

How do plant communities and flower visitors relate? A case study of semi-natural xerothermic grasslands

Damian Chmura^{1*}, Paweł Adamski², Zygmunt Denisiuk²

¹ Institute of Environmental Protection and Engineering, University of Bielsko-Biała, Willowa 2, 43-309 Bielsko-Biała, Poland

² Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31-120 Cracow, Poland

Abstract

The paper examines the relationships between the species composition of flower visitors and plants in the semi-natural xerothermic grasslands in southern and central Poland. Thirty 10 × 10 m permanent plots were laid out in total, mainly in nature reserves. The vegetation units studied were classified according to the Braun-Blanquet system; these were phytocoenoses of the *Festuco-Brometea* classes *Inuletum ensifoliae*, *Adonido-Brachypodietum pinnati* and the transitional plant community. Entomological research was performed using the Pollard method within the same plots. A particular site was visited only once and different sites were studied between April and August 2008. We applied, among others, co-correspondence-analysis Co-CA, detrended correspondence analysis (DCA) and redundancy analysis (RDA) to investigate the co-occurrence patterns of plants and flower visitors and their biotopic requirements. We found that the species composition of flower visitors cannot be predicted by floristic composition when the duration of the study is restricted to one day (but under similar weather conditions); however, there is a positive relationship between the species richness of insects and plants and a positive relationship between the number of plant species and the abundance of flower visitors. The Ellenberg moisture index and the cover of meadow species significantly explained the species composition of insects. The three various vegetation units and five dominant xerothermic species, i.e. *Adonis vernalis*, *Anemone sylvestris*, *Inula ensifolia*, *Linum hirsutum* and *Carlina onopordifolia* that were studied across time differed in the species richness of insects. Our results demonstrate that possible patterns in the species composition and the assembly rules of flower visitors are not apparent when the Pollard method is applied. Based on the data obtained using this method, the flower visiting assemblages seem not to be driven by competition and they primarily show a tendency to co-occur which can be an artifact. A plant-focused method that included a rarefaction analysis yielded more insightful results and shed more light on the differences between the dominant plants that shape the physiognomy of plant communities in a possible pollination specialization.

Keywords: calcareous vegetation, Co-CA, null model, entomofauna, species richness, sampling effort

Introduction

Grasslands are a vanishing and endangered habitat, due to changes in land use, the cessation of mowing and grazing and urbanization. Grasslands are one of the most species-rich and diverse plant communities in the agricultural landscape of Europe. The remnants of abandoned grasslands in Central and Western Europe are very important refuges for xerothermic species of plants and small animals [1–3]. Many case studies have addressed the processes of overgrowing by shrubs, trees and some forbs and have pointed to the need for the management

of these habitats [4–6]; they have focused on the maintenance of xerothermic plants but have not incorporated the species richness and diversity of pollinators. Some studies suggest that the persistence of pollinators influences ecosystem services [7] and vice versa. Pollinators are one of the most economically important groups of insects that assist in crop production [8]. Pollinator communities suffer from habitat fragmentation, which affects the species diversity and abundance of both insects and plants [9]. In a highly fragmented landscape, the species composition of pollinators in a given habitat may also be affected by the surrounding landscape [10]. This is particularly important for species whose reproductive stages live in different habitats [11] or for small-habitat patches. Fortunately, the effect of fragmentation may be mitigated by increasing habitat quality [12]. There is an enormous body of literature, including reviews and case studies, which demonstrates that not all visiting insects are pollinators (pollen vectors) because only a small fraction of them are effective pollinators and among the pollinators taxa, they can vary greatly in their effectiveness [13–15]. Therefore, in this work we use the term “flower visitor” and treat them as “potential” pollinators rather than “true” pollinators. This study examines the relationship between flower visitors and

* Corresponding author. Email: dchmura@ath.bielsko.pl

Handling Editor: Łukasz Łuczaj

This is an Open Access digital version of the article distributed under the terms of the Creative Commons Attribution 3.0 License (creativecommons.org/licenses/by/3.0/), which permits redistribution, commercial and non-commercial, provided that the article is properly cited.

