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ORIGINAL PAPER

Species-specific distribution of two sympatric *Maculinea* butterflies across different meadow edges

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Abstract An important consequence of habitat fragmentation is the increase of edge habitats. Environmental factors in the edges are different from those in the interiors, which causes changes in the distribution of plant and animal species. We aimed to study how edges affect the distribution of two butterfly species within meadow fragments. We therefore investigated the effect of distance from edge and edge type (road edge versus tree edge) on two sympatric large blue species (*Maculinea teleius* and *M. nausithous*). Our results showed that edge type had contrasting effects on the two species. *M. teleius* favoured both interiors and road edges, while *M. nausithous* preferred the tree edges. In the case of the latter species a strong positive edge effect was also found. This kind of within-habitat niche segregation is probably related to the different microenvironmental conditions at the edges. Foodplant density did not seem to limit the distribution of these species. Our results suggest that interiors of meadows are important for *M. teleius*, while tree edges maintain the habitats of the regionally rarer butterfly, *M. nausithous*.

Keywords Edge effect · Foodplant · Habitat use · Myrmecophily · Niche segregation

Introduction

Recently the destruction of natural and semi-natural habitats progressed very rapidly (Foley et al. 2005). In addition to being directly destroyed, extensive habitats were disrupted into small, isolated patches, a process known as habitat fragmentation (Saunders et al. 1991; Meffe and Carroll 1994; Tscharntke et al. 2002). The decrease in the extent of suitable habitats infers directly the decrease in populations due to the lack or lower availability of critical resources. However, the harmful effects of habitat destruction are not restricted only to the given area of the habitat. Even the loss of a relatively small part of the habitat could hinder the free movement or migration of species (Standovár and Primack 2001). An important consequence of habitat fragmentation is an increase of the ratio of edge to interior, because at the edges the populations are exposed to changed conditions (e.g. temperature, humidity, wind, light) partly influenced by the neighbouring habitat or association (Tscharntke et al. 2002). This environmental and biotic change associated with edges is termed edge effect (Saunders et al. 1991). Species react to edges different way; based on studying the population movements of arthropods, Duelli et al. (1990) grouped species according to their distribution around habitat borders.

In the edges of habitats the microenvironmental conditions are different from those in the interiors. This directly influences the structure of the vegetation and thereby the prevalence of animal species (Báldi and Kisbenedek 1999). In her review Murcia (1995) divided edge effects into three different types: (1) abiotic edge effects refer to changes in

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abiotic environmental factors, which are consequences of the proximity of a structurally different matrix around the habitat patch; (2) direct biological edge effects refer to the changes in abundance and distribution of species due to the direct physical proximity of edges; (3) indirect biological edge effects refer to the changes in ecological interactions among species (e.g. predation, pollination, competition, etc.). The fragmented forests, or rather the forest patches, are usually surrounded by a matrix of lower biomass and different structural complexity, e.g. pastures, cropland or secondary growth (Murcia 1995). These differences result in differences in microenvironmental factors, including temperature, humidity and light intensity on both sides of an edge (e.g. Matlack 1993; Jose et al. 1996; Báldi 1999; Urbina-Cardona et al. 2006).

From conservation point of view nature reserve should minimise the edge-to-area ratio to maximise the effective core area of the reserve (Debinski and Holt 2000). Though the species richness is generally higher in the habitat edges than in the habitat interiors (e.g. Kunin 1998), the situation can be different from this if we focus on the habitat specialist species, which have more conservation interest. For example, Magura and Ködöböcz (2007) showed an increase in total species richness of carabid beetles with decreasing habitat area in fragmented sandy grasslands, but if they analysed only the habitat specialists, they found the contrary result, i.e. specialists' richness decreased with decreasing habitat area. In case of butterflies, Krauss et al. (2003) found that the density of specialists and not that of generalists increased with increasing habitat area of calcareous grasslands.

