Co-existence of divergent communities at natural boundaries: spider (Arachnida: Araneae) diversity across an alpine timberline

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Abstract. 1. Habitat boundaries can contain high biodiversity because they potentially combine species from two habitat types plus additional boundary specialists. However, most research on animal communities is focused on uniform habitats.

2. Here, we assessed the degree to which the community change at a habitat edge is determined by the broad-scale spatial transition from one habitat to the other, or by fine-scale environmental influences. We compared the distribution of ground-dwelling spider species from open land to forest with the distribution around stand-alone trees at the boundary, the alpine timberline (Grisons, Switzerland).

3. Our results showed that spiders were more strongly influenced by local environmental conditions (40% of explained variation) than by the spatial position within the ecotone (24.5% of explained variation, with 15.6% overlap between the two). Spider communities differentiated according to light availability and corresponding changes in the ground vegetation.

4. Since the small area around a single tree at the studied timberline offered a similar broad spectrum of environmental conditions as the open land and forest together, it provided both habitats for species from the adjoining open land and forest as well as for some possible timberline specialists.

5. Accordingly, natural habitat boundaries may maintain very contrasting communities by providing a wide range of habitat conditions.

Key words. Arthropods, dwarf-shrub heath, ecotone, environment and space, forest, light, microspatial distribution, pitfall traps, Swiss Central Alps, vegetation structure.

Introduction

Spatial patterning of landscapes and its influence on the abundance and distribution of organisms remains one of the most fundamental issues in ecology (Ricklefs, 2004; Rahbek, 2005). Ecosystem management requires an understanding of the factors that drive species diversity. Landscapes exist as mosaics of numerous different patch types that interact with each other. Hence, knowledge about the ecology of habitat edges is critical for understanding which resources and interactions determine the distribution of organisms (Ries *et al.*, 2004). As land-use pressure often reduces the area of boundary habitats, their value in the conservation of habitats and species should be investigated (Harrison & Bruna, 1999; Brooks, 2000; Channell & Lomolino, 2000). Edges can be defined as ecotones between two plant communities, which are the transition zones between these communities (Holland *et al.*, 1991). The specific characteristics and value of the ecotonal flora and fauna have been known for a long time as 'edge effects', which are manifested as high diversity in microhabitats, a change in abiotic factors and species interactions and elevated species richness (Odum, 1971; Matlack, 1993; Murcia, 1995; Laurance *et al.*, 2002). Recently, ecotones were even found to be sources of speciation (Smith *et al.*, 1997; Schilthuizen, 2000).

However, our knowledge about biotic patterns and processes across natural boundaries and their extrapolation to landscapes

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is still limited (Ries *et al*., 2004). Only a small proportion of the edge literature deals with arthropods, although they account for the largest part of animal biodiversity (Wilson, 1992). Arthropods are important in a range of ecological processes (Didham *et al*., 1996), which should make them a main target for conservation. Existing studies on arthropods at habitat boundaries are often focused on anthropogenically created edges around clear-cuts, plantations or arable land (Duelli *et al*., 1990; Downie *et al*., 1996; Martin & Major, 2001; Rand *et al*., 2006; Matveinen-Huju *et al*., 2006). Comparatively few investigations have addressed natural ecosystems within the scope of edge ecology and arthropods (but see Heublein, 1983; Hänggi & Baur, 1998; Kotze & Samways, 2001; Magura *et al*., 2001; Ferguson, 2004). Still, these systems may provide advantages in assessing habitat associations and spatial patterns of organisms due to their equilibrium conditions and more stable populations (Maurer, 1980; Ricklefs, 2004).

