The effect of forest edge on ground-living arthropods in a remnant of unfertilized calcareous grassland in the Swiss Jura mountains

Autor(en): **Hänggi, Ambros / Baur, Bruno**

Objekttyp: **Article**

Zeitschrift: **Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society**

Band (Jahr): **71 (1998)**

Heft 3-4

PDF erstellt am: **22.07.2024**

Persistenter Link: https://doi.org/10.5169/seals-402720

Nutzungsbedingungen
Die ETH-Bibliothek ist Anbieterin der digitalisierten Zeitschriften. Sie besitzt keine Urheberrechte an den Inhalten der Zeitschriften. Die Rechte liegen in der Regel bei den Herausgebern.
Die auf der Plattform e-periodica veröffentlichten Dokumente stehen für nicht-kommerzielle Zwecke in Lehre und Forschung sowie für die private Nutzung frei zur Verfügung. Einzelne Dateien oder Ausdrucke aus diesem Angebot können zusammen mit diesen Nutzungsbedingungen und den korrekten Herkunftsbezeichnungen weitergegeben werden.
Das Veröffentlichen von Bildern in Print- und Online-Publikationen ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. Die systematische Speicherung von Teilen des elektronischen Angebots auf anderen Servern bedarf ebenfalls des schriftlichen Einverständnisses der Rechteinhaber.

Haftungsausschluss
Alle Angaben erfolgen ohne Gewähr für Vollständigkeit oder Richtigkeit. Es wird keine Haftung übernommen für Schäden durch die Verwendung von Informationen aus diesem Online-Angebot oder durch das Fehlen von Informationen. Dies gilt auch für Inhalte Dritter, die über dieses Angebot zugänglich sind.

Ein Dienst der *ETH-Bibliothek*
ETH Zürich, Rämistrasse 101, 8092 Zürich, Schweiz, www.library.ethz.ch

http://www.e-periodica.ch

MITTEILUNGEN DER SCHWEIZERISCHEN ENTOMOLOGISCHEN GESELLSCHAFT
BULLETIN DE LA SOCIÉTÉ ENTOMOLOGIQUE SUISSE
71, 343 – 354, 1998

The effect of forest edge on ground-living arthropods in a remnant of unfertilized calcareous grassland in the Swiss Jura mountains

AMBROS HÄNGGI[1] & BRUNO BAUR[2]

[1] Naturhistorisches Museum, Augustinergasse 2, CH-4001 Basel
[2] Institut für Natur-, Landschafts- und Umweltschutz (NLU), Abteilung Biologie, Universität Basel, St. Johanns-Vorstadt 10, CH-4056 Basel

The width of the edge zone is critical to the existence of interior habitat in any type of remnant. We used pitfall trapping to examine the effect of a sharp and a gradual forest edge on the distribution of ground-living arthropod species (spiders, staphylinid and carabid beetles and diplopods) on a forest-grassland transect in the northwestern Jura mountains, Switzerland. The grassland and forest habitats support distinct species assemblages. Both forest edge zones were found to have an elevated species richness of spiders and staphylinid beetles. However, species richness of carabid beetles and diplopods was not increased in the forest edge zones. At the habitat interface, the communities were composed of a mixture of open field and forest species and species that occur exclusively in the ecotone. Individuals of several species associated with forest were found to penetrate into the grassland. However, the arthropods did not move more than 3–6 m into the grassland at the sharp forest edge, and 6–12 m at the gradual forest edge. This indicates that even relatively small remnants of unfertilized calcareous grassland may contain a functional interior area for ground-living arthropods, which is not influenced by penetrating forest species.

Keywords: Araneae, Coleoptera, Diplopoda, biodiversity, calcareous grassland, forest edge, Jura mountains

INTRODUCTION

Compared with interiors of grasslands, forest-grassland edges typically have both different plant and animal species compositions and different community structures (POLLARD, 1968; SAUNDERS *et al.*, 1991). Specialized grassland species may be excluded from edge zones in small grassland fragments due to intrusion of edge-related physical effects and the penetration of forest species (LOVEJOY *et al.*, 1986; MATLACK, 1993). In this context, the edge zone is the grassland area adjacent to the forest in which forest and ecotone species penetrate. Edge width measures a marginal zone of altered microclimate and contrasting community structure distinct from the forest or grassland interior. Thus, edge effects make the functional interior area of a grassland remnant smaller than its actual area (LAURENCE & YENSEN, 1991). To assess the conservation value of small grassland fragments, it is essential to have an estimate of edge zone width.

In the northwestern Jura mountains of Switzerland, unfertilized calcareous grasslands were large and continuous at the beginning of this century, but since the 1950's changes in agricultural practices such as the use of modern machinery, chemical fertilizers, herbicides and pesticides, and new breeds of plants have reduced the size of these areas and split them into small and isolated fragments. For example, the total area of unfertilized calcareous grassland was reduced by 78% in the Passwang region 20 km south of Basel between 1950 and 1985 (ZOLLER *et al.*, 1986).

This overall reduction of the unfertilized grassland area and the isolation of the remnants has led to a dramatic loss of plant species within a short period (FISCHER & STÖCKLIN, 1997). For many plant and animal species the functional interior area of these scattered grassland remnants may even be smaller than their actual size, since most of them are at least partly surrounded by forest. Yet, little information is available about the influence of forest edges on arthropod communities in grasslands (SAMWAYS, 1994; NEW, 1995; but see HÄNGGI, 1993; BEDFORD & USHER, 1994; ŁUCZAK, 1997). In the present context, edge is considered as the physical boundary between two plant communities (i.e. forest and grassland), whereas the ecotone is the narrow overlap zone between adjacent plant communities (SAMWAYS, 1994).

This paper aims to examine the effect of an abrupt and gradual forest edge on the distribution of ground-dwelling arthropod species (spiders, staphylinid and carabid beetles and diplopods) on a forest-grassland transect. In particular, we addressed the following questions: (1) How far do forest and ecotone species of the four taxonomical groups penetrate into the remnant of unfertilized calcareous grassland? (2) Does the width of the edge zone differ between a sharp and a gradual forest edge? and (3) How much is the functional interior area of the grassland remnant reduced due to forest edge effects?

MATERIAL AND METHODS

Study site

The study was conducted on a 39 m wide remnant of nutrient-poor, dry calcareous grassland (belonging to the Teucrio-Mesobrometum type; ELLENBERG, 1988) near Movelier (5 km N of Delémont) in the northwestern Swiss Jura mountains (47°25' N; 7°19' E). A detailed description of the grassland vegetation is given in BAUR *et al.* (1996). The adjacent forest is dominated by beech (*Fagus sylvatica*).