Regarding the direct biological edge effects on butterflies we found some studies comparing edges with interiors or different types of edges at the community level (DeVries et al. 1997; Meek et al. 2002; Kitahara 2004). Another group of studies concentrated on investigating the edge effect on movement behaviour of butterflies (Schultz and Crone 2001; Schtickzelle and Baguette 2003; Ross et al. 2005; Conradt and Roper 2006). These demonstrated that the behaviour of butterflies changes significantly near edges. There are fewer studies regarding the edge effect at the population level. For example, Bergman (1999) studied the habitat utilisation of *Lopinga achine* females in open woodland and showed an edge effect on oviposition sites of butterflies, with more ovipositions at the edges of glades. The contrast in the structure of vegetation between the edge and matrix could largely determine the intensity and magnitude of edge effect. In this context Ries and Debinski (2001) investigated the response (crossing or turning back) of a habitat specialist (*Speyeria idalia*) and a generalist (*Danaus plexippus*) butterfly species to four types of prairie edges. The four edges under investigation differed in structural complexity, ranging from low-contrast to high-contrast. Based on direct tracking they found that the specialist species avoided the edges or turned back, while only high-contrast edges affected the generalist species negatively.

Though *Maculinea* butterflies are among the insects most frequently studied (Kühn et al. 2005), there are no direct edge studies regarding these butterflies (with the exception of some studies of habitat fragmentation). In the case of *M. teleius* and *M. nausithous*, Nowicki et al. (2005a; 2007) showed that patch area negatively affected the population density in Poland, while fragmentation affected it positively. Kőrösi (2005), who only investigated the abundance of *M. teleius* adults, found that the number of individuals increased with the size of habitat patches in Hungary. Regarding *M. nausithous* there is no contradiction in the recent results. All the studies (Anton et al. 2005; Loritz and Settele 2005; Nowicki et al. 2005b) showed that the species occurred with higher frequency and in higher densities in smaller patches than in larger ones. Kőrösi (2005) indicated that this species occupied primarily the shaded areas of forest edges.

Based on the above mentioned studies we hypothesise that both study species could be affected by the proximity of edges, but *M. teleius* negatively, while *M. nausithous* positively. Further we hypothesise that meadow edges characterised by trees, i.e. hard edges would benefit *M. nausithous*, but not *M. teleius*. Therefore the aim of the present study was to test the edge effect (edge versus interior) as well as the effect of edge type on microenvironmental factors and densities of foodplants available for *M. teleius* and *M. nausithous* and consequently on local prevalence of the two butterfly species.

Methods

Study species

Both study species (*M. teleius* and *M. nausithous*) are endangered throughout Europe, and show declining population trends (Wynhoff 1998; Van Swaay and Warren 1999). Habitat loss and habitat degradation due to agriculture intensification and abandonment of traditional management threaten the species in Hungary as well. Both study species occupy wet meadows and lay their eggs in the flowerheads of their foodplant, Great Burnet (*Sanguisorba officinalis*). The species are obligatory myrmecophiles. The primary host ant species of *M. teleius* is *Myrmica scabrinodis* (though four other ant species were recorded as hosts in Hungary: *Myrmica rubra*, *Myrmica salina*, *Myrmica specioides* and *Myrmica gallienii*), while the only host ant species of *M. nausithous* is *M. rubra* in Hungary (Tartally and Csősz 2004; Tartally and Varga 2005). After developing on the foodplant, caterpillars are adopted by given *Myrmica* host ants and then live in their nests as social parasites preying on ant broods (Thomas 1984; Thomas et al. 1989).

Study area

The study area was situated in the Szentgyörgyvölgyi stream valley at Velemér (Western Hungary, Őrség National Park, 46°44′N, 16°21′E, 204 m a.s.l.). The area of the valley along the stream was characterised by meadows and croplands disrupted by small paved and unpaved roads. Directly next to the stream there was a very dense alder tree strip with a height of 10–15 m. According to the traditional regime the first mowing of the year was in May and the second in late August or early September. Nowadays most of the meadows are mown once a year or every second or third year and there is no control on the timing of management during the season. None of the meadows in the valley were fertilised or treated with pesticides, and all are protected.

