Original article

Patch occupancy, number of individuals and population density of the Marbled White in a changing agricultural landscape

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ABSTRACT

Metapopulation theory predicts the occurrence of animals in habitat patches. In this paper, we tested predictions based on this theory, including effects of spatial autocorrelation, to describe factors affecting the presence, local number of individuals and density of the Marbled White butterfly *Melanargia galathea* in habitat patches spread across the agricultural landscape of southern Poland. This agricultural landscape has undergone significant changes in recent decades due to the country's political transformation and is currently characterized by a large proportion of fallow (abandoned) land. We compared 48 occupied habitat patches with 60 unoccupied ones. Positive spatial autocorrelation was found in the number and density of individuals in habitat patches. The probability of patch occupancy was higher for patches that were larger, had a higher proportion of edges, were located closer to the nearest neighbouring local population and to the nearest piece of fallow, contained a smaller area of cut grass, and also had more nectar resources. The number of Marbled Whites in habitat patches was positively related to the patch area, the distance to the nearest fallow and the abundance of nectar resources, but was negatively related to the density of shrubs. The density of individuals was positively related to abundance of flowers, proportion of edge in a patch and distance to the nearest fallow, but it was negatively related to patch area, vegetation height and grass cover. These results indicate that recent land-use changes in agricultural landscapes have had both positive and negative effects on the presence and local number of individuals and density of the Marbled White. These changes affect the metapopulation of the species through changes in habitat quality and landscape connectivity in the area surrounding habitat patches.

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1. Introduction

Metapopulation theory (Levins, 1969) helps to predict local population dynamics in habitat fragments and is useful in many areas of nature conservation (Yuttham et al., 2003). According to this theory, the size of habitat patches and the distance between them are important predictors of patch occupancy for a variety of species that occur unevenly in a landscape (e.g. Hill et al., 1996; Hokit et al., 1999). The dynamics of metapopulations in real landscapes have mostly been modelled using only these two variables on the presence/absence of a species in habitat patches (Hanski, 1994; Hanski et al., 1995; Hokit et al., 2001). The area of a patch is an indication of local population size – the number of individuals inhabiting that patch and their density. Small patches are less likely to be occupied because small local populations have a higher

probability of extinction than large populations occupying larger patches (Hanski, 1994; Hanski et al., 1995). The distance between patches is considered an index of the isolation of the patch. Isolated patches may be unoccupied because the colonization of empty patches and the demographic rescue of isolated local populations is limited. However, the probability of occupancy may be influenced by factors other than distance between patches and patch sizes (Sjögren-Gulve and Ray, 1996). One of these may be habitat quality (Thomas et al., 2001). High-quality patches may support more abundant and denser local populations and, therefore, their risk of extinction may be lower. In metapopulation studies of phytophagous arthropods it is tacitly assumed that habitat is largely synonymous with hostplant areas or with a single vegetation unit comprising hostplants; structural components are usually ignored (Dennis and Sparks, 2006). To fully understand metapopulation dynamics of the target species one has to identify habitat patches incorporating a resource-based definition (Dennis and Eales, 1997; Dennis et al., 2003, 2006). In this concept, a habitat patch is an area that may affect local populations at different times under different

conditions (Dennis and Sparks, 2006; Dennis et al., 2006). For this reason to identify habitat quality (and what a habitat patch is) one has to measure several resources and structural components that possibly affect the biology of the target species.

Only recently was it also found empirically that metapopulation dynamics may be affected by spatial autocorrelation (González-Megías et al., 2005). This means that measurements (occupancy, density, etc.) taken from nearby locations are often more similar than measurements taken from more widely separated locations (Beale et al., 2010).

Insects occupying semi-natural habitat patches spread across the agricultural landscape often fit into a metapopulation process. Insects which occur in the remnants of such habitats are also some of the most endangered species in Europe (Warren et al., 2001; Thomas et al., 2004), thus the knowledge about the factors affecting patch occupancy, number of individuals and their density may be important for the conservation of these species. A large number of insect species are dependent on unimproved grasslands or specific management schemes, thus the quality of these habitat fragments and the amount of resources therein may be of crucial importance to the persistence of populations of various species (e.g. Erhardt and Thomas, 1991; Sawchik et al., 2003). For example, grazing intensity affects vegetation height and microclimate which are important habitat quality factors for many grassland species (Thomas et al., 2001; Krauss et al., 2004). Many agricultural landscapes in central and eastern Europe have become more extensively managed since the beginning of the 1990s due to the region's political transformation (Lipsky et al., 1999; Van Swaay and Warren, 1999; Van Swaay, 2002). This has led to a less intensive pattern of land use or to total abandonment.

These changes may have important effects on the distribution and local number of individuals of species inhabiting agricultural landscapes. The effects of land abandonment may be positive as fallow may create new habitats (Balmer and Erhardt, 2000; Orłowski, 2005; Skórka et al., 2007; Skórka and Lenda, 2010) and could act as ecological corridors enabling the exchange of individuals among habitat patches. On the other hand, some specialist species occurring in open landscapes or dependent on specific management schemes may suffer from habitat loss or habitat deterioration due to this abandonment (Cremene et al., 2005).

