Insect Conservation and Diversity

Insect Conservation and Diversity (2012) **5,** 118–126 doi: 10.1111/j.1752-4598.2011.00138.x

Different habitat selection by two sympatric *Maculinea* butterflies at small spatial scale

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Abstract. 1. Worldwide extinction of species due to habitat loss and habitat degradation can be recognised among butterflies pronouncedly. Therefore, conservation biologists devote special attention to identify the most important ecological factors affecting distribution and survival of butterflies. These efforts have been dominated by landscape-scale studies, although variation in habitat quality at smaller spatial scales may be of crucial importance. This applies for the highly specialised *Maculinea* species, which usually do not form classic metapopulations.

2. *Maculinea nausithous* and *Maculinea teleius* use the same larval food plant and usually occupy the same habitats in Europe. Afforestation of meadows due to abandonment is a major threat for these species. However, few if any studies have assessed the effects that proximity of forest edges may have on the habitat selection by adult butterflies at the scale of local populations. Here, we aimed to test these effects within one habitat fragment based on an intensive mark–release–recapture sampling.

3. Distribution of *M. nausithous* was aggregated and its density was highly positively influenced by the proportion of afforested meadow edges, while *M. teleius* showed no preference for afforested edges. Despite their different within-habitat distribution, the movement of both species was restricted to smaller parts of the habitat.

4. Our results suggest that *M. nausithous* has a narrower niche in the study region, which is most likely due to that its only host ant can find suitable microclimatic conditions at the afforested edges of wet meadows. This implies that habitat patches are not equally used by the two species and hence different management approaches are desirable for their conservation.

Key words. Forest edges, grassland management, local adaptation, *Maculinea nausithous, Maculinea teleius,* myrmecophily, *Myrmica* ants, niche overlap.

Introduction

Global biodiversity crisis challenges both scientists and practitioners who aim at the long-term conservation of insect populations. Due to the enormous number of species, we often lack species-specific data on various factors affecting abundance and distribution of insects (New, 2009). Hence, management strategies for closely related species are often lumped together which hampers their successful conservation. It is true even for butterflies, which are of particular conservation concern due to long-lasting declines and regional extinctions in many species (Pullin, 1995; Wynhoff, 1998a; Thomas *et al*., 2004) and the feasibility of them being monitored (Thomas, 2005). There is some evidence that, for example, dispersal pattern and metapopulation dynamics of butterflies, which fundamentally determines their persistence, may greatly vary among species sharing an identical host plant (Gutierrez *et al*., 2001), among closely related species (Wahlberg *et al*., 2002; Kuras *et al*., 2003; Wang *et al*., 2004) and even among different populations of the same species (Mennechez *et al*., 2004; Schtickzelle *et al*., 2006).

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Identification of factors affecting the distribution of butterflies across different spatial scales is of primary importance for their successful conservation. Most of the previous studies concentrated on patch-occupancy patterns at landscape scale and used two different approaches. Early metapopulation studies examined the importance of habitat patch area and isolation (e.g. Hanski *et al*., 2000; Wilson & Thomas, 2002; Baguette & Schtickzelle, 2006), but there is an ample evidence that habitat patch quality should be explicitly considered as well (Thomas *et al*., 2001; McIntire *et al*., 2007), as long-term persistence of butterflies may be determined by habitat quality rather than by habitat configuration (Dennis & Eales, 1999; Fleishman *et al*., 2002). This implies that conservation efforts have to be concentrated on the maintenance of high quality habitat patches, which can be difficult because of the co-occurrence of several target species. In such cases, the identification of ecological resources and conditions for each species is essential (Turlure *et al*., 2009). Moreover, in metapopulation studies habitat quality and butterfly distribution within patches are typically assumed to be homogeneous. Although several authors have stressed the importance of habitat use and movement patterns within-habitat patches for long-term population dynamics (e.g. Mallet, 1986; Lindenmayer *et al*., 2003; Barton & Bach, 2005), they have received relatively little attention (but see Jeanson *et al*., 2003).