Field sampling

We have chosen 10 meadows (mean area = 2.5 ha) situated along a 2.5 km long section of the stream for sampling (Fig. 1). The meadows had not been mown until the end of August in the study year and had road and tree edges. We designated four 50 m long and 5 m wide transects on each meadow. One transect pair was designated at the so-called tree edge: one of the transects directly next to the trees at the stream (hereafter tree edge) and the other 15 m further inside parallel to the edge transect (hereafter tree interior). On the same meadow we used one transect pair in the same way at the so-called road edge. The road edge transect pair was situated next to a paved or unpaved road where there were no trees or bushes and only rare automobile traffic. On the other side of the road there was another meadow in all cases. One of the transects was directly at the edge (hereafter road edge), while the other was 15 m inside and

Fig. 1 Sample sites of *M. teleius* and *M. nausithous* in the Szentgyörgyvölgyi stream valley (Western Hungary, Őrség National Park). The dotted areas are wet meadows with presence of blooming foodplant of the butterfly species; the numbered meadows were selected for the study. The short parallel black-and-white dashed lines indicate the tree edge and tree interior transects, while the short parallel black lines indicate the road edge and road interior transects. The space photo was provided by the Fertő-Hanság & Őrség National Park Directorate

parallel to the previous one (hereafter road interior). The two interior transects on the same meadow were as far as possible from each other. We detected the number of *M. teleius* and *M. nausithous* individuals at each transect, walking along the transects in 2 min once everyday during the peak of flight period from the 24th to the 31st of July in 2006, eight times altogether. Within the 5 m wide transects the detectability of the two species was assumed to be constant. We paid attention not to count any individual more than once during each transect sampling. We carried out butterfly observations on sunny days without strong winds, from 9:00 a.m. until 4:00 p.m. After the 31st of July no more sampling was possible because of a long period of cold and rainy weather. To obtain unbiased data, the order in which meadows were sampled was varied between days. In the case of *M. nausithous* three meadows in which fewer than six individuals (probably transient animals) were observed during the study were excluded from the analysis. During every transect count we measured the temperature and the relative humidity using an electronic multi-purpose thermo-hygrometer (TFA 30.5007). We held the instrument in our shadow for 2 min. Wind speed was measured using Kaindl Windmaster 2 holding the instrument for 2 min above our head. We counted the blooming shoots of foodplant once on each transect in a 1 m wide strip. We did not investigate the flora of the study area, because on the basis of our earlier direct tracking study we had found that these butterflies rarely alight to feed on the nectar of plants different from the foodplant (Kőrösi et al. unpubl.).

Statistical analysis

We used linear mixed models to test the effect of edge type (tree versus road) and edge effect (edge transect *vs.* interior transect) on the number of butterflies detected per transect, the microenvironmental variables (temperature, humidity and wind speed) and the foodplant of the butterflies. We decided to analyse microenvironmental variables and foodplant in separate models (i.e. we did not include these variables in the models of the butterflies), since those were highly intercorrelated with edge type and distance from edge and also partly with each other. Before the analyses species densities were pooled over sampling days, while the microenvironmental variables were averaged for the whole sampling period. We assessed the normality of the distribution of the raw dependent variables using normal quantile plots. The three microenvironmental data proved to be normally distributed, while species densities and foodplant shoot density did not follow a normal distribution. In these cases we analysed the data using log-linear models employing the Poisson distribution (Faraway 2006). In all models we included effect of edge type (tree versus road) and edge effect (edge transect versus interior transect) and their interaction as fixed factors, but we discarded non-significant interactions ($P > 0.05$) using a manual stepwise backward selection procedure. Further, all models contained meadow as a random factor. We tested the significance of the fixed effects using the *F*-test. Conducting the model diagnostics, we always checked if the residuals of the models were normally distributed. To analyse the relationship between the butterflies' density and microenvironmental factors and foodplant, we performed Spearman rank correlations. We performed all statistical analyses using R software packages (version 2.2.0, R Development Core Team 2005).

Results

Altogether we registered 879 individuals of *M. teleius* and 92 individuals of *M. nausithous* during the study period. Analysing the effect of edge type (tree versus road) and edge effect (edge transect versus interior transect) on the density of *M. teleius*, we found a strong edge type effect, with more butterflies in road transects than in the tree transects (Table 1, Fig. 2). Although we did not show edge effect, the density was a bit higher at the road edges than at the road interiors. In the case of *M. nausithous* we found an edge effect on the density of butterflies, with higher densities at the edges (Table 1, Fig. 2). Furthermore, we showed a strongly significant edge type effect on the density of *M. nausithous*, i.e. we found the species more