plant species on various levels: at the level of the species compositions of two data sets of communities; in terms of species richness and diversity; and finally at the level of single species that shape the physiognomy of the distinguished vegetation units. There are some reports on the relationship between insect and plant species composition, using phytosociological data [16,17], but they do not cover all of those aspects. Our study was done under only one condition. We minimized the sampling effort to only one day in the case of the research on flower visitors. The main goal was to answer the question of which patterns are visible between plant and flower visitors during simultaneous field studies? To be more specific, we sought to answer the following questions: (i) do species-rich calcareous vegetation units attract species-rich entomofauna, i.e. especially flower visitors independent of the type of vegetation and the phase of the vegetation season; (ii) can the species composition of visiting insects be predicted based on plant species composition; (iii) do insect assemblages depend on local environmental factors or on the adjacent habitats as well, and; (iv) do dominant grassland plant species differ in the species diversity and richness of flower visitors?

Study areas

The studies were carried out in eight steppe nature reserves, one area proposed for reserve protection, one NATURA 2000 area situated in lowland in the Nida Basin of southern Poland (50°10'–50°40'N/19°50'–21°30'E) and two nature reserves in the Roztocze range of east-central Poland (51°12'22"N, 23°24'12"E; 50°48'9"N, 23°31'7"E; Tab. 1). The area of the Nida Basin is built mainly of Tertiary sediments (gypsum, marlstone, limestone) that are covered by Quaternary sediments (sands, clays, loess). The climate is temperate continental; mean annual precipitation is 550 mm, with maximum precipitation occurring in July and August; and the mean annual temperature is 8.2°C. An agricultural landscape prevails and woodlands occupy only small areas. The Roztocze range is built of Cretaceous rock (marlstone, gaize, limestone) with overlying younger limestone, sandstone and sands. The climate is temperate continental, mean annual precipitation reaches 700 mm and maximum precipitation occurs in June and July; insolation is highest in August. The area is dominated by a rural landscape with deciduous, fir and pine forests. Many sites are protected as landscape parks, nature reserves and a national park. In these locations, we chose thirty sites from one to four sites per location [18].

Material and methods

Vegetation sampling

For the studies, which included vegetation sampling and entomofauna sampling, thirty 10 × 10 m permanent study plots were established (Tab. 1). The study lasted from 24th April to 12th August 2008. For purpose of the present study, only simultaneous samplings of plants and insects were taken into account, i.e. the study site was visited only once. These plots were characterized by the presence of xerothermic species that are rare on the national scale, which were dominants or co-dominants: *Adonis vernalis* L., *Anemone sylvestris* L., *Inula ensifolia* L., *Linum hirsutum* L. and *Carlina onopordifolia* Besser. Phytosociologically, the plant communities can be classified as *Inuletum ensifoliae* Kozł. 1925, *Adonido-Brachypodietum pinnati* (Libb. 1933) Krausch 1960 of the *Festuco-Brometea* Br.-Bl. et R.

Tab. 1 Number of study plots site and vegetation units in the study areas.

Site	I.e.	A.-B.p.	Transitional community	Total
Dąbie		1		1
Góry Wschodnie	1			1
Lisieniec	1		1	2
Pińczów	3			3
Pasturka		1		1
Polana Polichno		3		3
Przęślin	1	1		2
Skotniki		1		1
Skowronno	1	2	1	4
Skowronno reserve			2	2
Stawska Góra		2		2
Wały	3		2	5
Winiary		2	1	3

A.-B.p. – *Adonido-Brachypodietum pinnati*; I.e. – *Inuletum ensifoliae*.

Tx. 1943 class with patches of a transitional plant community between them. The three vegetation units were studied over the entire study period, thus variation in time due to phenological phases in a given plant community did not affect the differences between plant communities. Vegetation sampling included floristic inventories and vascular plant cover estimation using the commonly applied Braun-Blanquet method. The so-called new Braun-Blanquet scale was used; that is, cover percentage was ranked on the 9-degree scale [19].