In this empirical study, we investigated the differentiation of epigeic spider communities across a natural boundary, the alpine timberline. We chose spiders as study organisms because they are abundant, species rich, and known to have well-defined habitat preferences (Cherrett, 1964; Coddington & Levi, 1991; Wise, 1993; Foelix, 1996), which makes them sensitive to edge effects and suitable for studying organism–habitat relationships. Moreover, because they are at the top of invertebrate food chains (Wise, 1993), spiders are likely to play an important role in shaping terrestrial arthropod communities and may therefore influence the distributions of other arthropods. The importance of vegetation structure in influencing spider distribution has long been noted (Robinson, 1981; Uetz, 1991; Downie *et al*., 1995). Recently, Frick *et al*. (2007) were able to show that a single spruce tree at the timberline offers habitats for a wide range of spider species with different abiotic requirements. It has been assumed that these requirements can be described as environmental gradients in moisture and shading, respectively (Huhta, 1971; Wise, 1993; Ferguson, 2004), which was confirmed in a recent analysis across Central Europe (Entling *et al*., 2007). However, we still do not know the unique and quantitative contribution of moisture and shading and the relative influence of other variables such as vegetation structure in determining spider distribution. Additionally, studies that differentiate between spatial and ecological influence are still scarce, although the importance of space in structuring communities has been discussed for years and approaches to integrate the new concepts into statistical analysis are manifold. In the current study, we analysed to which degree the community change at the alpine timberline is determined by the broad-scale spatial transition from one habitat to the other, or by fine-scale environmental influences. Moisture was relatively uniform across our study area due to the consistent inclination and the western exposition. We therefore focused on vegetation structure and the environmental gradient in shading. By investigating the spider distribution and its underlying factors, we also aimed to assess the value of boundaries, for example, the alpine timberline, in maintaining invertebrate communities. We specifically addressed four questions: (i) is community change at a timberline characterised by a broad-scale spatial transition from the open land to forest, or by fine-scale environmental influences? (ii) is vegetation structure or light more important in structuring epigeic spider communities? (iii) is an alpine timberline more species rich than the open land and forest, respectively? (iv) are there boundary species at a timberline that are absent from the adjoining habitats?

Methods

Study site

The study was conducted at Alp Flix (9°38′E, 46°31′N) in the Swiss Central Alps near the village of Sur in the canton Grisons, Switzerland. The alp is a southwest exposed terrace of 15 km^2 at 1950 m above sea level. It is surrounded by 3000 m mountain peaks and a valley. Our study area was a 300-m long stretch of timberline plus fragments of the adjoining Norway spruce forest (*Vaccinio-Piceion*) to the west and of the dwarf-shrub heath (*Juniperion nanae*) to the east. Each of the three parts covered approximately 3 ha. The site is located on a small slope inclined slightly towards the forest and is used for occasional cattle grazing throughout the vegetation period.

Study design and spider sampling

We differentiated between five habitat zones: the open land (dwarf-shrub heath) and forest, representing two macrohabitats, and three microhabitats linked to a single spruce tree at the timberline. These three microhabitats were defined by their location relative to the tree as: (i) next to the trunk (in figures and tables denoted as timberline trunk), (ii) at the end of branch cover (timberline branch), and (iii) in the adjoining open area outside of branch cover (timberline open). These five zones represented the whole gradient of habitat structures from forest to open land and thus allowed us to compare the macrospatial gradient across these two habitats with the microspatial gradient across the three areas around a tree.

In each of the five different habitat zones, we placed 15 pitfall traps. In the open land, forest and the open area at the timberline the traps were randomly positioned at least 15 m apart from each other. For placing the traps in the timberline zones at the end of branch cover and next to the trunk, the tree nearest to the trap in the open area at the timberline was chosen. Thus, the three microhabitats at the timberline were sampled at each of fifteen stand-alone trees. The mean distances between the traps in these three microhabitats were 4.1 m (timberline open–timberline branch), 4.5 m (timberline open–timberline trunk) and 1.5 m (timberline branch–timberline trunk). The traps consisted of white plastic cups with an upper diameter of 6.9 cm and a depth of 7.5 cm filled with a solution of 4% formaldehyde in water plus detergent (0.05% sodium dodecyl sulphate). Each trap was covered with a quadrangular transparent plastic roof (15 × 15 cm) fixed by three wooden rods 8 cm above-ground. Due to the proximity of cattle and the toxicity of the trapping liquid, we fenced off each trap with three plastic poles connected with ribbons. The traps were operated for 1 year. They were emptied monthly during the snow-free period (May 2005 to October 2005) and then left under the snow layer until May 2006, when

Table 1. Environmental conditions (mean ± SE) in the five different habitat zones (for definitions see text). $N = 15$ for each habitat.