Here, we tested a set of predictions from metapopulation theory using the Marbled White butterfly *Melanargia galathea*, which inhabits a changing agricultural landscape, to describe factors (adjusted for spatial autocorrelation) affecting the species' presence/absence, local number of individuals and density in habitat patches. We predicted that larger and less isolated patches should have a higher probability of occupancy than smaller and more isolated patches. Migration rate may be modified by the shape of the patch (Collinge and Palmer, 2002; Pfenning et al., 2004), thus in more irregular patches the ratio of edge to core area increases and the number of encounters of individuals with habitat boundaries increases as well. Consequently emigration rate should increase, leading to lower occupancy, number of individuals and density in the more irregular habitat patches. Furthermore, from the concept of ecological corridors and barriers (Turner et al., 2001; Hilty et al., 2006), we expected that fallow and watercourses may act as ecological corridors for the studied species and thus occupied habitat patches should be closer to these landscape elements, and local number of individuals and density should be higher there also. On the other hand, forests and human settlements may act as ecological barriers (Roland et al., 2000; Sutcliffe et al., 2002) thus they should negatively affect patch occupancy, local number of individuals and density. From the resource-based concept and knowledge on biology of the studied species we predicted that higher quality habitat patches (with higher abundance of flowers

and grass cover, taller vegetation height and lower density of shrubs) should have a higher occupancy probability than empty habitat patches. Accordingly, habitat patches of higher quality should be inhabited by a larger number of individuals and their density should be higher. Since the meadows differed in management intensity we predicted that mowing may be similar to local catastrophes (Aviron et al., 2007) leading to a temporary decrease of nectar sources and larval food plant availability. Therefore, the larger the proportion of the patch area that is regularly mown the lower the patch occupancy, number of individuals and their local densities should be.

2. Methods

2.1. Study species

The Marbled White is a typical insect of semi-natural habitats in the agricultural landscape. It is a large butterfly that can be found on various types of meadows that are rich in flowers (see Appendix A in the electronic Supplementary material). The adult flying period lasts from the final ten days of June to early August. The peak of the flying period is between July 10 and July 31. Larvae feed on various grass species, mainly Red Fescue *Festuca rubra*, Sheep's-fescue *Festuca ovina*, Tor-grass *Brachypodium pinnatum* and Yorkshire-fog *Holcus lanatus*. It is thought that several other grasses may be used, but the full range is not yet known. Adult butterflies often visit red-coloured flowers, especially *Centaurea* spp and *Cirsium* spp (Buszko and Masłowski, 2008; see Appendix A in the electronic Supplementary material).

2.2. Study area

The study area (179 km^2) was located east of the city of Tarnów (approx. 120,000 inhabitants), in south-eastern Poland (49° 59′–50° 06′ N, 20° 58′–21° 10′ E) (Fig. 1). The agricultural landscape is dominated by cereal crops (mostly wheat), which cover 30% of the study area; root crops (mostly potatoes and beet), cover 15%; grasslands cover 11%; fallow covers 19%; forests cover 14%; and human settlements cover 10%. Other habitats cover 1% of the study area. Land use is extensive. Most of the farms in the area are small: 82% of the farms are below 5 ha, 16% are 5–10 ha, and only 2% are larger than 10 ha. The average density of human population is 135 people/km^2.

In 2008 we surveyed all potential habitat patches (108 patches with a total area of 531 ha) of this species within the study area
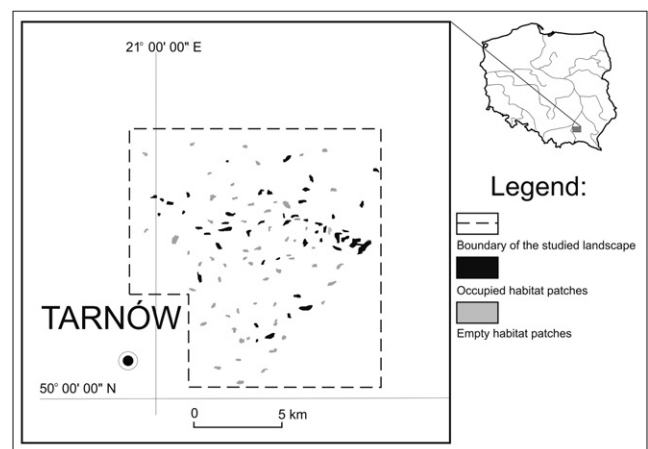

Fig. 1. Map of the study area (habitat patches enlarged for better visibility).

(Fig. 1). In this study, the potential habitat patches for the Marbled White were meadows with larval food plants and preferred nectar sources (*Centaurea* spp and *Cirsium* spp) (see Appendix A in the electronic Supplementary material).

2.3. Occupancy and abundance surveys

We searched for the presence of the Marbled White in all habitat patches in 2008. We were aware of all local populations of the Marbled White, as well as potential habitat patches due to our intensive surveys in the area in the years 2004–2007.

In all potentially suitable habitat patches for the Marbled White we established a 5 m-wide transect, where the presence, number of individuals and density of the species were noted. The length of the transect was proportional to the patch area ($r = 0.904$, $P < 0.001$) and varied between 20 m and 1960 m (mean $\pm$ SE: 413.5 ± 53.6 m). Two counts were performed between the 5th and 25th of July in each potential habitat patch. The patch was considered occupied when at least one individual was noted. Butterflies were surveyed between 10 a.m. and 4 p.m. during favourable weather conditions (maximum wind: 3 on the Beaufort scale, cloud cover up to 25%, temperature at least 20°C). The speed of the transect walk was approximately 200 m per 10 min. The order in which the potential habitat patches were checked was random. The index of local population size was estimated as the sum of individuals noted within transects during the two surveys and the density of individuals was calculated as the number of butterflies per hectare.

