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EDGE EFFECT IN DIFFERENT GROUPS OF ORGANISMS: VASCULAR PLANT, BRYOPHYTE AND FUNGI SPECIES RICHNESS ACROSS A FOREST-GRASSLAND BORDER

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Abstract: Six transects were established on the edges of two deciduous forests near Krosno (Carpathian Foothills) to compare the species richness pattern of vascular plants, bryophytes and fungi. The transects had the shape of a cross with one arm 10 m along the forest edge and the other across the edge, 50 m into the forest interior and 12 m into the grassland. They consisted of 2 × 2 quadrats.

The strongest edge effects were recorded for bryophyte, shrub and tree species richness, the weakest for herbaceous plant species richness. Overall vascular plant species richness and herbaceous species richness were higher in grassland than in the forest and peaked in grassland, 3 m from the forest edge. The shrub species richness was highest 1 m from the edge (in the forest) and the tree species richness 3 m from edge. Bryophyte species richness had roughly the same level across the grassland and within the first several meters of the forest, except for the 2 m zone on the edge itself where species richness was as low as in the forest interior. Fungi species richness was low in the grassland and on the forest edge and rose dramaticaly a few meters from the edge, remaining at the same level within the forest.

The species composition across the forest-grassland border was analysed using detrended correspondence analysis. It revealed that in the case of bryophytes the increase in species richness did not correspond to a change in species composition, such as might have been caused by a general increase in bryophyte density.

INTRODUCTION

Forest-grassland borders are a common component of human-dominated landscapes. Because of the division of land into different properties and patches of different land-use, most of the nemoral zone is nowadays divided into three zones: forest, forest edge and open space, differing strongly in their microclimate (BURGESS & SHARPE 1981, FALIŃSKI 1986).

Forest edges differ from the forest interior and open space in many environmental features such as light intensity and its spectral composition, air, litter and soil humidity and temperature minima and maxima (DIERSCHKE 1974, STOUTJESDIJK & BARKMAN 1992, MATLACK 1993). In comparison with open spaces are forests darker, moister and have fewer temperature extremes. For some factors, e.g. light, the forest edge microclimate has intermediate values between those of forests and open spaces. However, this is not always the case, because southern edges are in fact drier and warmer than open spaces, although northern edges in this case also have intermediate properties (STOUTJESDIJK & BARKMAN 1992).

Forest-grassland edges, both natural and artificial, have often been used as the standard example of an ecotone (ODUM 1971, ALLABY 1977, FORMAN & MOORE 1992, JENÍK 1992, but compare VAN DER MAAREL 1990). One of the features that ecotones were often believed to have is increased species richness (LEOPOLD 1933, ODUM 1971), although in the last few

Tab. 1. Transect characteristics.

No.	Woodland	Forest type	Grassland type	Edge orientation	Altitude a.s.l.
1.	Targowiska	*Tilio-Carpinetum corydaletosum*	hay meadow (*Arrhenatheretum elatioris*)	SW	280
2.	Targowiska	*Tilio-Carpinetum circaeaetosum*	hay meadow (intermediate between *Arrhenatheretum elatioris* and *Cirsietum rivularis*)	SE	280
3.	Łazy	intermediate between *Tilio-Carpinetum corydaletosum* and *Dentario glandulosae-Fagetum*	hay meadow (*Arrhenatheretum elatioris*)	S	360
4.	Łazy	*Dentario-Fagetum typicum*	hay meadow (*Arrhenatheretum elatioris*)	N	320
5.	Łazy	*Dentario-Fagetum lunarietosum*	former hay meadow (*Arrhenatheretum elatioris*)	S	370
6.	Łazy	*Dentario-Fagetum lunarietosum*	unmown *Arrhenatheretum elatioris* with many segetal weeds (oldfield)	S	380

