HABITAT REQUIREMENTS OF THE PROTECTED SOUTHERN FESTOON (*ZERYNTHIA POLYXENA*); ADULT, EGG AND LARVAL DISTRIBUTION IN A HIGHLY DEGRADED HABITAT COMPLEX

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Habitat quality affects the presence and size of butterfly populations. Resources for all life stages must be found in a given or few habitat patches. Southern festoon (*Zerynthia polyxena*) is a vulnerable, but locally abundant species in Hungary. The larva requires birthwort (*Aristolochia clematitis*) as food plant. We examined the small scale habitat use of adults and distribution of eggs and larvae among different vegetation types to reveal the requirements of the species in all life stages. Transect counts were conducted in a tree plantation complex comprising four types of vegetation. Number (±SE) of adults, eggs and larvae were lowest in poplar plantation (adult 0.3±0.2, egg 1.1±1.1, larva 0.6±0.3). Medium amount of butterflies were observed in open (adult 8.3±2.9, egg 3.1±2.6, larva 3.1±1.9) and black-locust (adult 9.4±4.2, egg 12.7±4.9, larva 4.1±1.1) habitat. Number of butterflies was highest in hummocks (adult 13.5±1.5, egg 12.9±5.7, larva 8.4±2.1). Adults avoided bare ground. We encountered most eggs in dense food plant patches with high plants. Food plant height also positively influenced the occurrence of the larvae. Although distribution of adults and juvenile forms showed quite similar patterns, we could also reveal some differences that caused by different environmental conditions in distinct vegetation types. Our study stresses the importance of habitat quality, which affects population size of butterflies even in a highly degraded habitat complex.

Keywords: habitat quality, habitat patch, life stage, resource use, tree plantations.

INTRODUCTION

The occurrence of a butterfly species can be significantly affected by the area, isolation and quality of the habitat (Thomas *et al.* 1992, Wahlberg *et al.* 2002). While some investigations considered patch geometry as the most relevant factor (Hanski *et al.* 1996, Thomas & Hanski 1997, Nowicki *et al.* 2007), other studies revealed that within-site variation in habitat quality is more important in predicting patterns of site occupancy (Thomas *et al.* 2001, Fleish-

MAN *et al.* 2002). Most ecological studies examining the role of habitat quality, area and isolation in butterfly occurrence and abundance pattern face the problem of habitat definition. Although defining a habitat patch is essential in these studies, adequate definition can be difficult, especially in continuous landscapes in which landscape elements do not help to identify suitable habitats. In the course of habitat definition specific requirements of all life stages should be considered, since different life stages use different resources and all of them should be found within reach. Habitats may consist of different vegetation patches, containing one or more resources for the species, but not necessarily all of them at once. In light of the fact that such resources at finer spatial scale do not necessarily overlap in the area occupied by the butterfly, determining the habitat patch solely on the basis of the presence of the food plant is not always appropriate (DENNIS *et al.* 2006).

In continuous landscapes, in which spatial limitation and isolation has little effect on the distribution of a given species, significance of habitat quality is relatively more important. Habitat quality can be described by structural factors, such as the amount of shade or light intensity (GRUNDEL *et al.* 1998), by main components of vegetation and food plant density (BATÁRY *et al.* 2007), or by the prevalence of sources of nectar, which can influence the density of adults within a suitable habitat (FISCHER 1998). Females and males can have different habitat requirements due to their different drives, such as finding suitable sites for oviposition or mating partners (BULL *et al.* 1985, MUNGUIRA *et al.* 1997, GRUNDEL *et al.* 1998). For some butterfly species, habitat permanence is also an important component of habitat quality (FISCHER *et. al.* 1998), while other species are adapted to changing environments (WARREN 1987). Vegetation management can also influence the quality of habitats, and therefore the habitat use of butterflies (SMALLIDGE & DONALD 1997).

Habitat quality requirements can be different for the given life stages, as they require different resources (DENNIS *et al.* 2006). The distribution and density of adult butterflies itself are not necessarily good predictors of oviposition sites (DOVER & ROWLINGSON 2005), because habitat requirements of eggs and larvae are usually narrower than those of the adults, therefore these stages determine essentially the distribution of butterfly species (THOMAS 1991, ELLIS 2003). Females try to choose the most appropriate places for egg laying. Oviposition sites may be chosen on the basis of structural parameters such as distance from the habitat edge (BERGMAN 1999), light intensity (MEYER & SISK 2001), fundamental rock (THOMAS 1983), area of bare ground (THOMAS *et al.* 1986), soil cover (FISCHER *et al.* 1998) or structure of shade (GRUNDEL *et al.* 1998). Food plant features, such as size and abundance, thickness of food-plant leaves' mesophyllum and organic nitrogen content are also important factors affecting the choice of oviposition site (BOURN & THOMAS 1993, ELLIS 2003). Other, non-food plant characteristics can also affect the selection of