The grassland remnant is situated on a SSE-facing slope (inclination 20–22°) at an elevation of 780 m. The humus layer is relatively thick (>20 cm) and contains some clay. Until 1993, the grassland was grazed by cattle and a moderate amount of artificial fertilizer was used. The south-facing forest edge was distinct with an abrupt change of the vegetation along the cattle fence (Fig. 1). Tree species at the forest edge included *Fagus sylvatica* (40 %), *Quercus petraea* (30 %), *Pinus sylvestris* (20 %) and *Acer pseudoplantanus* (10 %). The bushes of the forest edge consisted of *Viburnum lantana* (30 %), *Crataegus monogyna* (20 %), *Prunus spinosa* (20 %), *Rosa* sp. (20 %) and *Ligustrum vulgare* (10 %). The north-facing forest edge was gradual with bushes (*Corylus avellana* 90 % and *Rosa* sp. 10 %) extending 7 m across its original edge (indicated by a cattle fence; Fig. 1). Tree species found at the north-facing forest edge included *F. sylvatica* (70 %), *Q. robur* (20 %) and *Prunus avium* (10 %).

Sampling procedure

Pitfall traps were used to investigate the effect of forest edge on grassland-living arthropods. Traps were white plastic jars, 7 cm deep x 7 cm in diameter, containing about 50 ml formalin (4 %) with detergent. The traps were protected against rain by grey plastic roofs (measuring 18 x 18 cm) that were fixed horizontally about 10 cm above ground. Three parallel transects of traps were established 1 m apart from each other. In each transect the pitfall traps were placed at distances of 3 m, resulting in a total of 18 rows (Fig. 1). The transects run from the interior of the forest (6 m) over the open grassland (32 m) through a gradual forest edge (bushes in the grassland, 7 m) into the interior of the forest (6 m). All traps were emptied and reset fortnightly from 5 May to 24 July 1994, giving a total of 12 trap weeks.

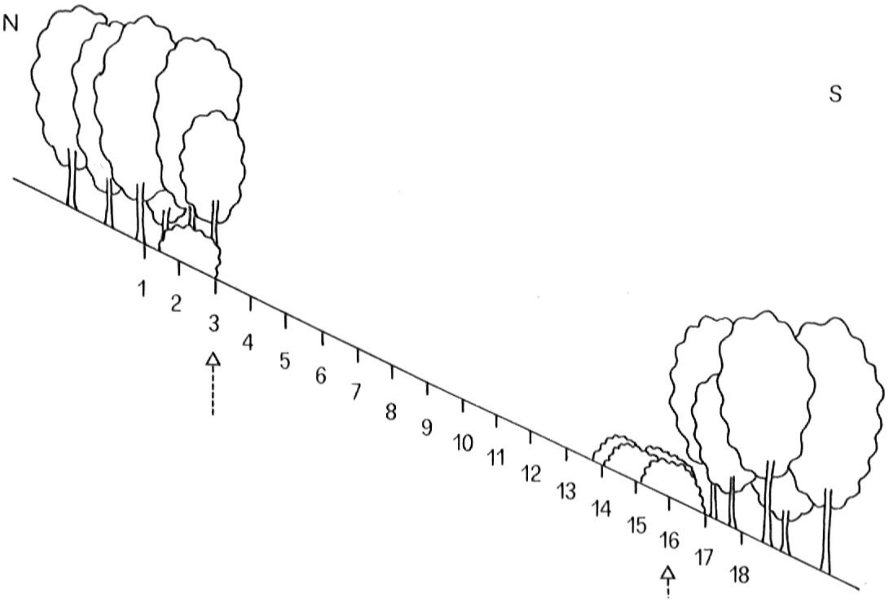


Fig. 1. Position of pitfall traps on the transects indicated by figures. Three parallel transects (1 m apart) with a distance of 3 m between traps were used. Arrows indicate the position of cattle fences.

All spiders, staphylinid and carabid beetles and diplopods caught in pitfall traps were identified to species level using standard keys. Nomenclature of spiders followed MAURER & HÄNGGI (1990). FREUDE *et al.* (1976) and LOHSE & LUCHT (1989) were used for carabid and staphylinid beetles and PEDROLI-CHRISTEN (1993) for diplopods. Detailed lists of species and abundances are available from the authors upon request. All arthropods collected are deposited in the Natural History Museum of Basel.

Data analysis

The catch data for each taxonomical group (spiders, staphylinids, carabids and diplopods) were analysed separately. The catch frequency for each species in all three replicate traps within a row was summed over the entire trapping period. For detailed analyses, a species was only considered if five or more individuals were recorded over the entire trapping period. This criterion was used to reduce the possibility of vagrant individuals affecting the results.

Arthropod species were categorized based on their relative abundances in particular habitats (cf. DUELLI *et al.*, 1990). Species with more than 67 % of the individuals caught in the forest (traps no. 1–3 and 16–18) are referred to as 'forest' species. Similarly, species with more than 67 % of the individuals collected in the grassland (traps no. 4–13) are termed 'open-habitat' species. Species associated with forest edge (more than 67 % of individuals collected in the traps no. 2–4 and 13–17 are termed 'ecotone' species. According to these critieria some species were assigned to two groups (e.g. forest and ecotone (f/e) or ecotone and open habitat (e/o); see Fig. 3).

RESULTS

Number of individuals recorded

A total of 3251 spiders belonging to 116 species were collected during summer 1994 (Tab. 1). The corresponding figures were 1034 individuals (68 species) for the staphylinid beetles, 853 individuals (33 species) for the carabid beetles and 351 individuals (8 species) for the diplopods (Tab. 1). In all taxa, a large proportion

Tab. 1: Total species lists with reference to codes in Fig. 3. Pitfall rows are indicated in italics in species with less than 5 individuals.

