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Influence of stand-alone trees on epigeic spiders (Araneae) at the alpine timberline

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We studied community composition and activity densities of spiders around stand-alone Norway spruce at the alpine timberline with respect to three interrelated parameters: (1) relative distance from tree trunk, (2) branch-, and (3) vegetation cover. Pitfall traps were positioned in an inner distance range (close to tree trunk), a median, and an outer distance range (at the outer limit of branch cover). Community composition: Linyphiid species numbers increased significantly towards the tree trunks where the branch cover was high, whereas lycosid and gnaphosid species numbers increased towards the edge where branch cover was low. Activity densities: 11 out of 14 species were significantly correlated with the relative distance to the tree trunk, ten with the branch cover, and two with vegetation cover. Open-land species preferred the outer distance range and forest species the inner distance range. *Caracladus avicula* is probably a habitat specialist of the alpine timberline.

Introduction

Structural heterogeneity of a biotope is one of the most important factors influencing animal communities and species diversity (Hatley & MacMahon 1980, Robinson 1981, Rosenzweig & Abramsky 1993, Niemelä *et al*. 1996, Horvath *et al*. 2000, Nentwig *et al*. 2004). The alpine timberline represents one of the most heterogeneous and biologically diverse living spaces of central Europe (Thaler 1989). Despite this, studies on small-scale distribution patterns of animal communities at the timberline are scarce. Our understanding of the influence of certain structural elements on these patterns is inadequate.

Spiders (Araneae) are an important, abundant and "megadiverse" (Coddington *et al.* 1996) group of epigeic arthropods whose species usually have strictly defined habitat preferences (Bauchhenss 1990, Wise 1993, Foelix 1996, Samu *et al.* 1999 and others). Thus, they are suitable indicative organisms for studying field-ecology problems.

We investigated the small-scale distribution patterns of epigeic spiders around stand-alone trees at the timberline in the Swiss Central Alps. The epigeic fauna around these single trees deserves special attention as the trees presumably offer microhabitats for forest species and represent a sharp boundary against the open

Fig. 1. Position of the study site in the Central Alps (400 km × 400 km, insert: 20 km × 20 km, modified after http://www.lib.utexas.edu/maps/switzerland.html; courtesy of the University of Texas Libraries, The University of Texas at Austin).

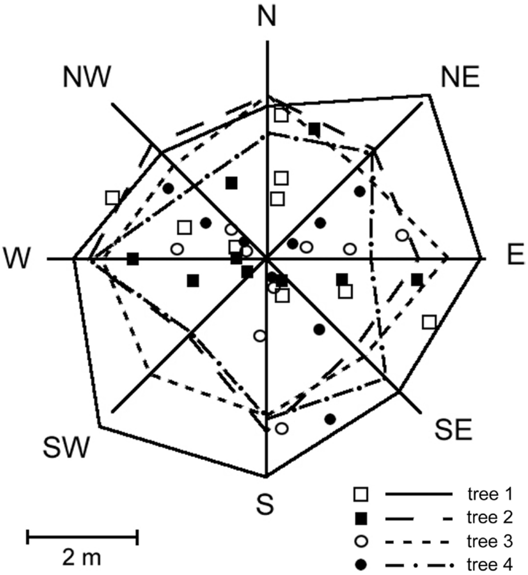

Fig. 2. Position of all traps (squares and circles) in relation to the outlines of all four trees as seen from above. The outer tips of the branches of all four trees are connected by lines. The main directions are indicated with lines equaling 400 cm.

dwarf shrub heath and alpine meadow. Thus, our working hypothesis is that the mosaic-like structured timberline harbors not only habitat specialists, but also species which are known from literature to inhabit mainly forests or open-land. To our knowledge, these stand-alone trees at the alpine timberline have never been studied before in this respect.

Methods

Study area

Alp Flix (GPS: 769 400/154 350; World Geodetic System 1984 coordinates: 46°31´8.41´´N, 9°38´47.12´´E) is situated in the Swiss Central Alps in the Canton Grisons and belongs to the village of Sur (Fig. 1). It is a southwest exposed terrace approximately 1000 m in breadth and situated at 1950 m above sea level. Adjacent to the terrace are mountain tops ca. 3000 m a.s.l. and a 400 m deep valley. We chose stand-alone Norway spruce (*Picea abies*) as study objects. They range from the southwestern border of the terrace, where the Norway spruce forest begins, to the dwarf shrub heath, dominated by *Juniperus communis* and *Rhododendron ferrugineum* combined with alpine meadow patches (Hänggi & Müller 2001). Occasional grazing by cattle occurs throughout the vegetation period.

Sampling of spiders

We selected four Norway spruce trees of similar age and size (ca. 12 m heigh and ca. 5 m wide; Fig. 2) that were at least 100 m apart and used pitfall traps for assessment of activity densities (Adis 1979). Tree 1 was the most exposed one with no other trees within a range of 30 m. Its lowest branches did not touch the ground. Tree 2 was the least exposed with the closest trees approximately 5 m away and with all lower branches touching the ground. Trees 3 and 4 were very similar in shape with some branches touching the ground; the next tree stood more than 15 m away.

Nine pitfall traps were placed around each tree, with three traps in each of three directions. Due to the high density of roots it was not possible to place the traps in all given directions (Fig. 2). We defined three distance ranges: an inner range, from the tree trunk up to approximately 1 m away; a median range, from ca. 1 m to ca. 2 m from the tree trunk; and an outer range, from ca. 2 m from the tree trunk to the outer border of the branch cover at approximately 3 m from the tree trunk (Fig. 2).

The traps consisted of white plastic cups with an upper diameter of 6.9 cm and a depth of 7.5 cm. We filled them with a solution of 4% formaldehyde and 0.05% SDS (sodium dodecyl sulphate, $C_{12}H_{25}NaO_4S$, as a tenside) to 3 cm under the upper rim. We fixed a quadrangular transparent plastic cover (15 × 15 cm) with three wooden rods 5 cm above the traps. The traps were emptied once a month between 15 May 2003 and 28 October 2003 (snow-free time) and the last time on 24 May 2004, when the snow started to melt.

The nomenclature of spiders follows that of Platnick (2005).