Flower visitor sampling

Simultaneously, the abundance and species composition of insects were assessed based on the Pollard “projected box” method. Squares covering 5 m² were demarcated within the study plots that had been established for the plant studies. The species composition and abundance of flower visitors in the squares was recorded for 30 minutes [20,21]. Each sampling was done on sunny days around midday. The projected box data were supplemented by information on flower visitor individuals that were observed on the whole study site. Apart from the common pollinators such as butterflies (Rhopalocera) and bumblebees (Bombini), other insects visiting the flowers or inflorescences were recorded as well. The majority of specimens were identified in the field, but in some cases it was necessary to collect insects for laboratory identification. Based on the habitat preferences of the imagos, the insects were assigned to four habitat groups (guilds): ubiquitous; forest; open and ruderal; open dry and xerothermic. Based on the literature [22], the plant species present in the grasslands were classified as food plants for entomofauna. The food plants for insects with pollenivorous larvae were not determined because there are no data about their preferences [23].

Data analysis

Indices of biodiversity (Shannon–Wiener index, Simpson index, Hill's Evenness N2/N1) [24] were calculated for each study plot with respect to insect and vegetation data. Simple linear regression analysis or Spearman rank correlations (Shapiro–Wilk test, $P < 0.05$) were employed to study the relationships

between plant and insect data in terms of species richness and cover/abundance. In order to calculate the total cover of plants, the medians for the new Braun-Blanquet values were used. The total sum of percentage cover for the plots varied between 96% and 163.5%. To calculate the abundance of insects for the plots, the total number of individuals was analyzed. The two species data matrixes were subjected to co-correspondence analysis (Co-CA), the latest ordination technique that examines the relationships between two communities [16]. Data on insects were treated as a dependent variable in this analysis. The predictive Co-CA model with the SIMPLS algorithm and permutation test to assess significant P -values for each ordination axes was applied using the “cocorresp” package in the R language and environment [25]. Detrended correlation analysis (DCA; for each data set separately) using CANOCO software [26] was another technique employed to examine the relations between plant and insect species composition. The relationship between sample scores of the first two DCA axes (eigenvalues) for the two communities was analyzed with Spearman rank correlations. DCA also helped to study any variation of species composition between the plots by the length of the gradient for the first axis. To evaluate the biotopic dependence of insects, redundancy analysis (RDA) followed by 999 Monte Carlo permutations was employed, with the Ellenberg indicator values as the environmental data. The mean arithmetic values of the indicator indices for light L , temperature T , continentality K and moisture F were computed on the basis of the presence/absence plant data [27]. To study the dependence of insect species composition on the biotopic groups of plants, five main plant groups were distinguished: meadow species, woodland species, xerothermic species, segetal-ruderal species and remaining species. The criteria for this division were the phytosociological affiliations of species; the nomenclature of the distinguished plant communities follows Matuszkiewicz [28]. A second RDA was performed with the cover of the plant species representing the above-mentioned groups.

In order to study the niche overlap of insects, the co-occurrence of species and differences in species richness, we used a Monte Carlo “null model” simulation to randomize each matrix in the data set using EcoSim 7.0 [29]. Niche overlap within insect communities was expressed by the Pianka index,

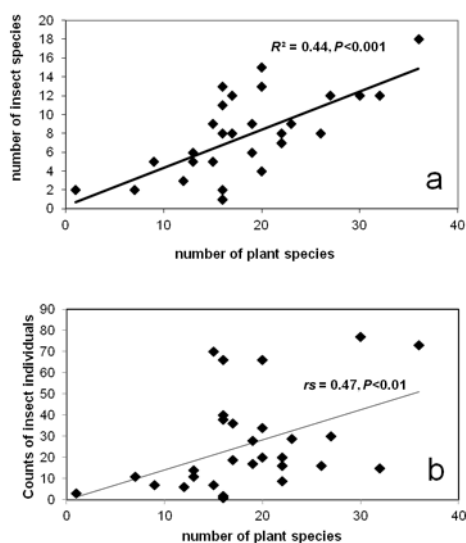


Fig. 1 Simple linear regression analysis of species richness of plants and insects (a) and the relationship between species richness of plants and number of insect individuals (Spearman rank correlation test; b).