Table 1 Linear mixed models for testing the effects of edge type (tree versus road) and distance from edge (edge transect versus interior transect) on the abundance of Scarce Large Blue (*M. teleius*) and Dusky Large Blue (*M. nausithous*), on three microenvironmental variables (temperature, humidity and wind speed) and on the foodplant (*S. officinalis*) of the butterflies

	Factor	*F*	*P*
Maculinea teleius	Edge type	26.016	**<0.001**
	Distance	1.032	0.319
Maculinea nausithous	Edge type	11.411	**0.002**
	Distance	19.923	**<0.001**
Temperature	Edge type	2.846	0.103
	Distance	2.305	0.140
Humidity	Edge type	2.090	0.160
	Distance	9.181	**0.005**
	Edge type × distance	8.020	**0.009**
Wind speed	Edge type	44.174	**<0.001**
	Distance	9.462	**0.005**
	Edge type × distance	5.579	**0.026**
Foodplant	Edge type	31.414	**<0.001**
	Distance	13.494	**0.001**

Bold *P* values indicate significant effects

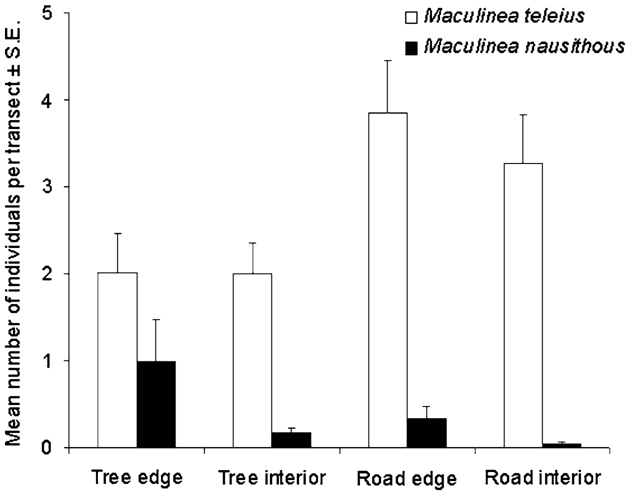

Fig. 2 Bars indicate means with SE of number of Scarce Large Blue (*M. teleius*) and Dusky Large Blue (*M. nausithous*) per transect count on two types of edges and interiors of meadows measured along 40 transects

prevalent at the tree transects—especially at the tree edge—than at the road edges (Fig. 2).

Regarding the microenvironmental parameters, we did not show either edge effect or edge type effect on air temperature (Tables 1, 2). In the case of relative humidity we found, in addition to a significant edge effect, a significant edge type—distance from edge interaction, which means that the edges were more humid than the interiors at the tree edges (Tables 1, 2). Finally, in the case of wind speed, we found both effects (edge effect and edge type effect) and a significant interaction. The tree edge was less windy than the tree interior. However, there was no similar difference between the road edge and road interior, which is the reason for the interaction (Tables 1, 2). Both the edge type and the distance from edge affected the foodplant density. The highest density was at the road interior and the lowest was at the tree edge (Tables 1, 2, Fig. 3).

Performing Spearman rank correlations between total density of *M. teleius* and foodplant shoot density and microenvironmental factors, we found that butterfly density correlated significantly negatively with air humidity ($r_s = -0.41$, $P = 0.009$) and significantly positively with foodplant shoot density ($r_s = 0.52$, $P < 0.001$). In case of *M. nausithous* we found a significantly negative relationship between butterfly density and wind speed ($r_s = -0.53$, $P < 0.001$) and also a significantly negative relationship between butterfly density and foodplant shoot density ($r_s = -0.40$, $P = 0.010$).