Parameters

Relative distance from tree trunk

The shape and outline of the trees were slightly different. Therefore, we calculated the position of the traps between the tree trunk and outer limit of branch cover as a number between 0.0 (trap at tree trunk) and 1.0 (trap at outer limit of branch cover). The distance between the tree trunk and the outer limit of the branch cover was measured in eight directions: N, NE, E, SE, S, SW, W and NW (Fig. 2). In this way, eight triangles were defined (Fig. 3). The outer tips of branches (D) were considered to lie on *c*: the distance between NE and E (Fig. 3). The relative position (*r*) of each pitfall trap (P) was defined as a proportion of the distance between the tree trunk (T) and the interpolated outer tip of the branches (D). This was calculated using the following equations:

$$r = t/d \tag{1}$$

$$d = \frac{ab\sin(\gamma)}{c\sin(180 - \alpha - \beta)} \tag{2}$$

$$\beta = \arcsin\left[\frac{b}{c}\sin(\gamma)\right] \tag{3}$$

$$c = \sqrt{a^2 + b^2 - 2ab\cos(\gamma)} \tag{4}$$

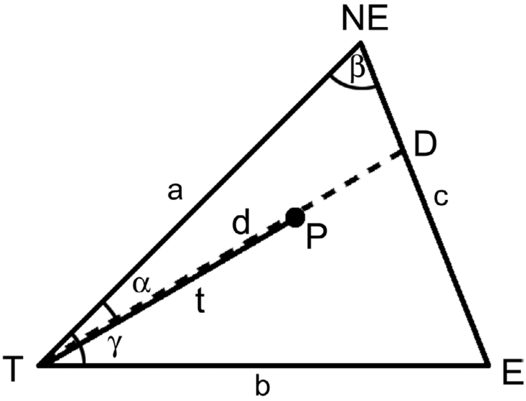

Fig. 3. Exemplary calculation of the relative distance (*r*) of a pitfall trap (P) situated between northeastern (NE) and eastern (E) directions from tree trunk (T). *See* text for calculation formulas and details.

with $\gamma = 45°$, and distances *a* (between T and NE), *b* (between T and E) and *t* (between T and P), and the angle α were measured in the field (Fig. 3).

Branch cover

We estimated the branch cover above every trap, upwards from the soil, in layers in each of five levels, i.e. level 5: 0–25 cm; level 4: 26–50 cm; level 3: 51–100 cm; level 2: 101–150 cm; level 1: above 150 cm from the soil surface. Then, we multiplied the branch cover as a percentage of a square around a trap at each level with the level number (e.g. cover of 80% at level 5: 0.8 × 5). We calculated the sum of these five numbers for every trap, resulting in an index between 0.0 (no cover) and 5.0 (total cover below 25 cm). Only the parts of an upper level that exceeded the cover of the lower level were considered. We used the average of two series of estimations by two persons in the field in early July. In addition, we calculated the total cover for all nine traps of each tree by summing up the mentioned indices. This resulted in a number between 0.0 (no cover) and 45.0 (total cover of all traps below a height of 25 cm) for each tree.

Vegetation cover

We assessed the vegetation cover using squares of 1 × 1 m around the traps. Herbs and shrubs that were at least 5 cm high and drooping branches touching the ground were taken into account. We used the average of two series of estimations by two persons on the basis of pictures of the surroundings of the traps made in early July 2003.

Data analyses

A Kolmogorov-Smirnov (KS) test illustrated that most of our data sets were not normally distributed. Transformation to a normal distribution of data was only possible with a combination of different transformation methods for different taxa. So, we used statistics for non-parametric data to get comparable results.

The significance levels of all correlation analyses were adjusted by a sequential Bonferroni correction at the 5% level (Rice 1989). However, this may sometimes have obscured true effects. For example, we relied mainly on the parameter "relative distance" (which is correlated with vegetation structure). The activity densities of eight out of 14 selected species were significantly correlated with the degree of vegetation cover without Bonferroni correction, while only two were significant after Bonferroni correction. In spite of this, we prefer the more cautious application of the sequential Bonferroni correction although its usefulness in ecological studies has been doubted (Moran 2003).

All statistics were calculated by SPSS (SPSS for Windows, Rel. 11.5.0. 2002. Chicago: SPSS Inc.) except for the post hoc Nemenyi test (program by Mario Barone from the Zoological Institute of the University of Bern).

Community composition

Total species numbers and activity densities (including values for linyphiids, lycosids, and gnaphosids separately) for the inner, median and outer distance ranges were compared with the Chi^2 test. In addition, the Spearman rank correlation coefficients (r_S) between species richness and relative distance from tree trunk, branch cover, and vegetation cover were calculated. We also compared the activity densities for species within each family and for all species together by calculating correlation coefficients as above.

Species associations between each distance range were calculated with the Czekanowski index (also known as Dice or Sørensen index) as proposed by Niemelä *et al*. (1996) and Thom *et al*. (2002). A presence/absence matrix using species, tree and distance range as parameters was created for this purpose.

Activity densities of selected species

Analysis for possible correlations between specimen counts per species and the three parameters mentioned above were performed using species that were represented by on average more than two specimens per trap (i.e. more than 72 individuals); 14 species of the total species pool of 69 (Frick *et al*. 2006; Appendix) satisfied this criterion (activity dominance in brackets): Hahniidae: *Cryphoeca silvicola* (3.2%); Linyphiidae: *Agnyphantes expunctus* (1.4%), *Bolyphantes luteolus* (3.2%), *Caracladus avicula* (7.5%), *Centromerus pabulator* (1.7%), *Improphantes nitidus* (4.1%), *Macrargus carpenteri* (1.8%), *Panamomops tauricornis* (1.3%), *Pelecopsis elongata* (5.4%), *Scotinotylus alpigena* (10.0%), *Scotinotylus clavatus* (1.4%), *Tapinocyba affinis* (3.6%); Lycosidae: *Alopecosa taeniata* (5.5%), *Pardosa riparia* (37.4%).