2.4. Patch characteristics

The following variables were measured for each patch:

1. Patch size (ha);
2. The index of the amount of edge taken as the ratio of patch perimeter to the perimeter of a circle of the same area. The formula for this index is $E = Pp/Pc$, where E is the index, Pp is the total length of the patch perimeter and Pc is the perimeter of a circle of the same area. Thus, in the case of circular patches, the index is one. The more irregular the habitat patch the higher the index is;
3. Distance to the nearest habitat patch (regardless of occupancy) (m);
4. Distance to the nearest occupied habitat patch (m);
5. Distance to the nearest permanent grassland (m). This variable represents any grassland regardless of its suitability for the Marbled White;
6. Distance to the nearest fallow (m);
7. Distance to the nearest watercourse (m) which may act as dispersal corridors for insects (Herzon and Helenius, 2008);
8. Percentage cover of forest within a distance of 500 m from the patch boundary;
9. Distance to the nearest building (m);
10. Proportion of the patch area where grass had been cut. The frequency of cutting grass, if it occurred, was 2–3 times per year. This is an index of habitat disturbance because cutting frequently occurred during the butterfly flight period;
11. Abundance of flowering plants as nectar sources for adult butterflies. 5–10 circular quadrats of 1 m diameter (0.79 m^2) were randomly recorded in each butterfly transect. The richness of plant species and flower abundance were estimated within these plots in the middle of July. We summed results across plant species to calculate the mean number of flowers/inflorescences per quadrat within the habitat patch (Skórka et al., 2007). The number of plant species was highly correlated with the number of inflorescences ($r = 0.836$, $P < 0.001$, $n = 108$) but the latter variable led to a slightly higher

proportion of variance explained in statistical models and was thus used in the analyses;
12. Ground cover (%) of grasses. Ground cover was estimated (to the nearest 10%) as the proportion of ground covered within the above quadrats;
13. Shrub density (individuals per ha). Shrubs were counted within the butterfly transects;
14. Mean height of vegetation (cm). 10 random measurements of the herbaceous layer per quadrat averaged across quadrats (see: Skórka et al., 2007).

The variables 1–2 describe patch geometry, variables 3–7 include characteristics potentially enhancing dispersal among habitat patches, variable 8 indicates a potential barrier for dispersal, variable 9 is a measure of anthropopressure, and the variables 10–14 describe habitat quality in the patch.

Patch characteristics 1–10 were calculated with ESRI Arcview GIS or directly in the field with the use of a GPS (Garmin GPSmap 60CSx). Variables 3–7 and 9 were measured as border to border distances.

2.5. Statistical analysis

The first analytical goal was to describe spatial aggregation in the patch occupancy, number of individuals and density of the species by means of Moran's *I* correlograms. A correlogram is a graph in which spatial autocorrelation values of a given parameter are plotted on the ordinate against distance classes among sampling points (Legendre, 1993; Legendre and Legendre, 1998). The spatial autocorrelation value at a given distance class indicates how predictable (positively or negatively) the measured variable (patch occupancy, number of individuals or density) is at a given point of the sampling framework. Autocorrelation Moran's index typically varies between -1 and $+1$, with non-significant values close to zero.

Taking into account our sampling design, we considered 12 distance classes chosen so that the number of meadow pairs was equal in each interval. We also manipulated the distance classes and intervals in various ways, changing the distance from 0.5 km to 10 km as well as altering the number of intervals but this had no impact on the final results. To test significance of the autocorrelation we estimated *P*-values based on 500 Monte Carlo simulations.

Spatial autocorrelation was calculated for both response variables and independent variables. This was done to check if the autocorrelation in dependent variables resulted from environmental gradients or from "internal" processes within local populations (e.g. dispersal).

We used autologistic regression to analyse factors influencing patch occupancy (Dormann, 2007). In the autologistic model spatial autocorrelation is taken into account by adding an autocovariate given by $Y = \rho WY$, in which W is the spatial relationship matrix, Y is the 0–1 vector and ρ is the autoregressive parameter. This is close to the standard autoregressive term in logistic regression (Segurado et al., 2006; Dormann, 2007), but the distance is defined in a continuous way, instead of using a neighbouring approach.

To analyse factors affecting the number of individuals and their density in the habitat patches we used simultaneous autoregression (SAR) which takes autocorrelation into account by changing the estimator of the vector of slopes using a generalized least-squares (GLS) (e.g. Selmi and Boulinier, 2001; Hawkins and Diniz-Filho, 2002). The general formulation for these models is $Y = \beta X + U$, and $U = \rho WY + \varepsilon$, where Y is a response variable, X the explanatory variable, β (beta) the function slope, ρ the autoregression parameter, W the matrix that contains neighbour weights indicating the relationships among spatial units, and ε is an error. Thus, SAR autocorrelation is incorporated into the model residual structure directly by the GLS approach, so space is taken into

account together with other predictor variables. Regression analysis is sensitive to the presence of outliers that frequently occur in the case of skewed distributions. We used natural log transformation to reduce the effects of outlier observations (Quinn and Keough, 2002). Moreover, in all regression models, variables were standardized to allow for a direct comparison of beta estimates (larger betas indicate stronger relationships between explanatory and dependent variables).

Akaike's Information Criterion corrected for small sample size (AICc) was used to identify the most parsimonious model from each candidate set. The model building procedure was as follows. Firstly, we built the model that included all dependent variables. Then we removed sequentially each variable to see how removal changes the AICc. We dropped the variable whose removal caused the highest decrease of AICc. We repeated this procedure for every reduced model. In the best models, when dropping variables did not further decrease the AICc, we sequentially excluded variables that had the largest confidence intervals of betas. Finally, we ranked the models according to their △ AICc values and used the model with the lowest AICc together with associated weight values (probability that a given model is the best) as that best describing the data (Burnham and Anderson, 2002). We consider models with △ AICc < 2 as equally good and all are reported as supporting the data. We used model averaging for estimates (betas) of parameters of interest (Burnham and Anderson, 2002). We also examined standard errors and associated confidence intervals of the betas and we report them as significant if the 95% confidence intervals did not overlap with zero. Recent literature increasingly advocates the use of AIC values as a standard model selection procedure (Burnham and Anderson, 2002). Using information criteria to select amongst candidate models obviates problems associated with multiple testing in classical statistics (Burnham and Anderson, 2002).

