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The importance of the gravel excavation industry for the conservation of grassland butterflies

Magdalena Lenda [a,*], Piotr Skórka [b], Dawid Moroń [c], Zuzanna M. Rosin [d], Piotr Tryjanowski [e]

[a] Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31-120 Kraków, Poland
[b] Institute of Environmental Sciences, Jagiellonian University, Gronostajowa 7, 30-387 Kraków, Poland
[c] Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland
[d] Department of Cell Biology, Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland
[e] Institute of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71 C, 60-625 Poznań, Poland

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ABSTRACT

Conservation biology often relies on the protection of (semi)natural habitat remnants. However, the ever increasing human population is taking over natural resources and habitats. Here, contrary to most other studies, we ask how human-associated severe changes in the environment can be used to enrich local biodiversity. We tested if industrial activity (gravel excavation) leads to the creation of habitats that support grassland butterflies and how these areas add to the richness of local species when compared to typical semi-natural habitats (grasslands). We also identified key factors affecting the richness, abundance, diversity and commonness of butterfly species to provide practical recommendations. Species richness, diversity index and the occurrence of rare species were higher in gravel-pit shores than in grasslands. The richness of butterfly species and their abundance were positively affected by the richness of plant species, shrub density and age of the gravel-pit but negatively by the cover of water reservoirs in the surrounding area and the isolation of gravel-pits from grasslands. Butterfly diversity was positively influenced by the richness of plant species and proximity of human settlement but negatively by area of the shore and isolation. Our study is the first one to show the high value of gravel-pits for the conservation of butterflies. We recommend the inclusion of gravel-pits in a system of ecological networks and management of their surroundings to improve the colonization rate of rare species. We suggests that directing interest to the possible positive effects of industrial development on biodiversity may support conservation efforts.

1. Introduction

Populations of many insects across Europe have declined rapidly (Thomas et al., 2004; Biesmeijer et al., 2006; Warren and Bourn, 2011). Many factors are responsible for this phenomenon, especially the intensification of agriculture (Van Swaay et al., 2010; Dover et al., 2011), habitat fragmentation (Van Swaay et al., 2010), urbanization (Clark et al., 2007), pollution (Mulder et al., 2005), invasive alien species (Moroń et al., 2009) and climate change (Settele et al., 2008). Great effort has been made to work out the specific actions and programs to stop this dramatic loss of species diversity with the emphasis put on the conservation of remaining (semi)natural habitats and increasing connectivity among them (Öckinger and Smith, 2006; Brückmann et al., 2010; Loss et al., 2011). Also, agri-environmental schemes in the European Union are being carried out in the hope that many insects inhabiting agricultural landscape will survive (Batáry et al., 2010). However, this attitude towards the conservation of species diversity faces many practical problems (Warren and Bourn, 2011). The creation and management of semi-natural habitats, the design of ecological corridors or stepping stones are costly and, hence, may be limited only to the local scale. The alternative or supplementary solution for the above problem is to look for the unrecognized advantages to biodiversity that are brought by human activity usually regarded as damaging to the environment. Man-made habitats, often associated with industrial or settlement development, may have high conservation value (Prach, 2003; Tropek and Konvicka, 2008; Lundholm and Richardson, 2010; Berg et al., 2011). Moreover, studies in such new habitats give an insight into the functioning of the ecosystem and the formation of animal and plant assemblages (Prach, 2003; Santoul et al., 2004). It has been shown that limestone quarries (Benes et al., 2003; Jukes et al., 2010; Tropek et al., 2010), road verges (Munguira and Thomas, 1992; Thomas et al., 2002; Saarinen et al., 2005), former open-surface coal mines (Holl, 2006) and landfills (Davis, 1989) may be refuges for rare plants and

* Corresponding author. Tel.: +48 12 370 35 63; fax: +48 12 632 24 32.
E-mail address: lendi.mag@gmail.com (M. Lenda).

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butterflies. The above mentioned studies suggest that the habitats created by industrial activity may significantly contribute to the conservation of species diversity and/or mitigate the negative results of human activity. In Europe, gravel-pits have become more and more common features in the landscape (Santoul et al., 2004; Skórka et al., 2006; Skórka, 2007). The excavation of aggregate (gravel, sand) has increased greatly because companies building roads and human settlements have created a huge market (Stryszewski, 2006; Galos, 2009). For example, in Poland the annual excavation of gravel and sand doubled between 2000 and 2006 (Stryszewski, 2006; Smakowska-Filipek and Smakowski, 2008). The results of this mining activity are various waterbodies with shores covered by diverse vegetation (Skórka et al., 2006; Bzdon, 2008). It is already recognized that gravel-pits are important habitats for some waterbirds (Santoul et al., 2004; Skórka et al., 2006). Shores of gravel-pits are wide (often up to 50 m) and are covered by many flowering plant species (Bzdon, 2008). The latter suggests that gravel-pit shores may be an important habitat for many butterfly species. To our knowledge, the value of gravel-pits for butterflies has not been studied to date. Therefore, in this study we explored the value of this habitat for butterflies by comparing their number, abundance, diversity and commonness of species with those found in a typical habitat of butterflies: extensively managed or recently abandoned meadows (Kruess and Tscharntke, 2002; Skórka et al., 2007; Dover et al., 2011). Further, we identified local- and landscape-level factors affecting the richness, abundance, diversity and commonness of butterfly species on gravel-pit shores to provide recommendations helpful in the management of this habitat for these insects.

2. Material and methods

2.1. Study area

The study was conducted in 2006 in 50 gravel-pits located in two provinces (Małopolska, Podkarpacie – total area 30,000 km^2) of southern Poland (Fig. 1 and Supplementary file). Gravel-pits were selected at random from our database of 209 gravel-pit complexes (total area 5000 ha) in Małopolska and Podkarpacie (Skórka et al., 2006; Skórka, unpublished). The mean ± SE size and age of the selected gravel-pits were 19.3 ha ± 3.2 ha (range: 1.1–89.0 ha) and 11.2 years ± 1.1 years (range: 3–34 years), respectively. The bedrock in the study sites is mainly composed of boulder clay, sand and glacial accumulation gravel (Zawiejska and Wyżga, 2010). Shores of the gravel-pits were covered by diverse vegetation, mostly dry grasslands and margin communities (class: *Festuco-Brometea; Trifolio-Geranietea sanguinei*), xeric sand grasslands (*Koelerio glaucae-Corynephoretea canescentis*), fresh and moderately moist meadows (*Molinio-Arrhenatheretea*), mesophilous communities of tall perennials (*Artemisietalia vulgaris* and *Convolvuletalia sepium*) and perennial ruderal communities (*Agropyretea intermedio-repentis*). Most numerous plant genera were: *Carex* (six species), *Trifolium* (7), *Vicia* (8) and *Veronica* (6). The intensiveness of gravel excavation was differentiated between gravel-pits. Most of them were extensively exploited and their relatively large fragments were abandoned after the aggregate extraction. Fourteen gravel-pits were intensively exploited (over 50% of area were in the exploitation) and ten were recently abandoned gravel-pits.