oviposition site, e.g., sward height (Tʜᴏᴍᴀs 1983, Tʜᴏᴍᴀs *et al.* 1986, Eʟʟɪs 2003). Microhabitat features can have a considerable effect on larval survival, as demonstrated e.g., in the case of *Coenonympha tullia* (Sᴇɪ & Pᴏʀᴛᴇʀ 2003). Occurrence of *Euphydryas aurinia* larvae was associated with high food plant cover and short grasses (Kᴏɴᴠɪčᴋᴀ *et al.* 2003).

Our aims were to determine factors affecting the small-scale habitat use of southern festoon (*Zerynthia polyxena*), including the use of food plant patches by adults and the distribution of eggs and larvae among food plant patches, and to reveal the resource requirements of the species in all life stages in a human-dominated landscape. We studied a population inhabiting a tree plantation habitat complex where food plant patches of various size and density occurred in four different vegetation types: poplar plantation, black-locust (*Robinia pseudo-acacia*) plantation, hummocks created by stubbings and clearings. We hypothesized that structural differences of food plant patches in different vegetation types has an effect on distribution and abundance of the southern festoon.

MATERIAL AND METHODS

The southern festoon (*Zerynthia polyxena* [Denis et Schiffermüller], 1775) is a papilionid butterfly distributed from Central and South Europe to the Southern Ural Mts. The northern edge of its range is in the Carpathian Basin, where the species occupies disturbed habitats with nitrogen-rich soil such as gallery forests, abandoned orchards and vineyards, clearings, poplar and black locust plantations and roadsides. The agricultural intensification, river control and urbanization caused a decline in natural disturbance of such habitats in Europe (Sᴍᴀʟʟɪᴅɢᴇ & Lᴇᴏᴘᴏʟᴅ 1997), thus butterflies requiring disturbed habitats have been forced to use human-dominated and artificially disturbed habitats (Rᴏʙᴇʀᴛsᴏɴ *et al.* 1995). Today most populations of the southern festoon can be found in black locust plantations, road verges, riparian woodlands and degraded deciduous forests (Báʟɪɴᴛ *et al.* 2006). In plantations, due to forestry management, the disturbed, nitrogen-rich soil provides excellent conditions for the food plant of the caterpillars.

The flight period is between late April and early June. Caterpillars hatch a week after the oviposition and pupate in July. In the study area the flight period started on the 26th of April in 2005. This species is oligophagous, but in Hungary its larval food plant is exclusively the birthworth (*Aristolochia clematitis*).

Study area

The population studied lives in a poplar (*Populus × euramericana*) plantation mixed with black-locust (*Robinia pseudo-acacia*) patches near Csévharaszt on the Hungarian Great Plain (47°18′59″N, 19°26′18″E). Four vegetation types were available for the butterflies: poplar- and black-locust plantations, hummocks and clearings. Hummocks created by the forestry during the earlier deforestation built-up from stumps of harvested trees merged to a 1.5–2 m high, narrow (~8 m) and long (~200 m) belt covered with soil. These structures were partly shaded and disturbed, which is ideal for birthworth. The larval food plant

was present in all type of vegetation, but in different quantity. Before the butterfly survey (between 3rd and 6th of May), a map of food plant patches of the study area was prepared with *ca.* 2-m precision using GPS Trimble GeoExplorer3 (Trimble Navigation Ltd., USA) (Fig. 1). Food plants appeared some days later than the start of the flight period in the study year. Transects were designated during the following days. In every available habitat type unit a transect was designated, so that each transect was inside in a distinct food plant patch. Each clump of food plants in which the density of shoots was at least five shoot per m^2 and which was separated by at least 10 m from other clumps, was considered a distinct patch. The mean food plant patch size was 1966 m^2 (SEM 450).

Study design and sampling

Altogether 23 large food plant patches were selected for sampling (Fig. 1). Each patch was located in one of the four vegetation types: 6 in poplar plantation, 7 in black-locust plantation, 6 in hummocks and 4 in clearings. To avoid pseudo-replication in each separated habitat type unit only one transect was designated. Transects (6 × 40 m) starting point and direction were selected randomly in every food plant patch. Each transect was divided into 4 m long and 1 m wide plots, and every second plot (altogether five plots per transect) was used for egg and larva census and vegetation survey.