Large blue butterflies of the genus *Maculinea* have been the focus of several ecological studies due to their unique life cycle (Settele *et al*., 2005). Moreover, they are among the most endangered butterflies (Van Swaay & Warren, 1999) and have become flagship species for nature conservation in Europe (Thomas & Settele, 2004). Population ecological studies revealed that *Maculinea* butterflies do not tend to exist in classic metapopulations (Nowicki *et al*., 2007), because populations are typically small, but remarkably demographically stable (Thomas *et al*., 1998) and mobility between habitat patches is quite low compared to other butterflies (Nowicki *et al*., 2005). Both features reduce the turnover of local populations and increase the importance of their dynamics. Nevertheless, few field studies have attempted to explore the habitat use and movement of *Maculinea* butterflies within local populations (but see Hovestadt & Nowicki, 2008; Kőrösi *et al*., 2008).

In the western regions of Hungary, afforestation due to abandonment is a major threat for grassland specialist insects. Afforestation leads to fragmentation of meadows and results in an increase of the proportion of afforested meadow edges. The closely related *Maculinea nausithous* (Bergsträsser, 1779) and *Maculinea teleius* (Bergsträsser, 1779) often co-occur on such wet meadows in Western Hungary and share the same host plant *Sanguisorba officinalis* (L.). Earlier landscape-scale studies indicate that *M. nausithous* shows a preference for afforested edges of meadows and abandoned grasslands, while *M. teleius* is usually more abundant in the interior parts of meadows and prefers open, regularly mown grasslands (Batáry *et al*., 2009; Kőrösi *et al*., 2009). In addition, several studies reported the different distribution of the two species in sympatric populations and suggested the existence of some subtle differences in their habitat use (Thomas, 1984; Wynhoff, 1998a; Nowicki *et al*., 2005, 2007; Van Langevelde & Wynhoff, 2009). However, these studies failed to assess the effects of afforested meadow edges on butterflies' distribution quantitatively.

Butterflies frequently move within-habitat patches, which may affect their distribution to some degree. Since distribution is not static and not independent from movement patterns, the analysis of distribution should be tightly coupled with the assessment of movement. However, only a few studies have concerned the within-habitat movement of *Maculinea* butterflies. These studies revealed that movement pattern of *Maculinea* species within-habitat patches is limited and does not follow a *random walk* model (e.g. Skórka *et al*., 2005; Hovestadt & Nowicki, 2008; Kőrösi *et al*., 2008), but the explanation for this pattern is still unclear.

In this study we aimed to reveal the effects of afforested meadow edges on the distribution of the two species and analyse their movement in a meadow complex where they co-occurred. We conducted an intensive mark–recapture sampling within a single population at a small spatial scale to reveal whether butterflies use the entire range of the habitat equally. We hypothesised, that some differences in the habitat selection by the two species would be found as *M. nausithous* will prefer afforested meadow edges, while *M. teleius* will be found in the interior parts of the habitat. We expected that density of *M. nausithous* will be higher along the afforested edges of meadows than in the interior parts, while density of *M. teleius* will not respond positively to afforested meadow edges. Finally, we expected that differences in the distribution of the two butterflies will be reflected in their movement patterns as well.

Materials and methods

Study site

The study area was located in the valley of the Kerca stream in the Őrség National Park (Western Hungary, 46°46′N; 16°18′E; 240 m a.s.l.). Our study site was a piece of a wet meadow in a mosaic landscape. Approximately half of the study site had been abandoned since 1995, while the other half had been mown erratically and seemed unsuitable for the butterflies in the sampling period and therefore was not sampled (Fig. 1a). In the abandoned part of the meadow, apart from a few patches of sedges (*Carex* spp.), willow shrubs (*Salix* spp.) and invasive weeds (*Solidago* spp.), the common food plant (*Sanguisorba officinalis*) of the two study species was growing at high densities in distinct patches. We designated 22 spatial units for sampling in these parts of the meadow (Fig. 1a). Designation of sampling units was arbitrarily adjusted to some landmarks (e.g. bushes), but within units the vegetation structure was quite homogeneous; size and shape of the 22 sampling units were variable (300–2200 m^2). The sampling area was surrounded by mixed deciduous forests (Fig. 1a). Both *Maculinea* populations occupying the study site could be regarded as single populations. According to another study in 2006, these populations are probably not isolated from others in the surrounding landscape (authors' unpubl. data). Outlines of the spatial units were measured using GPS (Trimble GeoExplorer 3, Sunnyvale, CA,