	Open land	Timberline open	Timberline branch	Timberline trunk	Forest
Open ground (percentage)	11 ± 2	9 ± 2	22 ± 3	31 ± 5	57 ± 7
Stone (percentage)	4 ± 1	3 ± 1	3 ± 0	3 ± 1	3 ± 1
Moss (percentage)	1 ± 0	3 ± 1	9 ± 2	9 ± 3	19 ± 4
Herb (percentage)	40 ± 5	36 ± 4	32 ± 3	25 ± 3	18 ± 6
Low dwarf-shrub (percentage)	26 ± 4	23 ± 4	20 ± 3	18 ± 3	2 ± 1
High dwarf-shrub (percentage)	20 ± 5	27 ± 5	18 ± 4	16 ± 3	2 ± 1
Branch close to ground (percentage)	0 ± 0	0 ± 0	20 ± 3	30 ± 4	2 ± 1
Branch distant from ground (percentage)	0 ± 0	2 ± 1	44 ± 4	68 ± 4	60 ± 8
Trunk (percentage)	0 ± 0	0 ± 0	1 ± 0	3 ± 1	3 ± 1
Small spruce (percentage)	1 ± 1	3 ± 1	4 ± 2	1 ± 1	0 ± 0
Tree smaller 2.5 m (n ha^{-1})	8 ± 8	263 ± 72	246 ± 66	289 ± 82	246 ± 56
Tree density (n ha^{-1})	0 ± 0	272 ± 49	373 ± 60	365 ± 63	1053 ± 107
Distance to closest trunk (metres)	41.6 ± 3.8	4.6 ± 0.6	1.4 ± 0.1	0.4 ± 0.1	1.8 ± 0.3
Distance to closest branch (metres)	40.1 ± 3.8	2.8 ± 0.4	0 ± 0	−1 ± 0.1	1.2 ± 0.3
Visible sky (percentage)	79 ± 1	63 ± 2	27 ± 2	14 ± 1	15 ± 0
Available radiation (percentage)	0.96 ± 0	0.79 ± 0.03	0.27 ± 0.04	0.10 ± 0.02	0.18 ± 0.02

they were emptied a last time. Only adult spiders were identified to species level, juveniles were excluded from the analyses. Nomenclature followed Platnick (2007).

Environmental variables

Sixteen environmental variables were measured at each of the 75 trap sites (Table 1). Ten variables represent structural categories of vegetation cover and were estimated for a rectangular area of 9 m^2 around each trap in June 2006. Tree branches were distinguished into close to ground (if below 50 cm) and distant from ground (if above 50 cm). Tree density (including trees higher than 2.5 m) and the number of trees below 2.5 m were calculated by counting the number of trees within a radius of 5 m. The proportion of visible sky and related available radiation (i.e. the fraction of direct radiation under the canopy relative to the direct radiation above the canopy) were obtained with hemispheric photographs taken with a Nikon Coolpix 900 digital camera with an FC-E9 fisheye lens attached on the SLM5 Hemiview Self Levelling Mount UM (Delta-T Devices Ltd, Burwell, Cambridge, UK) in July 2006 and the program HEMIVIEW 2.1.

Spatial variables

Techniques to integrate space into analyses of species distribution have greatly increased since Legendre and Fortin (1989). We used the geographical coordinates of all trap locations for assessing linear spatial gradients (Borcard & Legendre, 2002). To allow a more detailed identification of the spatial patterns, we obtained 41 additional spatial variables in a principal coordinates of neighbour matrices (PCNM) analysis (Borcard & Legendre, 2002; Borcard *et al.*, 2004) using the program SPACEMAKER 2 (Borcard & Legendre, 2003). PCNM variables were obtained by principal coordinate analysis (PCoA) of a truncated matrix of distances among sites. As the largest

distance between two adjacent trap sites, we used a truncation distance of 75 m (Borcard & Legendre, 2002). This technique allowed to distinguish between spatial and environmental influences on spider distribution. Nevertheless, it must be noted that only the microhabitats within the timberline were spatially replicated in our study. As the macrohabitats were not replicated, the designation of species as typical for one of the macrohabitats is only valid for the study area, and must not be generalised. In the following, we use terms such as 'forest spiders' in the sense of forest spiders in our study area.