Number of adults was counted twice a day at each transect, altogether 16 times, between May 13–26, 2005. Transects were visited in altered order to avoid effects of timing. Number of eggs and larvae was counted twice in each plot, at the first in the middle of the flight period in 11th–12th of May and the second time at 31st of May. Number and height of food plants, height of other plants and percentage of bare ground were measured at the
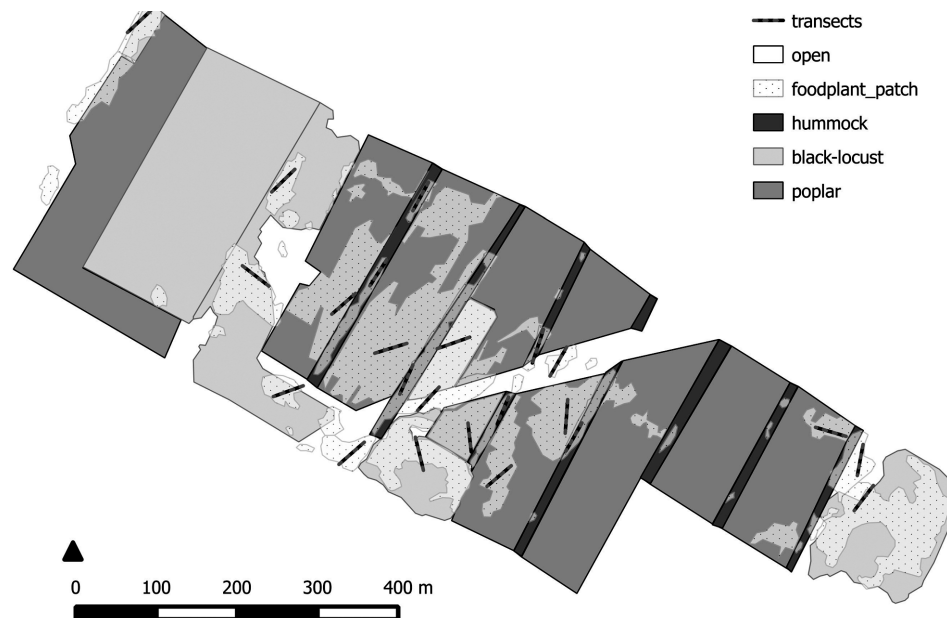

Fig. 1. Habitat map of the study area at Csévharaszt, Central Hungary.

same time. Light intensity was measured on each transect during the second survey by a photometer (LI-189 Quantum/Radiometer/Photometer) at 100 points 120 cm above the ground between 12:00 noon and 1:00 p.m.

Transects and sampling plots covered only a smaller part of a larger habitat complex, but the large density of adults, eggs and larvae made this possible. Sampling area upper limit was the necessary separation of transects to avoid semi-replication, while labour and time effort limited the frequency of egg and larval censuses.

Statistical analyses

Due to the overdispersion and heteroscedasticity in our dataset, and correlations among explanatory variables, we used conditional inference trees to analyse our data. Tree based methods are getting more popular in life sciences, but relatively new to field ecology (Low *et al.* 2006). This method is a variant of 'recursive binary partitioning' or 'trees', a class of simple regression models for prediction and explanation (Hothorn *et al.* 2006). It is a powerful and easy to understand statistical method, which can substitute regression models and produce similar or better results without the strict restrictions of parametric regression models (Hothorn *et al.* 2006). Nagy *et al.* (2010) showed the advantage of conditional inference tree method in a comparative study of two tree based methods and a regression method.

Generally, tree-based methods split the sample step by step into smaller and smaller groups according to mathematical conditions. Conditional inference tree uses regression estimation for splitting the sample into two groups at each node. The recursive binary partitioning is embedded into a well-defined framework of conditional inference procedures, hence both the overfitting and variable selection problem induced by a recursive fitting procedure are solved (Hothorn *et al.* 2006). If the outcome variable is measured on a continuous scale (as in the present study), the method is called regression tree whereas in case of a categorical outcome variable it is called classification tree (Nagy *et al.* 2010).

We carried out six regression tree analyses with quad type test statistic and Bonferroni correction. Number of adults, eggs and larvae as response variables were analysed separately. In the first three trees explanatory variable was only the vegetation category, while in the other three trees we used undergrowth parameters as explanatory variables: height of food plants, number of food plants, height of other undergrowth plants, percentage of bare ground and (only in the case of adults) light intensity. The separation of vegetation category and undergrowth parameters was necessary as vegetation type clearly influenced the undergrowth parameters (see Results). Conditional inference trees are not sensitive to the association between explanatory parameters, as the hierarchy of the outcome can show the connection among them. We also included the transect ID that each plot belonged to. We used the data of the first undergrowth survey in the case of eggs, because in that instance only 5.7% of the offspring were in the larval stage, and used the second survey in the case of larvae, when only 4.6% were still in egg stage. In the case of eggs another conditional inference tree was made, where presence or absence of eggs in a plot was the dependent variable. Undergrowth parameters by vegetation type were tested by Kruskal-Wallis test, and Multiple Comparison after Kruskal-Wallis test. Correlations of the undergrowth parameters with light intensity were tested by Spearman correlation tests. We used R 3.1.0 for statistical analysis (R Development Core Team 2014); the 'party' package was used for conditional inference tree analysis (Hothorn *et. al* 2006), the pgirmess (Giraudoux 2014) package was used for Multiple Comparison after Kruskal-Wallis test.

