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ORIGINAL PAPER

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The effects of Douglas-fir on tree-specific arthropod communities in mixed species stands with European beech and Norway spruce

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Abstract The ecological effects of planting exotic Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] in Central Europe are still poorly understood. The aim of this study was to answer the question of whether Douglas-fir affects tree specific arthropod communities in different mature forest types (Douglas-fir, spruce and beech dominated) in Southern Germany. Therefore, arthropod communities of stem and tree crown strata of Douglas-fir and spruce (*Picea abies* L.) were sampled in the years 1999–2001 using arboreal photo-eclectors and flight interception traps. Statistical analysis was conducted for all species and focused on conifer specialists at three levels: (1) species diversity, (2) guild structure and (3) community structure. Within the stem stratum, species diversity was significantly higher on spruce than on Douglas-fir independent of year and stand composition. This could not be explained by a single feeding guild, rather by species changing strata during the vegetation period. In contrast, species diversity in tree crowns was approximately the same for both conifer species. However, communities in Douglas-fir crowns were conspicuously different from those in spruce crowns, especially in the Douglas-fir dominated stand type. While zoophagous insects exhibited higher activity on Douglas-fir in 2000, xylophagous beetles were more abundant on spruce in 2001. In European beech stands with widely spaced Douglas-fir trees, the site specific and broad-leaved tree related fauna might be maintained. In addition, Douglas-fir with its resource of *Adelges cooleyi* and crowns that overtop the broad-leaved tree canopy, offer additional resources for several aphidophagous and thermophile species.

Keywords *Pseudotsuga menziesii* · *Picea abies* · Community structure · Canopy · Diversity · Ecological guilds · Coleoptera · Heteroptera · Neuropterida · Araneae

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Introduction

The planting of exotic tree species in German forests increased substantially in the second half of the 20th century. The main reason for the introduction of exotic tree species was an expected increase in timber production. One of the conifer species, which was expected to adapt well to the conditions of Central Europe was Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco]. It was introduced first in 1827 (cf. Knoerzer and Reif 2002). After a serious setback caused by Douglas-fir needle cast in the 1930s, Douglas-fir advanced to the most important introduced tree species in Germany. Fast growth and superior timber characteristics promoted their plantation. Because of the wide range of potential growing sites, including poor and non-productive ones, Douglas-fir provides a viable silvicultural alternative to the Norway spruce (*Picea abies* L.). Although the actual percentage of Douglas-fir in German state forest is still low (0.58% in Bavaria, 2.2% in Baden-Württemberg and Hesse; Biermayer 1999), there exists a general long term consensus that plantation of Douglas-fir will continue to increase in the future (Hanstein 1993; Wagner 2004). In addition, these aforementioned figures do not include private forests (Knoerzer and Reif 2002).

The ecological effects of an increased planting of Douglas-fir in Central Europe are still poorly understood (Bürger-Arndt 2000). The few published studies anticipate negative effects on arthropod communities. Kohlert and Roth (2000), Winter (2001), Winter et al. (2001) and Glatz et al. (2003) impart credence to this conjecture by reporting less diverse guilds of epigeic predators as well as saprophagous invertebrates in pure and mixed stands of Douglas-fir in Germany. Concerning tree specific arthropod communities, nearly no data exists. A few inconclusive studies were performed in the stem or lower crown stratum (Nick 1987; Kilchling 1993). As Simon (1995) pointed out, arthropod communities within trees change vertically; thus, communities in tree crowns are clearly differentiated from those observed on the stem strata. However, hitherto no comprehensive studies on the effects of planting Douglas-fir on tree crown communities in mature forest stands had been published. Previous studies were either in essence faunistic (Goßner and Bräu 2004), focused on a single guild (Goßner et al. 2005), or a single stand (Goßner and Simon 2002; Goßner and Utschick 2004). In this paper, for the first time, an analysis of various ecological and taxonomic groups in two vertical strata is presented.

The aim of our study was to answer the question of whether Douglas-fir affects tree specific arthropod communities in managed forests in Southern Germany. Therefore, communities of Douglas-fir were compared with those of Norway spruce. The main reasons for this comparison were: (1) Norway spruce is native to Germany with similar plant architecture (cf. Strong et al. 1984) and (2) Douglas-fir is discussed as an alternative to spruce at some sites. Different strata (stem, tree crown) as well as different ecological guilds of arthropods and different stand compositions were considered.

Methods

The study was conducted at three differently managed mature forest stand types (average tree age > 100 years) in southern Bavaria, Germany in the years 1999–2001. The stands are located in the forestry department of Ottobeuren (10°21′E 48°06′N) (spruce and beech dominated stand types, abbreviated as sp-dom and be-dom) and in a private forest near Edelstetten (10°25′E 48°17′N) (Douglas-fir dominated stand type, do-dom). The furthest distance between the stands is 24 km. Characteristics of the three stand types is presented in Table 1. All study sites were located in a landscape called "Schotterriedel" with soils of high nutrient content, promoting rapid tree growth. At both sites, the surrounding forest is dominated by spruce. Walentowski et al. (2001) described this region as "Collin and High Montane Beech Forests".

Tree crown communities of six Douglas-fir and six spruce trees, arranged in two replicates, were studied at each of the three stand types using flight interception traps (FIT) (Fig. 1; Winter et al. 1999). Stem communities were examined by four arboreal photo-eclectors (APE) (Fig. 1; Funke 1971) per tree species and stand type. FITs were installed in the core of each tree crown (mean installation height: Douglas-fir 27.8 ± 2.3 m, spruce 25.3 ± 3.1 m) and APE at 2 m height. Sampling jars were filled with a killing and preserving agent (1.5% $CuSO_4$-solution). A detailed description of trap types used and tree parameters is given in Goßner (2004). Crown strata were studied in the years 2000 and 2001, stem strata in the years 1999 and 2000 (except do-dom: 1999 and 2001). Traps were exposed from mid-March through mid-October (vegetation period), resulting in 215 trap days/year for FIT as well as for APE. Traps were emptied monthly and arthropods were transferred into alcohol (70%-ethanol) in the field.

Besides bark inhabiting fauna, APE also collects species that use the stem as a "highway" when changing strata during the vegetation period (Büchs 1990). We postulated that the captured assemblages would be tree species specific and denominated them as the tree crown and tree stem fauna of Douglas-fir and spruce, respectively. By the use of FIT and APE, activity densities of arthropods were measured as number of specimens and species.

Coleoptera and Heteroptera were analysed in tree crowns as well as in the stem stratum. Additionally in tree crowns, Neuroptera and in the stem stratum Araneae, both predaceous taxa, were included. This was done because of differences in habitat use (i.e. Neuropteran species are mainly crown living in forests; Gruppe and Schubert 2001) or trap specificity (i.e. in FIT, mainly "ballooning" spiders were sampled). The determination on species level was either done by one of us (Heteroptera: M.G.) or by other specialists (Coleoptera: F. Köhler, Bornheim and Dr. U. Simon, Freising; Neuroptera: Dr. A. Gruppe, Freising; Araneae: T. Blick,

Table 1 Characterisation of studied stand types

		do-dom	sp-dom	be-dom
Altitude (m a.s.l.)		550	620–645	620–645
Mean annual temperature (°C)		7–8	7–8	7–8
Precipitation (mm/a)		750–800	850–900	850–900
Tree species composition (%)	*P. menziesii*	57	2	1
	P. abies	32	80	29
	F. sylvatica	9	16	67
	Other broad-leaved trees	2	2	3
Mean tree height and SD (m)	*P. menziesii*	46.6 ± 2.5	42.9 ± 1.6	43.0 ± 1.5
	P. abies	38.3 ± 2.6	37.8 ± 1.5	39.5 ± 3.1
	F. sylvatica		30.7 ± 1.8	36.2 ± 1.2

do Douglas-fir (*Pseudotsuga menziesii*), *sp* spruce (*Picea abies*), *be* = beech (*Fagus sylvatica*), *dom* dominated