Relative distance from tree trunk

We separated the analysis into two sections. First we considered all trees as equal and pooled them for the analysis. Second, because of small natural differences between the trees, we considered the four trees separately. A Kruskal-Wallis (KW) test showed that four species out of 14 were present in different activity densities under the four trees. A post hoc Nemenyi test showed which trees differed from each other. Species with fewer than 18 specimens per tree (i.e. two specimens per trap on average) were excluded from the analysis of individual trees. We compared the activity density of each species (nine traps per tree, 36 traps in total) with the relative distance to the tree trunk using a Spearman rank correlation coefficient (r_S).

Vegetation cover and branch cover

We pooled the four trees for each analysis because possible differences in characteristics of the four trees do not bias the estimations of vegetation and branch cover around the traps. We calculated the Spearman rank correlation coefficient (r_S) for all trees together to correlate activity density data with the vegetation cover and branch cover.

Correlation between parameters

The Spearman rank correlation coefficients (r_S) were calculated for the following: relative distance–branch cover; relative distance–vegetation cover and branch cover–vegetation cover.

Results

Correlations between parameters

Relative distance was significantly correlated with branch cover ($r_S = –0.801$, $p < 0.001$) and vegetation cover ($r_S = –0.376$, $p = 0.024$). Branch and vegetation covers were also significantly correlated ($r_S = 0.505$, $p = 0.002$).

Community composition

Species richness

We recorded 69 species (Appendix). No differences were detected in species richness between distance ranges for individual families (Linyphiidae: $\chi^2 = 1.876$, df = 2, $p = 0.391$; Lycosidae: $\chi^2 = 0.400$, df = 2, $p = 0.819$; Gnaphosidae: $\chi^2 = 0.824$, df = 2, $p = 0.662$), and for all families together ($\chi^2 = 1.006$, df = 2, $p = 0.605$). Gnaphosids increased from four species in the inner distance range to seven and six species in the median distance range and in the outer distance range, respectively (Fig. 4). Lycosids increased (4–5–6 species) and linyphiids decreased (36–35–26) with distance to the tree trunk (Fig. 4).

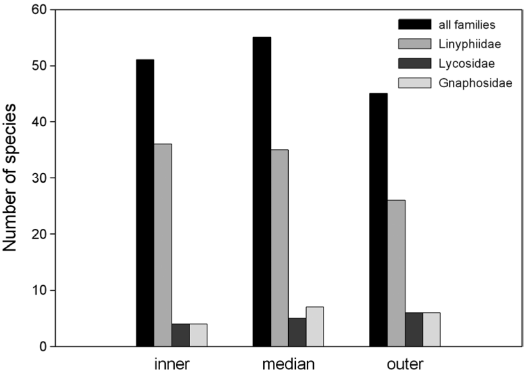

Fig. 4. Number of species of each family in each distance range. No significant differences between distance ranges were detected.

Differences in similarities in species composition between distance ranges were found (Czekanowski index of percentage similarity): the similarity between the inner and the median distance ranges was the highest for Linyphiidae and for all families together. The similarity between the median and outer distance range was highest for Lycosidae and Gnaphosidae (Table 1). All Czekanowski indices were found to be relatively high, i.e. above 0.68 (Table 1) showing significant overlaps (Coelho *et al.* 1997).

Activity densities

The total number of specimens increased by a factor of 1.7 from the inner to the outer distance range, i.e. from 1758 specimens in the inner distance range, to 2113 specimens in the median distance range and to 2395 specimens in the outer distance range (χ^2-test: $\chi^2 = 97.561$, df = 2, $p < 0.001$; Fig. 5). The number of collected specimens differed between distance ranges for all families separately (χ^2-test: Linyphiidae: $\chi^2 = 203.646$, df = 2, $p < 0.001$; Lycosidae: $\chi^2 = 924.991$,

Table 1. Czekanowski similarity indices for spider families, separated and together, for comparisons between inner–median, median–outer and inner–outer distance ranges.

	Inner–median	Median–outer	Inner–outer
Linyphiidae	0.87	0.69	0.68
Lycosidae	0.89	0.91	0.80
Gnaphosidae	0.73	0.92	0.80
Total	0.81	0.74	0.69

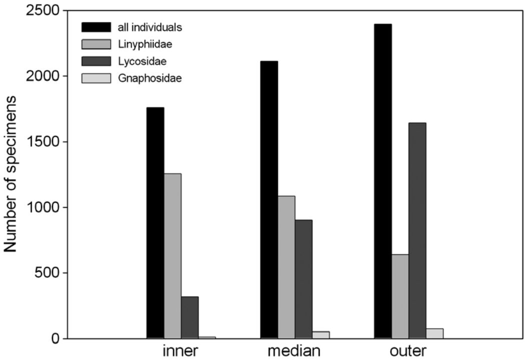

Fig. 5. Number of specimens of each family in each distance range. *See* text for significances.

df = 2, $p < 0.001$; Gnaphosidae: $\chi^2 = 43.956$, df = 2, $p < 0.001$; Fig. 5). From the inner to the outer distance range the number of specimens in the Linyphiidae halved: 1256 (inner range)–1086 (median range)–640 (outer range); 48.8% of the specimens belonged to three species: *S. alpigena, C. avicula* and *P. elongata*. Lycosidae specimens increased fivefold (318–900–1643) with *Pardosa riparia* counting for 82.0% of all lycosid specimens. Gnaphosidae specimens increased six fold (12–51–75) (Fig. 5).

Table 2. Influences of relative distance from the tree trunk, branch cover and vegetation cover on species richness and activity density per family. Abbreviations: *N* = total number of species, *n* = total number of trapped specimens, r_S = Spearman rank correlation coefficients, *p* = significance (**p* < 0.05, ***p* < 0.01, ****p* < 0.001), b = significant after Bonferroni correction (*p* < 0.05).