Statistical analysis

Numbers of spider individuals were pooled for each trap over the whole sampling period. Since the length of gradients was only 3.95 and 1.84 for the first two axes of a preliminary detrended correspondence analysis on spider communities (DCA), we used linear methods of ordination (ter Braak & Smilauer, 2002b). We conducted principal component analysis (PCA) to visualise the main trends of community variation across the habitat zones. The environmental variables recorded and the five habitat zones were included passively into the analysis for a first estimation of their influence (Fig. 1). Both analyses were run in the program CANOCO 4.5 for Windows (ter Braak & Smilauer, 2002a) on Hellinger-transformed species data (Legendre & Gallagher, 2001). To measure the relative contribution of spatial and environmental variables in explaining the variation of species assemblages, we partitioned the explained variation (Borcard *et al.*, 1992; Borcard & Legendre, 1994). This was achieved through a series of partial canonical redundancy analyses (RDA). We calculated the 'marginal' and 'conditional' effects of sets of environmental or spatial variables with the program VARCAN 1.0 (Peres-Neto, 2006) adopting the testing procedures described by Legendre and Legendre (1998). Marginal effects denoted the variation explained by a given set without considering other variables, whereas conditional
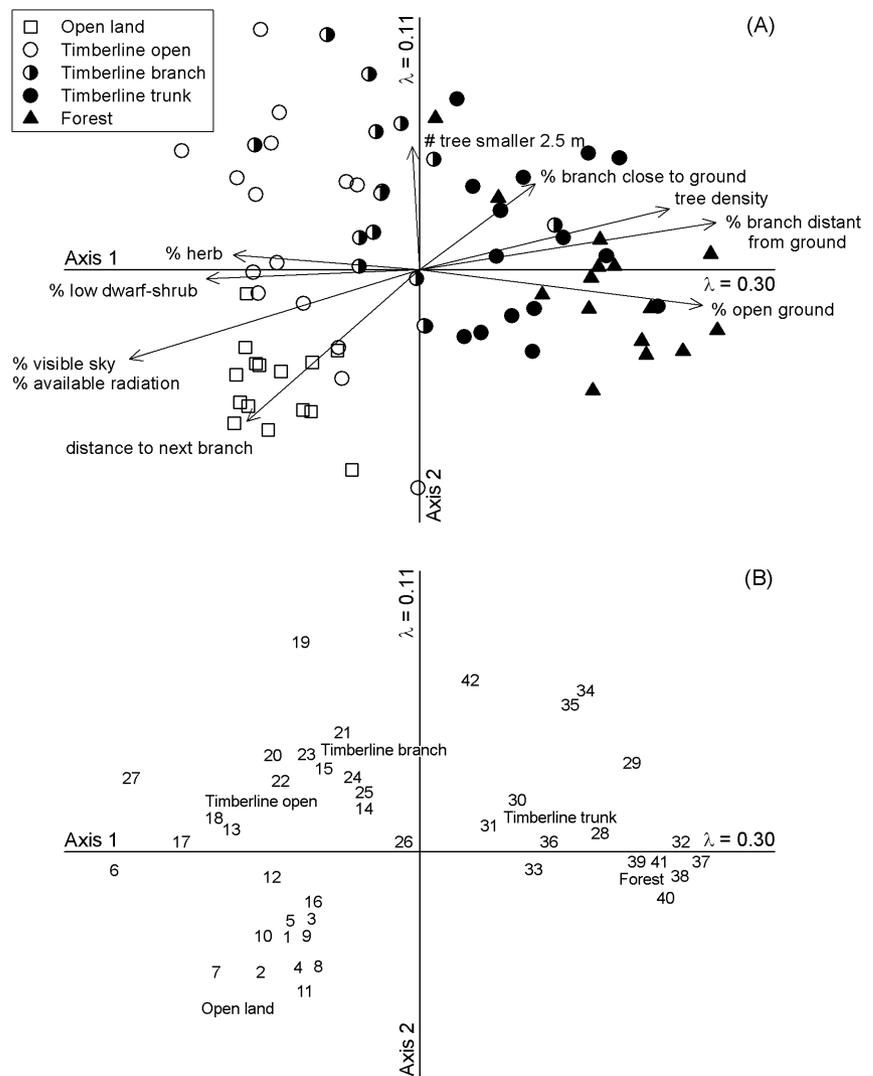
Fig. 1. Principal component analysis (PCA) of spider communities at the 75 trap locations in the five different habitat zones. In (a) passively included environmental variables are represented by arrows; their relative effect on the community differentiation is indicated by the length and direction of the arrows. Only environmental variables accounting for major influences are shown. In (b) the mean positions of the five habitat zones are shown; numbers denote single species with $N \geq 15$ individuals (for names see Table 4).

effects denoted the variation explained by a given set after removing the confounding effect of one or more other variables. VARCAN 1.0 also corrected for the biases in the method of variation partitioning influenced by both the number of explanatory variables and sample size (Dray *et al*., 2006; Peres-Neto *et al*., 2006). As explanatory variables, we used all 16 environmental variables recorded, since using the full set of predictors yields more accurate estimations of fractions than applying forward selection (Peres-Neto *et al*., 2006), as well as the geographical coordinates of all trap locations and the 41 PCNM variables (Fig. 2). The difference between two fractions of variation was tested by using 10 000 bootstrap samples. For estimating the marginal and conditional effects of each environmental variable on species variation, we contrasted them individually with the residual set of environmental predictors (Table 2).

To identify the compositional differences (= beta diversity) within and between assemblages of the five habitat zones (Table 3), we used permutational multivariate analysis of variance (Anderson,

Table 2. Independent, marginal (and dependent, conditional) contribution (percentage) of selected single environmental variables in explaining the spider community structure.