We also checked if there were any significant correlations among explanatory variables. Modified Pearson correlation coefficients that take into account the pattern in spatial autocorrelation (Dutilleul, 1993) were calculated. In correlations we applied Bonferroni correction due to the numerous pairwise tests that were not checking the hypotheses. Correlations were used to check for multicollinearity, which may lead to biased estimates of parameters for the predictors in models (O'Brien, 2007). It is believed that regression models are robust to multicollinearity if the correlation between variables is lower than $r = 0.6$ (Mertler and Vannatta, 2002). In our data, correlation values among variables were low and usually did not exceed $r = |0.3|$ (Appendix B in the electronic Supplementary material). We noted two stronger correlations (between "distance to the nearest habitat patch" and "distance to the nearest occupied habitat patch", and between "distance to the nearest habitat patch" and "distance to the nearest permanent grassland") were significant after Bonferroni correction (Appendix B in the electronic Supplementary material). Although the models could run with the raw data we checked if the use of corrected variables changed the final results. We performed simple regression between "distance to the nearest habitat" and "distance to the nearest occupied habitat patch". The same was done for "distance to the nearest permanent grassland". The extracted residuals represented parts of the variance of "distance to the nearest occupied habitat patch" and "distance to the nearest permanent grassland" not explained by the "distance to the nearest habitat patch". In each case, the simple regressions were highly significant (the first $F_{1,107} = 12.818$; $P < 0.001$, the second $F_{1,107} = 19.452$; $P < 0.001$) and the residuals maintained a strong and positive correlation with the original variables ($r^2 = 0.88$ and $r^2 = 0.83$). The autologistic model and SAR models with raw data gave the same results as those with corrected data. Therefore, in the paper we only present analyses of models with raw data.

All analyses were run in the SAM statistical software (Rangel et al., 2006). All estimates of statistical parameters (means, betas) are quoted ± 1 SE.

3. Results

We did not find significant autocorrelation in patch occupancy in any distance classes (Fig. 2a). However, positive spatial autocorrelation was found in the number of individuals within 1–2 km of the given patch (Fig. 2b). For the density of individuals we found significant positive spatial autocorrelation in occupied patches located within 3 km and significant negative autocorrelation at distances higher than 8 km (Fig. 2c). We did not find any significant spatial autocorrelation for all environmental variables at any distance classes (results not shown).

Forty eight potential habitat patches out of 108 were occupied by the Marbled White (occupancy = 0.44). The characteristic of the occupied and empty habitat patches are given in Table 1.

AICc selection procedure led to three equally good autologistic models of patch occupancy (Table 2). The probability of the presence of Marbled White in habitat patches increased with patch area
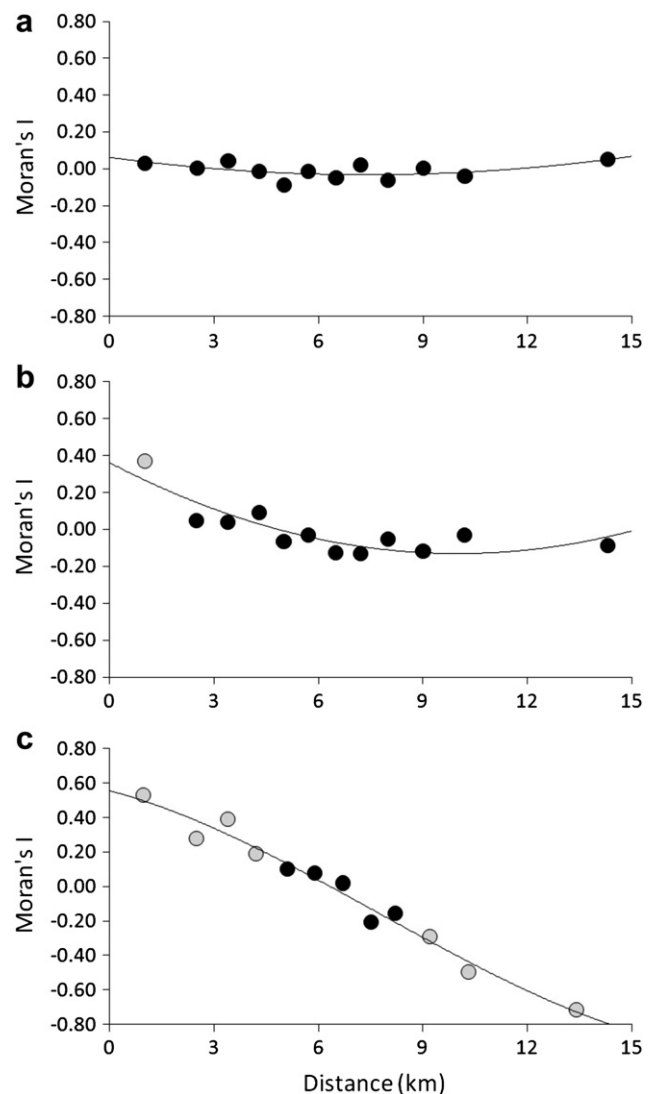

Fig. 2. Spatial autocorrelogram for (a) patch occupancy, (b) local number of individuals and (c) density of individuals. Grey circles indicate spatial autocorrelations significant at the level $\alpha < 0.05$.

Table 1
The characteristics of occupied ($N = 48$) and empty habitat patches ($N = 60$) of the Marbled White butterfly in the studied landscape. The asterix denotes the observations ln-transformed in the analyses of multivariate models.