		Relative distance	Branch cover	Vegetation cover
Number of traps →		36	36	36
Species richness				
Linyphiidae	r_S	–0.587	0.771	0.461
(*N* = 44)	*p*	***b	***b	**
Lycosidae	r_S	0.757	–0.706	–0.361
(*N* = 6)	*p*	***b	***b	*
Gnaphosidae	r_S	0.639	–0.371	–0.030
(*N* = 7)	*p*	***b	n.s.	n.s.
all families	r_S	–0.098	0.391	0.299
(*N* = 69)	*p*	n.s.	n.s.	n.s.
Activity density				
Linyphiidae	r_S	–0.536	0.692	0.569
(*n* = 2982)	*p*	***b	***b	***b
Lycosidae	r_S	0.814	–0.646	–0.082
(*n* = 2861)	*p*	***b	***b	n.s.
Gnaphosidae	r_S	0.651	–0.392	–0.094
(*n* = 138)	*p*	***b	n.s.	n.s.
all families	r_S	0.330	–0.047	0.381
(*n* = 6266)	*p*	n.s.	n.s.	n.s.

Correlation analyses of species richness and activity densities (specimen numbers)

We found significant correlations between the relative distance from the tree trunk and the number of species and specimens of Linyphiidae, Lycosidae and Gnaphosidae (Table 2). Linyphiidae decreased, while Lycosidae and Gnaphosidae increased (Table 2). Linyphiidae correlated positively with both branch and vegetation covers, i.e. the more pronounced the cover, the more species and specimens of linyphiids occurred. In contrast, lycosids correlated negatively with the branch cover but not with the vegetation cover, whereas the gnaphosids showed no correlations in both (Table 2). The total counts of species and specimens showed no correlations at all (Table 2).

Activity densities of selected species

Differences between trees

Ten species showed no significant differences in activity density under the four trees. However, four species, i.e. *A. expunctus* (KW: $\chi^2 = 10.867$, df = 3, $p = 0.012$; Nemenyi: $p < 0.05$), *B. luteolus* (KW: $\chi^2 = 14.342$, df = 3, $p = 0.002$; Nemenyi: $p < 0.01$), *C. pabulator* (KW: $\chi^2 = 18.136$, df = 3, $p < 0.001$; Nemenyi: $p < 0.01$), and *M. carpenteri* (KW: $\chi^2 = 9.940$, df = 3, $p = 0.019$, Nemenyi, $p < 0.05$), maintained significant differences at the 5%-level between trees 1 and 2. *C. pabulator* (Nemenyi: $p < 0.01$) also sustained different activity densities between trees 1 and 4. *See* Table 3 for numbers of specimens per tree.

For a more detailed comparison of the different abundances of these species under the four trees we calculated the total branch cover per tree for all nine traps. The values were 13.0 (tree 1), 26.8 (tree 2), 20.1 (tree 3), and 20.4 (tree 4) respectively. Tree 1 was the "lightest", and tree 2 the "darkest" of the four trees. *A. expunctus* avoided not only the outer distance ranges of trees 2–4 but also all distance ranges

Table 3. Influences of relative distance from the tree trunk, branch cover and vegetation cover on spider activity densities. Abbreviations: n = number of specimens, r_s = Spearman rank correlation coefficients, p = significance (*p < 0.05, **p < 0.01, ***p < 0.001), b = significant after Bonferroni correction (p < 0.05), X = excluded data, if fewer than 18 specimens.

		Relative distance				Relative distance, all trees	Branch cover, all trees	Vegetation cover, all trees
		Tree 1	Tree 2	Tree 3	Tree 4			
Number of traps →		9	9	9	9	36	36	36
Cryphoeca silvicola	r_s	X	–0.966	–0.804	–0.849	–0.779	0.839	0.489
	p	X	***	**	**	***b	***b	**
	n	8	97	50	45	200	200	200
Agnyphantes expunctus	r_s	X	–0.834	–0.420	–0.831	–0.554	0.676	0.490
	p	X	**	n.s.	**	***b	***b	**
	n	1	42	16	29	88	88	88
Bolyphantes luteolus	r_s	0.854	X	0.802	0.815	0.564	–0.589	–0.269
	p	**	X	**	**	***b	***b	n.s.
	n	102	13	29	58	202	202	202
Caracladus avicula	r_s	0.552	0.661	0.753	0.454	0.654	–0.429	–0.292
	p	n.s.	n.s.	*	n.s.	***b	**	n.s.
	n	87	144	118	121	470	470	470
Centromerus pabulator	r_s	X	–0.069	0.388	0.017	0.095	0.060	0.169
	p	X	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	n	2	38	28	38	106	106	106
Improphantes nitidus	r_s	–0.966	–0.870	–0.843	–0.842	–0.858	0.746	0.411
	p	***	**	**	**	***b	***b	*
	n	42	51	93	72	258	258	258
Macrargus carpenteri	r_s	0.186	X	X	0.785	0.583	–0.567	–0.387
	p	n.s.	X	X	*	***b	***b	*
	n	40	11	15	44	110	110	110
Panamomops tauricornis	r_s	X	–0.881	–0.901	–0.762	–0.865	0.710	0.366
	p	X	**	**	*	***b	***b	*
	n	12	35	16	20	83	83	83
Pelecopsis elongata	r_s	–0.617	–0.451	–0.059	–0.527	–0.291	0.313	0.200
	p	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	n	82	20	70	166	338	338	338
Scotinotylus alpigena	r_s	–0.858	–0.762	–0.762	–0.946	–0.748	0.887	0.612
	p	**	*	*	***	***b	***b	***b
	n	59	225	115	229	628	628	628
Scotinotylus clavatus	r_s	X	–0.905	X	–0.879	–0.716	0.817	0.585
	p	X	***	X	**	***b	***b	***b
	n	3	44	10	32	89	89	89
Tapinocyba affinis	r_s	–0.485	–0.586	0.114	–0.638	–0.404	0.536	0.341
	p	n.s.	n.s.	n.s.	n.s.	*	***b	*
	n	55	62	37	69	223	223	223
Alopecosa taeniata	r_s	0.763	0.879	0.797	0.895	0.686	–0.552	–0.032
	p	*	**	*	***	***b	***b	n.s.
	n	54	79	62	151	346	346	346
Pardosa riparia	r_s	0.678	0.767	0.683	0.833	0.739	–0.500	–0.036
	p	*	*	*	**	***b	**	n.s.
	n	440	790	558	557	2345	2345	2345
No. of sig. cases: p < 0.05		5 (55%)	8 (67%)	8 (67%)	10 (71%)	12 (86%)	12 (86%)	8 (57%)
No. of sig. cases: p < 0.01		3 (33%)	6 (50%)	4 (33%)	8 (57%)	11 (79%)	12 (86%)	4 (29%)
No. of sig. cases: p < 0.001		1 (11%)	2 (17%)	1 (8%)	2 (14%)	11 (79%)	10 (71%)	2 (14%)
No. of sig. cases after Bonferroni: p < 0.05		–	–	–	–	11 (79%)	10 (71%)	2 (14%)