calculated between the plots and among the dominant species in the blooming-phase: *Adonis vernalis*, *Anemone sylvestris*, *Inula ensifolia*, *Linum hirsutum* and *Carlina onopordifolia* and randomized with 1000 iterations. To study the co-occurrence of pollinating species among the distinguished guilds for the prepared matrix with the presence/absence data, the checkerboard score (C -score) was measured [30] and later randomized with 1000 iterations for computing random matrices in order to test whether the observed means and variance were larger or smaller than chance. A significantly higher value of the index indicates that the community is structured by species interactions [31]. To test whether insect communities differ in species richness between the three distinguished vegetation units, the rarefaction procedure was run for insect species number with 1000 iterations. The same procedure was applied to check differences in the activity of flower visitors on dominant plant species.

Results

Quantitative relations between plant and flower visitor data

The data include 153 plant species and 67 insect species. We found a significant positive relationship between insect and plant species richness (Fig. 1a) and also the Shannon–Wiener indexes ($R^2 = 0.14$, $P < 0.05$). The relationships between insects and plants were not significant for the evenness index ($R^2 = 0.06$, NS) and Simpson index ($R^2 = 0.12$, NS). There were no significant correlations between total plant cover and total counts of insects ($r_s = 0.22$, NS), but the number of plant species significantly explained insect counts (Fig. 1b). The generalized linear model revealed that both time (the duration of the vegetation season measured as the number of days from the beginning of study; $P = 0.0173$) and plant cover ($P = 0.0285$) explained the total counts of flower visitors ($F = 4.57$, adjusted $R^2 = 0.20$, $P = 0.017$).

Results of direct and indirect gradient analyses

There were no significant correlations between the DCA scores of plants and insects for DCA Axis 1 ($r_s = -0.05$, NS), nor for DCA Axis 2 ($r_s = -0.0001$, NS). The plant communities were characterized by a greater diversity, which was reflected in the longer gradient of the first two DCA axes (7.3, 3.2, respectively) as compared with insect assemblages (4.0, 4.29). In both cases the first two DCA axes explained ca. 17%. Based on 999 permutations for predictive co-correspondence analysis, the probabilities of a Type I error for the first two axes were 0.282 and 0.413. Total inertia was 6.6111. The RDA of insect data and the mean Ellenberg indicator values for the plots yielded chiefly non-significant results, except for the moisture index ($P = 0.018$). This was the only environmental variable that contributed significantly to the model. RDA with the cover of biotopic groups of plants revealed that meadow species cover significantly affected pollinator species composition ($P = 0.020$).

Biotopic groups of plants and insects

The largest share of calciphilous vegetation was comprised of xerothermic species, representatives of classes *Festuco-Brometea* and *Trifolio-Geranietea sanguinei* Th. Müll. 1964. Other frequently represented groups were meadow species of the *Molinio-Arrhenatheretea* R. Tx. 1937 class and of scrub-woodland vegetation (*Quercu-Fagetea* Br.-Bl. et Vlieg. 1937, *Rhamno-Prunetea* Rivas Goday et Garb. 1961; Fig. 2a). Amongst

the entomofauna, ubiquitous species dominated. Another frequent group included species of open areas and of dry open areas (Fig. 2b). The number and total cover of plant species known to be host plants for the entomofauna studied did not explain the insect species richness: the Spearman correlation coefficients were not significant for the number of plant species ($r_s = 0.04$, NS) or for the total cover of host plants ($r_s = -0.15$, NS). These parameters also did not explain the total counts of insects in grasslands ($r_s = -0.013$, NS and $r_s = -0.25$, NS, respectively).