Araneae

Species code in Fig.3	Species	Species code in Fig.3	Species
A01	Centromerus serratus (O.P.-CAMBR.,1875)	A30	Pocadicnemis pumila (BLACKWALL,1841)
A02	Micrargus herbigradus (BLACKWALL,1854)	A31	Callilepis schuszteri (HERMAN,1879)
A03	Haplodrassus silvestris (BLACKWALL,1833)	A32	Walckenaeria antica (WIDER,1834)
A04	Panamomops mengei SIMON,1926	A33	Clubiona neglecta O.P.-CAMBRIDGE,1862
A05	Tapinocyba pallens (O.P.-CAMBR.,1872)	A34	Zelotes pusillus (C.L.KOCH,1833)
A06	Saaristoa abnormis (BLACKWALL,1841)	A35	Micaria formicaria (SUNDEVALL,1831)
A07	Agyneta ramosa JACKSON,1912	A36	Meioneta mollis (O.P.-CAMBR.,1871)
A08	Monocephalus fuscipes (BLACKWALL,1836)	A37	Myrmarachne formicaria (DEGEER,1778)
A09	Maso sundevalli (WESTRING,1851)	A38	Haplodrassus signifer (C.L.KOCH,1839)
A10	Dysdera erythrina (WALCKENAER,1802)	A39	Alopecosa trabalis (CLERCK,1757)
A11	Linyphia hortensis SUNDEVALL,1829	A40	Eperigone trilobata (EMERTON,1882)
A12	Lepthyphantes tenebricola (WIDER,1834)	A41	Zelotes praeficus (L.KOCH,1866)
A13	Harpactea lepida (C.L.KOCH,1838)	A42	Drassodes cupreus (BLACKWALL,1834)
A14	Lepthyphantes flavipes (BLACKWALL,1854)	A43	Zelotes petrensis (C.L.KOCH,1839)
A15	Walckenaeria cucullata (C.L.KOCH,1836)	A44	Tricca lutetiana (SIMON,1876)
A16	Walckenaeria corniculans (O.P.-CAMBR.,1875)	A45	Euophrys aequipes (O.P.-CAMBR.,1871)
A17	Histopona torpida (C.L.KOCH,1834)	A46	Alopecosa cuneata (CLERCK,1757)
A18	Zora nemoralis (BLACKWALL,1861)	A47	Pardosa pullata (CLERCK,1757)
A19	Lepthyphantes pallidus (O.P.-CAMBR.,1871)	A48	Aulonia albimana (WALCKENAER,1805)
A20	Ceratinella scabrosa (O.P.-CAMBR.,1871)	A49	Drassodes pubescens (THORELL,1856)
A21	Walckenaeria atrotibialis (O.P.-CAMBR.,1878)	A50	Lepthyphantes tenuis (BLACKWALL,1852)
A22	Robertus lividus (BLACKWALL,1836)	A51	Phrurolithus festivus (C.L.KOCH,1835)
A23	Diplocephalus picinus (BLACKWALL,1841)	A52	Micrargus subaequalis (WESTRING,1851)
A24	Clubiona terrestris WESTRING,1862	A53	Alopecosa pulverulenta (CLERCK,1757)
A25	Diplostyla concolor (WIDER,1834)	A54	Phrurolithus minimus (C.L.KOCH,1839)
A26	Hahnia pusilla C.L.KOCH,1841	A55	Trochosa ruricola (DEGEER,1778)
A27	Microneta viaria (BLACKWALL,1841)	A56	Pardosa hortensis (THORELL,1872)
A28	Pardosa sp. (=saltans s. TÖPFER & HELV. 1990)	A57	Tegenaria picta SIMON,1870
A29	Lepthyphantes mengei KULCZYNSKI,1887	A58	Zora spinimana (SUNDEVALL,1833)
Pitfall row	Species with less than 5 individuals	Pitfall row	Species with less than 5 individuals
5	Agroeca cuprea MENGE,1873	*4*	Lepthyphantes keyserlingi (AUSSERER,1867)
6	Alopecosa accentuata (LATREILLE,1817)	*5,7,8,13*	Meioneta beata (O.P.-CAMBR.,1906)
17	Amaurobius fenestralis (STROEM,1768)	*4,5,8,11*	Meioneta rurestris (C.L.KOCH,1836)
14,18	Bathyphantes parvulus (WESTRING,1851)	*4*	Metopobactrus prominulus (O.P.-CAMBR.,1872)
4	Bianor aurocinctus (OHLERT,1865)	*14*	Micaria fulgens (WALCKENAER,1802)
16	Centromerus dilutus (O.P.-CAMBR.,1875)	*13*	Micaria pulicaria (SUNDEVALL,1831)
15	Centromerus sylvaticus (BLACKWALL,1841)	*13*	Micrommata virescens (CLERCK,1757)
16	Cicurina cicur (FABRICIUS,1793)	*4*	Oxyptila atomaria (PANZER,1810)
16,18	Clubiona compta C.L.KOCH,1839	*4,5*	Oxyptila nigrita (THORELL,1875)
4,7,9,10	Cnephalocotes obscurus (BLACKWALL,1834)	*11*	Pelecopsis parallela (WIDER,1834)
5	Crustulina guttata (WIDER,1834)	*5*	Pellenes tripunctatus (WALCKENAER,1802)
1	Cybaeus tetricus (C.L.KOCH,1839)	*7*	Philodromus collinus C.L.KOCH,1835
15,16,17	Diplocephalus latifrons (O.P.-CAMBR.,1863)	*3*	Pirata latitans (BLACKWALL,1841)
1,5,7,12	Drassodes lapidosus (WALCKENAER,1802)	*7*	Pirata uliginosus (THORELL,1856)
7,12	Enoplognatha thoracica (HAHN,1833)	*7,12,13*	Pocadicnemis juncea LOCKET & MILL.,1953
8	Erigone atra (BLACKWALL,1841)	*10,15,16*	Robertus neglectus (O.P.-CAMBR.,1871)
6,11,12	Euophrys frontalis (WALCKENAER,1802)	*10*	Segestria senoculata (LINNE,1758)
4	Euryopis flavomaculata (C.L.KOCH,1836)	*14*	Sintula cornigera (BLACKWALL,1856)
4	Euryopis quinqueguttata THORELL,1875	*5,7,11*	Talavera inopinata WUNDERLICH,1993
8	Evarcha arcuata (CLERCK,1757)	*4*	Tapinocyboides pygmaeus (MENGE,1869)
4	Gnaphosa bicolor (HAHN,1831)	*12,14*	Tiso vagans (BLACKWALL,1834)
5,14,18	Gongylidiellum latebricola (O.P.-CAMBR.,1871)	*9,10,13*	Trochosa robusta (SIMON,1876)
4	Hahnia nava (BLACKWALL,1841)	*6,13*	Trochosa terricola THORELL,1856
1,3	Hahnia ononidum SIMON,1875	*9,12,18*	Walckenaeria acuminata BLACKWALL,1833
4,6	Haplodrassus kulczynskii LOHMANDER,1942	*1,11,17,18*	Walckenaeria dysderoides (WIDER,1834)
1,3,15,17	Harpactocrates drassoides (SIMON,1882)	*2,14*	Walckenaeria obtusa BLACKWALL,1836
4,5,11	Heliophanus cupreus (WALCKENAER,1802)	*18*	Xysticus lanio C.L.KOCH,1824
4,10	Heliophanus flavipes (HAHN,1832)	*1,3,18*	Zelotes apricorum (L.KOCH,1876)
15	Lepthyphantes cristatus (MENGE,1866)	*8,11,13*	Zelotes latreillei (SIMON,1878)

Tab. 1 (cont.): Total species lists with reference to codes in Fig. 3. Pitfall rows are indicated in italics in species with less than 5 individuals.