2.2. Butterfly surveys

We established 50 transects (200 m long, 5 m wide), where the butterflies were counted with the Pollard method (Pollard and Yates, 1993). The location of the transect was established by the random generation of geographical coordinates at the selected gravel-pits. The transects were parallel to the shoreline and located in the middle of the shore. We defined shore as a land created during excavation of gravel that lies between water surface and other land use type (e.g. arable field, grassland, forest, see also: Supplementary file). In our sample of gravel-pits the mean width of the shore was 16 m ± 2 m (range: 5–58 m). Mean area of the shore ± SE was 4.7 ha ± 0.6 ha (range: 0.9–18.3 ha). We made seven surveys in each transect between the end of April and the end of August 2006. The surveys were done during favourable weather conditions (temperature of at least 18 °C, wind 3 or less on the Beaufort scale, cloud cover not greater than 25%). The total number of butterfly species (species richness), the total number of individuals (abundance) and Simpson's index of diversity were calculated for each transect. We used the Simpson's index because it is easily interpretable as the probability that two randomly selected individuals are of the same species (Simpson, 1949). Moreover, it is commonly used and is one of the least biased indices regardless of the abundance distribution model used and when sample size is small (Mouillot and Lepretre, 1999).

The number of occupied grid squares from the Polish Butterfly Atlas (Buszko, 1997) (http://motyle.info/forum/portal2.php?show=rozmieszczenie) based on field work done in 1986–1995 were used to provide a commonness (non-rarity) value for each species (Rosin et al., in press). A mean commonness score (C_s), weighted by species abundance, was then calculated for each transect. The formulae is as follow:

$$C_s = \frac{\sum_i^t (Ng \times Nind)}{Ntot}$$

where *Ng* is number of occupied grid squares by a given species in Poland derived from Polish Butterfly Atlas (Buszko, 1997), *Nind* is a number of individuals of a given species recorded during all counts in a given transect, *Ntot* is total number of individuals of all $(i, \ldots, t)$ species recorded during all counts in a given transect.

For our recorded species this score could, hypothetically, range from nine (if only *Colias erate* was recorded in a transect) to 873 for *Pieris napi* only. In our transects the score (averaged across all species recorded in a given transect) varied from 356 to 693.

To compare the number of species, abundance, diversity index and commonness of butterflies found at gravel-pit shores with those in grasslands we established a further 50 transects on extensively managed grassland or recently abandoned ones (<5 years). We chose grasslands in the vicinity of the studied gravel-pits (mean ± SE distance to the gravel-pits was 247 ± 12 m, range: 50–410 m) to keep such factors as the habitat patch size, bedrock and landscape composition similar to the transects on the shores. We chose extensively managed grasslands and recently abandoned grasslands because our earlier study showed that they are one of the most important and widespread butterfly habitats, covering about 11% of the study area (Skórka et al., 2007; Lenda and Skórka, 2010). The structure of agriculture in southern Poland is that fields and grasslands are usually small and elongated thus, are a little bit similar to the gravel-pit shores as far as shape is concerned. The mean ± SE grassland size was 6.1 ± 0.7 ha (range: 0.9–18.3 ha) and did not differ from the mean size of shore area (bootstrapped $t = 1.67$, $P = 0.096$). These grasslands were mown once a year in autumn or once every 2 or 3 years. Ten grasslands had not been managed for 4–5 years. No fertilizer was used in all meadows but two, where small amount of nitrogen and calcium (exact quantities not known) was applied occasionally in some years.

2.3. Variables measured in transects

The following environmental variables potentially affecting butterfly populations were determined in transects at gravel-pits:

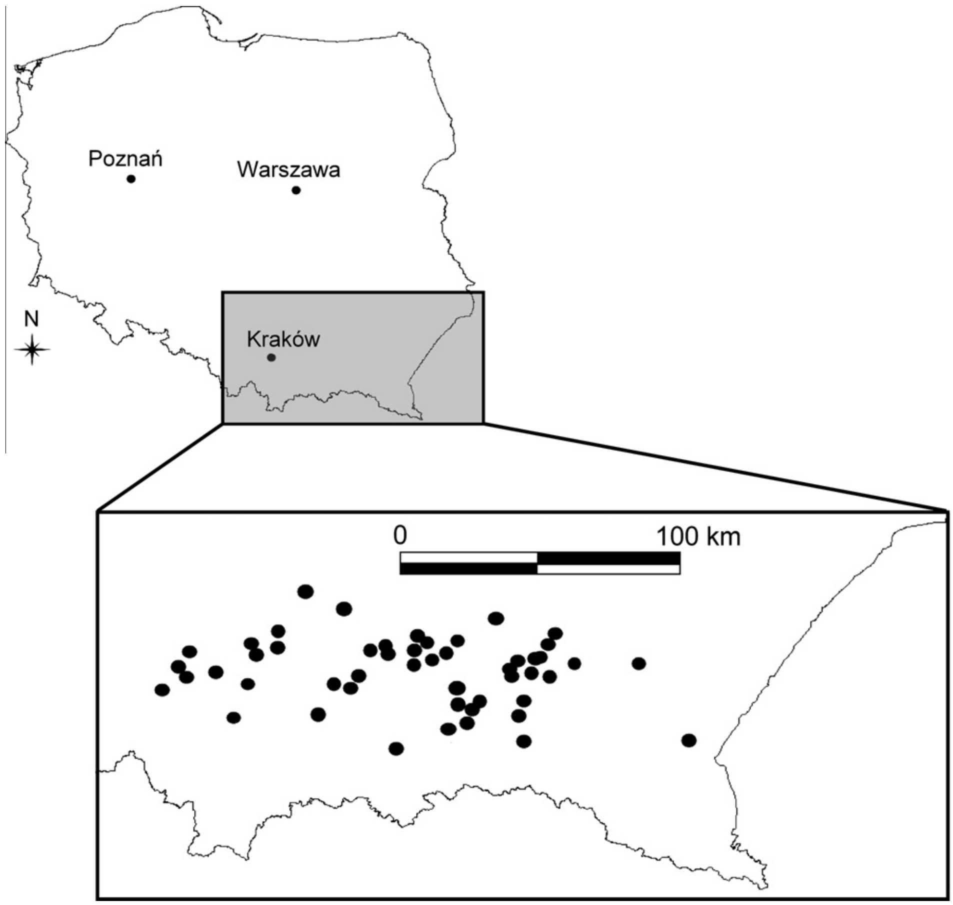

Fig. 1. Map of Poland and location of the region (shaded area) where gravel-pits were studied. Black dots indicate gravel-pits selected in this study.