years this view has been criticised (HARRIS 1988, YAHNER 1988, VAN DER MAAREL 1990). In the case of animals the predicted increase in species richness in ecotones sometimes proved true (HEUBLEIN 1983), sometimes not (HELLE & MUONA 1985), but it has not been tested for plant species richness on man-made forest boundaries. Most of the existing studies are of two kinds and both of them give incomplete information about plant species richness. The first kind are studies investigating the impact of edge proximity on forest vegetation (GYSEL 1951, WALES 1972, RANNEY et al. 1981, WILLIAMS-LINERA 1990, LAURENCE 1991, MATLACK 1994, DE CASENAVE et al. 1995). They do not deal with what happens outside the forest and thus do not give a full account of the ecotone species richness. The second kind are descriptive phytosociological studies, in which forest edge vegetation was sampled without regular comparison with adjacent woodland and grassland (TÜXEN 1952, MÜLLER 1962, PASSARGE 1967, BRZEG 1988 and many others). It was only DIERSCHKE (1974) and BALCERKIEWICZ & KASPROWICZ (1989) who sampled the whole vegetation across sharp forest-grassland boundaries. It is astonishing how little we know about forest edge patterns in bryophytes and fungi. Our knowledge is restricted here to notes that bryophytes increase in abundance on forest edges, because the wind blows away the leaf litter (GONSCHORREK 1977, BALCERKIEWICZ & KASPROWICZ 1989). In spite of an extensive literature search we did not find any papers concerning patterns of fungi distribution on forest edges.

In this paper for the first time the species richness and species composition patterns of vascular plants, bryophytes and fungi are compared using the data from six transects running from open space to the forest interior. The special concern of the authors was to find edge effects in these patterns. By an "edge effect" we understand the correlation of a phenomenon with the distance from the edge in a landscape composed of two habitats.

MATERIALS AND METHODS

The study area lies in the lowest part of the Polish Carpathians, in Doły Jasielsko-Sanockie, a hilly area with only slight variations in altitude (250-400 m a.s.l.). Deciduous forest communities are the potential natural vegetation of this region: *Tilio-Carpinetum*, dominated by *Carpinus betulus*, *Quercus robur*, *Fagus sylvatica* and *Abies alba*, and *Dentario glandulosae-Fagetum* (in places with a moister and cooler microclimate e.g. north-exposed slopes, hill tops), dominated by *Fagus sylvatica* with an admixture of mainly *Acer pseudoplatanus* and *Abies alba* (MATUSZKIEWICZ 1981, OKLEJEWICZ 1996). The shrub layer of these communities is very scarce, whereas the ground layer, though not very dense in summer, is lush in spring because of the massive appearance of a few geophyte species. The actual vegetation of the region is a fine mosaic of woodland, man-made grassland and fields. Most of woodland has retained its natural species composition owing to the less extensive introduction of conifers than in other regions of Poland, where they have severely altered the deciduous forest communities.

In 1995 and 1996 six transects in two woods were established across forest edges. Two transects were established on a plain on the edge of woodland near the village of Widacz (14 km SE from Krosno). Four transects were placed 5 km further east, on the edge of woodland on a hill near Łazy (Tab. 1). All the selected stands had been left uncut for some years, were not even-aged (usually 50-120 years) and had a particularly rich and natural woodland flora with many rare or protected species (e.g. *Lilium martagon*, *Veratrum lobelianum*, *Knautia dipsacifolia*, *Aconitum lasiocarpum*, *Arum orientale*, *Daphne mezereum*). The grassland communities (*Arrhenateretum elatioris* and *Cirsietum rivularis*), usually managed as hay meadows, were also floristically rich. The old cadastral maps from the mid-19th and beginning of 20th century (documenting land use at a scale of 1 : 2880) show that the forest edges have remained in the same position, although it was detected that over the period of last 50-90 years they have advanced up to 10 m into the grassland. In all sites on the very edge of the forest there was a thin (2-6 m) mantel of tree saplings and shrubs (*Corylus avellana*, *Prunus spinosa*, *Rubus* sp. div., *Cornus sanguinea*).

Each transect had the shape of a cross and consisted of 2 × 2 m plots (Fig. 1). The center of the cross was placed on the forest border. The longer arm of the cross ran at right angles to the forest edge, 50 m into the forest interior and 12 m into the grassland. The short arm of the cross consisted of two rows of five quadrats running parallel to the forest border. In total 234 (6 × 39) quadrats were sampled. Transects ran only 12 m into the grassland

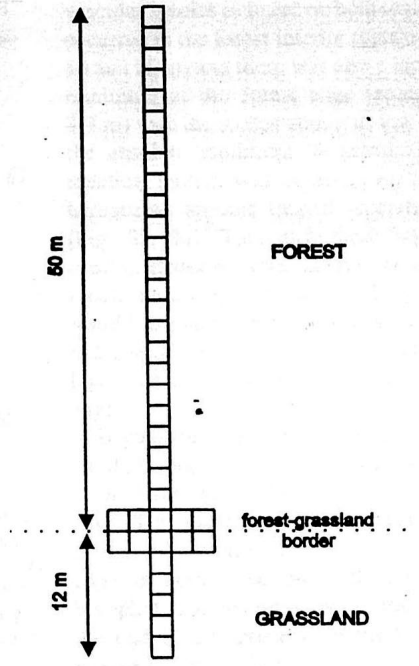

Fig. 1 The arrangement of quadrats in a study transect.

because they appeared to already have a typical floristic composition 2-8 m from the forest edge and longer transects might enter into another proprietor's land with different land-use. In the text the quadrats are labeled by the distance from their center to the edge plus the signs – negative for grassland and positive for forest.