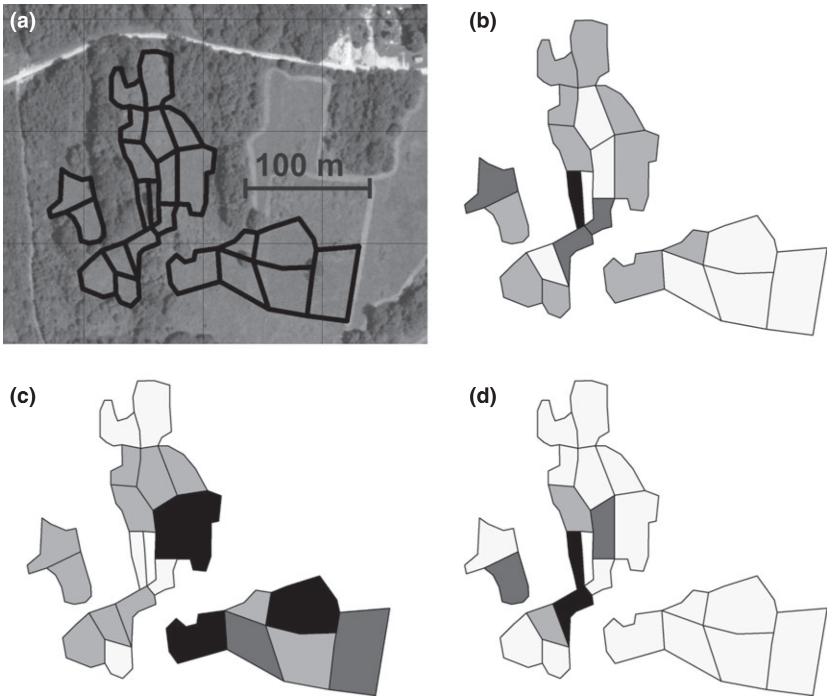

Fig. 1. (a) Aerial photo of the sampling area provided by the Őrség NP Directorate. Thick black lines delineate the 22 sampling units on the abandoned half of the meadow. Unsampled eastern and northern parts of the meadow were erratically mown, while the southern part was abandoned and covered by sedges. (b–d) Maps illustrating the distribution and spatial autocorrelation of (b) *forest proportion*, (c) *abundance* of *M. teleius* and (d) *M. nausithous*. Values are classified in equal intervals. Darker shading indicates higher values.

USA) and ArcView 3.3 (Redlands, CA, USA) was used to calculate perimeters, areas and distances.

Study species

According to recent phylogenic analyses *Maculinea* is a junior synonym of the clade *Phengaris* Doherty, 1891 (Fric *et al*. 2007). However, we will use the well-established genus name *Maculinea* to correspond with the vast majority of the literature. Both the dusky large blue (*M. nausithous*) and scarce large blue (*M. teleius*) are obligate social parasites of *Myrmica* ants. Females oviposit into the flowerheads of the great burnet (*S. officinalis*). After a few weeks of feeding on the seeds, caterpillars descend to the ground and await adoption by host ant workers, which carry them into their nest where caterpillars predate on the ant brood (Thomas, 1984). In Hungary, *Myrmica rubra* (L.) is the only known host ant of *M. nausithous*, while the primary host ant of *M. teleius* is *Myrmica scabrinodis* (Nyl.), although four additional ant species are also recorded as its host [*M. gallienii* (Bondroit), *M. rubra*, *M. salina* (Ruzsky), *M. specioides* (Bondroit)], but in the study region only *M. scabrinodis* and *M. rubra* were proved to tend *M. teleius* caterpillars (Tartally & Varga, 2008). In the study area, the flight period of the two butterflies overlaps (from mid July to mid August). Both species are listed by the Annex II of the Habitats Directive, since they show declining population trends throughout Europe (Wynhoff, 1998b).

Sampling method

The two sympatric populations were studied by mark–release–recapture (MRR) method. Sampling took place over 2 weeks in the peak time of the flight period of both butterflies (31 July–13 August 2003) and was conducted every day between 09:00 and 17:00 hours. Butterflies were captured by net, marked on the underside of their hindwing using fine tipped waterproof pen (Edding 140 S, Ahrensburg, Germany). Species and sex of each specimen were recorded together with the time and location (code of spatial unit) of the capture event, after which the butterflies were released. Duration of sampling in each spatial unit was proportional to its area in order to standardise the sampling effort. We endeavoured to capture almost all butterflies in each spatial unit. The food plant was superabundant throughout the study site (~20–50 flowerheads m^{-2}, for a comparison see Batáry *et al*., 2007; Dierks & Fischer, 2009) and did not seem to be a limiting factor for the butterfly populations, so we did not sample its abundance.