Table 1. Adult, egg and larva distribution in the four vegetation types.

	Adult (SE)	Egg (SE)	Larva (SE)
Poplar	0.3 (0.2)	1.1 (1.1)	0.6 (0.3)
Open	8.3 (2.9)	3.0 (2.6)	3.1 (1.9)
Black-locust	9.4 (4.2)	12.7 (4.9)	4.1 (1.1)
Hummock	13.5 (1.5)	12.9 (5.7)	8.4 (2.1)

RESULTS

Altogether 182 butterflies were observed over the course of 16 sampling occasions along the 23 transects. Southern festoon adults used the food plant patches in all of the four vegetation types, but their distribution was uneven (Table 1, Fig. 2). Number of adults was significantly lower in poplar plantations than in other types. Number of butterflies was significantly higher in transects with smaller percentage of bare ground. In transects where bare ground cover was >25%, number of food plants had a nearly significant positive effect on butterfly numbers (Fig. 3).

922 eggs were counted just after the peak of the flight period. Eggs were present in 28 out of the 115 sampling plots (14 hummock, 11 black-locust, 2 open, 1 poplar plots). Number of eggs was only marginally significantly higher in black locust and hummock plots than in open and poplar plots (Fig. 3). The result of 'conditional inference tree' analysis with the undergrowth parameters as explanatory variables showed, that the first node of the tree was host plant height (Table 3). Plots with higher than 45 cm host plants host-
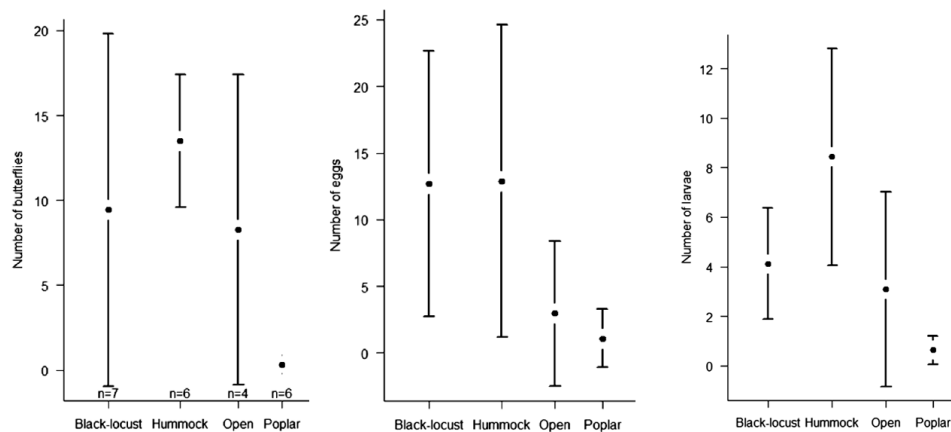

Fig. 2. Mean number of adults, eggs and larvae in the four vegetation types. Bars indicate 95% confidence intervals.

Table 2. Habitat characteristics of the four vegetation types examined during the first (1) and second (2) survey. Mean (±SE) number and height of food plants and mean (±SE) percentage of bare ground cover per plots in each type of vegetation and mean (±SE) light intensity/each transect in the four vegetation category.

	height of food plants (cm)		number of food plants		% cover of bare ground		height under-growth (cm)		light intensity (lux)
	1	2	1	1	2	2	1	2	2
Poplar	31.4 ±4.4	55.0 ±7.5	29.0 ±1.6	63.4 ±1.5	43.8 ±4.9	49.7 ±2.7	29.4 ±1.9	32.8 ±1.7	412.8 ±66.0
Open	53.8 ±9.2	149.5 ±15.1	23.5 ±1.6	17.7 ±2.9	4.5 ±1.1	51.5 ±2.1	23.0 ±1.4	26.0 ±2.58	1731.8 ±28.1
Black-locust	46.5 ±7.4	59.2 ±7.4	29.6 ±1.2	23.7 ±2.7	14.7 ±3.3	54.3 ±2.6	28.3 ±1.1	28.9 ±2.6	890.0 ±218.1
Hum-mock	129.6 ±24.3	137.2 ±18.3	37.5 ±2.0	20.7 ±3.1	4.2 ±1.2	63.3 ±4.9	29.2 ±1.2	29.2 ±2.8	1195.6 ±209.5

ed significantly more eggs than plots with smaller host plants. Host plant number significantly partitioned plots with smaller (< 45 cm) host plants into two groups; plots with more than 135 host plants hosted more eggs than plots with fewer host plants (Fig. 3).