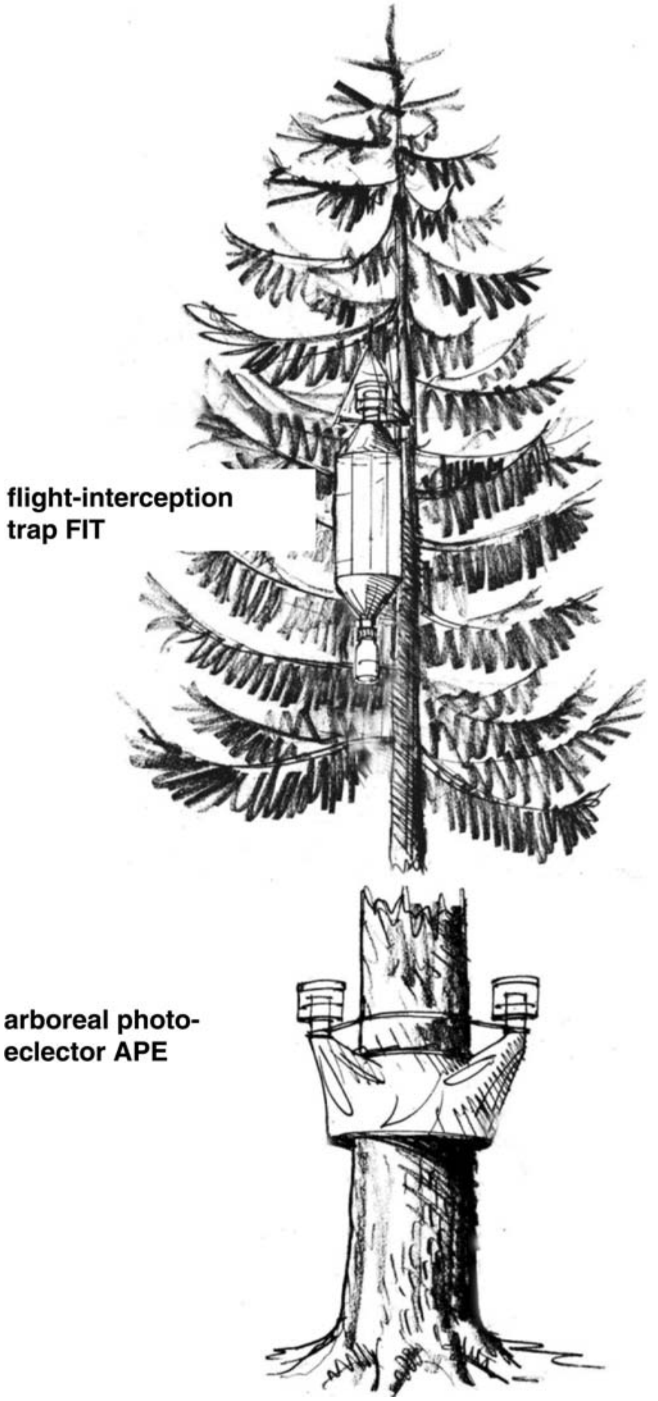


Fig. 1 Arrangement of traps

Hummeltal). Guild division was based on the literature (Heteroptera: Reuter 1908; Wagner 1952, 1966, 1967, 1971, 1973, 1975; Wagner and Weber 1978; Péricart 1972, 1987; Wheeler 2001; Dorow 2001; Wachmann et al. 2004; Coleoptera: Köhler 1996, 2000) and through the consultation of experts (F. Köhler, T. Blick). Main feeding behaviour of species was used as deciding factor. In Heteroptera, species with no clear preference of phytophagous and zoophagous feeding habits were defined as omnivorous. A complete species list including their ecological characteristics is presented in Goßner (2004) and Goßner and Bräu (2004).

Data analysis was conducted using Statistica 6.0 (StatSoft 2001), PC-ORD 4.10 for Windows (McCune and Mefford 1999) and EstimateS (Colwell 1997). For analysing differences in number of specimens or species between Douglas-fir and spruce a Mann–Whitney *U*-test (MWU-test) and a Repeated-Measure-ANOVA (RMA) were used. When using RMA, data were $\log(x+1)$ transformed to improve the normalities of the distributions (Sachs 1993). In all cases, also homogeneity of variances was tested after transformation (Levene-test). Between year differences were analysed by a sign-test. As α-diversity measure the α-value of the log-series, described as Fisher's alpha (Fisher et al. 1943), was selected because of its favourable statistical properties (May 1975; Southwood 1978; Taylor 1978; Wolda 1983). The computer program EstimateS generates a standard deviation for Fisher's alpha (Colwell 1997), which is then given in the figures and valided statistical tests (*t*-test, single-factor ANOVA) of the results. For synecological analysis a Detrended Correspondence Analysis (DCA) was performed using number of specimens per species (Jongman et al. 1995). Detrending was used to reduce the occurring arch effect. DCA is a method based on eigenanalysis and results in eigenvalues (for each axes), which are equivalent to the correlation coefficient. Resulting axes are a measure of β-diversity. In DCA a separate consideration of replicates was performed regarding tree crown but not stem communities. A Monte–Carlo-test (Dufrêne and Legendre 1997) was calculated to test if a particular species showed significantly higher numbers in one of the studied tree species separated by stand type. Species with significant values were presented in the ordination diagrams of a DCA. The calculation of RENKONEN-Index (cf. Mühlenberg 1993) allowed a statistical comparison of dominance structure (β-diversity) between Douglas-fir and spruce in different stand types. This is done by a Kruskal–Wallis-ANOVA followed by a Nemenyi post-hoc-test. Results with *P*-values below 0.05 were defined as significant.

Results

In stem and crown strata of Douglas-fir and spruce a total of 34 203 specimens (Col.: 19 238; Het.: 3 320; Neur.: 911; Ara.: 10 734) were caught and determined to species level. The observed 555 species (Col.: 352; Het.: 53; Neur.: 34; Ara.: 116) were used for further analysis. To evaluate the faunistic-ecological consequences of Douglas-fir: (1) diversity aspects, (2) guild structure and (3) whole community structure were considered.

Species diversity

Differences in the communities of stem and tree crown layers were analysed separately regarding species diversity. The species diversity pattern (α-diversity) was not significantly different between the two sampling years in both strata and regarding all captured species as well as conifer specialists (sign-test, $P > 0.10$ for all comparisons). Thus, both years were pooled.

In the stem stratum the α-diversity of arthropod communities of spruce was significantly higher than that of Douglas-fir regarding all captured species as well as conifer-specialist in spruce and beech dominated stands (Fig. 2a). However, no difference was found in the Douglas-fir dominated stand type.

Moreover, α-diversity on spruce and Douglas-fir stems differed significantly between the three different stand types regarding all species as well as conifer specialists (single-factor ANOVA, $P < 0.001$). However, this was unidirectional on both conifer species. In spruce and Douglas-fir highest overall diversity was found in the Douglas-fir dominated stand type and lowest in the spruce dominated stand type (Fig. 2a). However, α-diversity of conifer specialists decreased from the Douglas-fir (spruce $\alpha = 6.73$, Douglas-fir $\alpha = 6.38$) to the spruce (5.41/4.17) to the beech dominated stand type (3.96/2.91) on both tree species (Fig. 2a).

In tree crowns α-diversity was significantly higher on Douglas-fir compared to spruce in conifer dominated stands (do-dom, sp-dom, Fig. 2b). This was caused by euryoecous species and species living in more open habitats occurring in the Douglas-fir dominated stand type. There, no difference was observed regarding conifer specialists (Fig. 2b). In contrast, in beech dominated stand type species diversity was lower on Douglas-fir compared to spruce and this was attributed to conifer specialists to a high extend, which showed significant differences (Fig. 2b).

Additionally, significant differences in α-diversity were found between the three different stand types on spruce (all species $P < 0.01$, conifer specialists $P < 0.05$) and Douglas-fir (all species $P < 0.001$, conifer specialists $P < 0.01$) using a single-factor ANOVA. However, this was not uniform regarding the two conifer species. While species diversity on spruce was lowest in the spruce dominated stand type, on Douglas-fir it was lowest in the beech dominated stand type (Fig. 2b).

Guild analyses

In the stem stratum, results of both sampling years were not significantly different regarding all examined guilds (sign-test, $P > 0.10$ for all comparisons) and were therefore pooled.

All guilds exhibited higher numbers of specimens and species on stems of spruce when compared with Douglas-fir (except zoophagous specimens in the beech dominated stand type). This could be proven statistically only in a few cases: for mycetophagous mould-feeding specimens (all species and conifer specialists) as well as copro-/sapro-/necrophagous specimens and species (all species) in the Douglas-fir dominated stand type, zoophagous specimens and species (all species) in the spruce dominated stand type and xylophagous specimens (conifer specialists) and species (all species and conifer specialists) in the beech dominated stand type.