In each quadrat all vascular plants, bryophytes and macroscopic fungi were recorded. In the case of bryophytes and fungi herbarium specimens were usually collected to provide correct identification. Each transect was visited three or four times: end of May / beginning of June (to record vascular plants including spring ephemerals, and bryophytes), July or August (to record later appearing vascular plants), September (to record fungi during the period of their greatest appearance). The abundance of vascular plants in the herb and shrub layers was measured on a 0-10 scale (0 = absence, 1 = below 10% cover, 2 = 10-20%, etc.), whereas in the case of bryophytes and fungi only presence/absence were recorded. The abundance in the tree layer was expressed by the number of stems.

We compared the species richness pattern in two ways. Firstly by calculating the mean species richness of 2 × 2 m quadrats at each point from the edge. Secondly by creating 39 common species lists for all the six quadrat sets with the same locations in the transects (compare Fig. 1), e.g. flora of all grassland quadrats located 8 m from the forest edge. The Gini coefficient, an index of inequality in cumulative frequency distributions (WEINER & SOLBRIG 1984) was computed as a measure of edge effect strength. The coefficient can range from 0.0 (equal abundance at all distances from edge) to 1.0 (all individuals clustered at a single distance). The edge effect strength was calculated for the grassland and forest sides of the transect separately. If x = the sum of differences in mean species richness between all possible pairs of the distances, y = the sum of mean species richness scores at all distances, and z = the number of distances, the Gini coefficient in this case is calculated as

$$G = x/(y*(z-1))$$

The sign of the edge effect was calculated as a sign of a linear regression coefficient, with mean species richness as a dependent variable and distance from the edge as an independent variable. This was done separately for the grassland and forest sides of the transect, as in the case of the Gini coefficient.

In order to compare the species composition of each taxonomic group with environmental variables we applied detrended correspondence analysis (DCA, HILL & GAUCH 1980, TER BRAAK 1988) using the program CANOCO version 3.1 (TER BRAAK 1988). The environmental variables included: absolute distance from edge (regardless of whether in woodland or grassland), habitat type (grassland and grassland edge = 0, forest and forest edge = 1), leaf litter depth (0-3, 1: mean depth > 0 and < 1 cm, 2: depth = 1 to 5 cm, 3: depth > 5 cm), decaying wood cover (0-10 scale, as in plants) and presence of rubbish (cans, plastic, etc.) (0-2). Species composition was expressed as the scores on the first and second DCA axes. Its relation to environmental variables was expressed by linear regression coefficients.

RESULTS

Species richness

In the study plots there were 47 woody species (12 in the canopy layer, 24 in the shrub layer and 29 in the ground layer), 172 herbaceous vascular species, 24 bryophyte species and 93 macroscopic fungi species.

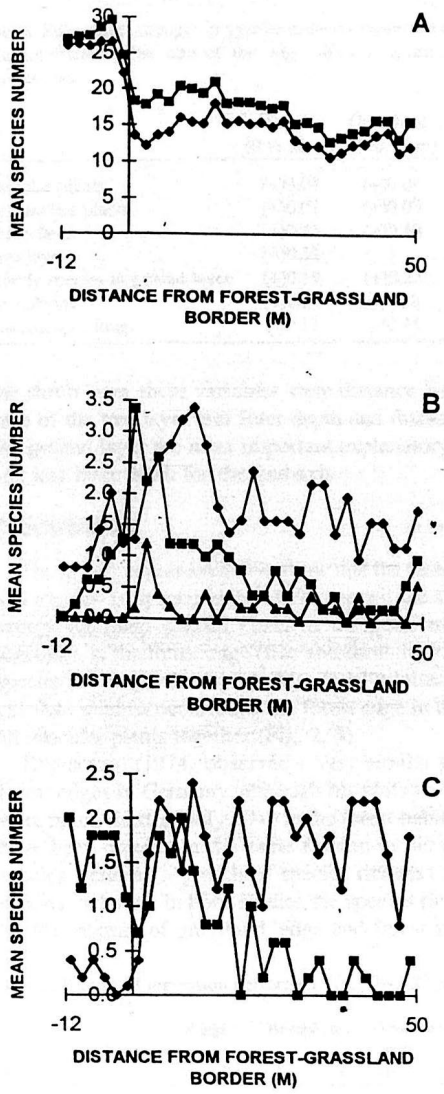

Fig. 2. Mean species richness of 2 × 2 m quadrats across the forest-grassland border. On the grassland side of the transect distances have negative values. Legend A: squares – all vascular plants, diamonds – herbaceous plants; B: diamonds – woody species in the ground layer (< 50 cm), squares – shrub layer (0.5-4.0 m), triangles – tree layer (> 4.0 m); C: squares – bryophytes, diamonds – macroscopic fungi.