(1) plant species richness, (2) index of flower abundance, (3) cover of bare ground (%), (4) density of shrubs (individuals per 100 m^2), (5) age of the gravel-pit (ha), (6) area of the shore, (7) distance to the nearest human settlement, (8) cover of water reservoirs in a 500 m radius around the transect, (9) distance to nearest forest, (10) distance to nearest grassland. To measure variables 1–3 in each transect we randomly selected three square plots (4 m^2). Within these plots we counted all plant species and measured their cover using the following scale: 1: <1%, 2: 1–10%, 3: 11–20%...11: 91–100%. The index of flower abundance was calculated as the number of flowering plant species multiplied by their cover scale. We used an upper value of the cover category for particular species in this calculation. Plant species were counted twice during the season (at the end of May and in the middle of July). Plant species richness used in the analyses is a sum of all plant species recorded during the two counts within a transect. The percentage cover of bare ground was noted in the same scale as plant species cover. Shrubs were counted on three square plots (100 m^2) within the transect and the mean figure was used in analyses. Age of the gravel-pit represents the number of years since the exploitation started. Variables 6–10 were read from aerial photos digitalized in Quantum GIS software and supported by direct measurements in the field by GPS.

2.4. Analysis

Before any analysis we checked if there was any spatial autocorrelation in the data by calculating Moran's statistics on correlograms (Legendre and Legendre, 1998). Since we did not find any evidence for statistically significant autocorrelation we used "traditional" statistical methods. To compare the total number of butterfly species, abundance, diversity index and commonness score between gravel-pit shores and meadows we used general linear mixed model (GLMM). Habitat type was introduced as a fixed effect, area of the shore and grassland was a covariate and pair ID was a random factor. GLMM was performed in SPSS version 19 for Windows (SPSS Inc.). A principal component analysis (PCA) was used to relate the abundance of the individual species to the habitat type (gravel-pit shore and grassland) using the CANOCO 4.5 package (Lepš and Šmilauer, 2003). We used bootstrapped *t*-tests to compare the abundance of particular species in these two habitats. This test is preferred over ordinary *t*-tests when sample sizes are small and unequal as in many cases of particular species in our data set (Flachaire, 1999; Meuwissen and Goddard, 2004). To compare the proportion of transects at which given species were recorded in gravel-pit shores and in meadows we used *G*-tests or the Fisher exact test (when frequencies were equal or lower than five). *T*-, *G*- and Fisher exact tests were done in Rundom Pro 3.12 software (Jadwiszczak, 2009). To identify factors affecting species richness, abundance, diversity and commonness at gravel-pit shores we used model selection procedures based on information theory (Burnham and Anderson, 2002). The Akaike information criterion corrected for small sample size (AICc) was used to identify the most parsimonious models from each candidate set (255 models tested for each dependent variable). Finally, we ranked all the models built according to their ΔAICc values and used models with the lowest AICc together with associated weight values (probability that a given model is the best) as that best describing the data. We considered models with ΔAICc lower than two as equally good (Burnham and Anderson, 2002). We used model averaging for estimates of function slopes of parameters of interest (Burnham and Anderson, 2002). Finally, the model weights were used to define the relative importance of each explanatory variable across the full set of models evaluated by summing weight values of all models that include the explanatory variable of interest (Burnham and Anderson, 2002).

When necessary we used logarithmic transformation to reduce the effects of outlier observations (Quinn and Keough, 2002). Our primary analysis showed that three variables (plant species richness, index of flower abundance and cover of bare ground) were strongly correlated between each other ($r > |0.700|$). Therefore, to avoid multicollinearity problems we left only one variable – plant species richness because this variable had a higher correlation with butterfly species richness and abundance. Moreover, in all regression models, variables were standardized to allow a direct comparison of beta estimates (larger values of betas indicate stronger relationships between explanatory and dependent variables).

Model selection and averaging were run in the SAM 4.0 statistical software (Rangel et al., 2010).

We considered that the function slopes (betas) were significant if their 95% confidence intervals (95% CI) did not overlap with zero. All statistical parameters (betas, means) are quoted with ± standard error (SE).

3. Results

3.1. Comparison of gravel-pit shores and grasslands

In total, we recorded 71 butterfly species on transects at gravel-pit shores whereas there were only 50 species on an equal number of transects on grasslands (Appendix, Supplementary file). Principal component analysis showed that species composition of the butterfly communities at gravel-pit shores was different from the communities in grasslands (Fig. 2). The first two axes of the PCA ordination explained 19% of the variation in butterfly species, of which the habitat type explained 93.5% (Fig. 2). Altogether, 23 species were unique to gravel-pits but only three species were unique to grasslands and this difference was statistically significant ($G_1 = 49.40$, $P < 0.001$, Appendix A). Moreover, there were 21 species that occurred on both gravel-pits and grasslands but their abundance and/or incidence on transects were significantly higher in gravel-pits than in grasslands (e.g. *Pyrgus malvae*, *Papilio machaon*, *Colias hyale*, *Callophrys rubi*, *Plebejus* sp., several species from the genus *Polyommatus*, *Argynnis* sp., *Boloria* sp., *Apatura* sp., see: Appendix A and Fig. 2). However, there were 13 species which did not differ in densities and occurrence on transects between gravel-pits and grasslands (e.g. *Thymelicus sylvestris*, *P. napi*, *Lycaena phlaeas*, *Cupido argiades*, *Melanargia galathea*, see: Appendix). Also, there were 15 species whose abundance were significantly higher and/or occurred in more transects in grasslands than in gravel-pits (*Thymelicus lineola*, *Lyceana dispar*, *Inachis io*, *Araschnia levana*, *Aphantopus hyperantus*. see: Appendix A and Fig. 2). In summary, species richness and Simpson diversity index were higher in transects on gravel-pit shores than on grasslands (species richness: GLMM $F_{1,45.9} = 162.271$, $P < 0.001$, Simpson diversity index: GLMM $F_{1,48.8} = 15.185$, $P < 0.001$, Fig. 3). Moreover, on average more common and widespread butterfly species occurred in grasslands than in gravel-pits as indicated by the commonness score (GLMM $F_{1,49.1} = 87.172$, $P < 0.001$, Fig. 3). However, the abundance of butterflies did not differ significantly between these habitat types (Fig. 3).