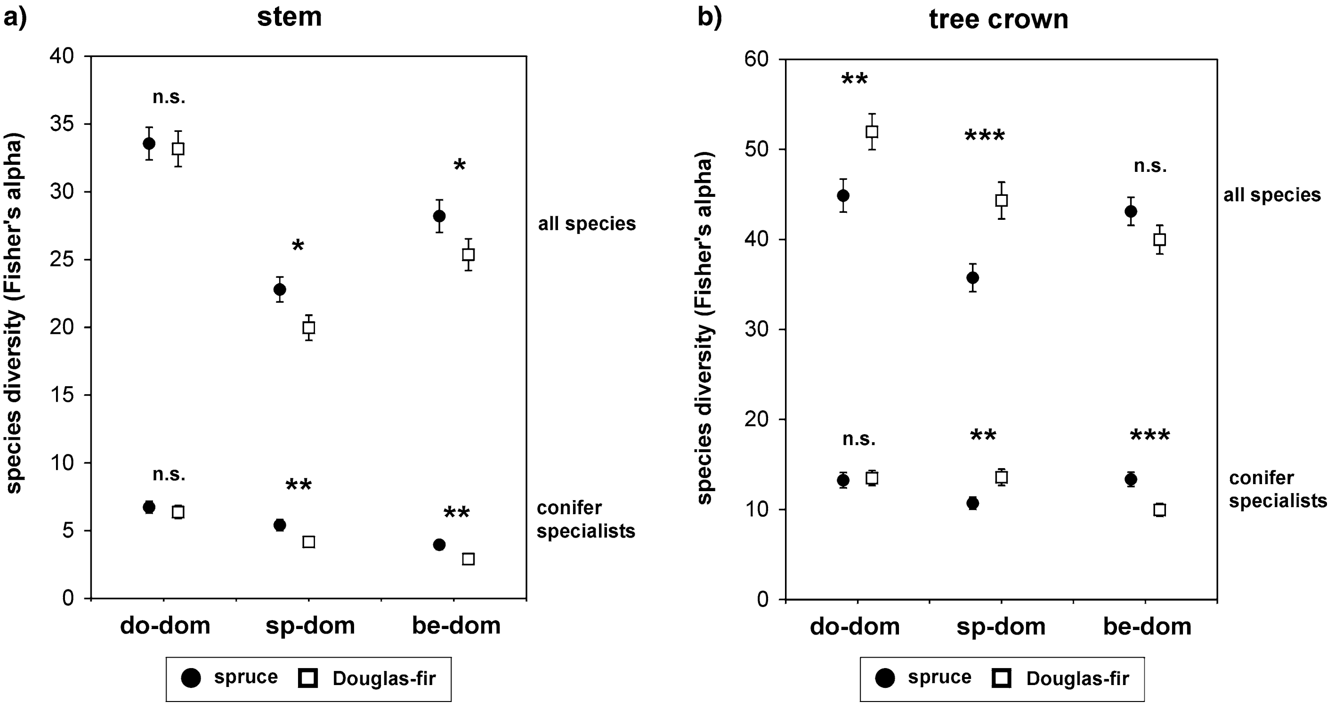


Fig. 2 Arthropod diversity in stem stratum (**a**) and crown stratum (**b**) of different stand types (means, standard deviation). *do* Douglas-fir, *sp* spruce, *be* beech, *dom* dominated; *t*-test: $*P < 0.10$, $**P < 0.05$, $***P < 0.01$, *n.s.* = not significant

Otherwise differences in the numbers of specimens and species were very low (Table 2).

In tree crowns, significant differences in guild structure occurred between the two sampling years. Because of this irregularity, both years were analysed separately.

Regarding specimens, in 2000 significant differences between Douglas-fir and spruce occurred only in the Douglas-fir dominated stand type. Mycetophagous mould-feeding, zoophagous and omnivorous species exhibited higher activity on Douglas-fir. Only fungi-feeding species exhibited a significantly higher abundance on spruce (Table 3). In 2001, the number of xylo- (all stand types) and zoophagous (except do-dom) insects was significantly higher on spruce compared with Douglas-fir (Table 3).

The different pattern on spruce and Douglas-fir between the two sampling years was most obvious in the xylo- and zoophagous guilds, illustrated in Figs. 3 and 4. In 2001, xylo- and zoophagous insects on spruce exhibited a significantly higher abundance than in the year 2000 (xylophagous: $P < 0.001$; zoophagous: $P < 0.01$). On Douglas-fir this could only be confirmed for xylophagous beetles ($P < 0.02$) (sign-test).

The results for species numbers were comparable to those for number of specimens, with a significantly higher number of zoophagous species found on Douglas-fir in the Douglas-fir dominated stand type in 2000 and a higher number of zoo- and xylophagous species on spruce in 2001 (Table 4). Consistent with the number of specimens, the number of omnivorous species was significantly higher on Douglas-fir in both years. However, the number of phytophagous species in the beech dominated stand type was higher on spruce compared with Douglas-fir.

Community analyses

In the stem stratum, the communities (all species and conifer specialists) exhibited a conspicuous gradient from Douglas-fir to spruce to beech dominated stand types on Douglas-fir as well as on spruce (Fig. 5a, b; right to left).

The communities of the two conifer species were separated along the second dimension in the ordination diagram (illustrated by a solid line in Fig. 5a, b), but the difference was very small, shown by the low eigenvalue (all species = 0.035, conifer specialists = 0.011). The most conspicuous difference between the communities on Douglas-fir and spruce occurred in the Douglas-fir dominated stand type (highest distance between data points of Douglas-fir and spruce in Fig. 5a, b). This was caused mainly by two conifer specialists (*Corticaria abietorum* No. 10, *Polydrusus pallidus* No. 22), which change between strata during the vegetation period, and some spider species (*Coelotes terrestris* No. 36, *Hahnia pusilla* No 41, *Lathys humilis* No. 42) (Fig. 5; Table 5).

In the tree crown stratum the communities of spruce and Douglas-fir were also influenced by the surrounding tree species composition. This was most obvious

Table 2 Number of specimens and species of different feeding guilds sampled on spruce (*sp*) and Douglas-fir (*do*) stems

Specimens	All species						Conifer specialists					
	do-dom		sp-dom		be-dom		do-dom		sp-dom		be-dom	
	sp	do	sp	do	sp	do	sp	do	sp	do	sp	do
Myceto-f (Col)	3	0	0	2	1	1	2	0	0	0	0	0
Myceto-m (Col)	277 a	94 b	180	100	52	43	216 a	66 b	130	26	26	19
Phyto (Col, Het)	1,848	1,078	1,313	1,033	1,280	759	1,687	980	1,137	845	991	528
Xylo (Col)	37	31	24	19	48	31	28	20	15	13	16 a	5 b
Zoo (Col, Het, Ara)	2,222	1,859	3,012 a	1,639 b	1,357	1,458	205	222	335	407	237 b	407 a
Csn (Col)	20 a	1 b	0	0	0	0	0	0	0	0	0	0
Omni (Het)	424	244	50	29	62	43	423	242	49	27	51	35

Species	All species						Conifer specialists					
	do-dom		sp-dom		be-dom		do-dom		sp-dom		be-dom	
	sp	do	sp	do	sp	do	sp	do	sp	do	sp	do
Myceto-f (Col)	2	0	0	2	1	1	1	0	0	0	0	0
Myceto-m (Col)	6	8	7	5	5	4	3	4	4	3	3	3
Phyto (Col, Het)	26	22	15	14	27	22	8	7	7	6	9	7
Xylo (Col)	14	12	9	9	11 a	5 b	8	7	5	4	5 a	1 b
Zoo (Col, Het, Ara)	108	106	87 a	65 b	81	79	14	15	13	9	4	4
Csn (Col)	6 a	1 b	0	0	1	0	0	0	0	0	0	0
Omni (Het)	4	3	3	4	4	4	3	2	2	2	2	2

Significantly different medians between tree species are indicated by different letters (MWU-test, $P < 0.05$)

be beech, *dom* dominated, *myceto* mycetophagous (*f* fungi, *m* mould), *phyto* phytophagous, *xylo* xylophagous, *zoo* zoophagous, *csn* copro-/sapro-/necrophagous, *omni* omnivorous, *Col* Coleoptera, *Het* Heteroptera, *Ara* Araneae

Table 3 Number of specimens of different feeding guilds sampled in tree crowns of spruce (*sp*) and Douglas-fir (*do*)