Table 2 Mean values (±SEM) of temperature, relative humidity and wind speed recorded in the four transect types

	Temperature (°C)	Humidity (%)	Wind speed (km h^{-1})
Tree edge	31.6 ± 0.2	45.2 ± 0.5	1.7 ± 0.2
Tree interior	31.8 ± 0.2	43.7 ± 0.6	2.7 ± 0.3
Road edge	31.6 ± 0.2	44.1 ± 0.4	3.3 ± 0.2
Road interior	31.6 ± 0.2	44.1 ± 0.5	3.4 ± 0.2

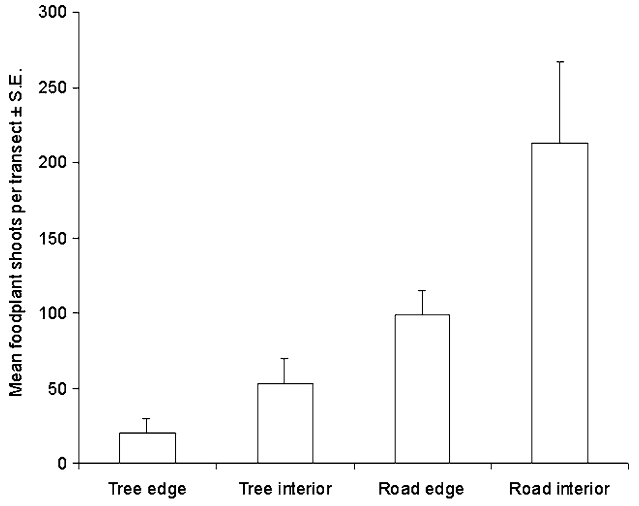

Fig. 3 Mean (±SE) foodplant (*S. officinalis*) shoot density on two types of edges and interiors of meadows

Discussion

In general we registered *M. teleius* in relatively high density. The species favoured the road edge and interior, while the rarer species, *M. nausithous* occurred more frequently at the edges of meadows, especially at the tree edge. So both hypotheses of the current study were supported by the results. In contrast to the distribution of butterflies, the behavioural responses of some species are well documented, e.g. Schultz and Crone (2001) found that a prairie lycaenid species (*Icaricia icarioides fenderi*) modified its behaviour within 10–22 m of the habitat boundary. Kuefler and Haddad (2006) showed different responses of four North-American Satyrinae butterfly species to boundaries with different contrasts. Ide (2002) reported seasonal changes in the microdistribution of *Lethe diana*. The males of the May–June and September–October generations preferred forest edges in contrast to the July–August generations, which preferred forest interiors; because of different light conditions. There are studies that reported association of butterfly species with habitat boundaries or edges, but these earlier papers described this in the case of a single species or in species that are in the same family and have different levels of habitat specialisation (Bergman 1999; Ries and Debinski 2001). In the present paper we compared two sympatric, congeneric species (*M. teleius* and *M. nausithous*), using the same foodplant (*S. officinalis*) and having a similar myrmecophilous strategy, and found that these species use different niches within the same habitat.

In the case of *M. teleius* we found a negative relationship between butterfly density and humidity and a positive relationship with foodplant shoot density. In our earlier study at Kunpeszér (Kiskunság National Park, Central Hungary) we showed a positive correlation between *M. teleius* density and foodplant density (Batáry et al. 2007). In contrast to our results, Nowicki et al. (2005a, 2007) found that foodplant density does not limit either the density of *M. teleius* or the density of *M. nausithous* at metapopulation level. Regarding *M. nausithous* we showed a negative relationship with foodplant shoot density and wind speed. Based on these results we can conclude that foodplant density does not seem to limit the distribution of *M. nausithous*. This supports the results of Anton et al. (2008), who found no correlation between the density of the foodplant and *M. nausithous* abundance. Butterfly density is often related to the abundance of foodplants growing under suitable conditions rather than to the total density of foodplants (Bourn and Thomas 1993). Figurny and Woyciechowski (1998) indicated that these two species select different flowerheads of the foodplant, *M. teleius* ovipositing on younger flowerheads that are closer to the ground, shorter, and contain fewer flowers. They found that ovipositing females search for sites visually according to the phenological stage of the flowerheads of the foodplant. Perhaps the developmental stage of the flowerheads could be different depending on the transect type of the present study due to the different microclimate. Further, Thomas and Elmes (2001) showed that the different developmental stages and sizes of foodplant flowerheads also separate the places where the two species oviposit.