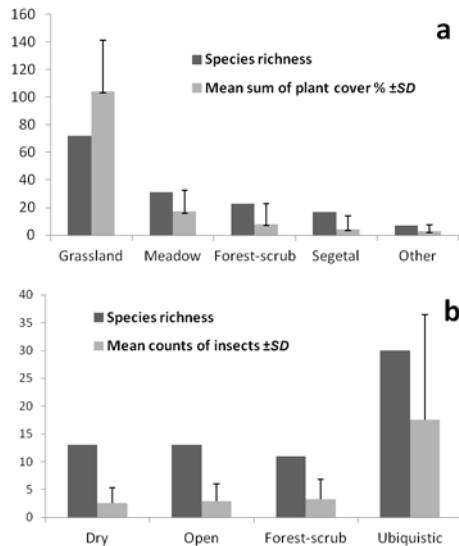


Fig. 2 Contribution of biotopic groups of plant species (a) and the contribution of biotopic groups of insect species to grasslands (b).

Null model of species diversity of entomofauna among sites, plant communities and five dominant plant species

The observed mean Pianka index of flower visitor communities between the plots was very low (0.0056) but was significantly higher than the mean 0 expected from chance ($P < 0.0001$). The observed variance was 0.0057 compared to 0 of the simulated matrices ($P < 0.0001$). The C-score of the distinguished guilds (15.14) was significantly lower than that expected from chance (17.80; $P < 0.004$). The observed variance score among the guilds (119.36) was not very different from the simulated value (70.77, NS). *Adonido-Brachypodietum pinnati* turned out to be the most abundant in terms of the observed insect species richness. However, the highest rarefied number of insect species was in the transitional community (Fig. 3a). The number of insect species and total density of specimens were highest on the flowers of *Inula ensifolia*. After rarefaction, however, species richness was highest on *Linum hirsutum* flowers (Fig. 3b). The mean Pianka index was 0.40, which was significantly higher than the mean simulated index (0.24); the same was true of the observed variance (0.19) versus the simulated variance (0.14).

Discussion

The relations between individual insect populations and the distribution of plant communities with host plants have been described [32,33]. There are some studies on the mutual dependence of insects and plants that demonstrate a positive correlation between plant species diversity and arthropod

diversity, including such groups of insects as herbivores, parasites and predators [34,35]. Among pollinators such a relationship has been demonstrated for bumblebees [36], hoverflies, solitary bees and large pollinators including social bees and butterflies [37,38]. Fontaine et al. [39] reported that increasing the functional diversity of both plants and pollinators led to the recruitment of more diverse plant communities. The functional diversity of pollinators influenced recruitment in terms of both the mean number of species and the mean number of plants. Feedback is implicated in this. Plant communities that are more diverse in terms of species richness and abundance are more attractive to pollinators. In our study, the number of species of flower visitors and their total counts on the plots increased with an increase of the vascular plant species that were present. It is important to stress the limitations of the method that was used in our study. The Pollard method in which the sampling lasted only 30 minutes (the time for vegetation sampling in the Braun-Blanquet method is similar for each plot) resulted in a relatively small number of species and total counts of insect individuals. As Ollerton and Cranmer showed [40], with an increasing sampling effort measured as the number of days of the study, the number of pollinators increases. A study that lasted less than ten days was unlikely to identify all of the pollinators of even a moderately generalized species. Moreover, other studies on the sampling of arthropod assemblages [16,26,41] of particular taxa, which used different methods, lasted several months over a period of two years or a site was visited at least twice a year. Plant cover turned out not to be a predictor of insect richness. Several studies have associated increased plant cover with increased numbers of insects. Martenko et al. [42] found a positive correlation between the cover of woody and perennial forbs and insect richness, which was not correlated with plant species richness. This observed pattern is the reverse of ours. Although we found a positive relationship between plant and insect species richness and diversity (Fig. 1a) and differences in the activity of flower visitors between vegetation types and individual dominant grassland plants (Fig. 3a,b), Co-CA failed to explain the patterns in the data. The ordination method, co-correspondence, which relates two community