Specimens	do-dom				sp-dom				be-dom			
All species	2000		2001		2000		2001		2000		2001	
	sp	do	sp	do	sp	do	sp	do	sp	do	sp	do
Myceto-f (Col)	17 a	4 b	11	19	5	6	26	6	5	14	25	15
Myceto-m (Col)	129 b	205 a	66	74	145	200	112	85	257	348	175	68
Phyto (Col, Het)	176	169	172	77	120	134	144	122	236	322	540	441
Xylo (Col)	81	63	330 a	151 b	69	105	669 a	147 b	152	113	503 a	151 b
Zoo (Col, Het, Neur)	193 b	374 a	328	325	175	180	295 a	157 b	269	345	551 a	240 b
Csn (Col)	3	5	3	5	1	3	1	3	6	8	3	0
Omni (Het)	35 b	405 a	57	115	13	46	150	135	18	23	106	74

Specimens	do-dom				sp-dom				be-dom			
Conifer specialists	2000		2001		2000		2001		2000		2001	
	sp	do	sp	do	sp	do	sp	do	sp	do	sp	do
Myceto-m (Col)	99	135	55	40	139	186	94	59	238	323	118	37
Phyto (Col, Het)	48	59	71	39	50	62	51	56	33	30	69	50
Xylo (Col)	68	18	315 a	130 b	55	80	644 a	132 b	107	65	439 a	97 b
Zoo (Col, Het, Neur)	70	128	143	146	73	57	145 a	79 b	88	78	232	104
Omni (Het)	29	394	53	108	9	45	135	134	7	12	93	59

Significantly different medians between tree species are indicated by different letters (Repeated-Measure-ANOVA, Scheffé post-hoc-test, $P < 0.05$)

be beech, *dom* dominated, *myceto* mycetophagous (*f* fungi, *m* mould), *phyto* phytophagous, *xylo* xylophagous, *zoo* zoophagous, *csn* copro-/sapro-/necrophagous, *omni* omnivorous, *Col* Coleoptera, *Het* Heteroptera, *Neur* Neuropterida

regarding all species in the year 2000. A clear separation of the communities in the three studied stand types (do-dom, sp-dom, be-dom) occurred in the DCA, more or less along dimension 1 (illustrated by a solid line in Fig. 6a). The communities in the Douglas-fir dominated stand type (do-dom) differed greatly from those in the

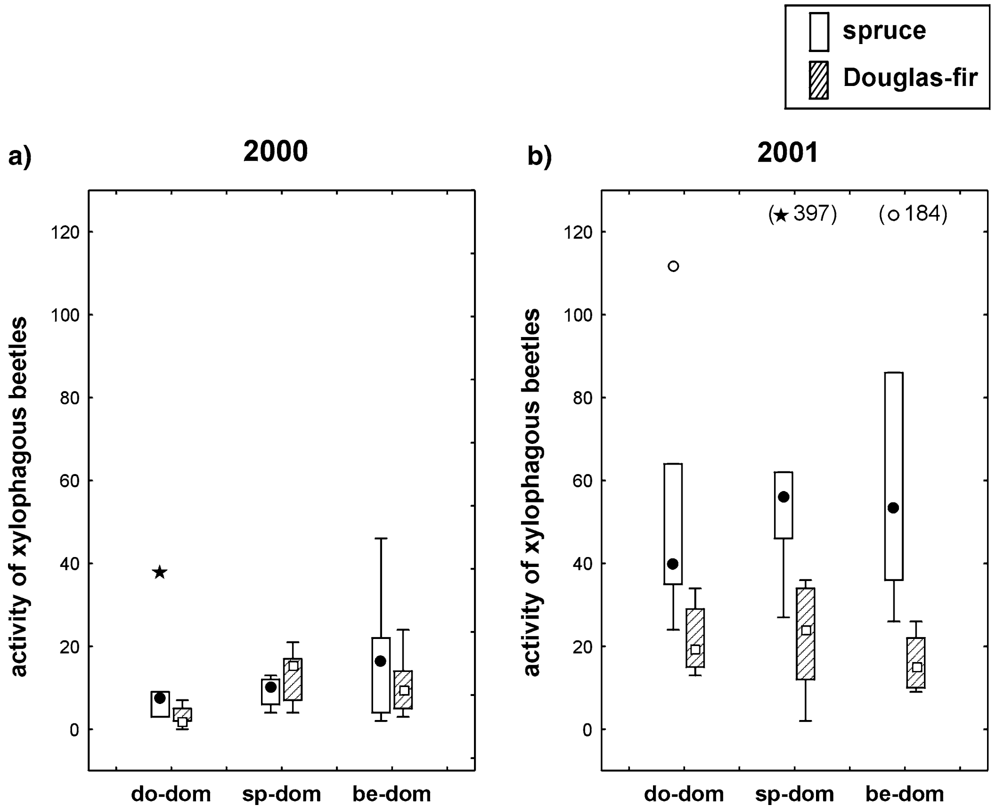
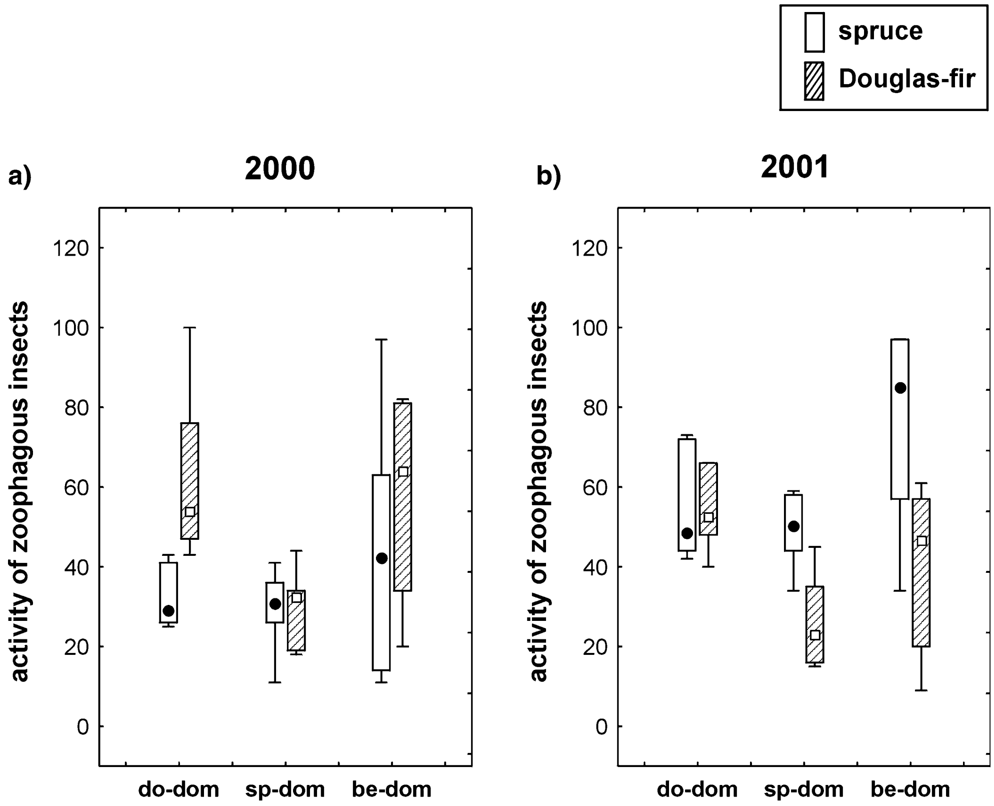


Fig. 3 Activity of xylophagous beetles (conifer specialists) on Douglas-fir (*do*) and spruce (*sp*) (median). Note that two values are not in the scale of the *y*-axis (in brackets). Box: 25%/75% percentiles, whisker: Min–Max-values. A *circle* indicates extreme values between one and three times the box length, an *asterisk* even larger value. *be* beech, *dom* dominated

Fig. 4 Activity of zoophagous insects (all species) on Douglas-fir (*do*) and spruce (*sp*) (median). Box: 25%/75% percentiles, whisker: Min–Max-values. *be* beech, *dom* dominated



other stand types during that year. Differences between the remaining communities of Douglas-fir and spruce were small in the crown stratum, indicated by a slight separation along dimension two (illustrated by a solid line in Fig. 6a), but more obvious compared with the stem stratum (higher eigenvalues). Regarding conifer

Table 4 Number of species of different feeding guilds sampled in tree crowns of spruce (*sp*) and Douglas-fir (*do*)