Variables	Code	Occupied				Empty			
		Mean	SE	Min	Max	Mean	SE	Min	Max
Patch area (ha)*	area	8.1	0.8	1.2	33.1	2.6	0.3	0.3	10.2
Index of edge proportion in patch*	ratio	1.58	0.05	1.11	2.41	1.32	0.03	1.01	1.91
Distance to the nearest habitat patch (m)*	npatch	189	18	29	660	218	13	43	432
Distance to the nearest occupied habitat patch (m)*	npop	275	22	59	670	381	27	100	1096
Distance to the nearest permanent grassland (m)*	ngrass	104	7	29	249	125	9	29	345
Distance to the nearest fallow land (m)*	fallow	151	10	53	288	244	12	81	432
Distance to the nearest watercourse (m)	water	375	44	0	899	352	36	0	845
Cover of forest within a 500 m radius from patch edge (%)*	forest	17	2	1	71	13	2	0	70
Distance to the nearest building (m)	build	331	37	10	885	390	34	10	869
Cover of the area of cut grass in the patch (%)	mown	23	2	3	65	67	3	29	100
Index of flower abundance	flower	75	4	31	120	44	3	1	89
Ground cover of grasses (%)	grascov	80	2	60	100	83	1	60	100
Shrub density (shrubs per 1 ha)	shrub	24	3	0	63	28	2	0	68
Vegetation height (cm)	vegh	91	5	31	150	88	4	36	147

(beta $= 1.789 \pm 0.712$), flower abundance (beta $= 1.742 \pm 0.683$) and proportion of edge in a patch (beta $= 1.335 \pm 0.439$) but decreased in habitat patches more distant from fallow (beta $= -1.181 \pm 0.402$) as well as from other occupied patches (beta $= -0.199 \pm 0.097$) (Table 2). Occupancy was also lower in habitat patches with a greater mown area (beta $= -2.730 \pm 1.137$) (Table 2).

The number of individuals varied from 5 to 234 individuals (mean $= 36.4 \pm 1.3$). AICc identified three equally good SAR models (Table 3). The total number of individuals in habitat patches was positively related to patch area (beta $= 4.194 \pm 1.729$), distance to the nearest fallow (beta $= 2.314 \pm 1.105$) and abundance of nectar resources (beta $= 1.625 \pm 0.875$) but negatively related to the density of shrubs (beta $= -2.574 \pm 1.780$; Table 3).

The density of individuals varied from 0.8 to 50.7 individuals per hectare (mean $= 9.7 \pm 1.6$). We found four SAR models that had the highest support by AICc (Table 4). The density of butterflies was positively related to abundance of flowers (beta $= 6.087 \pm 1.531$), proportion of edge in a patch (beta $= 0.776 \pm 0.362$) and distance to the nearest fallow (beta $= 2.281 \pm 1.014$) but negatively related to patch area (beta $= -1.714 \pm 1.425$), vegetation height (beta $= -1.547 \pm 0.606$) and grass cover (beta $= -0.304 \pm 0.125$).

4. Discussion

4.1. Spatial synchrony in (meta)population dynamics

Spatial autocorrelation may affect metapopulation dynamics (González-Megías et al., 2005). In a biological sense spatial

autocorrelation may lead to spatial synchrony that refers to coincident changes in occupancy, number of individuals and their density (Liebhold et al., 2004).

In our study we found significant spatial autocorrelation for the number of individuals recorded in a patch and their density but not for patch occupancy. The latter is a surprising result as one might expect that if the local density and number of individuals are spatially autocorrelated the same should be true for patch occupancy. We speculate that such a result is possible only if patch occupancy is constant over time e.g. the same patches are occupied in different seasons. In such a situation individuals may exchange only between occupied patches and, therefore, the positive spatial autocorrelation for number of individuals and their density could occur. We believe the autocorrelation we found results from dispersal of individuals. Other possible explanations of the presence of spatial autocorrelation are (1) that population dynamics depend on environmental gradients in space and (2) trophic interactions with populations of other species that are themselves spatially autocorrelated (Liebhold et al., 2004). However, we did not find any significant spatial autocorrelation for analysed environmental factors and we were not aware of any specific interactions between the Marbled White and any other species whose population dynamics could be spatially autocorrelated.

Much more difficult to explain is the negative autocorrelation found for the density of individuals. Negative spatial autocorrelation is rarely found in field studies (Griffith, 2006). It is hard to imagine the biological mechanism hidden behind such a spatial

Table 2
Candidate autologistic models with factors affecting probability of patch occupancy by the Marbled White. The fit of the best model $r^2_{McFadden} = 0.53$. Models with Delta <2 are considered as equally good. Codes of the variables see: Table 1.

Model	AICc	Delta	Weight
b0, b1 (area + fallow + flower + mown)	48.511	0.000	0.392
b0, b1 (area + fallow + flower + mown+ratio)	49.669	1.158	0.220
b0, b1 (area + fallow + flower + mown + npop + ratio)	49.731	1.220	0.213
b0, b1 (area + fallow + flower + grascov + mown + npop+ratio)	52.086	3.575	0.066
b0, b1 (area + fallow + flower + grascov + mown + npop+ratio + shrub)	53.820	5.309	0.028
b0, b1 (area + fallow + flower + grascov + mown + npatch+npop + ratio + shrub + vegh)	54.252	5.741	0.022
b0, b1 (area + fallow + flower + grascov + mown + npop+ratio + shrub + vegh)	54.263	5.752	0.022
b0, b1 (area + fallow + flower + grascov + mown + ngrass+npatch + npop + ratio + shrub+vegh)	54.844	6.333	0.017
b0, b1 (area + fallow + flower + grascov + mown + ngrass+npatch + npop + ratio + shrub + vegh + water)	56.381	7.870	0.008
b0, b1 (area + build + fallow + flower + grascov + mown+ngrass + npatch + npop + ratio + shrub + vegh+water)	57.202	8.691	0.005
b0, b1 (area + build + fallow + flower + gold + grascov+mown + ngrass + npatch + npop + ratio + shrub+vegh + water)	57.203	8.692	0.005
b0, b1 (fallow + flower + mown)	58.967	10.456	0.002
b0, b1 (area + build + fallow + flower + forest + gold+grascov + mown + npatch + npop + ngrass + ratio+shrub + vegh + water)	59.149	10.638	0.002
b0, b1 (fallow + mown)	64.318	15.807	0.000
b0, b1 (fallow)	119.145	70.634	0.000

Table 3
Candidate simultaneous autoregressive models with factors affecting number of individuals of the Marbled White in habitat patches. The fit of the best model $r^2 = 0.46$. Models with Delta <2 are considered as equally good. Codes of the variables see: Table 1.