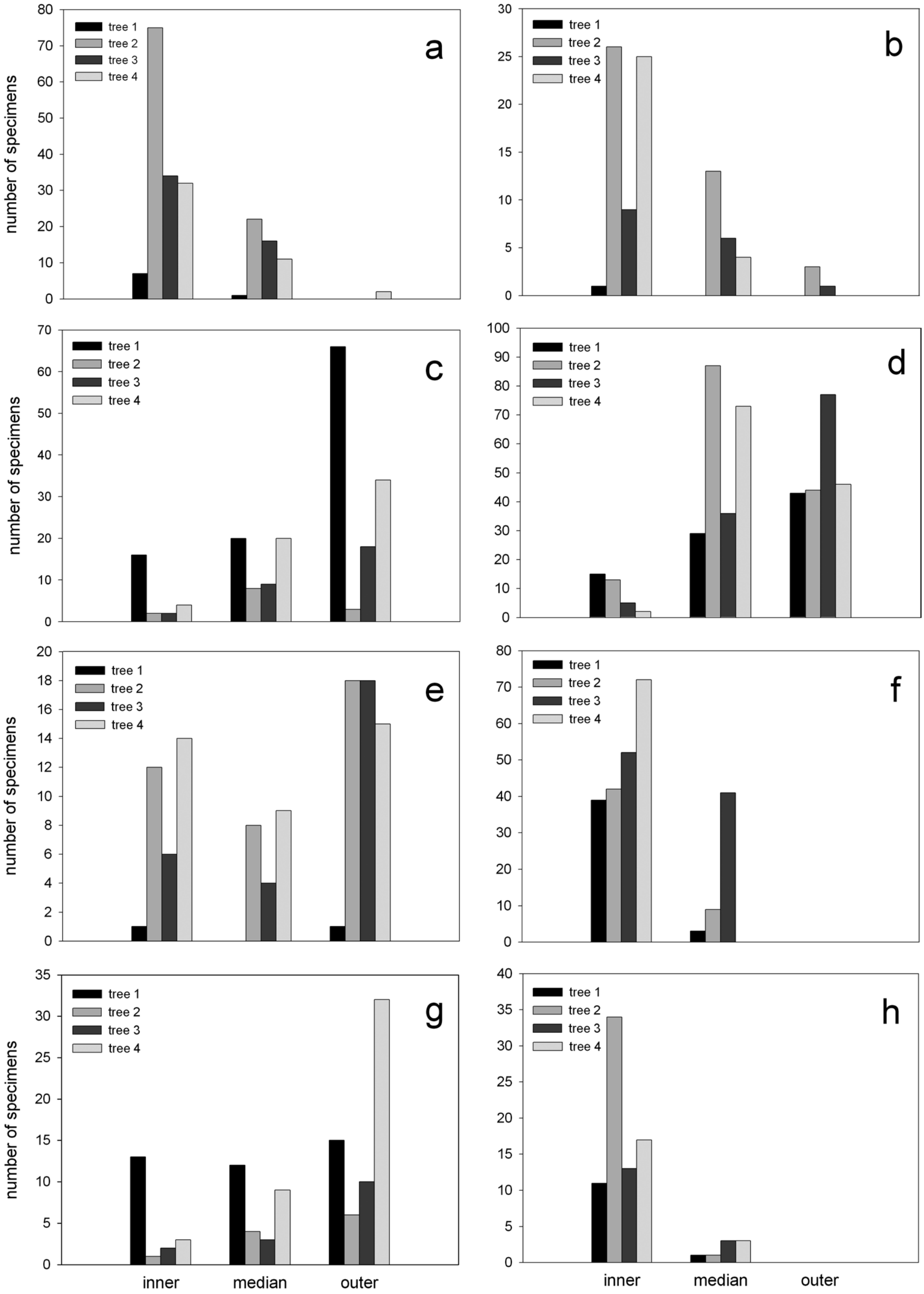

Fig. 6. Number of specimens per tree and in each distance range. (**a**) *Cryphoeca silvicola*; (**b**) *Agnyphantes expunctus*; (**c**) *Bolyphantes luteolus*; (**d**) *Caracladus avicula*; (**e**) *Centromerus pabulator*; (**f**) *Improphantes nitidus*; (**g**) *Macrargus carpenteri*; (**h**) *Panamomops tauricornis*.

of the "light" tree 1. The highest activity density for this species occurred under the "dark" tree 2 (Fig. 6b). In contrast, *B. luteolus* and *M. carpenteri* preferred not only the outer distance range of trees 2–4, but also all distance ranges of tree 1. Their lowest activity density occurred under the "dark" tree 2 (Fig. 6c and g). *C. pabulator* showed no preference (Fig. 6e).