The species richness pattern across the forest edge differed for each organism group but was very similar for the same group both on a scale of one quadrat and on a scale of summaric 6-quadrat floras (compare Figs. 2a and 3a, 2b and 3b, 2c and 3c).

Vascular species richness was higher on both scales in grassland and on the grassland edge than in the forest and on the forest edge (Figs. 2a, 3a). Of all the environments mean vascular species richness was highest in grassland 3 m from the edge and decreased in both directions. This pattern was very clear even within each separate transect: in the south facing transects the maxima of vascular species richness occurred at positions -1, -3, -3, 1, -5 m (transects 1, 2, 3, 5, 6 respectively) and in the north facing transect nr 5 at the position -9 m locality. The lowest scores of vascular species richness on both scales occurred in the forest interior (between 40 and 50 m) and there was also a local minimum at the forest edge (around 3-7 m) with the scores almost as low as the absolute minimum. A practically identical pattern was observed for the herbaceous species treated separately (Fig. 2a, 3a). Tree and shrub layer species richness were highest at the forest edge (Fig. 2b, 3b), peaking at 3 and 1 m respectively, whereas species richness of woody species in the ground layer had a maximum 11 m from the edge.

Bryophyte species richness had similarly high values in grassland and in the forest within 5 to 13 m from the edge. This plateau was intersected by a local minimum within 2 m from the edge in both directions. The lowest bryophyte species richness occurred at the end of the transect (in the forest interior) (Fig. 2c, 3c).

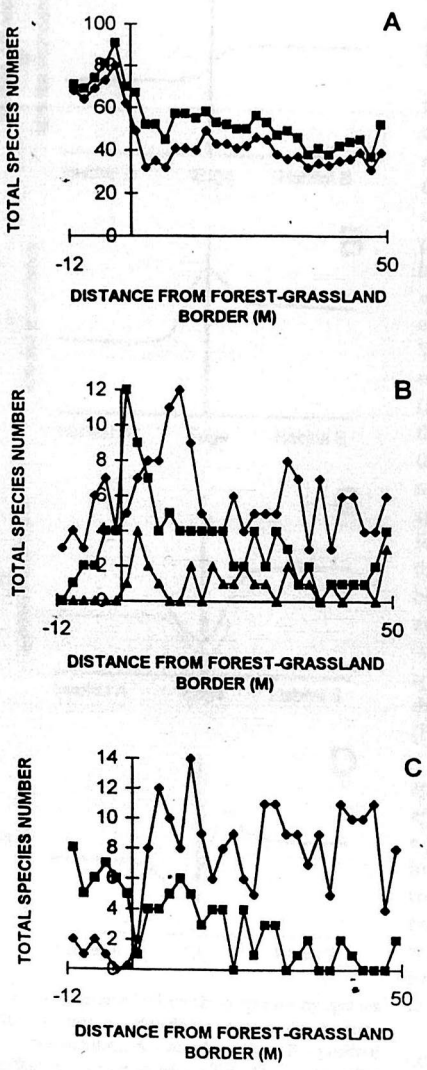

Fig. 3. The "floras" (overall species richness of six 2 × 2 m quadrats each from a different transect) in various distances from the forest-grassland edge. On the grassland side of the transect distances have negative values. Legend A: squares – all vascular plants, diamonds – herbaceous plants; B: diamonds – woody species in the ground layer (< 50 cm), squares – shrub layer (0.5-4.0 m), triangles – tree layer (> 4.0 m); C: squares – bryophytes, diamonds – macroscopic fungi.

Fungi species richness displayed yet another pattern than that of vascular plants and bryophytes (Fig. 2c, 3c). Grassland, grassland edge and forest edge species richness were very low but increased dramatically in the first 3 m from the edge and remained at the same level towards the forest interior.