Model	AIC	Delta	Weight
b0, b1 (area + flower)	473.491	0.000	0.440
b0, b1 (area + flower + shrub)	474.544	1.053	0.260
b0, b1 (area + fallow + flower + shrub)	475.363	1.872	0.173
b0, b1 (area + fallow + flower + mown+shrub)	476.387	2.896	0.103
b0, b1 (area + fallow + flower + mown + ngrass + shrub)	480.704	7.213	0.012
b0, b1 (area)	482.677	9.186	0.004
b0, b1 (area + build + fallow + flower + mown + ngrass+shrub)	483.188	9.697	0.003
b0, b1 (area + build + fallow + flower + mown + ngrass+shrub + water)	483.578	10.087	0.003
b0, b1 (area + build + fallow + flower + mown + ngrass+npatch + shrub + water)	485.780	12.289	0.001
b0, b1 (area + build + fallow + flower + forest + mown+ngrass + npatch + shrub + water)	488.727	15.236	0.000
b0, b1 (area + build + fallow + flower + forest + mown+ngrass + npatch + ratio + shrub+water)	492.835	19.344	0.000
b0, b1 (area + build + fallow + flower + forest + mown+ngrass + npatch + ratio + shrub + vegh + water)	496.787	23.296	0.000
b0, b1 (area + build + fallow + flower + forest + gold+mown + ngrass + npatch + ratio + shrub + vegh+water)	501.208	27.717	0.000
b0, b1 (area + build + fallow + flower + forest + gold+grasscov + mown + ngrass + npatch + ratio + shrub+vegh + water)	505.901	32.410	0.000
b0, b1 (area + build + fallow + flower + forest + gold+grasscov + mown + ngrass + npatch + npop + ratio+shrub + vegh + water)	511.105	37.614	0.000

pattern. Other authors chose not even to interpret negative spatial autocorrelation or to ignore it (Kerr et al., 2000; Kerr, 2001).

4.2. Effect of patch geometry on local populations of the Marbled White

Recent research on metapopulations among insects living in agricultural landscapes has demonstrated that habitat patch occupancy is often related to the size and isolation of patches (e.g. *Euphydryas editha*, Harrison, 1991; *Melitaea cinxia*, Hanski et al., 1995; *Hesperia comma*, Hill et al., 1996; *Lycaena helle*, Bauerfeind et al., 2009). Patch area and distance to the nearest neighbouring population also helped in predicting the presence/absence of the Marbled White in our study. Patch area was also significant in determining the number and density of butterflies. This relationship may predict local extinction in the patch network: small local populations are more susceptible to demographic extinction, and small resource areas to environmental stochasticity (Hanski, 1998). We found that density was lower in larger patches which is a pattern quite often found (Hambäck and Englund, 2005). These authors postulated that such a pattern is due to asymmetric dispersal between large and small patches. The predominant effect of dispersal on local densities may be confirmed by the spatial autocorrelation found in our study, given that dispersal is obviously distance-dependent.

Interpreting a negative density–area relationship as well as the positive impact of patch area on the number of individuals one might ask if saving several small patches is a better conservation solution for butterflies than a single large one. Although the density of individuals is higher in smaller patches as we demonstrated – smaller patches are probably more likely to occasionally lose their populations.

Moreover, *per capita* number of individuals in the habitat patch is sometimes more important for some reasons. Patch area is important in shaping the relationship between the number and density of individuals and we think that looking only at the density may sometimes be misleading. Thus, large meadows supporting larger populations seem to be most suitable habitats for the studied species from a conservation point of view.

In our study landscape, occupied patches also had a higher proportion of edges than empty ones. Most metapopulation models ignore patch shape, but simulation study and some empirical data suggest that patches that are more irregular may differ in migration rates (Pfenning et al., 2004; Levey et al., 2008). Our study meadows with the Marbled White had complex shapes and they possibly act as a net that enables the successful immigration of the butterflies which disperse outside habitat patches. Otherwise, we think that in our study system patch shape had a neutral or negative effect on emigration rate since the local number of individuals was independent of shape but the density of individuals was higher in more irregular patches. This requires further investigation as this interesting effect was also found in other species e.g. *Maculinea* butterflies (Nowicki et al., 2007). A possible explanation of this pattern is that once the dispersing Marbled White butterfly reaches

Table 4
Candidate simultaneous autoregressive models with factors affecting density of the Marbled White butterflies in habitat patches. The fit of the best model $r^2 = 0.37$. Models with Delta <2 are considered as equally good. Codes of the variables see: Table 1.