3.2. Factors affecting species richness, abundance, diversity and commonness

The model selection based on Akaike's criterion showed that eight models explaining butterfly species richness were equally good (Table 1). The best models explained over 50% of variation in the butterfly species richness (Table 1). Explanatory variables that were present in all best models were plant species richness (beta = 1.627 ± 0.348, 95% CI: 0.944–2.310, importance = 1.000) and cover of water in 500-m radius (beta = −1.427 ± 0.313, 95% CI: −2.040 to −0.813, importance = 1.000). The richness of butterfly species was also positively dependent on the density of shrubs at shores (beta = 0.459 ± 0.151, 95% CI: 0.177–0.742, importance: 0.438), distance to the nearest forest (beta = 0.397 ± 0.123, 95% CI: 0.156–0.638, importance: 0.390), age of the gravel-pit (beta = 0.317 ± 0.101, 95% CI: 0.120–0.514) but negatively with isolation (beta = −0.418 ± 0.131, 95% CI: −0.672 to −0.161, importance: 0.363).

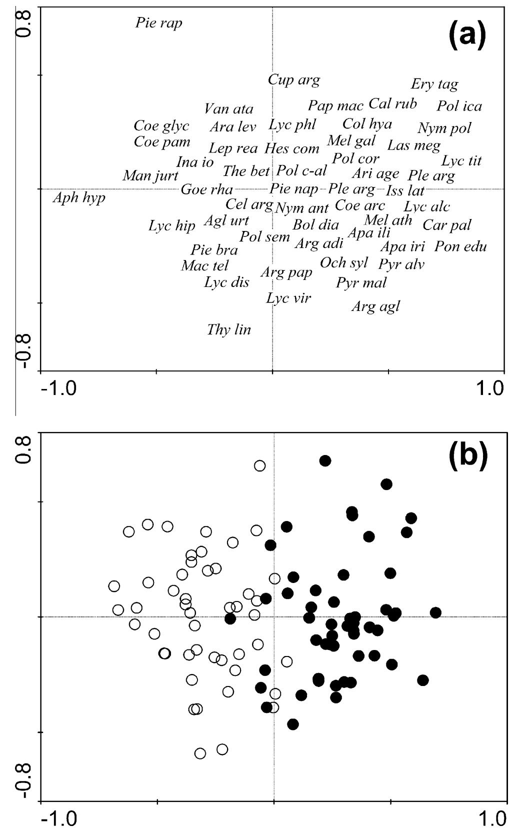

Fig. 2. PCA ordination plot of (a) species and (b) samples along the first and second PCA axis. Species occurring in less than ten patches have been omitted.

Model selection identified twelve equally good models describing the abundance of butterflies (Table 1). These best models explained 33% of variation on average (Table 1). The abundance of butterflies was negatively affected by cover of water in a 500-m radius (beta = −7.742 ± 2.143, 95% CI: −11.943 to −3.541, importance: 0.993) and isolation (beta = −4.703 ± 1.629, 95% CI: −7.896 to −1.511, importance: 0.654). Butterfly abundance was positively related to the richness of plant species (beta = 4.333 ± 1.445, 95% CI: 1.502–7.165, importance: 0.579), age of the gravel-pit (beta = 2.749 ± 0.874, 95% CI: 1.036–4.462, importance: 0.395), distance to nearest human settlement (beta = 2.740 ± 0.925, 95% CI: 0.927–4.552, importance: 0.347) and the density of shrubs (beta = 2.436 ± 0.779, 95% CI: 0.910–3.962). Model selection identified eleven equally good models describing the diversity of butterflies (Table 1). However, all best models explained little variation (5% on average) in butterfly diversity (Table 1). The only variables which 95% CI did not overlap with zero were area of the shore (beta = −0.628 ± 0.218, 95% CI: −1.055 to −0.201, importance: 0.670), the richness of plant species (beta = 0.470 ±

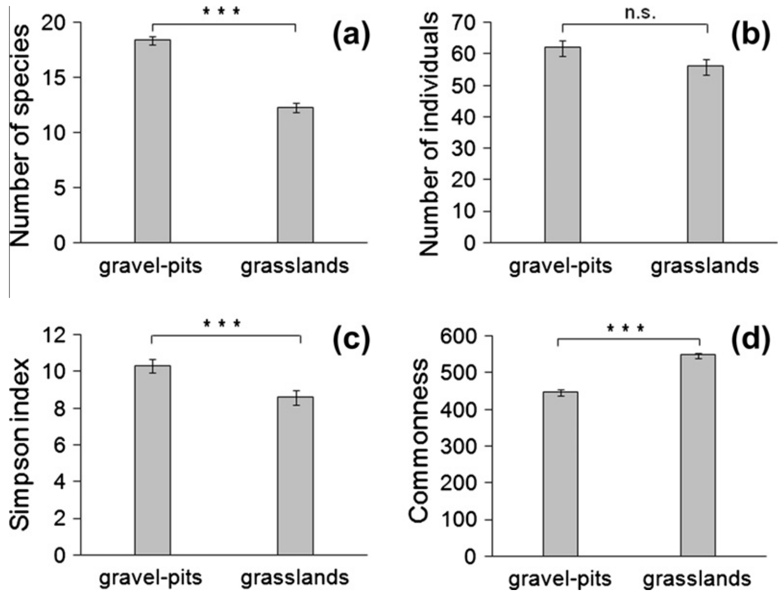

Fig. 3. Comparison of mean ± SE (a) number of butterfly species, (b) number of individuals (per 200 m transect), (c) Simpson diversity index and (d) commonness score on gravel-pit shores and extensively managed grasslands. Explanations: *** – $P < 0.001$, n.s. – non-significant.

0.158, 95% CI: 0.160–0.780, importance: 0.388), distance to nearest human settlement (beta = −0.306 ± 0.116, 95% CI: −0.551 to −0.061, importance: 0.295) and isolation (beta = −0.283 ± 0.126, 95% CI: −0.530 to −0.036, importance: 0.290). Model selection identified eleven equally good models describing commonness of butterflies (Table 1). However, all these best models explained little variation (<5%) in butterfly commonness scores (Table 1). Only four environmental variables in these models had slopes which 95% CI did not overlap with zero. The commonness score was negatively dependent on cover of water in a 500-m radius (beta = −7.547 ± 2.628, 95% CI: −12.698 to −2.396, importance: 0.392) and distance to nearest forest (beta = −5.900 ± 2.240, 95% CI: −10.291 to −1.510, importance: 0.328) and was positively related to the density of shrubs (beta = 7.485 ± 2.632, 95% CI: 2.327–12.643, importance: 0.381) and area of the shore (beta = 4.068 ± 1.899, 95% CI: 0.346–7.790, importance: 0.281).