In short, the observed different edge type effect on the *Maculinea* species (niche segregation) could be attributed to the pattern of microenvironmental factors, foodplant density and phenology, and further probably to other factors not yet investigated, such as edge effect on host ant presence (Dauber and Wolters 2004). The detailed explanation of this pattern could be the following. On the two edges we found different microclimate conditions (the tree edge was more humid and less windy than the road edge). These conditions directly determine the distribution of the butterflies and the density of their foodplant too. Consequently the negative correlation between the foodplant and *M. nausithous* is probably the result of the microclimatic conditions, as is the positive correlation between the foodplant and *M. teleius*. The butterfly species *M. teleius* and the foodplant Great Burnet have the same microclimatic requirements. Furthermore, *M. rubra*, the host ant of *M. nausithous*, favours the wetter meadow areas and is therefore probably the dominant ant species there (Dauber and Wolter 2004; Glinka and Settele 2005), while in the interiors of the meadows and in closer parts of road edges there could be a more diverse ant assemblage dominated by *M. scabrinodis*, which is the primary host ant of *M. teleius*. Presumably the two *Maculinea* species diverged so that in *M. nausithous* there could have been a shift in host ant species to the direction of *M. rubra*, which resulted in a preference of imagoes to a wetter microclimate (Elmes et al. 1998, Als et al. 2004). Finally the foodplant–host ant coincidence is a key question in the survival of these species. In the case of predacious species, such as *M. teleius*, the overlap is thought to be minimum 50%, whereas the coincidence of foodplant and host ant of *M. nausithous* is much lower (Thomas and Elmes 1998; Thomas et al. 1998). *M. teleius* achieves this level of co-occurrence by using several host ant species, while *M. nausithous* is highly specialized on an ant species that has a supercolony (*M. rubra*) (Elmes et al. 1998; Tartally and Varga 2005). The latter butterfly species may represent an evolutionary transition between the two strategy types, i.e. the predatory and cuckoo feeding strategies (Thomas 1991; Thomas and Settele 2004).

We investigated how different types of edges, which are generally thought to have negative effects from conservation point of view, do affect these highly specialised butterfly species. The conclusion for conservation is that interiors of meadows that are quite far from the tree edges are important for *M. teleius*, while tree edges at landscape scale level maintain the habitats of the rarer butterfly *M. nausithous* in this region. However, we did not investigate the effect of grassland management. The timing and intensity of management could also be critical in the survival of these species (Johst et al. 2006). Future studies should also focus on the relationship with host ants, as the presence of species might be a direct result of eclosion in the areas and as it might also have been influenced by previous mowing events.

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References

Als TD, Vila R, Kandul NP, Nash DR, Yen SH, Hsu YF, Mignault AA, Boomsma JJ, Pierce NE (2004) The evolution of alternative parasitic life histories in large blue butterflies. Nature 432:386–390

Anton C, Musche M, Hula V, Settele J (2005) Which factors determine the population density of the predatory butterfly

Maculinea nausithous. In: Settele J, Kühn E, Thomas JA (eds) Studies on the ecology and conservation of butterflies in europe. Vol 2. Species ecology along a European gradient: *Maculinea* butterflies as a model. Pensoft, Sofia, pp 57–59

Anton C, Musche M, Hula V, Settele J (2008) *Myrmica* host-ants limit the density of the ant-predatory large blue *Maculinea nausithous*. J Insect Conserv (in press). doi: 10.1007/s10841-007-9091-8

Báldi A (1999) Microclimate and vegetation edge effects in a reedbed in Hungary. Biodivers Conserv 8:1697–1706

Báldi A, Kisbenedek T (1999) Species-specific distribution of reed-nesting passerine birds across reed-bed edges: effects of spatial scale and edge type. Acta Zool Acad Sci H 45:97–114

Batáry P, Örvössy N, Kőrösi Á, Vályi Nagy M, Peregovits L (2007) Microhabitat preferences of *Maculinea teleius* (Lepidoptera: Lycaenidae) in a mosaic landscape. Eur J Entomol 104:731–736

Bergman K-O (1999) Habitat utilization by *Lopinga achine* (Nymphalidae: Satyrinae) larvae and ovipositing females: implications for conservation. Biol Conserv 88:69–74

Bourn NAD, Thomas JA (1993) The ecology and conservation of the brown argus butterfly *Aricia agestis* in Britain. Biol Conserv 63:67–74

Conradt L, Roper TJ (2006) Nonrandom movement behavior at habitat boundaries in two butterfly species: implications for dispersal. Ecology 87:125–132