Staphylinidae			
Species code in Fig.3	Species	Species code in Fig.3	Species
S01	Omalium caesum GRAV.,1806	S14	Drusilla canaliculata (F.,1787)
S02	Aleochara ruficornis GRAV.,1802	S15	Tachyporus chrysomelinus (F.,1775)
S03	Plataraea brunnea (F.,1798)	S16	Astenus gracilis (PAYK.,1789)
S04	Plataraea elegans (BENICK,1934)	S17	Ocypus aeneocephalus (GEER,1774)
S05	Anotylus sculpturatus (GRAV.,1806)	S18	Staphylinus caesareus CED.,1798
S06	Zyras haworthi (STEPH.,1832)	S19	Paederus littoralis GRAV.,1802
S07	Atheta elongatula (GRAV.,1802)	S20	Ocypus fulvipennis ER.,1840
S08	Philonthus decorus (GRAV.,1802)	S21	Zyras collaris (PAYK.,1800)
S09	Lathrimaeum atrocephalum (GYLL.,1827)	S22	Ocypus olens (MÜLL.,1764)
S10	Staphylinus fossor (SCOP.,1772)	S23	Zyras similis (MÄRK.,1844)
S11	Othius punctulatus (GOEZE,1777)	S24	Omalium rivulare (PAYK.,1789)
S12	Liogluta microptera (THOMS.,1867)	S25	Alaobia scapularis (SAHLB.,1831)
S13	Stenus impressus GERM.,1824	S26	Quedius curtipennis BERNH.,1908
Pitfall row	Species with less than 5 individuals	Pitfall row	Species with less than 5 individuals
5	Aleunota gracilenta (ER.)	*4*	Ocalea rivularis MILL.,1851
9	Astenus longelytratus (GRAV.,1806)	*11*	Ocypus compressus (MARSH.,1802)
4	Astenus procerus (GRAV.,1806)	*1*	Ocypus tenebricosus (GRAV.,1846)
17	Atheta fungi (GRAV.,1806)	*17*	Oxypoda alternans (GRAV.,1802)
18	Atheta negligens (MULS.REY,1873)	*17*	Oxypoda spectabilis MÄRK.,1844
17	Atheta pervagata BENICK,1975	*9*	Philonthus carbonarius (GRAV.,1810)
17	Domene scabricollis (ER.,1840)	*16*	Philonthus politus (L.,1758)
16	Enalodroma hepatica (ER.,1839)	*4,15*	Plataraea dubiosa (BENICK,1934)
15	Eusphalerum florale (PANZ.,1793)	*7*	Platydracus latebricola (GRAV.,1806)
2	Eusphalerum stramineum (KR.,1857)	*6,10*	Platydracus stercorarius (OL., 1795)
14	Falagria thoracica STEPH.,1832	*4,7*	Scopaeus sulcicollis (STEPH.,1833)
14	Gyrohypnus angustatus STEPH.,1833	*7*	Sepedophilus pedicularius (GRAV.,1802)
2,16,18	Habrocerus capillaricornis (GRAV.,1806)	*16,17*	Stenus fuscicornis ER.,1840
2,18	Homoeusa acuminata (MÄRK.,1842)	*5,13*	Sunius melanocephalus (F.,1792)
2	Ischnosoma longicorne (MÄKL., 1847)	*8,13*	Tachyporus dispar (PAYK., 1789)
8	Lathrobium multipunctum GRAV.,1802	*10,12*	Tachyporus hypnorum (L.,1758)
16	Leptusa ruficollis (ER.,1839)	*14*	Tachyporus nitidulus (F.,1781)
15	Liogluta longuiscula (GRAV.,1802)	*14*	Tachyporus obtusus (L.,1767)
8	Mycetoporus longulus MANNH.,1830	*17*	Xantholinus jarrigei COIFF.1956
7	Myrmoecia confragrosa (HOCHH.,1849)	*10*	Xantholinus linearis (OL.,1795)
5,17,18	Ocalea picata (STEPH.,1832)	*1,2,14,15*	Xantholinus tricolor (F.,1787)
Carabidae			
Species code in Fig.3	Species	Species code in Fig.3	Species
C01	Pterostichus burmeisteri HEER,1841	C09	Carabus problematicus HERBST,1786
C02	Abax ovalis (DUFTSCHMID,1812)	C10	Pterostichus melanarius (ILLIGER,1798)
C03	Pterostichus selmanni DUFTSCHMID,1812	C11	Harpalus latus LINNE,1758
C04	Carabus auronitens FABRICIUS,1792	C12	Pterostichus ovoideus (STURM,1824)
C05	Abax parallelus (DUFT.,1812)	C13	Carabus monilis FABRICIUS,1792
C06	Abax parallelepipedus (PILLER & MITT.,1783)	C14	Carabus convexus FABRICIUS,1775
C07	Molops piceus (PANZER,1793)	C15	Carabus nemoralis MÜLLER,1764
C08	Pterostichus madidus (FABRICIUS,1775)		
Pitfall row	Species with less than 5 individuals	Pitfall row	Species with less than 5 individuals
11	Amara lunicollis SCHIÖDTE,1837	*7*	Loricera pilicornis FABRICIUS,1775
12	Amara nitida STURM,1815	*13*	Microlestes maurus STURM,1827
11	Amara plebeja (GYLLENHAL,1819)	*15,17*	Nebria brevicollis (FABRICIUS,1792)
4,9	Amara similata (GYLLENHAL,1819)	*14*	Nebria salina FAIRMAIRE & LAB.,1854
12	Badister meridionalis PUEL,1925	*9*	Panagaeus bipustulatus (FABRICIUS,1775)
4,8	Calathus fuscipes (GOETZE,1777)	*1,3*	Philorhizus notatus (STEPHENS,1828)
5,8,10	Carabus purpurascens FABRICIUS,1787	*12*	Poecilus versicolor (STURM,1824)
1	Cychrus attenuatus FABRICIUS,1792	*18*	Trechus quadristriatus (SCHRANK,1781)
1,17	Licinus hoffmannseggi PANZER,1797	*2*	Trichotichnus laevicollis DUFTSCHMID,1812)
Diplopoda			
Species code in Fig.3	Species	Species code in Fig.3	Species
D1	Glomeris conspersa C.L.KOCH,1847	D4	Glomeris hexasticha intermedia LATZEL,1884
D2	Allajulis nitidus VERHOEFF,1930	D5	Tachypodoiulus niger (LEACH,1815)
D3	Glomeris marginata (VILLERS,1789)	D6	Cylindroiulus caeruleocinctus (WOOD,1864)
Pitfall row	Species with less than 5 individuals	Pitfall row	Species with less than 5 individuals
14,17	Glomeris connexa C.L.KOCH,1847	*17*	Rhymogona alemannica (VERHOEFF,1910)

of species were represented by 1–4 individuals (58 of the 116 (50 %) spider species, 42 of the 68 (62 %) of the staphylinid species, 18 of the 33 (55 %) carabid species, and 2 of the 8 (25 %) milliped species). These species were either rare or not susceptible to pitfall trapping. Altogether, the species with low catches contributed to 4 % of the total number of individuals caught (spiders 3.6 %, staphylinid beetles 6.6 %, carabid beetles 3.9 % and millipedes 0.9 %).