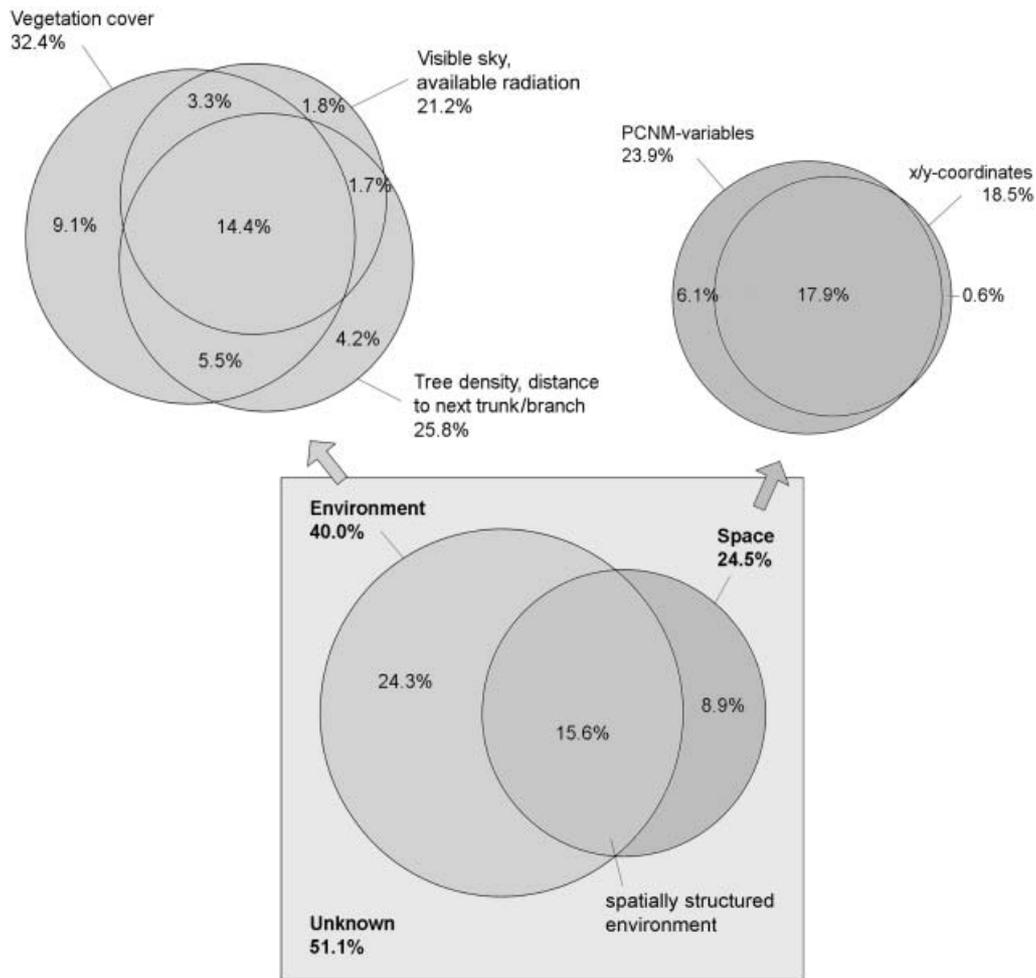|	
Visible sky	21.1 (1.5)
Branch distant from ground	20.8 (0.5)
Available radiation	19.4 (0.2)
Open ground	19.1 (0.5)
Tree density	16.4 (0)
Low dwarf-shrub	12.8 (0.3)
Distance to closest trunk	12.5 (1.6)
Trunk	11.8 (0.2)
Distance to closest branch	10.2 (2.4)
Herb	8.8 (0.5)
Moss	8.1 (0)
High dwarf-shrub	7.7 (0.6)
Branch close to ground	5.4 (1.3)
Tree smaller 2.5 m	3.2 (0.1)

Fig. 2. Variation partitioning (percentage) of the pooled species data into different environmental and spatial components. The area of the square and circles are proportional to the fraction of total variation explained. Values outside the symbols: marginal effects; values inside the symbols: conditional effects (see text). The two fractions 'environment' and 'space' were significantly different ($P = 0.02$), whereas the influence of the x/y coordinate did not differ from the one of the PCNM-variables ($P = 0.28$). The component 'vegetation cover' includes all environmental variables not listed explicitly in this figure, apart from 'tree smaller 2.5 m', which is part of the component 'tree density . . .'.