Data analysis

We modelled the abundance and density of butterflies applying different types of generalised linear models. Abundance was measured as the sum of the daily captures in each spatial unit and density was calculated as the abundance divided by the area of the spatial unit. Explanatory variables were the area of a 3-m wide zone along the afforested edge of the spatial units (*forest edge*), and the proportion of this zone to the area of the spatial units (*forest proportion = forest edge/unit area*). Three-metre width of the edge zone was assumed as a typical budding distance of *Myrmica* ant colonies (Hochberg *et al*., 1994) and a distance within forest edge may significantly influence the microclimatic conditions (Batáry *et al*., 2009). Since *forest proportion* was not independent from *forest edge*, the effects of the two variables were tested in separate models.

At first, we tested for spatial autocorrelation in the response and explanatory variables using global Moran's *I*-tests (Moran, 1948). Neighbour links were defined based on distances between the centroids of spatial units in the range of 0–55 m. In this way all spatial units had at least one neighbour, and being aware of limited movement of *Maculinea* butterflies within-habitat patches (Hovestadt & Nowicki, 2008; Kőrösi *et al*., 2008) we found this distance range biologically meaningful. We used row-standardised spatial weights (Bivand *et al*., 2009).

We specified two models for each response variable. In the first model, the environmental explanatory variable was *forest edge*, while the second model included *forest proportion*. In some cases logarithmic transformation of the explanatory variables highly improved the models' fit (see Table 1. for a list of all models tested). In all cases, we applied generalised linear models with Poisson error distribution using quasi-likelihood estimations. We plotted the deviance residuals against the fitted values of each model to check model fit (Faraway, 2006). Finally, we tested for spatial autocorrelation in the model residuals using Moran's *I*-tests (Moran, 1948; Dormann *et al*., 2007). For both species, data of males and females were analysed separately and pooled as well.

Explorative analysis of butterflies' movement distances was also performed. We considered the displacement between the first capture and the consecutive recapture of each butterfly as a move. Move length was measured as the Euclidian distance between the centroids of sampling units where the given individual was marked and recaptured. Moves were classified into two groups by that the marking and recapture had happened in the same sampling unit (*residents*) or in different ones (*emigrants*). Time length between the two captures in these two groups was compared by Wilcoxon rank-sum tests. Move lengths of emigrants were compared between sexes and species using the same statistics. All analyses were performed using packages *maptools* (Lewin-Koh *et al*., 2008), *spdep* (Bivand *et al*., 2008) and *faraway* (Faraway, 2008) of R 2.9.1 software (R Development Core Team 2009).

Table 1. List of generalised linear models specified and tested for both sexes of the two study species.

Species	Response variable	Explanatory variables
Maculinea teleius	Abundance	Forest edge
	Abundance	Forest proportion
	Abundance	log(forest proportion)
	Density	Forest edge
	Density	Forest proportion
Maculinea nausithous	Abundance	Forest edge
	Abundance	Forest proportion
	Density	Forest edge
	Density	Forest proportion

Table 2. Results of global Moran tests for spatial autocorrelation.

Variable	Moran's *I*	*P*-value
Forest edge	0.031	0.28
Forest proportion	0.25	< 0.05
Maculinea teleius abundance	0.08	0.17
M. teleius density	−0.12	0.72
Maculinea nausithous abundance	0.23	< 0.05
M. nausithous density	0.23	< 0.05

Results

A total of 171 and 1085 individuals of *M. nausithous* and *M. teleius*, respectively, were marked. Mean abundance of *M. nausithous* in sampling units was 13.7 (range: 1–50, median = 10), while that of *M. teleius* was 78.5 (range: 16–171, median = 65.5). Global Moran's *I*-tests showed a significant positive spatial autocorrelation for *forest proportion* of spatial units as well as for *abundance* and *density* of *M. nausithous* (Table 2). Although the global Moran's *I*-tests could not identify the exact location of positive spatial autocorrelation, the patterns could be illustrated by maps of the sampling area on which shading indicates the value of each variable (Fig. 1b,d). These maps show that spatial aggregation of *M. nausithous* coincides with high values of *forest proportion*.