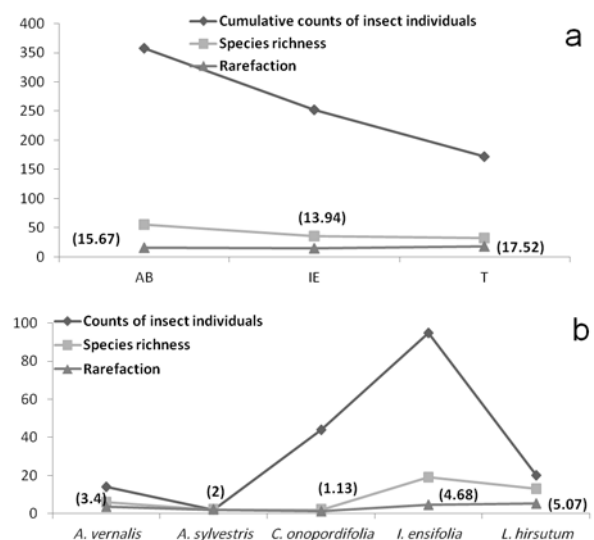


Fig. 3 a Comparison of observed and rarefied species diversity (in brackets) of insects found in the studied plant associations. b Comparison of observed and rarefied species diversity (in brackets) of flower visitors encountered on flowers of focal species. AB – *Adonido-Brachypodietum pinnati*; IE – *Inuletum ensifoliae*; T – transitional community.

compositions (plant and animal), was originally tested on the carabid beetle and vascular plant species along roadside verges in the Netherlands. Among others [16] found first two axes of Co-CA significant as well as high positive correlations between the first two axes of DCA. Also, it was reported that 28% of the variance in the species composition of water beetles was explained by wetland plants [41]. Due to the specific behavior of Carabidae, the method proved useful, unlike in our study with flying insects. Moreover, according to Lopes and Buzato [43], among native bees the variability of species number and abundance is significantly higher in fragmented landscapes. This phenomenon was probably an effect of local immigration. Another study [44] showed plant species composition to be a good predictor of seven functionally different arthropod groups (epigeic spiders, grasshoppers, ground beetles, weevils, hoppers, hoverflies and bees). In that work, all individual species, which are characteristic groups and community types, were good predictors of the species diversity of arthropods. For Aphidae bees (which dominated in our study) the percentage of the cross-validation fit was low (2.4%). In that study the vegetation units that were studied were more diverse: 10 semi-natural grassland types and one heathland type. In our study, the range of investigated plant communities was narrower. These were patches of plant associations classified to the *Cirsio-Brachypodium pinnati* alliance. In terms of species composition, the habitat requirements of these plant communities are similar [28]. Despite this, in terms of species richness, the type of community had an effect on flower visitors (Fig. 3b).

The phenological aspect of the relation of plant-visiting insects should be mentioned. Within the same study area, the numbers of insects and plants usually change during the vegetation season [25,45]. The period of imago activity for the majority of insects in the Northern Hemisphere is between May and August [46]. This is the result of the coincidence of the two main optimal temperatures for heat-labile animals and the availability of plant resources [47]. This means that on a plot with a dominance of early-flowering plants the abundance of possible pollinators should be lower.

Our finding that the moisture index affects insect species composition is in line with other studies [36,48]. Meadows with a higher meadow wetness index had a greater abundance of bumblebees than meadows with a lower wetness index. In our study, the wetness index was derived from known ecological responses of plants species. The significant explanatory power of moisture for the species composition of flower visitors agrees with the significant share of meadow species. This group was the second most represented in terms of both species richness and mean cover (Fig. 2a). Meadow species are known to be the most abundant source of floral resources [36]. A positive relationship has been described between insect richness and density of flowering ramets of plants [49]. Xerothermic grasslands are often places with a relatively high density of flowering plants. They can attract nectarivorous insects from the different types of habitats surrounding the study areas. As the majority of the investigated plots are situated in highly fragmented landscapes, the data on the relations between plant and pollinating insect diversity may contain artifacts as a result of the immigration of insects from the surroundings. As was mentioned, ubiquitous species prevailed in terms of both species richness and the number of individuals (Fig. 2b); these species are not stenotopic. Contrary to expectations, species typical for dry and xerothermic habitats did not have high shares. Analysis of the C-scores indicated that the insect communities