Table 3. Average Bray–Curtis dissimilarities within/between communities of all five habitat zones. Values in parentheses represent *t*-statistics of pairwise comparisons (all $P < 0.001$, corrected for multiple comparisons after Holm).

	Open land	Timberline open	Timberline branch	Timberline trunk	Forest
Open land	48.5				
Timberline open	54.5 (2.0)	49.9			
Timberline branch	65.0 (3.3)	56.3 (2.1)	51.8		
Timberline trunk	78.4 (4.3)	72.5 (3.6)	62.3 (2.4)	56.1	
Forest	89.8 (5.4)	82.3 (4.6)	73.1 (3.6)	64.3 (2.4)	55.2

2001; McArdle & Anderson, 2001) on the basis of Bray–Curtis distance measure as implemented in the program PERMANOVA (Anderson, 2005). For comparisons of abundance at the species level (Table 4), we used pairwise Kruskal–Wallis tests ($k = 9999$ Monte Carlo permutations), because a Levene's test indicated that variances of the species data were not homogeneous. These analyses were conducted with the program SPSS 14.0 for Windows including only species $N \geq 15$ individuals. All *P*-values were corrected for multiple comparisons after Holm (Legendre & Legendre, 1998).

Results

Spider community differentiation

We captured 6251 adult spiders belonging to 102 species and 14 families. The spider communities of the five distinct habitat zones differed clearly in their species compositions (Fig. 1a). The first PCA axis represented 30% of species variation. It correlated mainly with tree density and the proportion of visible sky and branch distant from ground, and separated the open land from forest. In representing another 11% of variation, the second axis separated the open land from the open area at the timberline, and (less clearly) the three different microhabitats within the timberline.

Variation partitioning revealed that 40% of variation in the species assemblages has been explained by the environment (Fig. 2). However, a large proportion of this variation (15.6% of the total variation explained) overlapped with the spatial structure of the environment. Together with a minor influence of pure spatial attributes (8.9%), almost 49% of species variation has been explained with the variables recorded. The influence of space resulted mainly from a linear gradient, represented by the x and y geographical coordinates, which alone determined 18.5% of species distribution. The variation explained by the environment was mainly attributable to factors directly influencing or resulting from the fraction of light reaching the ground (tree density, available radiation, proportion of visible sky, branch distant from ground and open ground). Most of them contributed about 20% of explanation each, although their influences overlapped highly (Table 2). In contrast, the type of ground vegetation (proportion of dwarf-shrub heath, herb, moss and branch close to ground) did not contribute much to the differentiation of the communities.

The multivariate analysis of variance on the species data showed that the communities found in the five habitat zones differed highly significantly from each other ($F = 12.5$, $P = 0.0001$). The largest dissimilarity was found between the open land and forest (Table 3). The timberline zone next to the trunk differed most strongly from the open land, whereas the open area at the timberline differed most strongly from the forest. In contrast, the most similar assemblages have been found in the open area at the timberline and the open land, and in the timberline zone next to the trunk and the forest, respectively. Species composition in the timberline zone at the end of branch cover seemed to be most similar with the communities in the other two zones at the timberline. Interestingly, the difference within the five habitat zones increased gradually along the gradient from the open land to the forest (Table 3).

Habitat preferences

All five habitat zones were dominated by certain species (Fig. 1b, Table 4). Two species dominated significantly in the open land, two in the open area at the timberline and four in the forest. Three additional species were significantly more frequent in one of the zones at the timberline than in either forest or open land. A comparison of frequencies by percentage indicates that most species seemed to prefer the open land whereas the forest was inhabited by a higher proportion of specialists. Regarding the zones at the timberline, the open area may have been most attractive followed by the zone next to the trunk. In contrast, few if any species seemed to prefer the zone at the end of branch cover.

Discussion

The distribution of epigeic spiders across the alpine timberline correlated most with the environmental factor light. Shading by woody plants is also the main factor for spider distribution among Central European lowland habitats (Entling *et al.*, 2007). By offering both open and completely shaded microhabitats (Table 1), the small area around a single tree provided habitats for the majority of species present in both open land and forest (Table 4). As a result, the distribution of the species found in this study across an area of 9 ha corresponded fairly well to the distribution within a few metres (Fig. 1a). Our findings indicate that due to the sensitivity of spiders to their environment, the differentiation of communities can act also on a very small scale if the landscape is heterogeneous enough. The question remains, however, how viable populations are in habitats as small as the area around a single tree.