The area of afforested edge zone (*forest edge*) had not any significant effect on butterflies' density or abundance in any one model. In the case of *M. teleius*, *forest proportion* had a significant negative effect on the abundance (Table 3). Although three sampling units with a *forest proportion* of zero had to be excluded from the analysis the use of log(*forest proportion*) improved the model fit. None of the predictors had any significant effect on the density of *M. teleius*. Contrarily, both the abundance and density of *M. nausithous* were positively affected by *forest proportion*, but models for density had much higher predictive values (Table 3). There were no remarkable differences between sexes in any cases. We found no significant spatial autocorrelation in the residuals of any models.

We recorded 77 moves of *M. nausithous* (males: 51, females: 26) and 483 of *M. teleius* (males: 157, females: 326). The frequency of residents was neither different between species (χ^2-test: $\chi^2 = 0.27$, $P = 0.61$) nor between sexes of each species (χ^2-test: *M. nausithous* $\chi^2 = 0.02$, $P = 0.89$; χ^2-test *M. teleius*: $\chi^2 = 0$, $P = 0.99$), which means that males and females, as well as the two species had the same probability to stay in a given sampling unit between two consecutive captures (Table 4). We found no significant differences in the time length between two captures of residents and emigrants, indicating that move length was not time-dependent. Move lengths of females were significantly longer than those of males in case of *M. teleius* ($W = 10625.5$, $P = 0.014$; mean move length of females: 68.06 m, and that of males: 58.19 m), and marginally insignificantly longer in case of *M. nausithous* ($W = 260$, $P = 0.088$; mean move length

Table 3. Generalised linear models results on the abundance and density of butterflies. Each row represents a different model. Predictive power indicates the proportion of variance explained by the model.

Species	Sex	Response	Predictors	Estimation (±SE)	*p*-value	Predictive power
Maculinea teleius	Males	Abundance	Forest_prop	−2.59 (1.05)	0.022	0.26
			log(Forest_prop)	−0.78 (0.23)	0.003	0.41
	Females	Abundance	Forest_prop	−2.56 (0.82)	0.005	0.36
			log(Forest_prop)	−0.64 (0.20)	0.004	0.39
	Both	Abundance	Forest_prop	−2.57 (0.83)	0.006	0.35
			log(Forest_prop)	−0.69 (0.19)	0.002	0.43
Maculinea nausithous	Males	Abundance	Forest_prop	2.5 (1.1)	0.033	0.23
	Females	Abundance	Forest_prop	2.2 (1.22)	0.088	0.13
	Both	Abundance	Forest_prop	2.39 (1.09)	0.041	0.21
	Males	Density	Forest_prop	4.20 (1.18)	0.002	0.43
	Females	Density	Forest_prop	4.06 (1.27)	0.005	0.34
	Both	Density	Forest_prop	4.15 (1.18)	0.002	0.42

Table 4. Number of butterflies that were recaptured in the same (residents) or in a different (emigrants) spatial unit than where they had been marked.

Species	Sex	No. of residents	No. of emigrants
Maculinea teleius	Males	46	111
	Females	97	229
Maculinea nausithous	Males	13	38
	Females	7	19

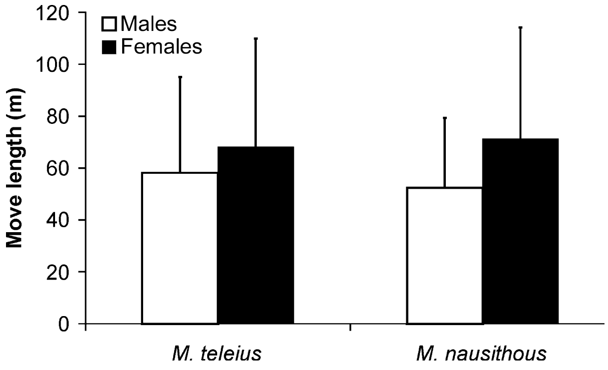

Fig. 2. Mean (+SD) of move lengths of butterflies. Females made significantly longer moves for *M. teleius*. For *M. nausithous* the difference was marginally significant.

of females: 71.26 m, and that of males: 52.39 m). We found no differences in move lengths between species (Fig. 2). Only two individuals of *M. teleius* took a longer move than 200 m, while the longest move taken by *M. nausithous* was 190 m.