Species	do-dom				sp-dom				be-dom			
All species	2000		2001		2000		2001		2000		2001	
	sp	do	sp	do	sp	do	sp	do	sp	do	sp	do
Myceto-f (Col)	3 a	1 b	3	7	2	4	6	3	2	6	6	7
Myceto-m (Col)	4	7	4	7	5	8	4	5	5	6	5	4
Phyto (Col, Het)	14	16	12	10	11	10	11	9	15	12	13 a	9 b
Xylo (Col)	14	18	21	23	22	20	25 a	25 b	21	25	32	24
Zoo (Col, Het, Neur)	46 b	55 a	45	48	40	50	41	36	42	57	51	45
Csn (Col)	3	5	3	2	1	3	1	2	4	4	2	0
Omni (Het)	2	6	2 b	5 a	4	4	5	4	4	6	4	4

Species	do-dom				sp-dom				be-dom			
Conifer specialists	2000		2001		2000		2001		2000		2001	
	sp	do	sp	do	sp	do	sp	do	sp	do	sp	do
Myceto-m (Col)	3	3	3	5	4	4	3	3	3	3	4	3
Phyto (Col, Het)	7	7	5	3	7	5	5	3	8	6	5 a	2 b
Xylo (Col)	11	7	16	14	15	10	16 a	15 b	11	13	18 a	13 b
Zoo (Col, Het, Neur)	16	21	19	19	16	19	14	16	15	12	16	17
Omni (Het)	1	2	1 b	2 a	2	3	3	3	2	2	2	2

Significantly different medians between tree species are indicated by different letters (Repeated-Measure-ANOVA, Scheffé post-hoc-test, $P < 0.05$)

be beech, *dom* dominated, *myceto* mycetophagous (*f* fungi, *m* mould), *phyto* phytophagous, *xylo* xylophagous, *zoo* zoophagous, *csn* copro-/sapro-/necrophagous, *omni* omnivorous, *Col* Coleoptera, *Het* Heteroptera, *Neur* Neuropterida

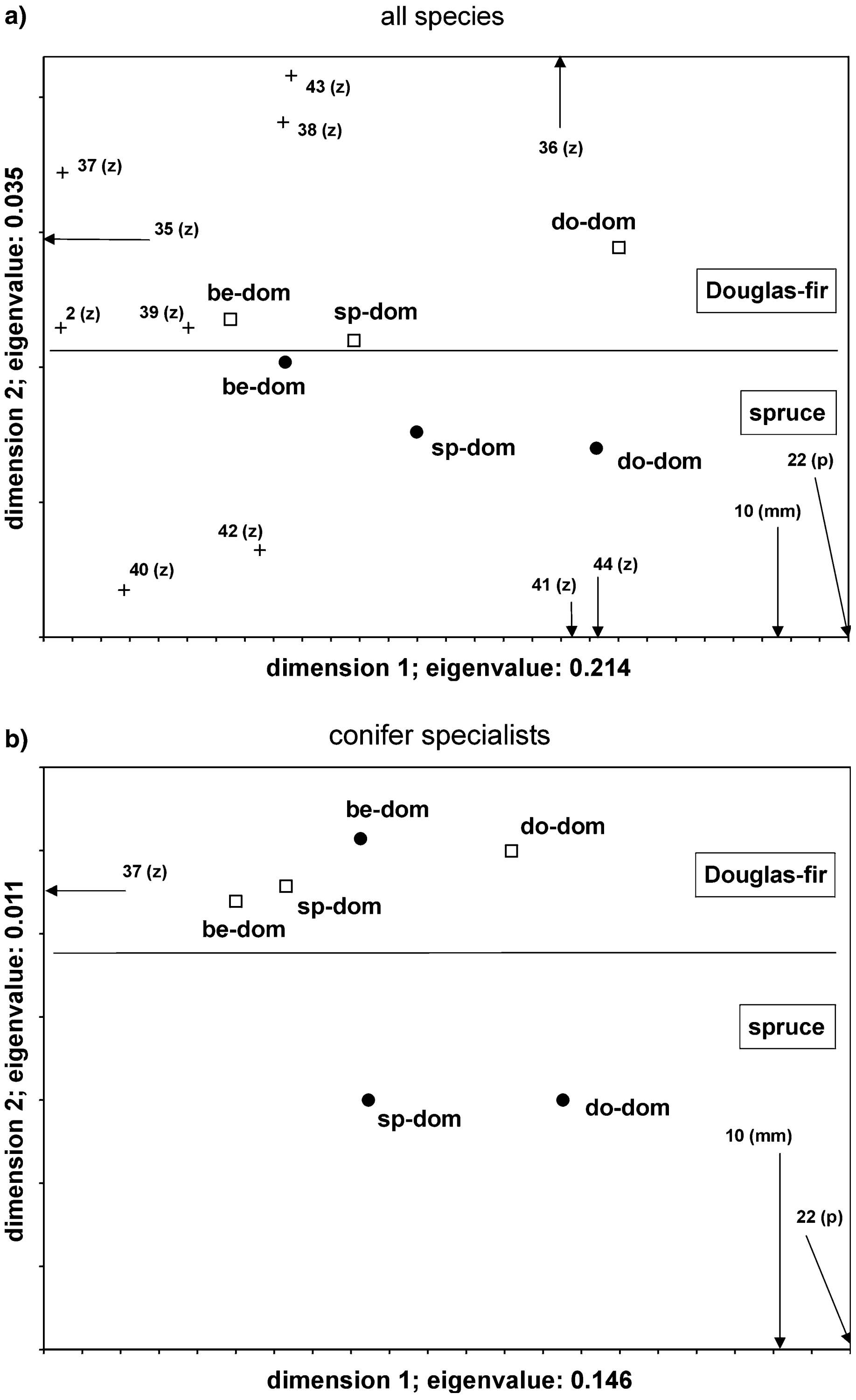


Fig. 5 Ordination diagrams (*DCA*) of arthropod communities on stems of Douglas-fir (*do open square)* and spruce (*sp filled circle*). Trees were pooled according to stand type. Species that exhibited differences between Douglas-fir and spruce by a Monte–Carlo-test ($P < 0.10$) are shown (+); the position of species outside the scale of the axes are indicated by the direction and length of *arrows*. The feeding habit of these species is given in brackets (*mm* mycetophagous-mould, *p* phytophagous, *z* zoophagous). *be* beech, *dom* dominated

specialists, also only the communities in the Douglas-fir dominated stand type (do-dom) were separated from the communities in spruce and beech dominated stands in an ordination diagram (Fig. 6b). In 2000, the most obvious difference occurred in the Douglas-fir dominated stand type and was mainly caused by higher abundances of zoophagous species on Douglas-fir (Fig. 6a, b; Table 5). Among these Coleoptera (*Anatis ocellata* No. 5) as well as Heteroptera (*Cremnocephalus alpestris* No. 24, *Orius minutus* No. 26) and Neuroptera (*Parasemidalis fuscipennis* No. 33, *Peyerimhoffina gracilis* No. 34) were found. A special situation was observed in 2001 regarding conifer specialists (Fig. 7). The larger difference in the communities of spruce and Douglas-fir (separated along dimension 1, illustrated by a solid line in Fig. 7) is explained by a relatively high eigenvalue

Table 5 Code of species of the ordination diagrams

Coleoptera	1	*A. rufotestacea* (Letzner 1845)	Heteroptera	23	*A. magnicornis* (Fallén 1907)
	2	*A. schoenherri* (Dejean 1837)		24	*C. alpestris* (Wagner 1941)
	3	*A. decempunctata* (Linnaeus 1758)		25	*D. lutescens* (Schilling 1837)
	4	*A. rufilabris* (Gyllenhal 1827)		26	*O. minutus* (Linnaeus 1758)
	5	*A. ocellata* (Linnaeus 1758)		27	*P. vitellinus* (Scholtz 1846)
	6	*A. subfuscus* (Müller 1764)		28	*P. varians* (Herrich-Schaeffer 1841)
	7	*A. vittatus* (Fabricius 1792)	Neuroptera	29	*C. pygmaea* (Enderlein 1906)
	8	*B. nebulosus* (Forster 1771)		30	*H. fenestratus* (Tjeder 1932)
	9	*C. lama* (Mulsant 1847)		31	*H. micans* (Olivier 1792)
	10	*C. abietorum* (Motschulsky 1867)		32	*H. pini* (Stephens 1836)
	11	*C. lambiana* (Sharp 1910)		33	*P. fuscipennis* (Reuter 1894)
	12	*C. abietis* (Ratzeburg 1837)		34	*P. gracilis* (Schneider 1851)
	13	*C. luteus* (Fabricius 1787)	Araneae	35	*A. accentuata* (Walckenaer 1802)
	14	*E. abietis* (Fabricius 1792)		36	*C. terrestris* (Wider 1834)
	15	*E. quadripustulatus* (Linnaeus 1758)		37	*C. silvicola* (Koch 1834)
	16	*L. alternans* (Erichson 1845)		38	*D. rudis* (Sundevall 1833)
	17	*M. nitida* (Gyllenhal 1827)		39	*Di. elevatus* (Koch 1838)
	18	*M. castanipes* (Paykull 1800)		40	*D. socialis* (Sundevall 1833)
	19	*P. chalcographus* (Linnaeus 1761)		41	*H. pusilla* (Koch 1841)
	20	*P. exsculptus* (Ratzeburg 1837)		42	*L. humilis* (Blackwall 1855)
	21	*P. pityographus* (Ratzeburg 1837)		43	*P. elongata* (Wider 1834)
	22	*P. pallidus* (Gyllenhal 1834)		44	*S. senoculata* (Linnaeus 1758)