Factors driving spider community differentiation

Neutral theory of biodiversity and biogeography is able to reproduce certain patterns of species distribution without considering habitat conditions and niche properties (Hubbell, 2005). Nevertheless, the two classic models of communities shaped by environmental factors and biological interactions are still widely supported (Peterson & Holt, 2003; Eyre *et al.*, 2005). The relationship between species diversity and habitat features seems to be strongly dependent on the organisms and region (Jeanneret *et al.*, 2003; Schweiger *et al.*, 2005). Habitat preferences of spiders are well documented and several underlying environmental factors have been proposed (Samu *et al.*, 1999; Entling *et al.*, 2007). All of these factors deal with physical properties of the environment, which influence either light and moisture conditions or specific demands of spiders on their environment (e.g. places for hunting, courtship, prey availability, protection from enemies and desiccation). Because of interactions between environmental conditions and vegetation characteristics, the quantitative importance of these different factors has remained speculative. In our study, variables connected with light availability (e.g. proportion of open ground and visible sky) had a greater influence on spider communities than the type of ground vegetation in which the spiders live (Fig. 1, Table 2). The rather large effect of the component 'vegetation cover' on species variation (Fig. 2) is a direct result of the inclusion of the two variables 'open ground' and 'branches distant from ground' into this component.

Our study demonstrates the possible overestimation of environmental effects on species distribution when space is not taken into account (Borcard *et al.*, 1992). Space overlapped with almost 40% of the total environmental influence and accounted for 18% of the total variation explained (Fig. 2). This

Table 4. Numbers of spider individuals (*N*) and their distribution by percentage across the five habitat zones. The order follows the species' dominance in one of the habitat zones (in bold). Letters behind numbers denote habitats significantly different from each other according to pairwise Kruskal–Wallis tests (all *P* < 0.05, corrected for multiple comparisons after Holm). Only species with $N \geq 15$ are shown. Codes refer to Fig. 1b. Mean number of individuals and species per pitfall trap, respectively, and Simpson diversity for each habitat zone are additionally included at the bottom.

Code	Species	Family	Total *N*	Open land	Timberline open	Timberline branch	Timberline trunk	Forest
1	*Meioneta alpica*	Linyphiidae	18	**89b**	11a	0a	0a	0a
2	*Gnaphosa leporina*	Gnaphosidae	32	**88b**	9a	3a	0a	0a
3	*Pardosa mixta*	Lycosidae	18	**72b**	22ab	6ab	0a	0a
4	*Macrargus carpenteri*	Linyphiidae	42	**69c**	17bc	7abc	7ab	0a
5	*Drassodes cupreus*	Gnaphosidae	20	**60c**	30bc	5ab	5ab	0a
6	*Alopecosa pulverulenta*	Lycosidae	639	**57c**	37c	5b	0a	0a
7	*Thanatus formicinus*	Philodromidae	59	**56b**	36b	8a	0a	0a
8	*Alopecosa accentuata*	Lycosidae	26	**54c**	35bc	8abc	0a	4ab
9	*Ozyptila atomaria*	Thomisidae	18	**50c**	28bc	17abc	6ab	0a
10	*Zelotes talpinus*	Gnaphosidae	47	**47b**	38b	13ab	0a	2a
11	*Pardosa blanda*	Lycosidae	150	**44c**	42bc	13ab	1ab	0a
12	*Drassodes pubescens*	Gnaphosidae	27	**41c**	30bc	19abc	4a	7ab
13	*Halpodrassus signifer*	Gnaphosidae	79	**33c**	32bc	15ab	10a	10a
14	*Minicia marginella*	Linyphiidae	16	13a	**69a**	13a	6a	0a
15	*Gonatium rubens*	Linyphiidae	22	18ab	**59b**	18ab	5a	0a
16	*Arctosa renidescens*	Lycosidae	64	23ab	**58b**	13ab	5ab	2a
17	*Bolyphantes luteolus*	Linyphiidae	109	23c	**56d**	12b	9b	0a
18	*Agyneta cauta*	Linyphiidae	128	24c	**55c**	19bc	2ab	0a
19	*Alopecosa taeniata*	Lycosidae	429	2a	**52b**	30b	7a	9a
20	*Tenuiphantes mengei*	Linyphiidae	180	21b	**44c**	14b	16b	5a
21	*Bolyphantes alticeps*	Linyphiidae	44	7ab	**39b**	23ab	2a	30ab
22	*Xysticus luctuosus*	Thomisidae	40	15ab	38b	**48b**	0a	0a
23	*Micaria aenea*	Gnaphosidae	48	15b	25ab	**44b**	0a	17b
24	*Metopobactrus prominulus*	Linyphiidae	15	13a	20a	**40a**	27a	0a
25	*Caracladus avicula*	Linyphiidae	196	20ab	11a	**38b**	13ab	17ab
26	*Pelecopsis radicicola*	Linyphiidae	84	10a	19ab	**35b**	30ab	7a
27	*Pardosa riparia*	Lycosidae	1953	30c	27c	**31c**	11b	1a
28	*Panamomops tauricornis*	Linyphiidae	70	0a	0a	3a	**80b**	17b
29	*Scotinotylus alpigena*	Linyphiidae	146	0a	0a	5a	**62b**	33b
30	*Pelecopsis elongata*	Linyphiidae	54	0a	0a	33b	**50b**	17ab
31	*Mansuphantes pseudoarciger*	Linyphiidae	18	6a	22ab	11ab	**50b**	11ab
32	*Improphantes nitidus*	Linyphiidae	136	1a	0a	3a	**49b**	46b
33	*Scotargus pilosus*	Linyphiidae	17	0a	0a	18ab	**47b**	35ab
34	*Tapinocyba affinis*	Linyphiidae	249	1a	8b	32c	**44c**	15b
35	*Robertus truncorum*	Theridiidae	105	0a	9ab	31b	**36b**	24b
36	*Mughiphantes cornutus*	Linyphiidae	23	0a	0a	9a	9a	**83a**
37	*Cryphoeca silvicola*	Hahniidae	134	0a	0a	1a	25b	**74c**
38	*Porrhomma pallidum*	Linyphiidae	42	0a	0a	7ab	19b	**74c**
39	*Mughiphantes mughi*	Linyphiidae	38	0a	3ab	8ab	21b	**68c**
40	*Agnyphantes expunctus*	Linyphiidae	52	0a	0a	12ab	31b	**58c**
41	*Scotinotylus clavatus*	Linyphiidae	114	0a	0a	6ab	43bc	**51c**
42	*Centromerus pabulator*	Linyphiidae	319	3a	30bc	25abc	10ab	**32c**
	Mean number of individuals			100	112	89	65	51
	Mean number of species			18	18	16	16	14
	Simpson diversity			0.74	0.79	0.76	0.83	0.86