Discussion

Distribution of butterflies

In this study we identified an environmental variable (proportion of afforested edges) which had clearly different effects on the within-habitat distribution of two *Maculinea* species. *Maculinea nausithous* butterflies aggregated in the vicinity of forest edges, while *M. teleius* did not show any sign of a non-random spatial distribution. Although the abundance of the latter species was negatively affected by *forest proportion*, it was likely due to the significant negative correlation between *forest proportion* and the area of spatial units (Spearman's $\rho = -0.61$, $P = 0.002$). Thus, the negative relationship between *M. teleius* abundance and *forest proportion* simply reflects to that number of butterflies in spatial units was positively correlated with unit area, which is an obvious result if we assume a random (or uniform) spatial distribution. Note, that density of *M. teleius* could not be explained by any predictors. In contrast, the density of *M. nausithous* was significantly higher where the proportion of afforested edge zones was higher. This result together with the significant positive autocorrelation of both *M. nausithous* density and *forest proportion* clearly proves that *M. nausithous* prefers the afforested edges of meadows. These are in agreement with a landscape-scale study, which showed a contrasting distribution of these species across different meadow edges (Batáry *et al*., 2009). In that study, we compared only the relative abundances of the two species in two different edge types (tree edges vs. road edges) on several meadows and we ignored the internal parts of the meadows. However, in the present study we mapped the spatial distribution of both species throughout the entire area of a single, though complex habitat patch, we found different distributions and we revealed a quantitative relationship between the density of *M. nausithous* and the proportion of afforested edges. To our knowledge, this is the first study that has identified a single environmental variable explaining the different within-habitat distribution of these two closely related butterfly species.

To explain the observed pattern we assume that the abundance of *Myrmica rubra*, the only host ant of *M. nausithous*, is the highest at the afforested edges of meadows, since this ant prefers more humid and cooler microhabitats than other *Myrmica* species in Hungary and often forms supercolonies in the most humid microhabitats (Csősz, 1999). In some wetland habitats of *Maculinea* butterflies in Western Europe *M. rubra* can be the predominant ant species (e.g. Anton *et al*., 2008; Dierks &

Fischer, 2009), but in Hungarian meadows occupied by both *M. nausithous* and *M. teleius*, *M. rubra* is equally abundant to *M. scabrinodis* (Tartally & Varga, 2008). In addition, Van Langevelde and Wynhoff (2009) reported that *M. rubra* prefers vegetation edges (such as forest edges) in the Netherlands, while Dauber and Wolters (2004) found higher density of *M. rubra* at the edges compared to the centres of meadows and fallow lands. Based on all these literary data we suspect that the preference for afforested meadow edges by *M. nausithous* is an adaptive behaviour as it increases the probability of deposited eggs to fall within the foraging range of a host ant colony. This would be in line with the findings of Wynhoff *et al.* (2008), who observed that *M. nausithous* laid more eggs on host plants where *M. rubra* was present beneath. Furthermore, they found in a re-introduced population of *M. nausithous* that the presence of butterflies greatly coincided with the presence of *M. rubra*. Contrarily to *M. nausithous*, we found that the density of *M. teleius* was not affected by the proximity of forest edges. It was more evenly distributed throughout the study area, and it was highly abundant also in more open parts of the habitat, where ant communities may consist of more species. This butterfly can be reared by several *Myrmica* species (Tartally & Varga, 2008; Witek *et al.*, 2008) and this lower host-specificity may assure a sufficient food plant–host ant coincidence throughout the entire study site. However, as we did not sample the ants in this study, this explanation must be empirically tested. We also ignored the host plant, although butterflies certainly recognise it and the two study species have different flowerhead preferences for oviposition (Thomas, 1984; Figurny & Woyciechowski, 1998; Thomas & Elmes, 2001). Microclimatic conditions along forest edges may increase the incidence of flowerheads in the suitable phenological stage for oviposition of *M. nausithous*.