Model	AICc	Delta	Weight
b0, b1 (area + fallow + flower + ratio)	339.283	0.000	0.288
b0, b1 (area + fallow + flower + grascov+ratio)	339.315	0.032	0.283
b0, b1 (area + fallow + flower + grascov + ratio + vegh)	340.064	0.781	0.195
b0, b1 (area + flower + ratio)	340.763	1.480	0.137
b0, b1 (area + fallow + flower + grascov + river + ratio+vegh)	342.374	3.091	0.061
b0, b1 (area + flower)	344.303	5.020	0.023
b0, b1 (area + fallow + flower + grascov + npop + ratio+vegh + water)	346.003	6.720	0.010
b0, b1 (area + fallow + flower + grascov + mown + npop+ratio + vegh + water)	349.848	10.565	0.001
b0, b1 (area + fallow + flower + grascov + mown + npop+ratio + shrub + vegh + water)	351.166	11.883	0.001
b0, b1 (area + build + fallow + flower + grascov + mown+npop + ratio + shrub + vegh+water)	353.857	14.574	0.000
b0, b1 (area)	355.712	16.429	0.000
b0, b1 (area + build + fallow + flower + grascov + mown+ngrass + npop + ratio + shrub + vegh + water)	358.474	19.191	0.000
b0, b1 (area + build + fallow + flower + gold + grascov+mown + ngrass + npop + ratio + shrub + vegh+water)	364.971	25.688	0.000
b0, b1 (area + build + fallow + flower + forest + gold+grascov + mown + ngrass + npop + ratio + shrub+vegh + water)	369.836	30.553	0.000
b0, b1 (area + build + fallow + flower + forest + gold+grascov + mown + ngrass + npatch + npop + ratio+shrub + vegh + water)	373.005	33.722	0.000

a patch it probably remains there. The studied species, when it is in the habitat patch, responds negatively to habitat boundaries and avoids them (unpublished observations). Avoidance of habitat patch boundaries was found in several species and it also seems to have positive effects on the population density of some butterflies (e.g. Kuussaari et al., 1996; Schtickzelle and Baguette, 2003; Conradt and Roper, 2006).

4.3. Effect of land-use changes on the isolation of habitat patches

Distance to the nearest occupied patch was larger in empty patches than in occupied ones. This pattern of occurrence for the Marbled White is also similar to other butterfly species (Thomas and Harrison, 1992; Hanski et al., 1995; Thomas and Hanski, 1997; Bergman and Landin, 2001). However, our results also clearly indicate that recent changes in land use have important consequences for metapopulation processes and act mostly through modifications of habitat connectivity at the landscape scale. Proximity of fallow had positive effects on patch occupancy but negative effects on the local number of individuals and their densities. This indicates that abandoned fields may act as dispersal corridors for this species. Fallow may also be a habitat for the Marbled White, however we did not find any local populations occupying abandoned fields. This may be because of low grass cover in abandoned arable fields (larval food plants) and the swift invasion of alien goldenrods that overgrow most other plants, including nectar sources (Moroń et al., 2009). Therefore, due to their low quality, fallow may be a poor habitat for the Marbled White to reproduce. As this species can feed on several flowering plants another possibility is that fallow may be viewed as nectar sites, which reduce the population density in nearby meadow patches. However, from our field experience and data gathered on flora composition in fallow we believe it is not an important source of nectar for this species. Richness of flowers in the meadows occupied by Marbled White were higher than in fallow where invasive alien goldenrods often predominate (Skórka and Lenda, 2010). Moreover, goldenrods bloom mostly in August and this only slightly overlaps with the Marbled White flight period, therefore butterflies may use this plant as a nectar resource mostly at the end of the flight period. However, this does not change the possibility that fallow may enhance dispersal because low quality ecological corridors may promote animal movement, and increase gene flow among populations in fragmented landscapes (Haddad and Tewksbury, 2005).

We did not find significant effects on the occupancy and local number of individuals of the distance to nearest potential habitat patches that may be a result of the predominance of fallow in the studied landscape. Similarly, the proximity of habitats possibly acting as ecological corridors between various grasslands and watercourses did not affect the presence, number of individuals and the density of Marbled White in the agricultural landscape. In other studies, numbers of insect populations in agricultural landscapes were positively affected by the presence of permanent grasslands as well as watercourses in the vicinity (e.g. Öckinger and Smith, 2006; Diekötter et al., 2008). It is possible that in such a diverse landscape fallow may be a more effective corridor than any other habitat type because of its predominance in the landscape (Skórka and Lenda, 2010). However, this requires further testing.

4.4. Effect of land use on the quality of the butterfly habitat

Changes in land use in the agricultural landscape also had significant effects on habitat patch quality. In the landscape surrounding habitat patches these changes mostly had positive consequences for local populations of the Marbled White. Within the habitat patches, however, the changes were both positive and detrimental. Firstly, where there had been a cessation of farmland management, grass in larger parts of the habitat patches occupied by the Marbled White remained uncut, which seemed to have positive effects on patch occupancy. In our study area, habitat patches were of heterogeneous quality. This was because different parts of the meadows had various owners; some of them cut the grass on their land, others left the area unmanaged or cut the grass occasionally in some years (see Appendix A in the electronic Supplementary material). The frequent cutting of grass is probably analogous to the catastrophes that may lead to local extinctions (Aviron et al., 2007). In the case of the studied butterfly, the frequent cutting of grass may remove larval food resources as well as directly kill larvae. Thus, the cessation of farmland management may be positive (at least in the early years; see Skórka et al., 2007).

However, later, the arrival and spread of shrubs may lead to substantial habitat deterioration (see: Erhardt, 1985). Some parts of the habitat patches that were not managed for several years became overgrown with shrubs (mostly Hawthorn *Crataegus* spp. and young birches *Betula* spp.). The high density of shrubs had negative effects on the local number of butterflies. Dense shrubs could simply swamp areas frequented by butterflies but could also result in a higher predation rate. Shrubs are nest or perching sites for many birds that hunt adult butterflies and their larvae (Gardner and Thompson, 1998; Tremblay et al., 2001). Indeed, the density of small insectivorous birds is often positively related to shrub density in meadows (Laiolo et al., 2004; Skórka and Lenda, 2010). Thus, a high predation rate may also be responsible for the lower number of individuals of the studied species in shrubby meadows.