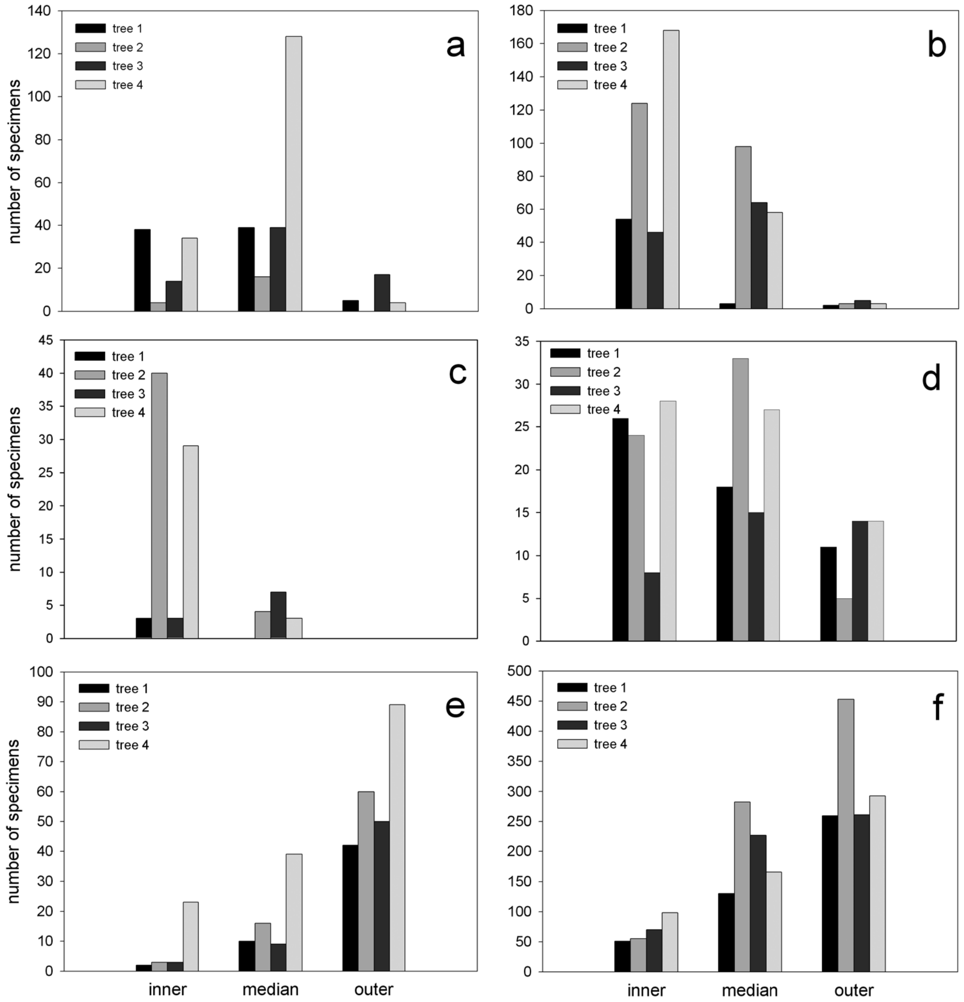

Fig. 7. Number of specimens per tree and in each distance range. (**a**) *Pelecopsis elongata*; (**b**) *Scotinotylus alpigena*; (**c**) *Scotinotylus clavatus*; (**d**) *Tapinocyba affinis*; (**e**) *Alopecosa taeniata*; (**f**) *Pardosa riparia*.

Relative distance

The observed activity densities of 11 (*C. silvicola*, *A. expunctus*, *B. luteolus*, *C. avicula*, *I. nitidus*, *M. carpenteri*, *P. tauricornis*, *S. alpigena*, *S. clavatus*, *A. taeniata*, *P. riparia*) out of 14 species were significantly correlated with the distance from the tree trunk. Their activity densities in the inner, median and outer distance ranges of each tree are shown in Figs. 6 and 7.

C. silvicola, *A. expunctus*, *I. nitidus* and *P. tauricornis* decreased in numbers from the inner to the outer distance range (Fig. 6a, b, f and h, respectively). *S. alpigena* and *S. clavatus* showed the same tendency in all trees but tree 3, where both species occurred in highest numbers in the median distance range (Fig. 7b and c, respectively). For these species, Spearman rank correlation coefficients (r_S) of activity density and relative distance was negative at $p < 0.05$ (Table 3). In addition, *C. silvicola* (Fig. 6a), *A. expunctus* (Fig. 6b), *P. tauricornis* (Fig. 6h), and *S. clavatus* (Fig. 7c), occurred most frequently around the "dark" tree 2, while the lowest number of specimens was found around the "light" tree 1 (*see* above).

The activity densities of *B. luteolus*, *M. carpenteri*, *A. taeniata* and *P. riparia* were positively and significantly correlated with the relative distance to the tree trunk and the pooled data for all trees (Figs. 6c and g, 7e and f, respectively; Table 3). *C. avicula* showed a similarly significant positive correlation for the pooled data for all trees (Table 3); however, the pattern differed for trees 2 and 4, with the highest number of specimens collected in the median distance range (Fig. 6d).

For *C. pabulator*, *P. elongata* and *T. affinis* correlation between the activity density and the relative distance was not significant at $p < 0.05$ (Table 3). For *C. pabulator*, the median distance range showed the lowest number of specimens (Fig. 6e), with *P. elongata* showing the highest (Fig. 7a). *T. affinis* displayed different tendencies between trees, decreasing in number from the inner to the outer distance range in trees 1 and 4 and maintaining the highest activity density in the median distance range in trees 2 and 3 (Fig. 7d).

Branch cover

A significant correlation was found between the number of individuals collected and the degree of branch cover in ten species (Table 3): *C. silvicola*, *A. expunctus*, *B. luteolus*, *I. nitidus*, *M. carpenteri*, *P. tauricornis*, *S. alpigena*, *S. clavatus*, *T. affinis*, *A. taeniata*. Among these ten species, a positive correlation was present in *C. silvicola* and all linyphiids but *B. luteolus and M. carpenteri*, where we found a negative correlation as in *A. taeniata* (Table 3). *C. avicula*, *C. pabulator*, *P. elongata*, and *P. riparia* showed no significant correlations (Table 3).

Vegetation cover

A positive correlation with the degree of vegetation cover was found in two species, i.e. *S. alpigena* and *S. clavatus* (Table 3).

Discussion

Community composition

The increase of lycosids and gnaphosids in specimen numbers with relative distance from the tree trunk is probably due to the preferences of many species of these free-hunting spiders for open habitats like alpine meadows (Grimm 1985, Pajunen *et al.* 1995, Thaler & Buchar 1994, 1996, Buchar & Thaler 1995, 1997). This hypothesis is also supported by the negative correlation of the lycosids with branch cover. Linyphiids made up the majority of forest species rarely found in open land, reflected by the negative correlation with relative distance and the positive correlation with branch cover (Thaler 1995b, 1999).