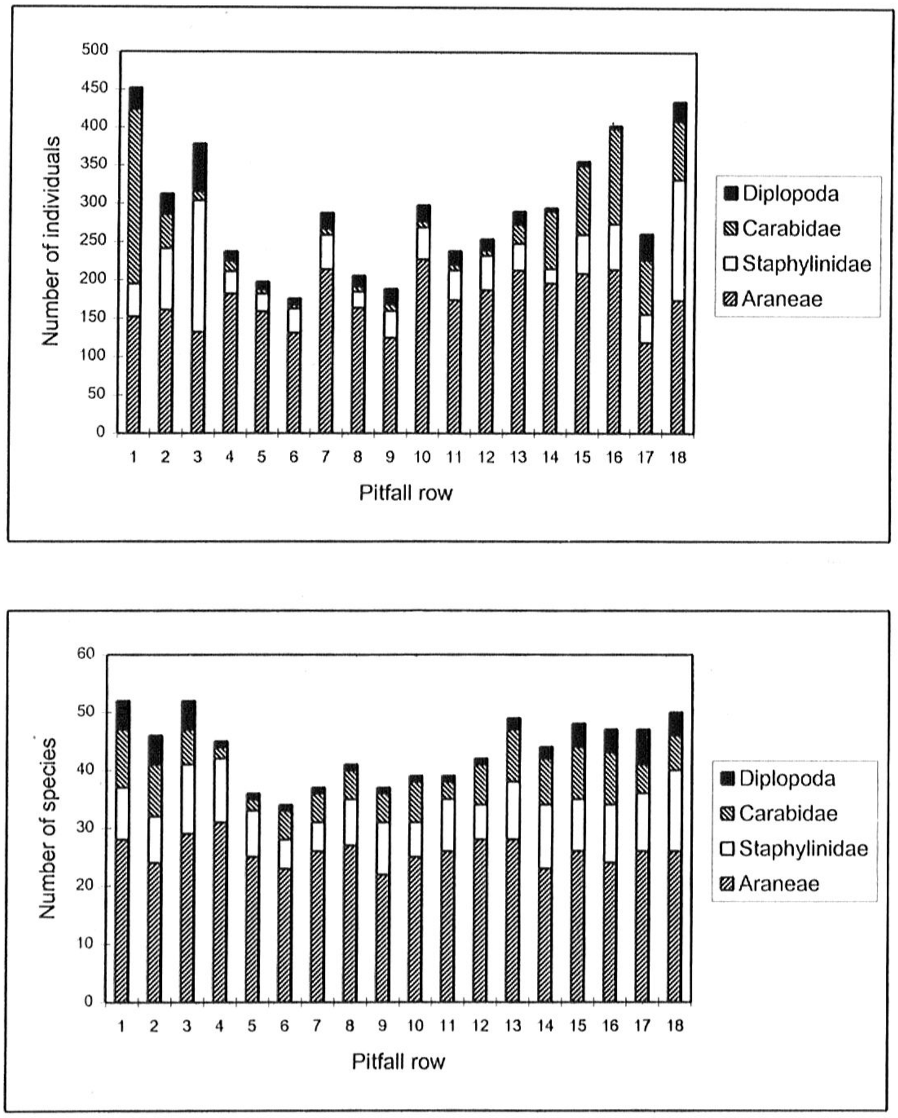


Fig. 2. Number of individuals (top) and species (bottom) of four groups of arthropods caught along the transect (only species with ≥ 5 individuals recorded). Positions of the traps as in Fig. 1.

In the following analyses we omitted species with less than five individuals.

Over the entire transect significant differences in catch frequency were found in all taxonomical groups (X^2-test, in all taxonomical groups $P < 0.001$; Fig. 2, top). In general, catch frequency was higher in the forest than in the grassland. In staphylinid beetles and diplopods, the number of individuals trapped increased in the forest edge zones and decreased towards the interior of the grassland. In spiders and carabid beetles, the differences in mean number of individuals caught per trap row were not as pronounced as in the other two groups.

Species richness

Species richness is presented for each taxonomical group over the entire transect in Fig. 2, bottom. Both forest edge zones were found to have a slightly elevated species richness of spiders and staphylinid beetles (Tab. 2 and Fig. 2, bottom). No similar trend was observed in carabid beetles and diplopods.

Tab. 2. Number of species recorded in different types of habitats along the transect. Data from two rows of pitfall traps are combined. See Fig. 1 for positions of traps.

Taxonomical group	Habitat type (pitfall row no. in transect)								
	Forest	Ecotone	Grassland				Ecotone		Forest
	(1+2)	(3+4)	(5+6)	(7+8)	(9+10)	(11+12)	(13+14)	(15+16)	(17+18)
Diplopods	5	5	1	1	1	1	3	4	6
Carabid beetles	10	7	6	6	7	7	11	11	7
Staphylinid beetles	11	18	11	10	9	11	16	14	15
Spiders	31	45	30	33	29	32	37	30	29
Total	57	75	48	50	46	51	67	59	57

Fig. 3 shows the spatial distribution and abundance of individual species collected over the transect. Species names are given in Tab. 1. In most species the majority of the individuals were trapped either in the grassland or in the forest as indicated by an abrupt decline in catch frequency at the edge of their preferred habitat. Thus, the grassland and forest supported distinct species assemblages. However, there were some species (e.g. the spiders A27 *Microneta viaria* (Blackwall, 1841) and A28 *Pardosa saltans* Töpfer & Helversen, 1990), which appear to favour the edge zone over both the open grassland and the forest interior. At the habitat interface the communities were composed of a mixture of forest and grassland species and some ecotone species (i.e. species with individuals occurring predominantly in the edge zone).

Our classification of the species according to their relative abundance in particular habitats (Fig. 3) revealed in most cases the same classification as described in the literature (e.g. Marggi, 1992).

Edge effect

Individuals of several 'forest' and 'ecotone' species penetrated 6 m and farther into the grassland (e.g. the staphylinid beetle S04 *Plataraea elegans* (Benick, 1934) and the spider A04 *Panamomops mengei* Simon, 1926; Fig. 3). The two forest edges differed in the number of 'forest' and 'ecotone' species that were caught in the 6 m-wide grassland strip. In each taxonomical group more 'forest' and 'ecotone' species were found in the grassland strip adjacent to the gradual forest edge than in the grassland strip adjacent to the sharp forest edge (Fig. 3). This indicates that the type of forest edge may affect the extent to which forest- and ecotone-living arthropods penetrate into the grassland.