(= 0.239). Xylophagous beetles, which were significantly more abundant on spruce than on Douglas-fir, were most important in this case (Fig. 7; Table 5). Among these, mostly bark beetles (*Cryphalus abietis* No. 12, *Pityophthorus exculptus* No. 20, *Pityophthorus pityographus* No. 21), but also one Anobiidae (*Ernobius abietis* No. 14) and one Curculionidae (*Magdalis nitida* No. 17) were observed. Moreover, three zoophagous (*Leptophloeus alternans* No. 16, *Hemerobius fenestratus* No. 30, *H. pini* No. 32), one phytophagous (*Parapsallus vitellinus* No. 27) and one mycetophagous species (*C. abietorum* No. 10) were significantly more abundant on spruce during this year. On the other hand, two xylophagous species, the long-horn beetle *Clytus lama* (No. 9) and the bark beetle *Pityogenes chalcographus* (No. 19) as well as the zoophagous lacewing *Coniopertyx pygmaea* (No. 29) significantly preferred Douglas-fir (Monte–Carlo-test).

Further analysis on the effect of stand composition for differences in dominance structure between the communities in tree crowns of Douglas-fir and spruce were performed using the RENKONEN-Index. In both years, significant differences between stand types were calculated by a Kruskal–Wallis-ANOVA regarding all species (Fig. 8a) and conifer specialists (Fig. 8b). However, different results were observed in the two study years (Fig. 8a, b). While in 2000 the communities exhibited a significantly higher β-diversity (lower RENKONEN-values) in Douglas-fir dominated compared with spruce and beech dominated stand types, in 2001 β-diversity was lowest in this stand type (Fig. 8a, b).

Discussion

This study demonstrates that Douglas-fir in Southern Bavaria harbours a species-rich community, although Douglas-fir was introduced to Central Europe no more than 177 years ago (Knoerzer and Reif 2002). Therefore, the long held opinion that neophytes do not provide niches for native species cannot be accepted in this circumstance. However, the results of our study point out that there is obviously a variable influence on tree specific arthropod communities when Douglas-fir replaces spruce. Results of spot check studies on stem and lower crown fauna of Douglas-fir in comparison to spruce and Silver fir (*Abies alba* Mill.), respectively, by Nick (1987) and Kilchling (1993) as well as on caterpillar droppings from Douglas-fir and spruce crowns by Kolb (1996) drew similar conclusions. As Kohlert and Roth (2000) and Winter (2001) reported, not only tree specific arthropods but also taxa living in and on the forest floor are affected by Douglas-fir when compared to spruce. Winter (2001), Winter et al. (2001) and Glatz et al. (2003) found similar results when Douglas-fir stands were compared with pine stands. Therefore, an influence of Douglas-fir on arthropod communities seems to occur in all strata, although exceptions exist (Engel 2002). However, the present study emphasises that the influence is not unidirectional. Effects depended strongly on: observed stratum, year of investigation, examined guild and stand composition.

Dependency of results on the observed stratum

In the stem stratum, lower species diversity could be observed on Douglas-fir compared to spruce and this was confirmed for almost all examined guilds. In close to ground strata, a reduced number of specimens and species of different taxa of Douglas-fir stands in comparison to stands of indigenous tree species seem to be a general pattern (Kohlert and Roth 2000; Winter 2001; Winter et al. 2001; Glatz et al. 2003).