The density of nectar sources positively affected the presence, number and density of individuals of the species in the studied meadows. When studying the Glanville Fritillary butterfly *M. cinxia* in Finland, Moilanen and Hanski (1998) found that immigration was increased and emigration reduced in patches containing high densities of flowers. This indicates that additional resources help support larger populations and/or enhance population persistence (Sutcliffe et al., 1997a,b). Thus, the quality of a patch can, to some extent, acts as a substitute for patch area (Hanski and Ovaskainen, 2000) and enhances the predictive power of metapopulation models (Thomas et al., 2001). This has important practical implications. Planting wild flowers, especially those favoured by the studied butterfly, may greatly enhance the persistence of local populations, especially in small meadows.

Vegetation height negatively affected density of the Marbled White. This may be explained by tall vegetation preventing flight among flowers. If the vegetation is very tall not every flower is available as nectar sources for butterflies because some plant species overgrow others. Other studies also indicate that vegetation height may be a key factor affecting density of individuals (Reeder et al., 2005; Skórka et al., 2007).

The finding that grass cover negatively affects butterfly density is somewhat surprising. Various grass species are larval food plants for this butterfly thus the opposite effect was expected. Bearing in mind that grass cover was relatively high (Table 1) it is probable this resource is in excess for butterflies even when their cover is low. When grass cover is high it may limit access to nectar resources for the butterflies in a similar way as tall vegetation does and it may explain the observed relationship.

In butterfly studies, food plants have usually been considered the major limiting resource for most species and the area containing food plants was regarded as a habitat patch. Only recently has more attention been given to other important resources leading to the development of the resource-based concept of butterfly habitats (Dennis and Sparks, 2006; Dennis et al., 2006). Our

findings strongly support this concept, showing that habitat quality is determined by factors other than just food plant availability. The novelty of our study is that we have shown that different components of habitat quality may affect local populations in complicated ways with some factors affecting only the density of individuals (grass cover, vegetation height) or the number of individuals (density of shrubs) while others (nectar resources) may affect patch occupancy, number of individuals and their density. We believe that the resource-based concept of butterfly habitat may be a useful framework especially in conservation biology and may be developed by adding structural complexity of the habitat because our results clearly show that management regime and structure of the vegetation may be regarded as an additional demand (resource) influencing local populations. Our results support other findings (e.g. Fred et al., 2006; Nowicki et al., 2007) that various measures of habitat quality should be incorporated in metapopulation models to improve their predictive power because, as we have shown, the effect of habitat quality be as important as patch area.

4.5. Barriers and anthropopressure do not affect the butterfly occurrence and abundance

Our analysis showed that the proximity of forests had no negative effects on the occupancy of habitat patches by Marbled White. One might expect the opposite result, as forests are inevitably barriers for grassland butterflies (e.g. Roland et al., 2000). On the other hand, it is easy to imagine that forests may create specific microclimatic conditions favoured by butterflies. They may protect them from the wind, and enable butterfly activity even during windy days. Indeed, we noted that in meadows located in forested areas, various species of butterflies are active (frequent flights) on windy days when in the open landscape butterfly activity is low (unpublished data). Moreover, the edges of forests are often rich in flowers, thus they could even be sources of individuals for grassland habitat patches in the neighbourhood (unpublished data; see also: Kujawa, 1997; Öckinger and Smith, 2007). Therefore, the possible negative effects of forest presence in proximity to habitat patches may be counter-balanced by their positive effects. However, this requires further experimental and behavioural investigation.

The proximity of human settlements did not affect local populations of the Marbled White. This indicates that this species and its habitats are resistant to increased human activity near villages or human disturbance is too low to have negative effects. The results of other studies are equivocal. Some studies did not find any effect of anthropopressure on butterfly populations (e.g. Collinge et al., 2003; Nowicki et al., 2007), while others found an effect, mostly at low spatial scales (Kitahara and Fujii, 1994; Clark et al., 2007).

4.6. Management recommendations

Our study provides guidelines on how to manage meadows for the Marbled White butterfly. A large area of fallow increases connectivity. In other landscapes where agriculture is more intensive, connectivity among grasslands may be achieved by setting aside fields. Meadows with this species should be extensively managed. The frequency of cutting grass should be low, carried out in the late summer or early in spring once a year and plants should be cut at a height of at least 15 cm to enable the development of larvae and pupae. Alternatively, parts of the meadow should be left unmanaged for several years as they could be breeding places for the butterfly (see Cremene et al., 2005). It is recommended to plant favourable nectar sources within habitat patches (Kardol et al., 2008). This could increase population density and probably

decrease emigration from the patch. Nectar sources for the Marbled White are also frequently used by other pollinators, thus these plants could act as flowering hotspots attracting other insects (Maccherini et al., 2009). The abandonment of land, although favourable for this species at the beginning leads to the expansion of shrubs adversely affecting local populations of the studied species. Shrubs should be removed from the meadows and, as stated earlier, low-intensive cutting of grass should prevent their succession.

5. Conclusions

Recent changes in land use in south-eastern Poland have modified the suitability of the agricultural landscape for species inhabiting semi-natural habitat patches. Our study shows that these changes have had significant effects on metapopulation processes and local population dynamics but the effects have acted in the opposite direction as far as meta(population) persistence is concerned. The large number of former arable fields increased habitat connectivity at the landscape scale, which may be positive to habitat occupancy, but at the habitat patch level may lead to a lower local number and density of individuals. Further studies should focus on modelling and solving which factors are the most important for population persistence of the studied species.

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Appendix. Supplementary material

Supplementary material associated with this paper can be found, in the online version, at doi:10.1016/j.actao.2010.07.002

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