In general positive edge effects in species richness on both sides (grassland and forest) of the transect occurred in all vascular plant groups. In bryophytes there was a strong positive edge effect on the forest side and a small negative edge effect on the grassland side. In fungi we recorded a small negative edge effect on both sides of the transect (Tab. 2).

Species composition

The analysis of species composition using detrended correspondence analysis revealed that both distance from the edge and other factors had different impacts on each group of organisms (Tab. 3).

Distance from the edge was significantly ($P < 0.05$, t-test) correlated with the scores of the first DCA axis of all vascular plants and the shrub layer, and with the second DCA axis of bryophytes, tree layer and herbaceous plants. There were no significant correlations between distance from the edge and fungi or woody species in the ground layer DCA scores.

The environmental variables taken into account (distance from edge, presence of rubbish, leaf litter depth, decaying wood cover and habitat type) explained more than half of the variance in the first two axes of DCA for herbaceous plants, all vascular plants together and bryophytes. Their explanatory value for the tree layer, shrub layer and woody species in the ground layer was less and the least one for fungi (the first DCA axis explained only ca. 4% of the variance in the fungi species-environment biplot, Tab. 3).

Tab. 2. Edge effect strength in species richness expressed as Gini coefficient. The sign of the edge effect is given in parentheses.

	Forest (0 to 50 m)	Grassland (0 to 12 m)
Vascular plants	(+)0.08	(+)0.04
Herbaceous plants	(+)0.07	(+)0.03
Shrub layer	(+)0.46	(+)0.48
Tree layer	(+)0.52	-
Woody species in ground layer	(+)0.19	(+)0.23
Bryophytes	(+)0.56	(-)0.13
Macroscopic fungi	(-)0.17	(-)0.45

For fungi the most important explanatory variables were habitat type for the 1st DCA axis and distance from edge for the 2nd axis. In the case of bryophytes these were decaying wood and habitat type respectively. For vascular plants together and herbaceous plants on both axes, habitat type was the most important variable. In the case of the shrub layer these variables were distance from the edge and decaying wood, and in the case of the tree layer leaf litter depth and distance from the edge. For the woody species in the ground layer the most important explanatory variables were habitat type for the 1st axis and leaf litter depth for the 2nd axis.

DISCUSSION

The results presented above show that the forest-grassland edge is a zone with both maxima and minima of species richness. In general the species richness of all the investigated groups except for fungi peaked either at the grassland edge (herbaceous plants, vascular plants together), at the forest edge (tree and shrub layer) or near the forest edge (bryophytes, woody species in the ground layer). Also local minima of species richness with values close to the absolute minima occurred at the forest edge in the case of bryophytes, herbaceous plants and all vascular plants together (Fig. 2, 3).

DIERSCHKE (1974) observed a very similar pattern of vascular plant species richness on forest edges in Germany, although his plots had a different shape and size, and the transects were much shorter (only 10 m in the forest habitat). The vascular plant species richness could have been ordered in the same fashion in his transects as in this study, i.e. grassland edge species richness > grassland species richness > forest species richness ≥ or = forest edge species richness. In both studies the species richness peak at the grassland edge was caused by the mixture of grassland, edge and forest species, whereas the zone of lowered species

Tab. 3. Results of regression performed by CANOCO 3.1 on detrendended correspondence analysis scores.

	Fungi		Bryophytes		Vascular plants		Herbaceous plants		Shrub layer		Tree layer		Woody species in ground layer	
DCA axis	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd
Fraction of variance explained by variables	0.04	0.02	0.16	0.36	0.42	0.28	0.52	0.27	0.17	0.12	0.21	0.19	0.21	0.03
Distance from edge	-0.04	-0.15	0.02	0.39*	0.25*	-0.13	0.14	-0.23*	0.45*	-0.22	0.26	-0.47*	0.12	0.11
Rubbish	-0.03	0.02	-0.13	0.18	-0.18*	-0.12*	-0.13*	-0.07	-0.14	-0.15	-0.49*	-0.42*	-0.17	-0.10
Leaf litter depth	0.05	-0.13	0.04	0.55*	0.56*	0.21*	0.62*	0.28*	-0.02	-0.28	-0.52*	0.29	-0.13	-0.13
Decaying wood	-0.03	0.09	0.47*	-0.46*	0.10	0.14*	0.07	0.10	0.28*	0.34*	0.26	-0.09	0.21*	-0.08
Habitat	0.34*	0.09	-0.02	0.76*	0.66*	-0.44*	0.77*	-0.36*	0.03	-0.31*	-	-	0.22	0.07