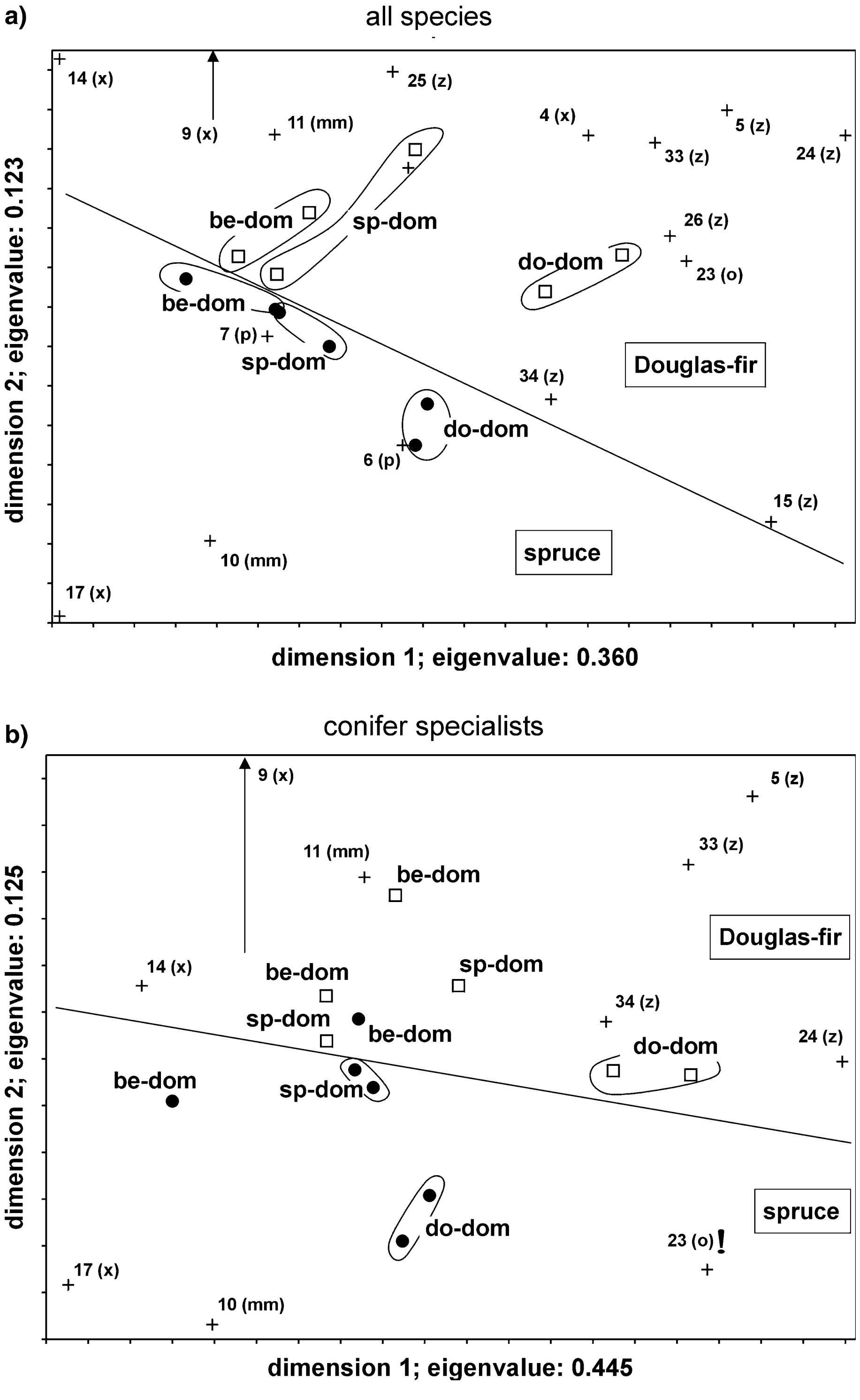


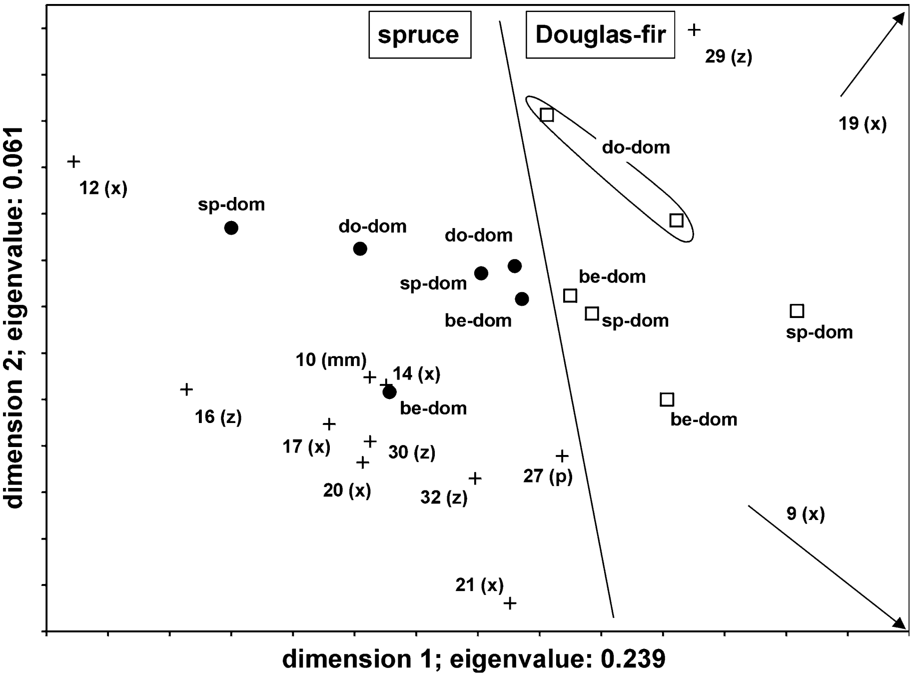
Fig. 6 Ordination diagrams (*DCA*) of arthropod communities in tree crowns of Douglas-fir (*do open square)* and spruce (*sp filled circle*) in the year 2000. Trees were pooled according to replicates. Species that exhibited differences between Douglas-fir and spruce by a Monte–Carlo-test ($P<0.10$) are shown (+); the position of species outside the scale of the axes are indicated by the direction and length of *arrows*. The feeding habit of these species is given in brackets (*mm* mycetophagous-mould, *o* omnivorous, *p* phytophagous, *x* xylophagous, *z* zoophagous). *be* beech, *dom* dominated; **!** significantly more abundant on Douglas-fir (Monte–Carlo-test)

In contrast, the diversity of arthropod communities in the tree crown stratum was approximately the same on Douglas-fir as compared to spruce, but the results strongly depend on the year of investigation, examined guild and stand composition. In some cases, the species diversity and number of specimens or species of a particular guild (e.g. zoophagous) was even higher in Douglas-fir crowns.

Dependency of results on the year of investigation

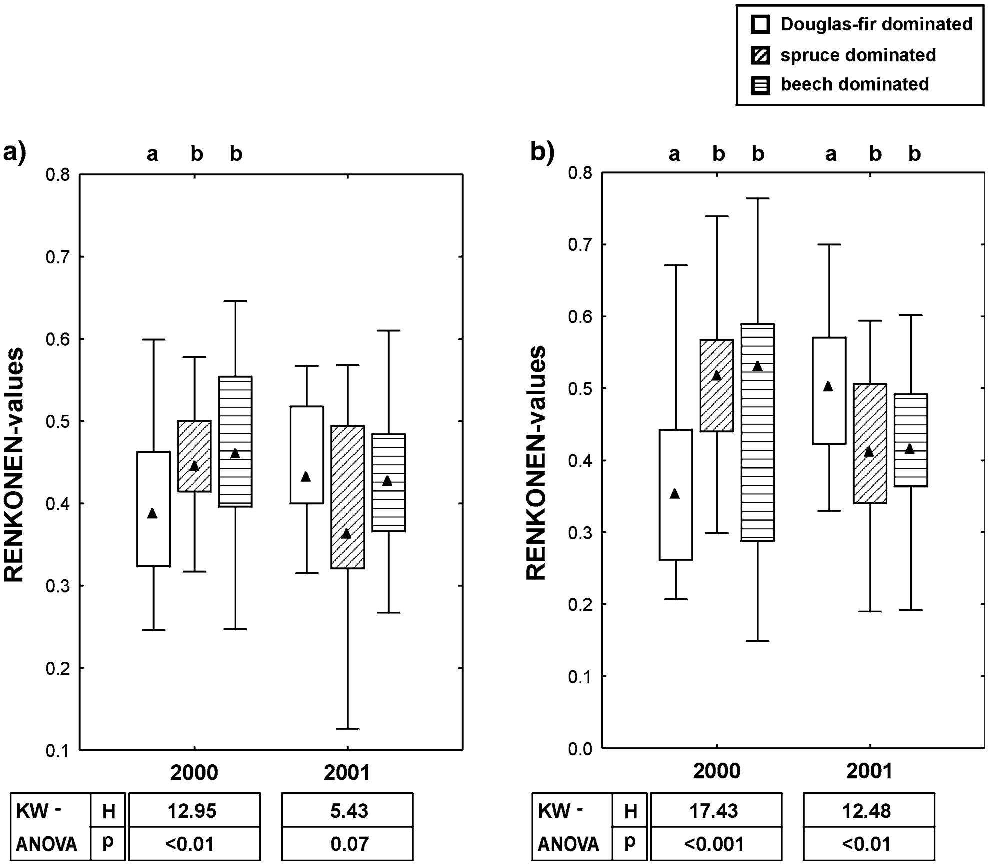
While fluctuations in population densities between years did not change the general "between tree species pattern" of arthropod communities in the stem stratum, tree crown communities were strongly affected and this might lead to a different evaluation of Douglas-fir. Considering the results of the year 2000,

Fig. 7 Ordination diagrams (*DCA*) of arthropod communities (conifer specialists) in tree crowns of Douglas-fir (*do open square*) and spruce (*sp filled circle*) in the year 2001. Trees were pooled according to replicates. Species that exhibited differences between Douglas-fir and spruce by a Monte–Carlo-test ($P < 0.10$) are shown (+); the position of species outside the scale of the axes are indicated by the direction and length of *arrows*. The feeding habit of these species is given in brackets (*p* phytophagous, *x* xylophagous, *z* zoophagous). *be* beech, *dom* dominated



Douglas-fir would have been positively assessed regarding the maintenance of high species diversity, but negatively for the year 2001. As a consequence reports based on a 1 year study need to be interpreted with caution and final conclusions are difficult to draw from this study.

Fig. 8 Differences in dominance structure (RENKONEN-Index) of the tree crown communities regarding all species (**a**) and conifer specialists (**b**) between Douglas-fir and spruce in different stand types (median). Significantly different medians are indicated by different *letters* at the top of the figure (Nemenyi post-hoc-test: $P < 0.05$). Box: 25%/75% percentiles, whisker: Min–Max-values



Dependency of results on the examined guild

Effects of Douglas-fir on tree specific communities in tree crowns depended more on guilds than on taxonomic systems (cf. Goßner 2004). Therefore, guild structure is the better measure to evaluate Douglas-fir under nature conservation aspects. The observed higher diversity on spruce compared to Douglas-fir stems could not be traced back to a single feeding guild but might be explained by lower suitability of Douglas-fir bark for some species that change from ground to crown stratum during the vegetation period (Goßner 2004). The roughly cracked, furrowed, cork like bark of mature Douglas-fir has a more textured surface than scaly spruce bark (Erlbeck et al. 1998). This coarse bark might be a less suitable "highway" to tree crown than less structured spruce bark. However, an increase in bark structure does not generally result in a decrease of vertical arthropod activity (Nicolai 1985, 1994; Goßner 2004). In the present study communities in tree crowns of Douglas-fir compared with spruce were more diverse in Douglas-fir and spruce dominated stands. However, spruce stems exhibited higher diversity of arthropods than Douglas-fir in all stands. Therefore, difference in bark structure of Douglas-fir is the most likely explanation for the observed lower diversity on Douglas-fir compared to spruce stems in the present study.

Additionally, as observed in the beech dominated stand type, crown diversity of Douglas-fir was lower than that of spruce. Because Douglas-fir bark is likely a less suitable "highway" to the tree crown, it may be assumed that for some species Douglas-fir is depended on a permanent colonisation from neighbouring spruce. We suspect that the increased distance between conifers in the beech stand inhibits crown-to-crown migration from spruce to Douglas-fir.