The habitat quality, especially the microclimate, reflected by the vegetation cover, plays a decisive role in the small scale distribution of spider species (Bauchhenss 1990, Wise 1993, Downie *et al.* 1995, Foelix 1996, Samu *et al.* 1999). The inner distance range of a tree, preferred by the linyphiids in our study, is characterized by higher humidity and lower and more stable temperature as compared to the outer distance range (Larcher 2001). Our data correspond to those of Hatley and MacMahon (1980) on spiders in a sage (*Artemisia tridentata*) community. They showed that as compared with free hunters (like lycosids and gnaphosids) web-building species, like the linyphiids, preferred higher humidity and lower temperature as well as denser vegetation. So the similar patterns of spider species richness and activity densities presented in Hatley and MacMahon (1980) and in our study could possibly be extrapolated to a wider variety of biotopes. Therefore these results may be of importance for our general understanding of the distribution and species diversity of predatory invertebrates.

Pajunen *et al.* (1995), in a study about epigeic forest spiders in southern Finland, found similar patterns of species and specimen counts for the Linyphiidae, Lycosidae, and Gnaphosidae. They attempted an explanation of these patterns through the availability of suitable prey items (Otto & Svensson 1982) and through habitat preferences. However, as shown by Huhta (1971), the activity density of springtails in forest soils does not influence the size of populations of spiders feeding on them. There is insufficient knowledge, however, on the prey spectra of many spiders. Springtails (Collembola) play a major role for small linyphiids (Nentwig 1987, Nyffeler 1988, 1999) and for boreal forest-dwelling species (Huhta 1971), while lycosids feed mainly on larger prey items like Diptera, Homoptera, Coleoptera, Heteroptera and other spiders (Edgar 1969, Nentwig 1987, Nyffeler 1999).

An additional possible explanation concerns the importance of three-dimensional vegetation structural elements (Cherret 1964, Coulson & Butterfield 1986, Downie *et al*. 1995, Pajunen *et al*. 1995, Pearce *et al*. 2004). This could be especially true for web builders and could explain the preferences for branch- and vegetation-covered habitats by the linyphiids.

Activity densities of selected species

The majority of species correlated with the parameters studied. This confirms the importance of a particular structural element, i.e. stand-alone spruce trees in an alpine environment. They offer different microclimatic conditions to the "open" surroundings (Larcher 2001, Zweifel *et al*. 2002). Microclimatic factors depend largely on vegetation structure (Larcher 2001), in our case mainly on branch and vegetation cover. However, these parameters are difficult to measure and quantify and could only be estimated in this study. Furthermore, all three parameters were significantly correlated with each other. Thus we focused mainly on the relative distance of spider catches to the tree trunk, indicating particular microclimatic conditions. The data on branch and vegetation cover should therefore be treated here as complementary. In addition, differences in vegetation cover may influence the occurrence of spiders not only due to different microclimate but also to mechanical barriers.

Differences between trees

Four species (*A. expunctus*, *B. luteolus*, *C. pabulator* and *M. carpenteri*) were significantly different in terms of their specimen numbers under trees 1 and 2. This may be explained by the fact that tree 1 had the lowest degree of branch cover up to 1 m above the ground (total cover 13.0), while tree 2 had the highest among the four trees studied (total cover 26.8). As was expected, the forest species *A. expunctus* (Maurer & Hänggi 1990, Heimer & Nentwig 1991, Muster 2001) preferred the "dark" tree 2 and the inner distance ranges of the other trees. In contrast, the open land species *B. luteolus* (Palmgren 1973, Maurer & Hänggi 1990, van Helsdingen *et al*. 2001) and *M. carpenteri* with different habitat preferences (Thaler 1983) showed the opposite trend i.e. they preferred the "lighter" areas. This is also consistent with findings of *M. carpenteri* in meadows and dwarf shrub heath (Thaler 1995b, Muster 2001). The differences could also be due to different surroundings of trees (alpine pasture on the one hand, dwarf shrub heath on the other hand); however, the proportions of these two did not markedly differ in the surroundings of the trees.

Relative distance to tree trunk, branch cover, and vegetation cover

Eleven out of fourteen species were significantly influenced by the distance from the tree trunk. Nine of these (all except *C. avicula* and *P. riparia*) correlated also with the branch cover. Only two were found to correlate with vegetation cover (*S. alpigena*, *S. clavatus*). This could indicate that microclimatic factors related to shading were more important than the structure of the vegetation layer.

B. luteolus, *C. avicula*, *M. carpenteri*, *A. taeniata* and *P. riparia* preferred the outer distance range with a significant decrease in specimen numbers towards the tree trunk (Figs. 6c and d, 7e and f, respectively). The correlation with the branch cover was negative (not significant in *C. avicula* and *P. riparia*). Both data sets show that the species avoid dark areas under the trees. *B. luteolus* and *P. riparia* are known to prefer open habitats (Maurer & Hänggi 1990, Thaler 1995a, Muster 2001). The habitat preferences of *M. carpenteri* (*see* above) and *A. taeniata* were more difficult to assess. Kronestedt (1990) discussed the occurrence of *A. taeniata* in different types of forests, e.g. coniferous and birch forests, and in more shady and mesic habitats. In our study site, *A. taeniata* clearly preferred the less shaded outer distance ranges of the trees and correlated significantly and negatively with the degree of branch cover (Fig. 7e and Table 3). It should also be kept in mind that old data may be unreliable due to confusion with *Alopecosa aculeata* (Kronestedt 1990).

One could speculate that these open-land species occurred under stand-alone trees merely by chance and so should have no ecological influence. Also Pearce *et al.* (2005) observed higher abundances of open habitat specialists in small spruce patches within a clear-cut area than in other forested habitats. However, in our study they occurred mostly in high numbers (especially *P. riparia*) and thus should have a considerable impact.

C. avicula is known as a litter dweller in subalpine forests rather than in alpine meadows where it has been found less often (de Lessert 1910, Maurer & Hänggi 1990, Thaler 1995a, Muster 2001). As it is a rare species that has usually been found in smaller numbers (e.g. Thaler 1999, Muster 2001) these conclusions should be re-evaluated. Our results based on 470 specimens suggest that *C. avicula* appears in highest numbers at the timberline, at least on Alp Flix. So, *C. avicula* possibly can be classified as a habitat specialist of the timberline with a tendency towards more open and light areas.