demonstrates very impressively how ecological phenomena can be spatially structured and that species and physical variables are distributed neither uniformly nor at random (Legendre, 1993). Pure spatial variation may reflect biological processes without relationship to the environmental variables recorded, such as growth, predation, competition, reproduction or social aggregation for example (Borcard *et al.*, 1992). The high amount of unexplained variation can be understood by considering that it may not only represent real stochasticity but also unmeasured, potentially explainable environmental effects.

Microspatial distribution at boundaries

Our study at the timberline indicates that also spatially limited structures can be of great importance in providing a wide range

of habitats. These findings are consistent with other studies suggesting small-scale distribution of invertebrates. Antvogel and Bonn (2001) identified different ground beetle assemblages within a few metres in an alluvial forest; Maudsley *et al.* (2002) revealed highly spatially variable distribution patterns of overwintering arthropods within an individual hedgerow; Juen and Traugott (2004) found distinct spatial distribution patterns of arthropod predator communities in an organically cultivated 0.3-ha field and Romero and Vasconcellos-Neto (2005) demonstrated how changes in the architecture of a single plant species influences the microspatial distribution of a strictly associated spider species. Furthermore, the current study underlines the suitability of boundary habitats for assessing distribution patterns and their determining factors, at least for invertebrates, which is essential for nature conservation. Due to the edge effects and their well-known influences on these organisms in patchy habitats (Downie *et al.*, 1996; Magura *et al.*, 2001) relationships can be investigated to a great extent, even when time and effort are restricted (Antvogel & Bonn, 2001). Understanding the small-scale distribution of organisms reveals their suitability as bio-indicators, which today becomes increasingly important in the context of nature conservation and management (Spellerberg, 1993). The community differentiation between microhabitats around a single tree found in our study clearly confirms the suitability of spiders to indicate changes in habitats and the environment as suggested in other studies (Marc *et al.*, 1999; Pearce & Vernier, 2006).

Conclusion

This study demonstrates how habitat boundaries may maintain very contrasting communities by providing a wide range of habitat conditions. The epigeic spider communities at an alpine timberline were strongly influenced by the local environment and differentiated according to light preferences of single species. The occurrence of nearly all species from the adjoining open land and forest patches as well as some possible habitat specialists around single trees at the timberline highlights the potential of heterogeneous microspatial structures in preserving arthropod communities.

Acknowledgements

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