Considering the 'forest' and 'ecotone' species of the four taxonomical groups, a higher proportion of staphylinid species than carabid and diplopod species were found in the grassland strip adjacent to the gradual forest edge (Fig. 3). This suggests that different taxonomical groups show different responses to the forest edge.

DISCUSSION

The present study shows that species richness in ground-living arthropods slightly increased in the forest edge zone and that individuals of several forest species showed little movement into the adjacent grassland. Most studies of edge effects on invertebrate communities have shown that abundance, richness and diversity usu-

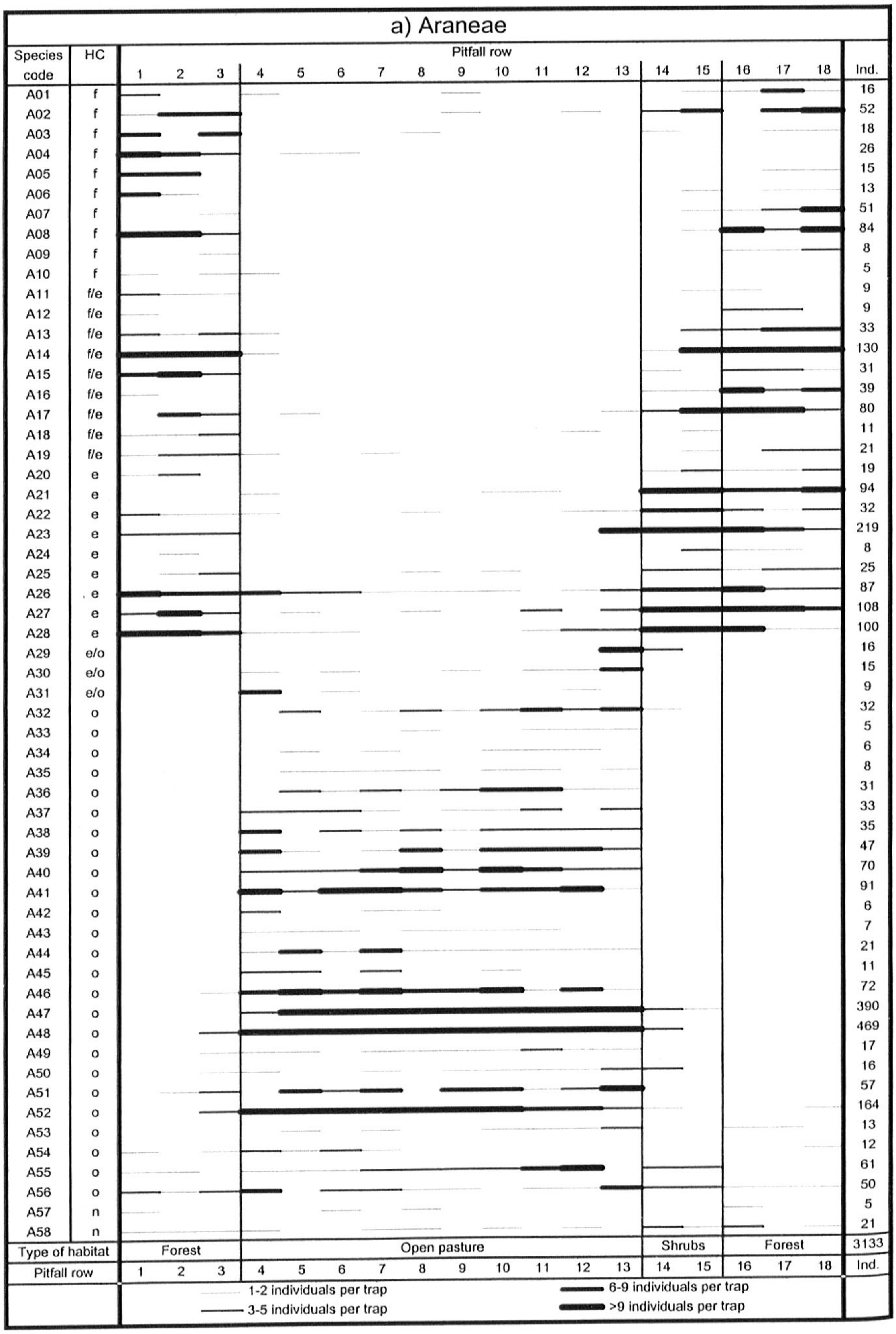
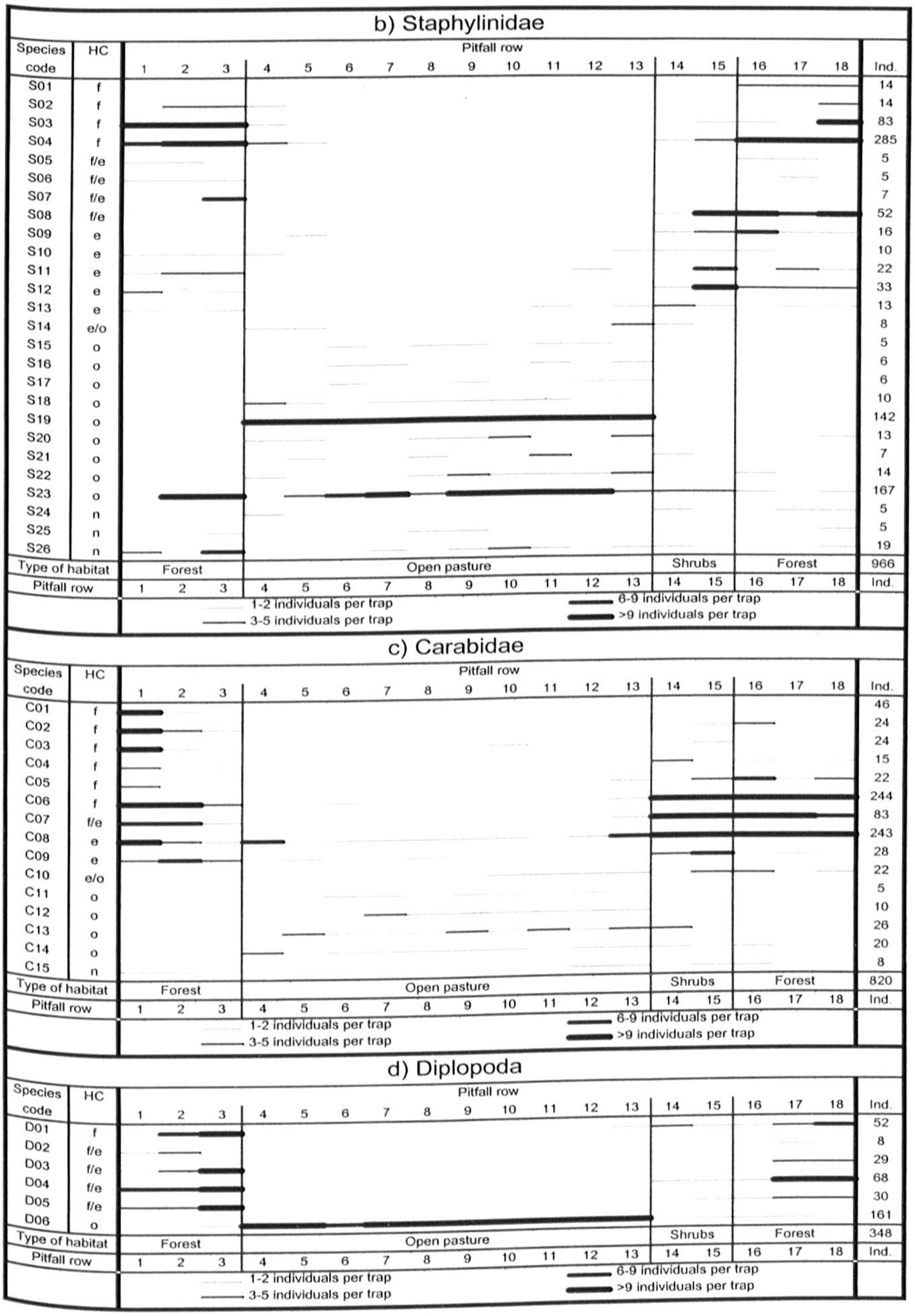