After the flight period 471 larvae were counted in the plots. Larvae were present in 48 of the 115 plots. Larvae number was significantly higher in plots of hummock vegetation type than in black-locust, open and poplar type. The second node of the conditional inference tree was only marginally non-significant and partitioned black-locust and open plots from poplar plots (Fig. 3). The regression tree with the undergrowth parameters showed that food plant height partitioned the sample into three category, plots with the highest number of larvae were plots with higher than 75 cm food plants, fewer larvae were in plots with food plants between 75 and 60 cm, and the lowest number of larvae were in plots with shorter than 60 cm food plants (Fig. 3).

The four vegetation types differed in number of food plants, height of food plants, cover of bare ground and light intensity (Table 2). Relying on

Table 3. Results of conditional inference trees on the habitat characteristics as dependent and vegetation type as independent variables. Significant values are bold.

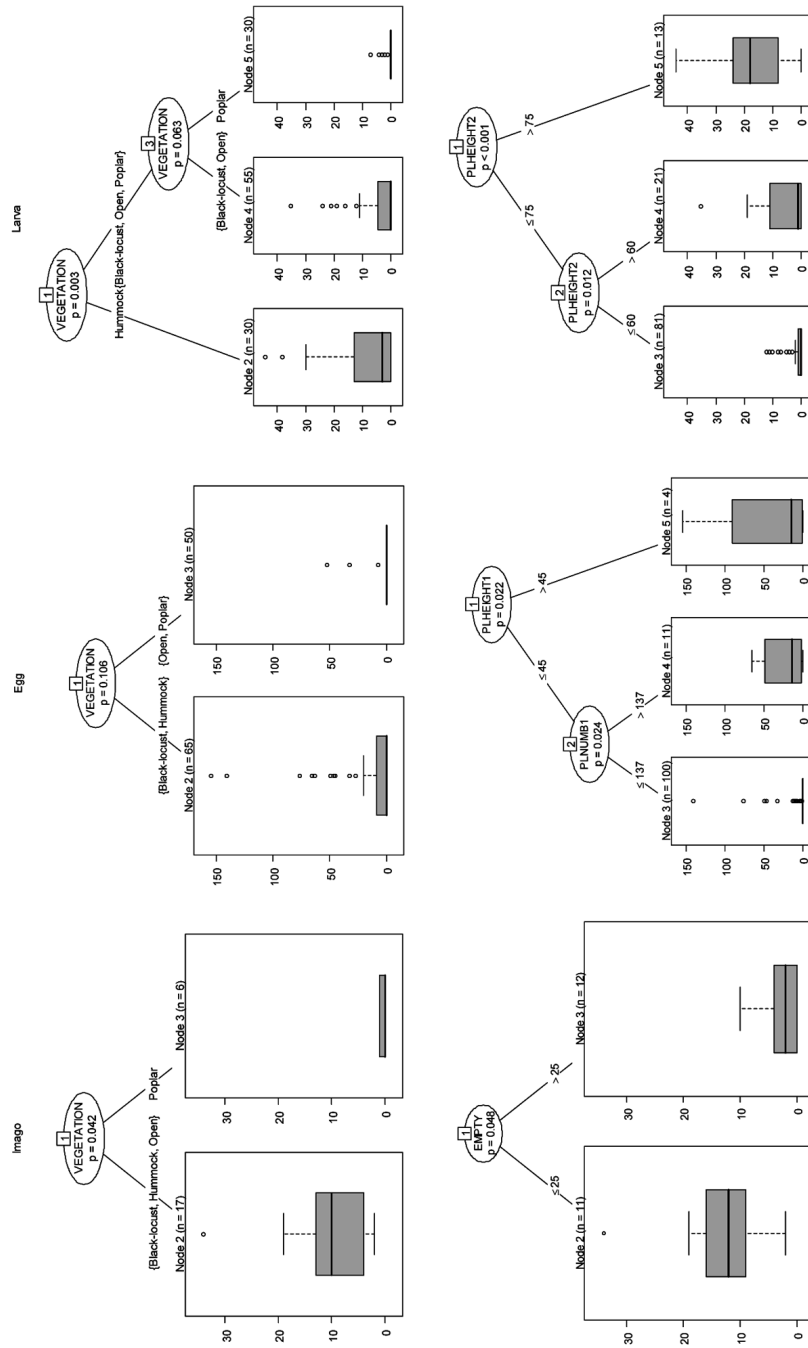| habitat parameter	group1	group2	p
bare ground	black-locust, hummock, open	poplar	**<0.001**
food plant height1	black-locust, hummock, open	poplar	**0.013**
food plant height2	hummock	black-locust, open, poplar	0.117
food plant number2	hummock	black-locust, open, poplar	**0.001**