* $P < 0.05$, t-test

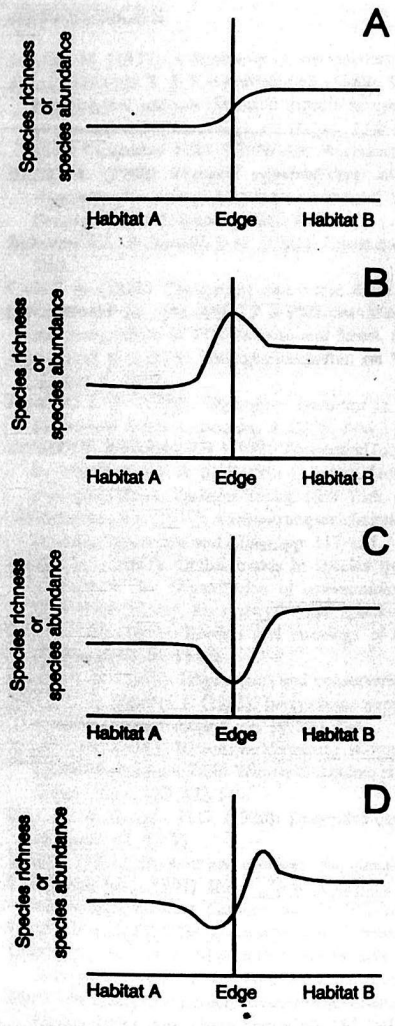

Fig. 4. Four patterns which can be displayed by species richness or species abundance across the ecotone between two habitats. A – no edge effect, B – positive edge effect, C – negative edge effect, D – double edge effect.

richness occurred in places where the dense mantel of shrubs prevented the growth of both meadow and forest species, as well as bryophytes.

The herbaceous species richness pattern across the forest-grassland boundary is consistent with what we know about species richness patterns in grasslands and forests. Grasslands show a high species richness, even on a small scale, as in this study, due to high plant density and small plant size. Forests have low species richness on a small scale, which increases at a larger scale due to environmental heterogeneity (CAIN 1938, WILLIAMS 1964, GRUBB 1987). In this study on both scales analysed grassland herbaceous (and vascular) species richness were higher than forest species richness (Fig. 2a, 3a). At the extreme edge, however, we can notice neighbouring local maxima and minima of species richness. This looks as if the forest-grassland border was asymmetrical: the high species richness at the grassland border was a superposition of grassland, scrub and woodland species, whereas the wooded side of the edge not only lacked grassland species, but also many woodland species, displaying a minimum of species richness (Fig. 2a, 3a).

Positive edge effects in shrub and tree species richness as recorded in this study agree with the results of most other authors, e.g. RANNEY et al. (1981) from forest islands in Wisconsin, and DE CASENAVE et al. (1995) from Chaco semi-arid forest in Argentina, but not with those of WILLIAMS-LINERA (1990) who observed a rather uniform species richness across the edge of a tropical forest in Panama.

Although in this study bryophytes did not occur at the very edge, i.e. in the "mantel" community, further into the forest interior they displayed a positive edge-oriented pattern (Fig. 2c, 3c). An edge-oriented pattern (increased abundance of bryophyte cover at forest edges) was already recorded in bryophytes in Central European deciduous forests by GONSCHORREK (1977), and BALCERKIEWICZ & KASPROWICZ (1989). In all cases this increase was explained by the lower leaf litter cover near the edge due to the activity of wind, which enables the establishment of mosses. This phenomenon was named "bryophytisation" (OLACZEK 1972, BALCERKIEWICZ & KASPROWICZ 1989). It must be stressed that although in this study bryophyte species richness displayed a positive edge effect (Tab. 2), the actual species composition did not completely depend on the distance from the edge (Tab. 3). Thus, proximity of the forest edge means rather a quantitative, not qualitative, change. This discrepancy does not concern the shrub layer, where both species richness (Tab. 2) and species composition (Tab. 3) were strongly affected by the proximity to the edge.

Our results show that, contrary to our expectations, fungi species richness showed a negative edge effect in the ecotone, and species composition showed no significant edge-oriented patterns. We must, however, bear in mind that not the whole mycelia but only the fruiting bodies were recorded, their density being much smaller and more changeable than the density of green plant stems in meadow or forest. Moreover, the mycelia are clones, often larger than the clones of green plants, which causes a larger spatial heterogeneity of fungi assemblages in comparison with herbaceous to plants or even trees. Thus, more extensive research is needed. Designing the study we expected that fungi would be better indicators of edge conditions than plants (or at least complementary to them). We presumed this because most cap fungi are saprophytes, strongly dependent on soil and litter moisture, and this factor shows a wider edge zone than light intensity (MATLACK 1993) – the main factor influencing the distribution of plants (ODUM 1971). On the other hand a similar lack of a clear correlation of the fungal flora with plant assemblages and environmental variables has been reported by most authors dealing with "fungi sociology" (e.g. NESPIAK 1959 and LISIEWSKA 1963).