In tree crowns, differences in guild structure were most conspicuous within two guilds in the present study: xylophagous and zoophagous insects. Douglas-fir dead wood seems to be a less suitable substrate for breeding when compared with spruce. This might be because of a lack of time since the introduction of the neophyte Douglas-fir for adaptation processes to occur. As Goßner (2004) pointed out, densities of beetles emerging from crown dead wood by incubation in the lab were perceptibly lower in Douglas-fir compared to spruce. Particularly species, which breed in the bark cortex were negatively affected by Douglas-fir. This confers with studies on breeding densities (beetles per area), which examined infestation of trees thrown by storms (Luitjes 1976) and the experimental inoculation of harvested stems (Führer and Mühlenbrock 1983; Wainhouse and Beech-Garwood 1994). Bringmann (2001) also found less species of long-horn beetles using Douglas-fir as breeding substrate compared with spruce. However, hardwood borers might be less affected or even show higher infestation of Douglas-fir compared with indigenous tree species (Doom and Luitjes 1972; Eidmann 1987; Goßner 2004). This result may also be related to wood properties. Douglas-fir decomposes much slower than Norway spruce (Jochum and Roeder 1995).

The tree crown structure of Douglas-fir is different from that of spruce. Because of horizontal twigs in Douglas-fir compared with pendulate twigs in studied spruce trees, the structure of Douglas-fir crowns can be defined as more open than spruce crowns (Erlbeck et al. 1998). Additionally, Douglas-fir crowns overtopped the surrounding spruce and beech trees in the present study. Because of these differences in structure, different microclimatic conditions may be expected which may lead to additional differences in arthropod communities. As one example in the present study, the Ceramycidal *C. lama* may be mentioned. As Jonsell et al. (1998), Sverdrup-Thygeson and Ims (2002) and Müller et al. (2004) reported, favourable conditions for many saproxylic beetles including several Cerambycidae are found in sun exposed dead wood. Therefore, the higher abundance of *C. lama* on Douglas-fir compared to spruce might be a consequence of dryer and warmer microclimatic conditions in overtopping tree crowns of Douglas-fir. This coincides with the study of Schubert (1998) and Gruppe and Schubert (2001) on shade intolerant tree species like pedunculate oak (*Quercus robur* L.) and European larch (*Larix decidua* Mill.). They demonstrated that the warmer microclimatic conditions in tree crowns of these trees support thermophilic species. The different microclimatic conditions might also have led to differences in occurrence of mycetophagous insects feeding on mould in the present study. While some species preferred spruce, others preferred Douglas-fir (cf. also Goßner and Simon 2002) and this might be caused by differences in food quality of spruce and Douglas-fir dead wood, especially for mould species. Future investigation on mould species on Douglas-fir and spruce are needed to prove this hypothesis.

The high abundance of zoophagous insects in tree crowns of Douglas-fir seems to be a consequence of the Douglas-fir woolly aphid (*Adelges cooleyi*) which followed its host plant from the country of origin (Pacific Northwest) (Bogenschütz 1996). As Goßner et al. (2005) demonstrated aphidophagous insects exhibited significantly higher densities of activity in Douglas-fir when compared to spruce.

Surprisingly, the phytophagous guild exhibited insignificant differences between Douglas-fir and spruce in the tree crown layer, except species number in the beech dominated stand type. It is assumed that effects on native arthropod communities by neophytes mainly occur in the phytophagous guild because of a lack of co-evolutionary processes. This could be proven for herbaceous plants (Schmitz 1991, 1998, 2001; Zimmermann and Topp 1991; Jobin et al. 1996; Bürki and Nentwig 1997; Klipfel and Tscharntke 1997; Schmitz and Werner 2000) as well as for trees (Southwood et al. 1982; Strong et al. 1984; Ashbourne and Putman 1986; Goßner and Gruppe 2003; Goßner 2004; Goßner and Simon 2005). Why this hypothesis has to be rejected for Douglas-fir in the present study might have two reasons:

(a) because of similar secondary plant compounds of spruce and Douglas-fir no special adaptation is necessary to colonise Douglas-fir (Burzlaff 1998) and (b) because the studied region is situated outside the natural growth range of spruce (Walentowski et al. 2001), thus spruce may also be designated as an exotic species and therefore specialists might be lacking on this tree species as well. Both factors can explain the phenomenon in part. It may be that most species adapted to spruce followed the expansion of spruce plantations during the last ~400 years (Kaiser and Purps 1991; Hanstein 1993). However, monophagous beetle specialists are also missing on spruce in the present study (Böhme 2001). Future investigations are necessary to answer the question if these species are able to use Douglas-fir as a food resource.

Dependency of results on the stand composition

Differences between Douglas-fir and spruce are strongly dependable upon stand composition. In the stem stratum, differences in species diversity between Douglas-fir and spruce were lowest in the Douglas-fir dominated stand type, but community structure showed the highest β-diversity in this stand type. The special structure of this stand (open, highly developed herb layer) had strong effects on the communities, but these were not unidirectional in the two conifer species. Several arthropod species were more strongly supported by Douglas-fir and others by spruce. This might possibly be traced back to different bark structure. In tree crowns, as already discussed above, different microclimatic condition and varying distances between single conifer trees in stands of different composition resulted in different patterns of arthropod communities.

Similarity of arthropod community structure in tree crowns of Douglas-fir and spruce was lowest in the Douglas-fir dominated stand type in 2000, but in the beech dominated stand type in 2001. In the year 2000, the abundance of native aphids was low (Goßner 2004); therefore, the relatively high density of Douglas-fir woolly aphid resulted in a concentration of aphidophagous species on Douglas-fir in the Douglas-fir dominated stand during this year (Goßner et al. 2005). This effect might explain the low similarity values between the two conifer species. However, differences in aphidophagous communities cannot explain the observed differences between and within year pattern in β-diversity completely. The high abundance of xylophagous beetles in 2001 with the differences in habitat use as explained before led to higher β-diversity in the spruce and the beech dominated stand type in 2001 compared with 2000 and with the Douglas-fir dominated stand type in the same year.

Because the impact of Douglas-fir on arthropod communities is extremely complex, a highly differentiated assessment of planting Douglas-fir is necessary. Although the tree specific arthropod communities are not generally less diverse than those of indigenous spruce (at least in tree crown layer), the changing influence on arthropod communities in Douglas-fir may affect functional aspects of forest ecosystems. As Goßner and Utschick (2004) pointed out, arthropods are lacking in tree crowns of Douglas-fir in winter and this results in lower bird activity, especially in pure stands. The longer flight distance to profitable food resources might be problematic for birds during extreme climatic conditions. On the other hand aphidophagous insects might profit from the new food resource *A. cooleyi* on Douglas-fir, especially during years of low native aphid abundance. This might increase population densities of native aphidophagous species and thus may prevent outbreaks of insect pests and increase stability of forest ecosystems (Goßner et al. 2005). Additionally, the lower suitability of Douglas-fir for species breeding in the bark cortex may be assessed positively concerning forest protection. Namely, spruce is highly susceptible to outbreaks of these species at lowland forest sites. However, adaptation processes of bark beetles to Douglas-fir might occur in the future, demonstrated by the high abundance of *P. chalcographus* in the crowns of Douglas-fir, especially in the Douglas-fir dominated stand. The eventual adaptation by these species to Douglas-fir would then negate this current immunity advantage from a silvicultural perspective.

Conclusions and recommendations for forest practice

It is not the question whether Douglas-fir should be planted or not, but in which stand composition it may be combined with an adequate level of ecological functionality. Because effects of planting Douglas-fir on native arthropod communities increase with its proportion of total tree species, a small total percentage of Douglas-fir is recommended and pure stands of Douglas-fir should be avoided in future forest management. Considering the results of our study, this may occur best in hardwood (beech) stands with widely spaced Douglas-fir trees. With a maximum admixture of 30% Douglas-fir by basal area (being roughly equivalent to 10% stem count) in a European beech stand, the site and broad-leaved tree related fauna may be maintained. In addition, Douglas-fir with its resource of *A. cooleyi* and crowns overtopping the broad leaved tree canopy offer an additional resource for several aphidophagous and thermophile species. Even though some spruce specialists will not be able to colonise Douglas-fir in this stand type, these species are not threatened at the landscape scale, where spruce will remain the most common tree species.

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