Fig. 3. Conditional inference trees show the effect of vegetation type and undergrowths parameters on the abundance of the three life stages. Nodes show the separating value of the effective parameters with their significance level, while branches show the mean and size of grouped samples. 'EMPTY': percentage of bare ground; 'PLHEIGHT1': food plant height at the first survey; 'PL-HEIGHT2': food plant height at the second survey; 'PLNUMB1': food plant number at the first survey.

Table 4. Comparing undergrowth parameters of vegetation types. Results of Multiple Comparison after Kruskal-Wallis test.

	Food plant height 1			Food plant number 1			Food plant number 2		
	observed difference	critical difference	difference	observed difference	critical difference	difference	observed difference	critical difference	difference
Black-locust–Hummock	7.9	9.5	False	9.7	10.0	False	9.3	10.0	False
Black-locust–Open	5.2	10.7	False	1.5	11.2	False	11.4	11.2	True
Black-locust–Poplar	0.4	10.0	False	4.1	10.0	False	1.8	10.0	False
Hummock–Open	13.2	11.1	True	8.3	11.6	False	2.2	11.6	False
Hummock–Poplar	8.3	10.4	False	13.8	10.3	True	11.1	10.3	True
Open–Poplar	4.9	11.5	False	5.6	11.6	False	13.3	11.6	True

	Bare ground 1			Bare ground 2			Height of undergrowth		
	observed difference	critical difference	difference	observed difference	critical difference	difference	observed difference	critical difference	difference
Black-locust–Hummock	6.5	20.9	False	22.5	21.9	True	1.4	20.9	False
Black-locust–Open	9.3	23.6	False	17.8	24.7	False	28.7	23.6	True
Black-locust–Poplar	49.3	22.0	True	31.2	21.9	True	2.7	24.3	False
Hummock–Open	2.8	24.3	False	4.8	25.4	False	27.4	24.3	True
Hummock–Poplar	55.9	22.8	True	53.8	22.7	True	4.0	22.8	False
Open–Poplar	58.7	25.2	True	49.0	25.4	True	31.4	25.2	True

Kruskal-Wallis tests some vegetation type characters differed in the four vegetation type. Food plant height was different in the four vegetation categories at the first survey (df = 3, χ^2 = 11.0, p = 0.011), it was higher in hummocks than in open transects based on Multiple Comparison test after Kruskal Wallis (Table 4) (observed difference = 13.2, critical difference = 11.1, p = 0.05). The difference became non-significant for the second survey (df = 3, χ^2 = 3.7, p = 0.291). Food plant number at the first survey was significantly higher in hummock vegetation type than in others (df = 3, χ^2 = 13.2, p = 0.004), while at the second survey it was significantly higher in hummock and open patches than in black locust and poplar patches (df = 3, χ^2 = 15.3, p = 0.002) (Table 4). Similarly, light intensity was also significantly higher at hummocks and open patches than in black locust and poplar ones (df = 3, light intensity χ^2 = 12.7, p = 0.005). Bare ground cover was significantly higher in poplar patches than in all other vegetation types (first survey: df = 3, χ^2 = 12.1, p = 0.007, second survey: df = 3, χ^2 = 47.6, p < 0.01) (Table 4). Height of undergrowth at the first survey was significantly higher in black-locust, and hummock, than in open and poplar quadrates (df = 3, χ^2 = 14.5, p = 0.002) (Table 4). During the second survey, there was no significant difference in height of undergrowth (df = 3, χ^2 = 3.6, p = 0.307). There was a negative correlation between light intensity and percentage of bare ground cover per transects (S = 3131.36, *p* = 0.01, rho = –0.55), while we found a positive correlation between light intensity and number of host plants in the first (S = 1136, *p* = 0.04 rho = 0.44), and second survey (S = 631.66, *p* < 0.01, rho = 0.69). There was no significant correlation between light intensity and height of host plants nor in the first (S = 2030.02, *p* = 0.99 rho = –0.003), neither in the second survey (S = 1274.15, *p* = 0.08, rho = 0.37).