4. Discussion

Our results demonstrated that shores of gravel-pits are important habitats for butterflies. Firstly, the total number of butterfly species was higher in gravel-pits than in the equal sample of grasslands. The same was true for the mean number of butterfly species per transect. This indicates that gravel-pits contribute to the local species pool of butterflies. Secondly, transect occupancy and the abundance of some butterflies was much higher on gravel-pits than in grasslands (e.g. *Pyrgus alveus, Thymelicus acteon, Aricia agestis*). Thus, shores of the gravel-pits may be a superior habitat for these species than grasslands. Thirdly, species that are rarer than those found in extensively managed or abandoned grassland were mostly found in gravel-pits. This suggests that shores of gravel-pits may be important habitats from a conservation point of view because they are inhabited by uncommon or rare species (e.g. *P. alveus, C. erate, Polyommatus bellargus, Lycaena alciphron*).

Gravel-pits are a special transient habitats that need continuous disturbance to maintain their characteristics in a longer period of time. Vegetation is very diverse there and are often in early successional stages (Bzdon, 2008). The constant expanding of the excavation area and the activity of machines often cause a substantial mosaic of habitats within one gravel-pit (Supplementary file). Bzdon (2008) showed that gravel-pits had over twice as many plant species than surrounding control areas. Also, the specific fine grained bedrock substrates and lower moisture in gravel-pits (Řehounková and Prach, 2006; Pakulnicka, 2008) may be favoured by some rare plants there (e.g. *Astragalus glycyphyllos*, *Centaurium pulchellum*, *Fumaria officinalis*, *Sedum maximum, Veronica spicata*). This may also be an explanation of the greater richness of species and diversity of butterflies found at gravel-pit shores in our study because these insects are often strictly linked with specific plant species at certain stages of their lives (e.g. Settele et al., 2000). The richness of plant species was the most important predictor of the number of butterfly species, their abundance and diversity in our study. However, it is difficult to establish if it is a casual relationship, because butterflies and plants tend to respond to the same environmental factors, rather than depending on each other (Hawkins and Porter, 2003; Wolters et al., 2006). The relationship between plants and butterflies seems to be weaker at larger, biogeographical spatial scale (Hawkins and Porter, 2003; Stefanescu et al., 2004) than at local scale (Skórka et al., 2007; Kitahara et al., 2008) as it was in this study. Soil disturbance caused by the excavation of gravel allows pioneer plants to colonize these areas (Bzdon, 2008). The early succession stages of vegetation at gravel-pits is also partially kept after the cessation of gravel excavation, mostly for recreation and relaxation, including anglers fishing on shores (authors' unpublished data). They create patches of bare ground with sparse short vegetation that is an important microhabitat requirement for some butterfly species (Thomas and Harrison, 1992). This disturbance regime maintains early successional stages at many old gravel-pits because lots of people use gravel-pits for the above mentioned purposes. However, it would be beneficial if some of the old-gravel-pits in our study area were managed (e.g. shores could be grazed and shrubs could be removed) to avoid habitat deterioration due to vast invasion of shrubs. Currently, in all studied by us gravel-pits, vegetation developed naturally and no post-extraction management was applied. Several butterflies that had high occupancy and abundance at gravel-pits are typical species for calcareous grasslands (*T. acteon*, *Polyommatus coridon*, *P. bellargus*, *L. alciphron*). Dry calcareous grasslands are the most endangered butterfly habitat in Europe (WallisDeVries et al., 2002; Wenzel et al., 2006; Sang et al., 2010) and gravel-pits may become a surrogate habitat for some

Table 1
Best models describing species richness, abundance, diversity and commonness of butterflies on the shores of gravel-pits. For each model the number of predictors (k), variance explained by the model (r^2), the Akaike information criterion score (AICc), the difference between the given model and the most parsimonious model (Δ) and Akaike weight (w) are listed. Explanations of variable codes: Plant – plant species richness, Shrub – density of shrubs, Build – distance to the nearest human settlement, Water – cover of open water in a 500 m radius around the transect, Forest – distance to nearest forest, Isolation – distance to nearest grassland, Area – size of the gravel-pit shore, Age – age of the gravel-pit.

No.	Model	k	r^2	AICc	Δ AICc	w
	Species richness					
1	Plant + Water	2	0.55	220.876	0	0.080
2	Plant + Water + Shrub	3	0.57	221.130	0.254	0.071
3	Plant + Water + Forest	3	0.57	221.238	0.362	0.067
4	Plant + Water + Isolation	3	0.56	222.154	1.277	0.042
5	Plant + Water + Forest + Shrub	4	0.58	222.364	1.487	0.038
6	Plant + Water + Isolation + Shrub	4	0.58	222.590	1.714	0.034
7	Plant + Water + Forest + Age	4	0.58	222.642	1.765	0.033
8	Plant + Water + Age	3	0.56	222.702	1.826	0.032
	Abundance					
1	Plant + Water	2	0.31	414.696	0	0.060
2	Plant + Water + Isolation	3	0.34	415.193	0.497	0.047
3	Water + Isolation + Age	3	0.33	415.303	0.606	0.045
4	Water + Isolation	2	0.30	415.418	0.722	0.042
5	Plant + Build + Water + Isolation	4	0.36	415.726	1.030	0.036
6	Plant + Water + Isolation + Age	4	0.35	416.329	1.633	0.027
7	Water + Isolation + Shrub	3	0.32	416.439	1.742	0.025
8	Plant + Build + Water	3	0.32	416.453	1.757	0.025
9	Plant + Water + Shrub	3	0.32	416.516	1.820	0.024
10	Plant + Water + Age	3	0.32	416.552	1.855	0.024
11	Water + Isolation + Shrub + Age	4	0.35	416.554	1.858	0.024
12	Plant + Build + Water + Isolation + Age	5	0.38	416.640	1.944	0.023
	Species diversity (Simpson index)					
1	Age	1	0.05	242.013	0	0.044
2	Plant + Age	2	0.09	242.216	0.202	0.040
3	Plant	1	0.04	242.476	0.463	0.035
4	Build + Area	2	0.07	242.983	0.970	0.027
5	Isolation + Area	2	0.07	242.999	0.986	0.027
6	Shrub + Area	2	0.07	243.226	1.213	0.024
7	Build	1	0.02	243.477	1.464	0.021
8	Age	1	0.01	243.917	1.903	0.017
9	Shrub	1	0.01	243.951	1.938	0.017
10	Isolation	1	0.01	243.960	1.947	0.017
11	Area + Age	2	0.06	243.963	1.950	0.017
	Commonness					
1	Water	1	0.03	526.974	0	0.049
2	Shrub	1	0.02	527.313	0.339	0.042
3	Forest	1	0.02	527.814	0.840	0.033
4	Area	1	0.01	528.221	1.247	0.027
5	Forest + Shrub	2	0.05	528.465	1.490	0.023
6	Isolation	1	0.01	528.497	1.522	0.023
7	Water + Shrub	1	0.05	528.531	1.556	0.023
8	Plant	1	<0.01	526.554	1.580	0.022
9	Age	1	<0.01	528.555	1.581	0.022
10	Build	1	<0.01	528.555	1.581	0.022
11	Water + Area	2	0.04	528.896	1.922	0.019