Despite many studies on the habitat use of these closely related butterflies, the role that afforested meadow edges play in the spatial segregation of the two species has not been evaluated quantitatively. Wynhoff *et al.* (2008) found a very low spatial overlap between *M. nausithous* and *M. teleius* in a re-introduced population and they revealed that the occupancy of 1 m^2 plots by both species was primarily influenced by vegetation composition and presence of host ants. However, these predictors correlated, hence their effects were confounded. Some authors found differences in the flowerhead selection for oviposition of the two species, but did not explain the discrepancy in the spatial distribution of adult butterflies (Thomas, 1984; Figurny & Woyciechowski, 1998; Thomas & Elmes, 2001). This is partly due to that microhabitat preferences of butterflies and host ants may vary with geographic location and climate. We stress that our results cannot be generalised across the whole European distribution range of the studied *Maculinea* species. The preference of *M. nausithous* for afforested meadow edges may rather be regarded as a local adaptation.

Movement characteristics of butterflies

Despite their different distributions, we did not find any significant differences in the movement characteristics of the two butterfly species. The lack of time-dependence in butterflies' move lengths suggests that they did not follow the rules of a pure random walk, which is a widely used null-model for animal movement (e.g. Blackwell, 1997). We found a higher mobility of females, which is common in butterfly populations (e.g. Kuussaari *et al.*, 1996; Baguette *et al.*, 1998) and is likely a consequence of different resource distribution and/or foraging strategies of males and females. However, mean move length of both species was unexpectedly short indicating that the majority of butterflies stayed within smaller parts of the sampling site. Only two individuals took moves in the range of the largest distances (~240 m). Limited within-habitat movement of the two species was already suggested (Thomas, 1984) and quantitatively demonstrated (Hovestadt & Nowicki, 2008). In the present study, the small size of the study area may explain the low value of mean move length (Schneider, 2003). Furthermore, in a typical mark–recapture study short distances are more frequently sampled than long distances (e.g. Ovaskainen *et al.*, 2008). Although specific tests would be needed to evaluate whether butterflies' movement can be characterised by a random walk model (see Hovestadt & Nowicki, 2008), nevertheless, given the high sampling intensity and the very short mean move length compared to the spatial dimensions of the study site, we suppose that the results reflect to the inherent movement behaviour of butterflies. However, we stress that our study concerns movements only within habitat patches (i.e. routine movements, see Van Dyck and Baguette (2005)) and thus no inference on dispersal rates can be made.

Implications for conservation

Our results may help conservationists to discover new populations of *M. nausithous* in Western Hungary. Afforested meadow edges can be identified from aerial photos and thus, combined with expert knowledge, potential habitats where efforts of field surveys should be concentrated can be designated easily. According to our results, *M. nausithous* may have a narrower niche in the study region than *M. teleius*, which results in smaller and more isolated populations of the former species (see also Buszko *et al.*, 2005). The implication for conservation may be that afforestation alone does not seem to threaten the populations of *M. nausithous*, but it is certainly not beneficial for *M. teleius* as it increases habitat fragmentation. However, in the study region afforestation of wet meadows is a side effect of cessation of mowing, which leads to the disappearance of *S. officinalis* and invasion of alien goldenrod (see also Skórka *et al.*, 2007). Abandoned meadows become unsuitable for both study species independently on afforestation (authors' unpubl. data). Therefore, the appropriate management of the remaining habitat patches is a crucial element of their successful conservation. For example, timing and frequency of mowing fundamentally influence the survival of large blue butterflies (Johst *et al.*, 2006), thus further research on the effects of different mowing regimes on *Maculinea* populations are urgently needed (see Grill *et al.*, 2008; Kőrösi *et al.*, 2009). In our study region, habitat management can be strictly supervised by the National Park in a few small habitat patches only. Therefore, landscape characteristics cannot be considered for the maintenance of networks of butterfly populations and conservational efforts are concentrated to these single habitat patches. Our study suggests that excessive afforestation of meadows must be prevented by regular management for the successful conservation of both *Maculinea* species, and special attention should be paid to the maintenance of afforested meadow edges in favour of the regionally rarer *M. nausithous*.

Acknowledgements

The authors are indebted to Gabriel Nève and two anonymous referees for their valuable comments on a previous draft of the manuscript and to Laura Sutcliffe for linguistic corrections. We thank the Őrség National Park Directorate for research permissions. Research was funded by the EC within the RTD project MacMan (EVK2–CT–2001-00126) and partly by the NKTH project Faunagenesis (NKFP 3B023-04). Special thanks to Edina Prondvai and Szabolcs Sáfián for their assistance in field work.

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Accepted 1 February 2011

Editor: Jacobus Boomsma
Associate editor: Karsten Schonrogge