It is worth pointing out that in the case of bryophytes the sign of an edge effect in species richness was different on both sides of the transect (Tab. 2), as their species richness displayed a negative edge effect on the grassland side, and a positive one on the forest side. This result is a strong argument for consequently distinguishing both sides of the ecotone and making more studies across the ecotone, not only from the ecotone in one direction, which has usually been the case for plants on forest edges (e.g. GYSEL 1951, RANNEY et al. 1981, MATLACK 1994). For the clarification of edge effect terminology in ecology we propose to distinguish the following responses in the ecotone (Fig. 4): no edge effect (variable has an intermediate value in the ecotone – Fig. 4a), positive edge effect (variable has maximum in the ecotone – Fig. 4b), negative edge effect (variable has minimum in the ecotone – Fig. 4c), double edge effect (variable has both maximum and minimum in the ecotone close together – Fig. 4d).

The results clearly show that the forest-grassland border has different characters for various taxonomic groups. For herbaceous plants it is rather a transition zone classified as an ecocline (VAN DER MAAREL 1990, JENÍK 1992), as the edge effects in their species richness were very weak (Tab. 2), whereas in the case of bryophytes and fungi, which show a marked decline in species richness at the forest edges (Fig. 2c, 3c, Tab. 2), it resembles rather a sea-land border with an empty tidal zone, termed by VAN DER MAAREL (1990) a true ecotone.

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REFERENCES

ALLABY M. (1977): *A dictionary of environment*. Macmillan Press Ltd., New York.

BALCERKIEWICZ S. & KASPROWICZ M. (1989): Wybrane aspekty synantropizacji ujawniające się na granicy kompleksów leśnych (Selected aspects of synanthropisation appearing in forest boundaries). In: *Wpływ gospodarki leśnej na środowisko (Impact of forestry activities on environment)*. Scientific seminar, Sękocin, 10-11 November 1988, SGGW-AR, Warszawa, pp. 7-21.

BRZEG A. (1988): Przeglad systematyczny zbiorowisk okrajkowych dotąd stwierdzonych i mogących występować w Polsce (A systematic survey of "saum"-communities found and possibly occurring in Poland). *Fragm. Florist. Geobot.* 34: 385-424.

BURGESS R.L. & SHARPE D.M. (1981): *Forest island dynamics in man-dominated landscapes*. Springer, New York.

CAIN S. A. (1938): The species-area curve. *Amer. Midl. Naturalist* 19: 573-581.

DE CASENAVE J.L., PELOTTO J.P. & PROTOMASTRO J. (1995): Edge-interior differences in vegetation structure and composition in a Chaco semi-arid forest, Argentina. *Forest Ecol. Managem.* 72: 61-69.

DIERSCHKE H. (1974): Saumgesselschaften im Vegetations- und Standortsgefälle an Waldrändern. *Scripta Geobot.* 6: 1-246.

FALIŃSKI J. B. (1986): *Vegetation dynamics in temperate lowland primeval forest. Ecological studies in Białowieża forest. Geobotany 8*. Dr W. Junk Publishers, Dodrecht.

FORMAN R. & MOORE P.N. (1992): Theoretical foundations for understanding boundaries in landscape mosaics. In: HANSEN A.J. & DI CASTRI F. (eds.), *Landscape boundaries: consequences for biotic diversity and ecological flows*, Springer-Verlag, New York, pp. 236-258.

GONSCHORREK J. (1977): Aushagerungserscheinungen im *Luzulo-Fagetum* des Wesergebirges. In: DIERSCHKE H. (ed.), *Vegetation und Klima*, pp. 117-125.

GRUBB P.J. (1987): Global trends in species richness in terrestrial vegetation: a view from the northern hemisphere. In: *Organization of communities: past and present*, The 27th Symposium of the British Ecological Society, Aberystwyth 1986, Blackwell, Oxford, pp. 99-118.

GYSEL L.W. (1951): Borders and openings of beech-maple woodlands in Southern Michigan. *J. Forest. (Washington)* 49: 13-19.

HARRIS L.D. (1988): Edge effects and conservation of biotic diversity. *Conservation Biol.* 2: 330-332.