Fig. 3. Catch frequency of abundant arthropod species (≥ 5 individuals recorded) plotted against position on the transect: a) Araneae; b) Staphylinidae; c) Carabidae; d) Diplopoda. Positions of traps as in Fig. 1. The thickness of the horizontal line indicates the abundance of each species. HC refers to the classification of the species to a particular habitat type (f = forest; e = ecotone; o = open habitat). Species codes are explained in Tab 1.



ally increase towards the edge of habitats (HEUBLEIN, 1983; DUELLI *et al.*, 1990; DENNIS & FRY, 1992; BEDFORD & USHER, 1994). In our study, the edge zone included both forest and grassland. In spiders and staphylinid beetles, the species assemblages of both habitats overlapped over a short distance. This resulted in an elevated species richness at the forest edge. A highly structured forest edge may also provide a more complex habitat structure and thus additional niches for a variety of animals. However, we used pitfall trapping to record ground-living arthropods. This method does not consider invertebrates living in the vegetation or on bushes. Taking into account animals living in these niches, species richness might even be higher in the edge zone.

The edge effect and ecotone are not clearly definable discrete units (SAMWAYS, 1994). Each animal species responds differently to the boundary and the environmental characteristic of spatially variable conditions. In addition, biotic interactions may also influence the species distribution pattern. Forest edge may be regarded as a zone which experiences the climate-buffering effects of a tree canopy, but has not the lateral protection afforded by trees to one side. Based on abiotic variables, estimates of edge zone width reached 50 m into the interior of the forest (MATLACK, 1993). The width of the edge zone may vary, primarily determined by the size of the adjacent habitats and the degree of difference between the habitat types. In nature, spatial patterns may be abrupt or gradual as it was the case in the present study. Furthermore, the orientation of the edge may influence the width of the edge zone (FRAVER, 1994). It is possible that different results would be obtained for similarly structured edges with other orientation.

The structural similarity between habitats is also important in controlling the degree of interchange of animals across the edge (cf. edge permeability; STAMPS *et al.*, 1987). When the difference is pronounced, the level of exchance is reduced, and when adjacent habitats are more similar, the number of species crossing the edge will be greater (BAUER, 1989; DOWNIE *et al.*, 1996). In this context, we did not consider the possibility of small-scale movements shown by some arthropod species (cf. MORSE, 1997). For example, small-scale movements of spiders in a forest-grassland edge zone can be explained as a response to changing weather conditions, as seasonal behaviour of different developmental stages in certain species, or as sex-specific behaviour after mating (HEUBLEIN, 1983). Seasonal migrations may not be detectable in the present study due to the relatively short sampling period (May to July). However, small-scale movements of some species as a response to differences in ground temperature cannot be excluded.

Another study using transects of pitfall traps across forest edges on Monte San Giorgio (Southern Switzerland) showed that ground-living spiders penetrate 3–8 m into open meadows (HÄNGGI, 1993). Different spider species responded differently to the forest edge, as found in the present study in all four taxonomical groups.

The size of the habitat island, edge to size ratio and habitat similarity are important in the context of conservation strategies. With increasing fragmentation of the landscape, edges of land patches are becoming proportionately greater relative to interiors (MADER, 1981). In many cases the remnants may be too small or too isolated from other grasslands to function in the same capacity as larger unbroken grassland ecosystems (e.g. SAUNDERS *et al.*, 1991). Extremely narrow grasslands or belts of pasture may be perceived by invertebrates to be essentially all edge, rather than edge and interior habitat (BEDFORD & USHER, 1994). The results of our study indicate that the extent of this effect depends, among other factors, on the structure of the forest edge and varies from 3–12 m for the arthropods considered. This suggests that remnants of unfertilized calcareous grassland wider than 30 m may contain a functional interior area for grassland specialists among the ground-living arthropods.

ACKNOWLEDGEMENTS

We are grateful to T. Blick for identifying the spiders, F. Wittwer the staphylinids, H. Luka the carabids and A. Pedroli-Christen the diplopods. We also thank C. Dolt, G. Hofer, S. Liersch, K. Schweizer and M. Wurtz for assistance and A. Baur, A. Erhardt and C. Kropf for constructive comments on the manuscript. Financial support was received from the Swiss National Science Foundation (Priority Programme Environment, IP Biodiversity, grant No. 5001–44620), the Emilia Guggenheim-Schnurr Stiftung der Naturforschenden Gesellschaft Basel-Stadt and the Freiwillige Akademische Gesellschaft, Universität Basel.

ZUSAMMENFASSUNG

Die Grösse der durch externe Einwirkungen beeinflussten Randzone ist für das Vorhandensein einer habitatcharakteristischen Kernzone in kleinen Restflächen von entscheidender Bedeutung. Auf einer kleinen (39 m breiten) Restfläche einer Juramagerweide in der Nordwestschweiz wurde der Einfluss der Waldrandstruktur (scharf abgeschnitten oder abgestuft) auf die lebensraumspezifische Verteilung von bodenlebenden Arthropoden (Spinnen [Araneae], Kurzflügelkäfer [Staphylinidae], Laufkäfer [Carabidae] und Tausendfüsser [Diplopoda]) mit Hilfe von Becherfallen untersucht. Die Magerweide wie auch der Wald beherbergten unterschiedliche Artengemeinschaften. Bei beiden Waldrändern wurde eine erhöhte Artenvielfalt bei den Spinnen und Staphyliniden gefunden. Carabiden und Diplopoden hingegen zeigten keine erhöhte Artenvielfalt am Waldrand. Im Übergangsbereich Wald/Weide (Ökoton) bestehen die Gesellschaften aus einer Mischung von echten Wald- und Offenlandarten sowie aus spezifischen Ökotonarten. Individuen von verschiedenen Waldarten drangen auch in die Magerweide ein. Allerdings wurden sie nur in einem 3–6 m breiten Streifen entlang des scharf abgeschnittenen Waldrandes und in einem 6–12 m breiten Streifen entlang des abgestuften Waldrandes gefangen. Dies deutet darauf hin, dass auch relativ kleine Restflächen von Magerweiden für bodenlebende Arthropoden noch eine lebensraumtypische Kernzone enthalten dürften.