endangered butterflies inhabiting such grasslands. Also, many other grassland butterflies found suitable habitats at gravel-pits. The exception was butterflies linked, at some stages of their lives, with grass and these species usually had lower densities at gravel-pit shores (e.g. *Maniola jurtina*, *Aphantopus hyperantus*).

Shrubs positively affected the number of species and their abundance. However, it seems this variable positively affected mostly common and widespread species. Dense shrubs may diminish habitat suitability for some pioneer or specialist butterfly species (Smallidge and Leopold, 1997; Stefanescu et al., 2009; Lenda and Skórka, 2010). On the other hand, shrubby shores may be attractive sites for some other butterflies like *Nymphalis polychloros* and *Apatura* sp. (Söderström et al., 2001). It seems that the appropriate management of this habitat is the keeping or the creation of a mosaic of naturally developed shrubs that may provide shelter for some butterflies and patches of bare ground or sparse vegetation (Sparks and Parish, 1995; Dover et al., 1997; Talsma et al., 2008; Pradel and Fischer, 2011).

Species richness and abundance of butterflies increased with the age of gravel-pits. The theory of secondary succession suggests that species richness should be dominated by mobile generalists with high dispersal capacity, while later stages are expected to develop a higher floristic and structural complexity (Brown and Southwood, 1987; Krauss et al., 2009). Thus, conservation value has been assumed to increase with the age of habitat (Davis, 1979; Tropek et al., 2010) and for plants, there is some evidence of increasing conservation value with increasing successional age in abandoned quarries (Novak and Konvicka, 2006). Our results are in line with this prediction. Also, after a successful colonization event and establishment the species' population size usually increases for a certain period of time which may be explanation for the observed positive relationship between age of the gravel-pit and abundance of butterflies.

Habitat area is regarded one of the most important factors affecting species richness and abundance (Rosenzweig, 1995; Krauss et al., 2009). Interestingly, area of the gravel-pit shore did not affect species richness nor abundance of butterflies. This might suggests that both small and large gravel-pits are equally good habitats for butterflies. It was shown that endangered butterfly species respond more positively to heterogeneity than to area (Jarošik et al., 2011). However, our transects were of constant size, thus, lower proportion of shore was sampled on larger gravel-pits and, therefore, for the species richness, this conclusion must be taken with caution. We also found that area negatively affected species diversity and positively commonness of species. These results are difficult to explain because diversity index is calculated from both species richness and abundance, and these were not affected by the area. Models for diversity index and commonness explained very little variation (<5%) thus any interpretation in such case is doubtful. Landscape composition also influenced the richness of butterfly species as well as their abundance, diversity and commonness. The cover of water reservoirs negatively affected the richness of species and their abundance. We are not aware of other studies that found similar results. It is possible that a large surface of water may act as a barrier for butterflies, thus lowering their dispersal rate. Flight above large water reservoirs may be of high energy cost as well as being quite risky because butterflies during such flight had no opportunity to rest. Moreover, butterflies flying over a water surface may be easy to capture by birds hunting in flight. Such species as the Common Swift *Apus apus*, Sand Martin *Riparia riparia*, Barn Swallow *Hirundo rustica* are common at gravel-pits and capture insects in flight above the water surface (Cramp, 1988). Thus, from a practical point of view, it may be profitable for butterflies to have smaller gravel-pits with islets on them that could enable a spontaneous and successful colonization all suitable parts of this habitat by butterflies (this could be also beneficial for waterbirds that nest on islets). Gravel-pit shores that were surrounded by higher cover of water reservoirs had less common species. However, this result should be treated with caution because this model explained little (<5%) variation in the commonness score.

In our study the number of species and diversity index were negatively related to distance to the nearest grassland patch in the vicinity of gravel-pits. This indicates that the number of butterfly species at gravel-pits may be limited by colonization rates due to habitat isolation. This is in line with studies in butterfly populations in other habitats (e.g. Haddad, 2000; Matter et al., 2009; WallisDeVries and Ens, 2010). Grasslands in the surrounding of gravel-pits may play two important roles. Firstly, they are probably a local pool of species that may colonize gravel-pit shores. Secondly, grasslands may act as stepping stones making the matrix more permeable and, thus, enabling the migration of other species (e.g. usually occurring on railway sides or rare in our study area – dry grasslands) so that they successfully reach suitable habitats in gravel-pits (Dennis et al., 2006). This has a useful consequence for conservation. In gravel-pits isolated from grasslands (e.g. located in intensively managed farmland) and located far from other dispersal corridors, the number of butterfly species may be increased by the assisted colonization of individuals from other habitats (Loss et al., 2011). This could be done both in the case of rare and endangered species as well as common ones that provide ecosystem services (Kevan, 1999). The richness of butterfly species was positively dependent on the distance to the nearest forest. This indicates that the proximity of forest somehow negatively affects the richness of species. Since many of the butterflies occurring at gravel-pits prefer open, sunny areas the proximity of forests may negatively affect microclimatic conditions for these species (Chen et al., 1993; Davies-Colley et al., 2000). Recent studies suggest that proximity of forests may positively affect species richness of grassland butterflies (Dover and Settele, 2009; Berg et al., 2011; Öckinger et al., 2012). However, most of the forests in the study area are pine plantations and forest edges do not provide attractive resources for butterflies (see: Ohwaki et al., 2007; Vu, 2009). It seems to be confirmed by the negative relationship between the commonness score and distance to the nearest forest. Moreover, forests may be barriers to movement for many grassland butterflies (Roland et al., 2000). Fry and Robson (1994) showed experimentally that even very simple structures (tarpaulins) could reduce the movement of grassland butterflies thus forests near gravel-pits may add to the isolation of the latter habitat. We found that the abundance of butterflies was lower in the proximity of human settlements. The negative effect of human settlement on butterflies was found in several other studies and settlements may alter habitat quality and landscape permeability (Stefanescu et al., 2004; Clark et al., 2007). Contrary to this, the Simpson diversity index was higher in the proximity of human settlement, although this variable explained little variance in diversity index. Higher diversity in the proximity of human settlements may be also explained by lower butterfly abundance, especially if these butterflies were the most common species. If the abundance of species is more equal the value of diversity indices increases.