DISCUSSION

Our study demonstrated that distribution of different life stages of the southern festoon butterfly was highly uneven among food plant patches in different vegetation types. Although distribution of adults and juvenile forms showed quite similar patterns, we could also reveal some differences that can be explained by different environmental conditions in distinct vegetation types.

Adult butterflies clearly avoided poplar patches, but their abundance in the other three vegetation types was fairly similar, in other words, they used them equally. This pattern largely coincided with the cover of bare ground and none of the other environmental variables had significant effect on it. However, we suppose that light intensity may play a crucial role in affecting butterfly movement and distribution. Our observations on *Z. polyxena* individuals suggest that the activity of this species is highly dependent on di-

rect sunlight (Kőrösi *et al.* unpubl. data), and we suggest that poplar stands were avoided by the butterflies because light intensity was probably below a certain threshold. Moreover, light intensity was negatively correlated with bare ground cover. Possibly, bare ground cover described better the amount of sunlight on an area during the whole development period of the southern festoon, than once measured light intensity. Measurement of light intensity was far less precise and detailed than that of other environmental variables, and presumably this also may have caused that it did not prove to have a significant effect. Our result that bare ground and shaded microhabitat type had a negative effect on adult abundance confirms the conclusion of Čelik (2012) that the area of host plant stands in sunny locations is strongly related with male and weakly with female adult numbers. They showed the importance of sunny food plant patches and the significance of resource overlapping. Size or amount of food plants had no effect on imago abundance, similarly to our study (Čelik 2012). Flight activity of adult butterflies in search for nectar sources and resting places could mask the female's search for suitable oviposition sites, therefore the adults may spend time in areas with few or low quality larval food plant. However, the lack of a significant food plant effect on adults could be the result of the fact that we did not differentiate genders during our survey. Different habitat use of males and females is possible, particularly in light of male dominance in sex ratios, which was observed during in earlier MRR studies in 2003–2004 in Hungary (Örvössy *et al.* unpubl. data) and in Slovenia (Čelik 2012). Male dominance can lead to male harassment on females, causing different behaviour and habitat use of the two sexes. Females fly longer distances, while males have a smaller home range (Čelik 2012). Another explanation for the lack of larval food plant effect on adults might be that food plants, which occurred in high abundance, were not a limiting factor in the study area and the study did not include areas without food plants. There are studies where the availability of larval resources did not affect the abundance of females, e.g. *Parnassius apollo* (Fred *et al.* 2006), while other large-scale studies suggest that population size of monophagous butterflies linearly increases with the density of larval food plants (Krauss *et al.* 2004, Batáry *et al.* 2007) or that adult abundance is positively correlated with the larval food plant, as in the case of *Euphydryas aurinia* (Munguira 1997).

Distribution of eggs showed a bit different pattern from butterflies as their presence and number was lower in open and poplar patches than in hummocks and black locust patches. This means that butterflies used the food plant patches in open areas, but did not lay many eggs there. Eggs were more abundant in plots where food plants were bigger and food plant number was higher. Food plant number was significantly higher in hummock (first survey), and in hummock and open patches (second survey). Food plants were

significantly taller in hummock than in other vegetation types at the first survey. At the second survey the pattern was similar, but the difference was not significant. Seemingly, the number and size of food plants together can jointly explain the egg distribution. Egg distribution could differ from adult distribution in other butterfly species as well, such as *Hypochrysops halietus*, where adult density was high in a track without vegetation, but larvae were present only on the food plant (DOVER & ROWLINGSON 2005). Other studies showed that adults preferred the same habitat suitable for egg-laying, so egg density was greater where adults were more abundant, as in the case of *Aricia artaxerxes* (ELLIS 2003). Our observations on *Z. polyxena* individuals suggest that the activity of this species is highly dependent on direct sunlight (KŐRÖSI *et al.* unpubl. data). However, clearings could be too dry for eggs, and drought can be a critical factor in the larval development (SCHWEIGER *et al.* 2006). Clearings were not only dry, but were more exposed to occasional night frosts during the egg and early larval stages.

Hummocks and black-locust patches were the best oviposition sites, an observation that was confirmed by a latter study (BATÁRY *et al.* 2008), probably due to the large number and size of food plants, which had a positive relationship with the amount of larvae. Hummocks are nitrogen-rich and sunny enough to be the most suitable habitat for the food plant. To lay eggs in an area with sufficient food plant is necessary, since excessive egg load can lead to defoliation of the food plants, as in the case of *Zerynthia cretica*, which forces larval searching for food plant with increased mortality (DENNIS 1996). Although egg density depended on food plant density at this scale, in a latter study on egg distribution we showed that at the level of individual food plant shoots the surrounding food plant density had no significant effect on egg density (BATÁRY *et al.* 2008).