The activity densities of six species (*C. silvicola*, *A. expunctus*, *I. nitidus*, *P. tauricornis*, *S. alpigena*, *S. clavatus*) correlated negatively with the relative distance to the tree trunk and positively with the branch cover and the animals preferred the "dark" tree 2. These findings are in good accordance with literature data. All six species are known to occur mostly in litter of coniferous forests (de Lessert 1910, Maurer & Hänggi 1990, Thaler 1995a, 1999, Muster 2001). *C. silvicola* and *I. nitidus* seem to be restricted to forests, while the other species also occur in dwarf shrub heath. Our data (only two specimens of *C. silvicola* and no specimens of *I. nitidus* in the outer distance range) support these observations (Fig. 6a and f). Remarkably, *P. tauricornis* and *S. clavatus* were also totally absent from the outer distance range and occurred mostly in the inner distance range (Figs. 6h and 7c). The few specimens of both species that were found in the median distance range occurred in traps with high vegetation cover nearby. It can be assumed that these localities offer microclimatic conditions similar to those in the litter layer of coniferous forests, their preferred habitat.

These marked differences in the activity densities of the 14 selected species seem to be partly in contrast to the results revealed by the Czekanowski indices for the families. However, the Czekanowski index accounts for the occurrence or absence of a species only, thereby neglecting individual numbers. Differential occurrence of a species in different distance ranges is thus often overlooked when using this index alone.

Three species (*C. pabulator*, *P. elongata* and *T. affinis*) did not significantly correlate with relative distance from the trunk. Of these, *T. affinis* was positively correlated with the branch cover. Furthermore this species is known as a forest species with additional occurrence in dwarf shrub heath and meadows (Maurer & Hänggi 1990, Muster 2001).

In conclusion, while the alpine timberline occupies only a small area, it shows high structural heterogeneity and offers habitats for numerous open-land species, forest species, and possibly also habitat specialists. Thus, the alpine timberline may play a key role in future conservation efforts. Our data show that the mosaic pattern of structural elements is reflected by a wide variety of spider species with different and strictly defined habitat preferences. This is especially important in a landscape where the original forests were highly fragmented by human activities. Depending on their dispersal abilities, forest species could use stand-alone trees as stepping stones between larger forest areas. In this way, stand-alone trees may be important for habitat coherence. As the critical area for the long term survival of spider species is rather small (below 1 ha at least for open-land species; Hänggi 1991), future research should focus special attention on such biotopes.

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Appendix. List of all species caught in this study with numbers per distance range and total number.

	Inner	Median	Outer	Total
Amaurobiidae				
Coelotes terrestris	0	0	1	1
Dictynidae				
Mastigusa arietina	0	3	0	3
Gnaphosidae				
Drassodes cupreus	0	2	4	6
Drassodes pubescens	1	4	6	11
Gnaphosa leporina	1	2	7	10
Haplodrassus signifer	9	23	26	58
Micaria aenea	1	18	31	50
Micaria pulicaria	0	1	1	2
Zelotes talpinus	0	1	0	1
Hahniidae				
Cryphoeca silvicola	148	50	2	200
Linyphiidae				
Agnyphantes expunctus	61	23	4	88
Agyneta cauta	1	7	35	43
Anguliphantes monticola	8	1	0	9
Bolephthyphantes index	0	5	2	7
Bolyphantes alticeps	3	8	14	25
Bolyphantes luteolus	24	57	121	202
Caracladus avicula	35	225	210	470
Centromerus arcanus	1	0	2	3
Centromerus pabulator	33	21	52	106
Ceratinella brevis	0	0	1	1
Erigonella subelevata	1	9	5	15
Evansia merens	0	0	2	2
Gonatium rubens	1	3	4	8
Improphantes nitidus	205	53	0	258
Lepthyphantes nodifer	1	0	0	1
Macrargus carpenteri	19	28	63	110
Mansuphantes pseudoarciger	20	7	1	28
Maro lehtineni	1	3	4	8
Metopobactrus schenkeli	0	0	1	1
Micrargus alpinus	4	1	0	5
Mughiphantes cornutus	43	8	0	51
Mughiphantes mughi	7	2	0	9
Obscuriphantes obscurus	0	1	0	1
Panamomops tauricornis	75	8	0	83
Pelecopsis elongata	90	222	26	338
Pelecopsis radicicola	1	4	2	7
Pityohyphantes phrygianus	1	2	0	3
Porrhomma campbelli	2	1	1	4
Porrhomma pallidum	28	7	2	37
Scotargus pilosus	5	2	0	7
Scotinotylus alpigena	392	223	13	628
Scotinotylus clavatus	75	14	0	89
Stemonyphantes conspersus	8	5	0	13
Tapinocyba affinis	86	93	44	223
Tenuiphantes cristatus	1	2	4	7
Tenuiphantes jacksonoides	1	0	0	1
Tenuiphantes mengei	4	12	17	33
Tenuiphantes tenebricola	6	0	0	6
Thyreostenius biovatus	7	2	0	9
Walckenaeria antica	5	3	9	17
Walckenaeria languida	0	1	0	1
Walckenaeria mitrata	0	0	1	1
Walckenaeria monoceros	1	0	0	1
Liocranidae				
Agroeca proxima	2	2	0	4
Lycosidae				
Alopecosa pulverulenta	1	2	53	56
Alopecosa taeniata	31	74	241	346
Arctosa renidescens	0	3	42	45
Pardosa blanda	12	16	40	68
Pardosa riparia	274	805	1266	2345
Trochosa terricola	0	0	1	1
Philodromidae				
Philodromus collinus	1	0	0	1
Philodromus vagulus	1	0	0	1
Thanatus formicinus	0	4	15	19
Sparassidae				
Micrommata virescens	1	0	1	2
Theridiidae				
Robertus truncorum	17	12	3	32
Steatoda phalerata	0	1	0	1
Thomisidae				
Xysticus audax	2	5	8	15
Xysticus gallicus	0	1	0	1
Xysticus luctuosus	0	1	7	8