Dauber J, Wolters V (2004) Edge effects on ant community structure and species richness in an agricultural landscape. Biodivers Conserv 13:901–915

Debinski DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. Conserv Biol 14:342–355

DeVries PJ, Murray D, Lande R (1997) Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. Biol J Linn Soc 62: 343–364

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

Elmes GW, Thomas JA, Wardlaw JC, Hochberg ME, Clarke RT, Simcox DJ (1998) The ecology of *Myrmica* ants in relation to the conservation of *Maculinea* butterflies. J Insect Conserv 2:67–78

Faraway JJ (2006) Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. Chapman Hall, Boca Raton

Figurny E, Woyciechowski M (1998) Flowerhead selection for oviposition by females of the sympatric butterfly species *Maculinea teleius* and *M nausithous* (Lepidoptera: Lycenidae). Entomol Gen 23:215–222

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. Science 309:570–574

Glinka U, Settele J (2005) The effect of ant communities and spatial pattern for *Maculinea nausithous*. In: Settele J, Kühn E, Thomas JA (eds) Studies on the ecology and conservation of butterflies in Europe. Vol 2. Species ecology along a European gradient: *Maculinea* butterflies as a model. Pensoft, Sofia, p 72

Ide J-Y (2002) Mating behaviour and light conditions cause seasonal changes in the dispersal pattern of the satyrine butterfly *Lethe diana*. Ecol Entomol 27:33–40

Johst K, Drechsler M, Thomas JA, Settele J (2006) Influence of mowing on the persistence of two large blue butterfly species. J Appl Ecol 43:333–342

Jose S, Gillespie AR, George SJ, Kumar BM (1996) Vegetation responses along edge-to-interior gradients in a high altitude tropical forest in peninsular India. Forest Ecol Manage 87:51–62

Kitahara M (2004) Butterfly community composition and conservation in and around a primary woodland of Mount Fuji, central Japan. Biodivers Conserv 13:917–942

Kőrösi Á (2005) Habitat-use of wetland *Maculinea* species—a case study. In: Settele J, Kühn E, Thomas JA (eds) Studies on the ecology and conservation of butterflies in Europe. Vol 2. Species ecology along a European gradient: *Maculinea* butterflies as a model. Pensoft, Sofia, p 132

Krauss J, Steffan-Dewenter I, Tscharntke T (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? J Biogeogr 30:889–900

Kuefler D, Haddad NM (2006) Local versus landscape determinants of butterfly movement behaviors. Ecography 29:549–560

Kühn E, Gwillym S, Thomas J , Settele J (2005) Bibliography on *Maculinea* ecology and related topics (state: September 2005). In: Settele J, Kühn E, Thomas JA (eds) Studies on the ecology and conservation of butterflies in Europe. Vol 2. Species ecology along a European gradient: *Maculinea* butterflies as a model. Pensoft, Sofia, pp 259–283

Kunin WE (1998) Biodiversity at the edge: a test of the importance of spatial ''mass effects'' in the Rothamsted Park Grass experiments. Proc Natl Acad Sci USA 95:207–212

Loritz H, Settele J (2005) Changing a butterfly's landscape. persistence of the Dusky Large Blue in managed grasslands. In: Settele J, Kühn E, Thomas JA (eds) Studies on the ecology and conservation of butterflies in Europe. Vol 2. Species ecology along a European gradient: *Maculinea* butterflies as a model. Pensoft, Sofia, pp 221–224

Magura T, Ködöböcz V. (2007) Carabid assemblages in fragmented sandy grasslands. Agric Ecosyst Environ 199: 396–400

Matlack GR (1993) Microenvironment variation within and among forest edge sites in the Eastern United States. Biol Conserv 66:185–194

Meek B, Loxton D, Sparks T, Pywell R, Pickett H, Nowakowski M (2002) The effect of arable field margin composition on invertebrate biodiversity. Biol Conserv 106:259–271

Meffe GK, Carroll CR (1994) Principles of conservation biology. Sinauer Associates, Sunderland

Murcia C (1995) Edge effects in fragmented forests: implications for conservation. Trends Ecol Evol 10:58–62