HELLE P. & MUONA J. (1985): Invertebrate numbers in edges between clear-fellings and mature forests in northern Finland. *Silva Fenn.* 19: 281-294.

HEUBLEIN D. (1983): Räumliche Verteilung, Biotoppräferenzen und kleinräumige Wanderungen der epigäischen Spinnenfauna eines Wald-Wiesen-Oekotons; ein Beitrag zum Thema "Randeffekt". *Zool. Jahrb. Syst. Oekol. Geogr. Tiere*. 110: 473-519.

HILL M. & GAUCH H.G. (1980): Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42: 47-58.

JENÍK J. (1992): Ecotone and ecocline: two questionable concepts in ecology. *Ekológia (ČSFR)* 11: 243-250.

LAURENCE W.F. (1991): Edge effects in tropical forest fragments: Application of a model for the design of nature reserves. *Biol. Conservation* 57: 205-219.

LEOPOLD A. (1933): *Game management*. Charles Sribner's Sons, New York.

LISIEWSKA M. (1963): Mikoflora zespołów leśnych Puszczy Bukowej pod Szczecinem (Mycoflora of forest communities in the Beech Forest near Szczecin). *Monogr. Bot.* 15.

MATLACK G.R. (1993): Microenvironment variation within and among deciduous forest edge sites in the eastern United States. *Biol. Conservation* 66: 185-194.

MATLACK G.R. (1994): Vegetation dynamics of the forest edge: Trends in space and successional time. *J. Ecol.* 82: 113-123.

MATUSZKIEWICZ W. (1981): *Przewodnik do oznaczania zbiorowisk roślinnych Polski (A guide for the identification of Polish plant communities)*. PWN, Warszawa.

MÜLLER T. (1962): Die Saumgesselschaften der Klasse *Trifolio-Geranietea sanguinei*. *Mitt. Florist.-Soziol. Arbeitsgem.* N.F. 9: 95-140.

NESPIAK A. (1959): Studia nad udziałem grzybów kapeluszowych w zespołach leśnych na terenie Białowieskiego Parku Narodowego (Studies on the contribution of fungi in the forest plant communities of Białowieża National Park). *Monogr. Bot.* 8.

ODUM E.P. (1971): *Fundamentals of ecology*. Ed. 3. W.B. Saunders, Philadelphia.

OKLEJEWICZ K. (1996): Charakterystyka geobotaniczna Dołów Jasielsko-Sanockich (Geobotanical description of the Jasło-Sanok Basin). *Zesz. Nauk. Uniw. Jagiellon. Prace Bot.* 27: 1-93.

OLACZEK R. (1972): *Formy antropogenicznej degeneracji zbiorowisk leśnych w krajobrazie rolniczym Niżu Polskiego (Forms of anthropogenic degeneration of forest communities in the agricultural landscape of Polish Lowlands)*. PhD. Thesis, Łódź University.

PASSARGE H. (1967): Über Saum Gesellschaften in norddeutschen Flachland. *Feddes Repert.* 89: 133-195.

RANNEY J.W., BRUNER M.C. & LEVENSON J.B. (1981): The importance of edge in the structure and dynamics of forest islands. In: BURGESS R.L. & SHARPE D.M. (eds), *Forest island dynamics in man-dominated landscapes*, Springer, New York, pp. 67-95.

STOUTJESDIJK P. & BARKMAN J.J. (1992): *Microclimate, vegetation and fauna*. Opulus, Uppsala.

TER BRAAK C.J.F. (1988): *CANOCO – a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal component analysis and redundancy analysis (version 2.1)*. Agricultural Mathematics Group, Wageningen.

TÜXEN R. (1952): Hecken und Gebüsche. *Mitt. Geogr. Ges. Hamburg* 50: 85-117.

VAN DER MAAREL E. (1990): Ecotones and ecoclines are different. *J. Veg. Sci.* 1: 135-138

WALES B. (1972): Vegetation analysis of northern and southern edges in a mature oak-hickory forest. *Ecol. Monogr.* 42: 451-471.

WEINER J. & SOLBRIG O.T. (1984): The meaning and measurement of size hierarchies in plant communities. *Oecologia* 61: 334-336.

WILLIAMS C.B. (1964): *Patterns in the balance of nature*. Academic Press, New York, London.

WILLIAMS-LINERA G. (1990): Vegetation structure and environmental conditions of forest edges in Panama. *J. Ecol.* 78: 356-373.

YAHNER R. H. (1988): Changes in wildlife communities near edges. *Conservation Biol.* 2: 333-339.

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