5. Conclusions

Our results provide evidence that man-made habitats may be remarkably good for biodiversity. Gravel-pits as well as other man-made habitats (quarries, coal mines) are a consequence of industrial development throughout the world. It has been suggested these sites may be valuable refuges for many organisms especially in regions that are intensively farmed and heavily industrialized (see: Lundholm and Richardson, 2010; Tropek and Konvicka, 2011). Although they can be restored to their original use, it is much cheaper to keep them as water reservoirs. Also, in such post-industrial sites the spontaneous succession may act as a much more efficient way of the biodiversity conservation than special restoration actions as it was demonstrated for limestone quarries (Tropek et al., 2010). Industrial and infrastructure developments in several Eastern European countries, which are a consequence of joining the European Union, will lead to changes in seminatural habitats. It is regarded as a huge threat to many habitats with high biodiversity (Reidsma et al., 2006; Hartel et al., 2010; Tryjanowski et al., 2011) However, as we have shown, this industrial development may also bring positive effects and it would be worthy to put more emphasis on finding the positive effects of human activity and working out solutions which may make this activity beneficial for wild animals and plants (Lundholm and Richardson, 2010). In the case of gravel-pits, excavation is steadily increasing and many new gravel-pits have appeared (Skórka, 2007). We estimated that gravel-pits cover over 5000 ha with over 600 km of shoreline in our study region (Skórka et al., unpublished). This is a large amount of habitat available for butterflies (the study region covered a mere 10% of the country's total area). More studies are required in order to understand the value of gravel-pits for other organisms, and to work out recommendations that will help extraction companies to create habitats in new gravel-pits that will be a sanctuary for biodiversity and will allow the possible negative effects of gravel excavation to be mitigated. We think that gravel-pit shores are good sites for the creation of ecological networks (Jongman, 2004). Ecological networks are landscape-scale systems of interconnecting corridors, nodes and patches designed to mitigate effects of habitat fragmentation (Samways, 2007). Because most of the gravel-pits are created in agricultural landscapes, the ecosystem functioning of the landscapes would be enhanced (e.g. higher number of species and their diversity, more ecosystem services, microclimate changes) by gravel-pits. They may provide both habitat for the persistence of organisms and probably corridors for the their movement towards extensive intact habitat. However, the benefit of gravel-pits might be temporary if succession is allowed to continue so that the open areas are entirely covered by shrubs and woodland. Therefore, gravel-pit shores should be managed to remove shrubs periodically, mostly at older gravel-pits.

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Appendix A

List of all species recorded within transects at gravel-pit shores and grasslands. Abundance is the mean number of individuals per 200 m in transects where a given species was recorded. Occurrence is the number of transects with a given species. The total number of sites for both gravel-pits and grasslands, was 50. *T*-tests were based on 10,000 bootstrap iterations. Fisher exact (F. exact) tests were used when frequencies were equal or lower than 5, otherwise 2 × 2 *G*-tests with Williams correction were used. Species that had statistically higher densities and/or had higher occupancy of transects at gravel-pit shores than in grasslands are bolded.

Species	Abundance ± SE				Occurrence			
	Gravel-pit	Grassland	*t*-test	*P*	Gravel-pit	Grassland	Statistic	*P*
Erynnis tages	8.5 ± 1.4	4.8 ± 0.8	2.31	0.045	30	12	*G* = 3.30	<0.001
Carcharodus alceae	2.8 ± 1.4	–	–	–	4	0	F. exact	0.117
Pyrgus malvae	3.4 ± 0.4	3.1 ± 0.5	0.53	0.601	26	16	*G* = 8.44	0.004
Pyrgus alveus	2.1 ± 0.5	–	–	–	15	0	F. exact	<0.001
Carterocephalus palaemon	2.1 ± 0.3	–	–	–	14	0	F. exact	<0.001
Thymelicus lineola	4.9 ± 0.5	9.0 ± 1.0	−3.78	<0.001	35	34	*G* = 0.09	0.762
Thymelicus acteon	1.6 ± 0.2	–	–	–	9	0	F. exact	0.003
Thymelicus sylvestris	5.2 ± 1.6	4.0 ± 0.9	0.61	0.554	5	4	F. exact	1.000
Hesperia coma	2.5 ± 0.5	2.5 ± 0.5	0.05	0.966	17	8	*G* = 9.61	0.002
Ochlodes sylvanus	5.0 ± 0.7	3.8 ± 1.5	0.74	0.501	14	13	*G* = 0.10	0.750
Anthocharis cardamines	3.8 ± 2.4	–	–	–	4	0	F. exact	0.117
Papilio machaon	2.0 ± 0.2	1.8 ± 0.4	0.35	0.718	22	9	*G* = 16.60	<0.001
Pieris brassicae	5.0 ± 0.4	7.1 ± 0.9	−2.13	0.047	28	27	*G* = 0.08	0.777
Pieris rapae	4.9 ± 0.8	9.1 ± 1.0	−3.26	0.003	19	34	*G* = 18.71	<0.001
Pieris napi	5.3 ± 0.8	4.2 ± 0.5	1.20	0.247	27	29	*G* = 0.32	0.570
Pontia edusa	1.6 ± 0.2	–	–	–	14	0	F. exact	<0.001
Leptidea reali	2.2 ± 0.3	2.6 ± 0.4	−0.75	0.462	12	14	*G* = 0.41	0.525
Colias erate	1.0	–	–	–	1	0	F. exact	0.785
Colias croceus	1.2 ± 0.2	–	–	–	5	0	F. exact	0.056
Colias hyale	2.0 ± 0.3	1.3 ± 0.2	1.88	0.082	14	7	*G* = 6.55	0.010
Gonopteryx rhamni	4.5 ± 0.4	4.7 ± 0.5	−0.42	0.682	23	27	*G* = 1.27	0.260
Hamearis lucina	2.0 ± 1.0	–	–	–	3	0	F. exact	0.242
Lycaena phlaeas	2.0 ± 0.3	2.6 ± 0.5	−0.92	0.400	16	12	*G* = 1.63	0.202
Lycaena helle	1.0	2.1 ± 0.3	–	–	1	7	F. exact	0.059
Lycaena dispar	2.1 ± 0.6	3.6 ± 0.5	−2.14	0.048	11	14	*G* = 0.93	0.335
Lycaena virgaureae	2.7 ± 0.3	1.7 ± 0.7	1.36	0.336	12	3	*G* = 16.95	<0.001
Lycaena tityrus	2.9 ± 0.4	1.8 ± 0.4	2.11	0.047	23	9	*G* = 20.40	<0.001
Lycaena alciphron	1.0 ± 0.0	–	–	–	10	0	F. exact	0.001
Lycaena hippothoe	–	3.4 ± 0.7	–	–	0	11	F. exact	<0.001
Thecla betulae	1.4 ± 0.2	1.1 ± 0.1	1.16	0.256	11	10	*G* = 0.12	0.728
Callophrys rubi	3.7 ± 0.3	1.8 ± 0.4	4.08	0.002	19	5	*G* = 27.35	<0.001
Satyrium ilicis	1.0 ± 0.0	–	–	–	2	0	F. exact	0.495
Cupido minimus	4.0 ± 0.7	–	–	–	4	0	F. exact	0.117
Cupido argiades	3.3 ± 0.6	2.4 ± 0.2	1.30	0.205	18	17	*G* = 0.09	0.767
Celastrina argiolus	1.2 ± 0.1	2.0 ± 0.2	−3.86	<0.001	16	9	*G* = 5.63	0.018
Phenagris nausithous	1.0 ± 0.0	4.0 ± 0.7	−4.58	0.002	2	14	*G* = 19.64	<0.001
Phenagris teleius	–	2.3 ± 0.4	–	–	0	6	F. exact	0.027
Plebejus argus	3.7 ± 0.5	1.8 ± 0.3	3.18	0.004	21	8	*G* = 18.86	<0.001
Plebejus idas	1.0 ± 0.0	–	–	–	2	0	F. exact	0.495
Plebejus argyrognomon	1.6 ± 0.2	1.0 ± 0.0	2.55	0.067	15	2	*G* = 37.96	<0.001
Aricia agestis	3.4 ± 0.3	1.4 ± 0.2	4.84	0.001	15	10	*G* = 2.79	0.094
Polyommatus semiargus	1.2 ± 0.1	4.3 ± 0.9	−3.54	0.082	11	3	F. exact	0.041
Polyommatus icarus	7.8 ± 0.7	4.3 ± 0.7	3.50	0.001	35	12	*G* = 46.58	<0.001
Polyommatus bellargus	1.4 ± 0.2	–	–	–	6	0	F. exact	0.027