Nowicki P, Pępkowska A, Kudłek J, Skórka P, Witek M, Woyciechowski M (2005a) Landscape scale research in butterfly population ecology. *Maculinea* case study. In: Settele J, Kühn E, Thomas JA (eds) Studies on the ecology and conservation of butterflies in Europe. Vol 2. Species ecology along a European gradient: *Maculinea* butterflies as a model. Pensoft, Sofia, pp 140–143

Nowicki P, Witek M, Skórka P, Settele J, Woyciechowski M (2005b) Population ecology of the endangered butterflies *Maculinea teleius* and *M nausithous* and the implications for conservation. Popul Ecol 47:193–202

Nowicki P, Pępkowska A, Kudłek J, Skórka P, Witek M, Settele J, Woyciechowski M (2007) From metapopulation theory to conservation recommendations: lessons from spatial occurrence and abundance patterns of *Maculinea* butterflies. Biol Conserv 140: 119–129

R Development Core Team (2005) R: a language and environment for statistical computing. Foundation for Statistical Computing, Vienna. http://www.R-project.org

Ries L, Debinski DM (2001) Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. J Anim Ecol 70:840–852

Ross JA, Matter SF, Roland J (2005) Edge avoidance and movement of the butterfly Parnassius smintheus in matrix and non-matrix habitats. Landsc Ecol 20:127–135

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. Conserv Biol 5:18–32

Schtickzelle N, Baguette M (2003) Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in fragmented landscapes. J Anim Ecol 72:533–545

Schultz CB, Crone EE (2001) Edge-mediated dispersal behavior in a prairie butterfly. Ecology 82:1879–1892

Standovár T, Primack RB (2001) A természetvédelmi biológia alapjai (Principles of conservation biology). Nemzeti Tankönyvkiadó, Budapest

Tartally A, Csősz S (2004) Data on the ant hosts of the *Maculinea* butterflies (Lepidoptera: Lycenidae) of Hungary. Természetvédelmi Közlemények 11:309–317

Tartally A, Varga Z (2005) Host-ant specificity of *Maculinea* species in Hungary, connections with parasitoids and host plants. In: Settele J, Kühn E, Thomas JA (eds) Studies on the ecology and conservation of butterflies in Europe. Vol 2. Species ecology along a European gradient: *Maculinea* butterflies as a model. Pensoft, Sofia, pp 94–98

Thomas JA (1984) The behaviour and habitat requirement of *Maculinea nausithous* (the Dusky Large Blue Butterfly) and *M teleius* (the Scarce Large Blue) in France. Biol Conserv 28:325–347

Thomas JA (1991) Relationship between butterflies and ants. In: Dennis RLH (ed) Ecology of butterflies in Britain. Oxford Scientific Publications, Oxford, pp 149–154

Thomas JA, Elmes GW (1998) Higher productivity at the cost of increased host-specificity when *Maculinea* butterfly larvae exploit ant colonies through trophallaxis rather than by predation. Ecol Entomol 23:454–464

Thomas JA, Elmes GW (2001) Food-plant niche selection rather than the presence of ant nests explains oviposition patterns in the myrmecophilous butterfly genus *Maculinea*. Proc R Soc Lond B Biol 268:471–477

Thomas JA, Settele J (2004) Evolutionary biology: butterfly mimics of ants. Nature 432:283–284

Thomas JA, Elmes GW, Wardlaw JC, Woyciechowski M (1989) Host specificity among *Maculinea* butterflies in Myrmica ant nests. Oecologia 79:452–457

Thomas JA, Clarke RT, Elmes GW, Hochberg ME (1998) Population dynamics in the genus *Maculinea* (Lepidoptera: Lycenidae). In: Dempster JP, McLean IFG (eds) Insect populations. Chapman & Hall, London, pp 261–290

Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C (2002) Characteristics of insect populations on habitat fragments: a mini review. Ecol Res 17:229–239

Urbina-Cardona JN, Olivares-Pérez M, Reynoso VH (2006) Herpetofauna diversity and microenvironment correlates across a pasture-edge-interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. Biol Conserv 132:61–75

Van Swaay CAM, Warren MS (1999) Red data book of European butterflies (Rhopalocera). Nature and environment series no. 99. Council of Europe, Strasbourg

Wynhoff I (1998) The recent distribution of the European Maculinea species. J Insect Conserv 2:15–27