REFERENCES

Bauer, L.J. 1989. Moorland beetle communities on limestone 'habitat islands'. I. Isolation, invasion and local species diversity in carabids and staphylinids. *J. Anim. Ecol. 58*: 1077–1098.

Baur, B., Joshi, J., Schmid, B., Hänggi, A., Borcard, D., Stary, J., Pedroli-Christen, A., Thommen, G.H., Luka, H., Rusterholz, H.-P., Oggier, P., Ledergerber, S. & Erhardt, A. 1996. Variation in species richness of plants and diverse groups of invertebrates in three calcareous grasslands of the Swiss Jura mountains. *Revue Suisse Zool. 103*: 801–833.

Bedford, S.E. & Usher, M.B. 1994. Distribution of arthropod species across the margins of farm woodlands. *Agric. Ecos. Environ. 48*: 295–305.

Dennis P. & Fry, G.L.A. 1992. Field margins: can they enhance natural enemy population densities and general arthropod diversity on farmland? *Agric. Ecos. Environ. 40*: 95–115.

Downie, I.S., Coulson, J.C. & Butterfield, J.E.L. 1996. Distribution and dynamics of surface-dwelling spiders across a pasture-plantation ecotone. *Ecography 19*: 29–40.

Duelli, P., Studer, M., Marchand, I. & Jacob, S. 1990. Population movements of arthropods between natural and cultivated areas. *Conserv. Biol. 54*: 193–207.

Ellenberg, H. 1988. *Vegetation Ecology of Central Europe*. Cambridge University Press, Cambridge, 731 pp.

Fischer, M. & Stöcklin, J. 1997. Local extinctions of plants in remnants of extensively used calcareous grasslands 1950–1985. *Conserv. Biol. 11*: 727–737.

Fraver, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River Basin, North Carolina. *Conserv. Biol. 8*: 822–832.

Freude, H., Harde, K.W. & Lohse, G.A. 1976. *Die Käfer Mitteleuropas*. Band 2, Adephaga 1. Goecke & Evers, Krefeld, 302 pp.

Hänggi, A. 1993. Minimale Flächengrösse zur Erhaltung standorttypischer Spinnengemeinschaften – Ergebnisse eines Vorversuches. *Bull. Soc. neuchât. Sci. nat. 116*: 105–112.

Heublein, D. 1983. Räumliche Verteilung, Biotoppräferenzen und kleinräumige Wanderungen der epigäischen Spinnenfauna eines Wald-Wiesen-Ökotons; ein Beitrag zum Thema "Randeffekt". *Zool. Jb. Syst. 110*: 473–519.

Laurence, W.F. & Yensen, E. 1991. Predicting the impacts of edge effects in fragmented habitats. *Biol. Conserv. 55*: 77–92.

Lohse, G.A. & Lucht, W.H. 1989. *Die Käfer Mitteleuropas*. 1. Supplementband mit Katalogteil. Goecke & Evers, Krefeld, 346 pp.

Lovejoy, T.E., Bierregaard, R.O., Rylands, A.B., Malcolm, J.R., Brown, K.S., Quintela, C.E., Harper, L.H., Powell, A.H., Powell, G.V.N., Schubart, H.O.R. & Hays, M.B. 1986. Edge and other effects of isolation on Amazon forest fragments. *In*: SOULÉ, M.E. (ed.), *Conservation Biology: The Science of Scarcity and Diversity*, pp. 257–285. Sinauer Associates, Sunderland, Mass.

ŁUCZAK, J. 1997. *Ecotonal systems on the border of the Kampinos Forest and their importance to spiders*. Proceedings of the 16th European Colloquium of Arachnology. Wyższa Szkoła Rolniczo – Pedagogiczna, Siedlce, pp. 211–219.

MADER, H.-J. 1981. Untersuchungen zum Einfluss der Flächengrösse von Inselbiotopen auf deren Funktion als Trittstein oder Refugium. *Natur und Landschaft 56*: 235–242.

MARGGI, W.A. 1992. *Faunistik der Sandlaufkäfer und Laufkäfer der Schweiz (Cicindelidae & Carabidae) Coleoptera. Teil 1*. Documenta Faunistica Helvetiae 12. Centre suisse de cartographie de la faune (CSCF), Neuchâtel, 477 pp.

MATLACK, G.R. 1993. Microenvironment variation within and among forest edge sites in the Eastern United States. *Biol. Conserv. 66*: 185–194.

MAURER, R. & HÄNGGI, A. 1990. *Katalog der schweizerischen Spinnen*. Documenta Faunistica Helvetiae 12. Centre suisse de cartographie de la faune (CSCF), Neuchâtel, 412 pp.

MORSE, D.H. 1997. Distribution, movement, and activity patterns of an intertidal wolf spider *Pardosa lapidicina* population (Araneae, Lycosidae). *J. Arachnol. 25*: 1–10.

NEW, T.R. 1995. *An Introduction to Invertebrate Conservation Biology*. Oxford University Press, Oxford, 194 pp.

PEDROLI-CHRISTEN, A. 1993. *Faunistique des mille-pattes de Suisse (Diplopoda)*. Documenta Faunistica Helvetiae 14. Centre suisse de cartographie de la faune (CSCF), Neuchâtel, 248 pp.

POLLARD, E. 1968. Hedges IV. A comparison between the Carabidae of a hedge and field site and those of a woodland glade. *J. Appl. Ecol. 5*: 649–657.

SAMWAYS, M.J. 1994. *Insect Conservation Biology*. Chapman & Hall, London, 358 pp.

SAUNDERS, D.A., HOBBS, R.J. & MARGULES, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol. 5*: 18–32.

STAMPS, J.A., BUECHNER, M. & KRISHNAN, V.V. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. *Am. Nat. 129*: 533–552.

ZOLLER, H., WAGNER, C. & FREY, V. 1986. Nutzungsbedingte Veränderungen in Mesobromion-Halbtrockenrasen in der Region Basel: Vergleich 1950–1980. *Abh. Westfäl. Mus. Naturk. 48*: 93–107.

(received May 29, 1998; accepted after revision August 17, 1998)