Larvae showed a different distribution from eggs and butterflies, since they were significantly most abundant in hummock patches. Larvae number was also lower in poplar patches than other vegetation types, but this difference was marginally non-significant. We recorded larvae in much more plots than eggs, probably because eggs are usually laid in small clusters by females and caterpillars may disperse to reduce competition. Larvae number was significantly affected by food plant height, indicating that food plant biomass may be an important factor in larval survival and development. Food plant height was highest in hummocks and lowest in poplar patches, just like the number of larvae. The fact that larval distribution differed from egg distribution suggests that larval survival was highest in hummock patches. Number of larvae was highest in hummocks, medium amount was observed in black-locust and open patches and only occasionally was observed in poplar plantation. The difference in significance of egg and larval distribution might mean

that the initial distribution of the recruits changed during larval development. This phenomenon could be explained by the fact that females do not necessarily can select the best host and larvae may reject the given plant individual they hatched on (BERNAYS & CHAPMAN 1994). It is also possible that larvae moved from less suitable microhabitats and/or had a higher mortality rate on them. Egg-laying is time consuming, besides choosing the best oviposition places, females should also optimise the number of eggs laid. This can lead to aggregated egg distribution, as larvae were less aggregated, larval movement is likely. Larval movement could reduce competition among conspecifics, compensate weak maternal choice or changes in habitat quality after egg-laying. Adults strongly preferred hummocks and black-locust patches. Egg distribution showed similar pattern, although it was not so pronounced. This pattern changed when larvae hatched. Hummocks hosted most of them; black-locust and open patches had fewer larvae while poplar plots were almost free of larvae. This pattern change could be the result of different egg and larval survival in the four vegetation types. As black-locust was coming to leaves, transects in black-locust patches became more shaded therefore, it may be turn to an ecological trap, since after the egg-laying period it became less suitable for larval development than in hummocks.

Changes in habitat quality during larval development were the result of both the growing shading of black-locust trees, and the proliferation of undergrowth, which could delay or inhibit the development of food plant and/or larvae. Lower temperatures might force the larvae to leave the hatching place because of either increasing mortality or decreasing growth rate. MEYER and SISK (2001) found that canopy cover is an important factor in mortality of eggs and larvae, since too much light can dry out eggs, while overshading may reduce food plant vigour. Our results showed that the height of food plants positively affected both presence and density of larvae. This emphasizes the importance of a sufficient amount of food plant to avoid defoliation and larval starvation (DENNIS 1996).

The traditional food plant based definition of habitat patch would fail in the case of the southern festoon in the study area. Though food plants itself were available in the study site in large quantity, however, the suitability of food plant patches was different in the four habitat types. The poplar plantation seems to be the poorest habitat for this species; each of the three studied life stages was less numerous there. At first sight suitable food plant patches of the poplar habitat were not used by the butterflies and therefore can be regarded as low quality habitats or even an ecological trap (ROBERTSON *et al.* 2013), as its quality is decreasing during the butterfly's life-cycle. Defining the habitat based on all the necessary resources (DENNIS *et al.* 2006, VANREUSEL *et*

al. 2007) would lead to more precise habitat maps, in contrast to those based merely on food plant distribution.

This study showed the importance of within-patch habitat quality, as the different life stages of this butterfly were revealed to have different habitat requirements, a result that is in concordance with other studies (Thomas 1991, Ellis 2003, Dover & Rowlingson 2005). We did not investigate the effects of size or isolation of habitat patches in this study area, which is relatively large and easily penetrable for the southern festoon. In our study we could point out the importance of habitat quality on the fine scale distribution of *Z. polyxena* and proving that within-site variation in habitat quality is very relevant to site occupancy of this species, as in the case of *Melitaea cinxia* (Thomas *et al*. 2001), *Polyommatus bellargus* (Thomas *et al*. 2001), *Thymelicus acteon* (Thomas 1983, Thomas *et al*. 2001) and *Speyeria nokomis* (Fleishman 2002).

Since the importance of human-dominated habitats is increasing due to the decline of natural habitats and decrease of natural disturbance (Robertson *et al*. 1995), the state of these plantation complexes can strongly affect the survival and reproduction of southern festoon and can offer alternative habitats for them, similarly to other insect species living in riparian forests (Allegro & Sciaky 2003). Human created habitats, like plantations can also act as ecological trap for butterflies (Robertson *et al*. 2013), therefore study on real habitat requirements of all the life stages is necessary to facilitate long-term survival of protected butterfly species.

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