(*continued on next page*)

Appendix A (*continued*)

Species	Abundance ± SE				Occurrence			
	Gravel-pit	Grassland	*t*-test	*P*	Gravel-pit	Grassland	Statistic	*P*
Polyommatus coridon	2.8 ± 0.7	–	–	–	12	0	F. exact	<0.001
Argynnis paphia	2.3 ± 0.6	3.8 ± 0.7	−1.60	0.151	10	6	*G* = 2.57	0.109
Argynnis aglaja	5.0 ± 0.6	2.0 ± 0.4	4.17	0.001	17	13	*G* = 1.55	0.212
Argynnis adippe	2.2 ± 0.5	1.5 ± 0.5	1.00	0.360	10	2	F. exact	0.028
Argynnis laodyce	–	1.0	–	–	0	1	F. exact	1.000
Issoria lathonia	5.0 ± 0.8	2.2 ± 0.3	3.17	0.012	25	6	*G* = 42.66	<0.001
Boloria selene	1.0 ± 0.0	–	–	–	2	0	F. exact	0.495
Boloria dia	4.4 ± 0.7	1.0 ± 0.0	4.78	0.003	11	5	*G* = 6.12	0.013
Vanessa atalanta	2.4 ± 0.4	4.3 ± 0.6	−2.69	0.013	17	16	*G* = 0.09	0.764
Inachis io	1.8 ± 0.5	6.9 ± 0.8	−5.71	<0.001	15	19	*G* = 3.22	0.073
Aglais urticae	1.9 ± 0.3	3.4 ± 0.5	−2.60	0.023	16	9	*G* = 5.62	0.018
Polygonia c-album	1.1 ± 0.1	1.1 ± 0.1	−0.23	0.882	11	8	*G* = 1.21	0.271
Nymphalis antiopa	1.5 ± 0.3	1.8 ± 0.4	−0.50	0.620	11	9	*G* = 0.51	0.476
Araschnia levana	4.4 ± 0.7	3.2 ± 0.4	1.42	0.188	7	15	*G* = 6.96	0.008
Nymphalis polychloros	1.0 ± 0.0	–	–	–	11	0	F. exact	<0.001
Melitea athalia	2.2 ± 0.4	–	–	–	14	0	F. exact	<0.001
Apatura iris	3.4 ± 0.5	1.7 ± 0.3	1.97	0.096	11	3	F. exact	0.041
Apatura ilia	3.6 ± 0.7	1.3 ± 0.3	2.76	0.030	12	3	F. exact	0.023
Pararge aegeria	1.2 ± 0.2	–	–	–	4	0	F. exact	0.117
Lassiomata maegera	2.7 ± 0.5	2.0 ± 0.6	0.90	0.394	15	3	F. exact	0.003
Coenonympha tulia	1.0 ± 0.0	–	–	–	3	0	F. exact	0.242
Coenonympha arcania	2.2 ± 0.5	–	–	–	12	0	F. exact	<0.001
Coenonympha glycerion	1.0 ± 0.0	6.7 ± 1.3	−4.31	0.014	7	9	*G* = 0.57	0.449
Coenonympha pamphilus	3.2 ± 0.5	5.4 ± 0.5	−3.04	0.005	22	25	*G* = 0.71	0.398
Aphantopus hyperantus	2.6 ± 0.6	9.1 ± 0.9	−5.86	<0.001	14	40	*G* = 57.80	<0.001
Maniola jurtyna	1.7 ± 0.3	4.1 ± 0.4	−4.63	<0.001	11	22	*G* = 10.49	0.001
Erebia medusa	2.5 ± 0.5	–	–	–	2	0	F. exact	0.495
Melanargia galathea	5.1 ± 0.7	3.4 ± 0.6	1.75	0.091	22	18	*G* = 1.34	0.247
Hyponephele lycaon	2.0 ± 0.7	–	–	–	4	0	F. exact	0.117

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2012.01.014.

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