are not competitively structured; the observed value of the index was not higher than the simulated index. Furthermore, the null model showed a significant positive pattern of species co-occurrence, thus indicating that the species co-occur more often than is expected from chance. Such an interpretation of C-scores that were lower than the simulated values was given by [50], but in a completely different type of assemblage, bat parasite communities. The non-significant result of comparison of the observed and expected C-score variance suggests that the species were assigned to guilds randomly rather than based on co-occurrence behavior. This may result from the overrepresentation of ubiquitous species and short one-day observations of visiting insects. The number of flower visitor species differed between the five most abundant and dominant plant species (Fig. 3). The differences in the number of insects between plant communities were affected mainly by the presence of dominant species that differed in flower structure, size and attractiveness to insects. Most studies of this type are devoted to particular groups of flower visitors such as bees and bumblebees and do not take into account all of the potential pollinating species and flower visitors that are present in particular plant communities. The patterns observed in small groups cannot be generalized to all flower-visiting insects. The mobility of the investigated animals and the abundance of flowers are the main reasons why flower visitors/pollinating assemblages are not driven by competition. They show a tendency to co-occur rather than compete. Those two factors may be the reason why the species composition of the plants that provide food resources and microhabitats for these insects is not a crucial factor in the assembly rules of flower visitor communities. Another, and probably the most important factor, is restriction of Pollard method. Our results demonstrate that possible patterns in species composition and assembly rules of flower visitors are not apparent when the Pollard method is applied. Based on the data obtained using this method, flower-visiting assemblages do not seem to be driven by competition and they primarily show a tendency to co-occur, which may be artifact. A plant-focused method including rarefaction analysis yielded more insightful results and shed more light on the differences between the dominant plants that shape the physiognomy of plant communities in possible pollination specialization. However, this study does suggest that maintenance of the high biodiversity of grasslands should provide enough resources for all groups of flower visitors including pollinators. Conservation and management practices aimed at preserving large areas of grassland and preventing fragmentation will promote natural ecological processes and the proper functioning of ecosystems in the agricultural landscape.

Acknowledgments

This work was funded by the Ministry of Science and Higher Education, grant No. P04 G 025 28. We thank Piotr Skórka and the two anonymous reviewers for their many valuable comments on the draft of this paper.

Authors' contributions

The following declarations about authors' contributions to the research have been made: design of the study: DC; field research: DC, PA, ZD; analyzing data: DC; writing manuscript: DC, PA.

References

1. Cremene C, Groza G, Rakosy L, Schileyko AA, Baur A, Erhardt A, et al. Alterations of steppe-like grasslands in Eastern Europe: a threat to regional biodiversity hotspots. *Conserv Biol.* 2005;19(5):1606–1618. <http://dx.doi.org/10.1111/j.1523-1739.2005.00084.x>
2. Öckinger E, Eriksson AK, Smith HG. Effects of grassland abandonment, restoration and management on butterflies and vascular plants. *Biol Conserv.* 2006;133(3):291–300. <http://dx.doi.org/10.1016/j.biocon.2006.06.009>
3. Dzwonko Z, Loster S. Changes in species composition of an abandoned limestone grassland in relation to climatic conditions. *Pol J Ecol.* 2011;59(4):687–698.
4. Dzwonko Z, Loster S. Changes in plant species composition in abandoned and restored limestone grasslands – the effects of three and shrub cutting. *Acta Soc Bot Pol.* 2008;77(1):67–75.
5. Wahlman H, Milberg P. Management of semi-natural grassland vegetation: evaluation of a long-term experiment in southern Sweden. *Ann Bot Fenn.* 2002;39:159–166.
6. Bąba W, Kurowska M, Kopała-Bąba A, Wilczek A, Długosz J, Szarejko I. Genetic diversity of populations of *Brachypodium pinnatum* (L.) P. Beauv.: expansive grass in a fragmented landscape. *Pol J Ecol.* 2012;60(1):31–40.
7. Tschardtke T, Klein AM, Krüss A, Steffan-Dewenter I, Thies C. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol Lett.* 2005;8(8):857–874. <http://dx.doi.org/10.1111/j.1461-0248.2005.00782.x>
8. Kremen C, Williams NM, Aizen MA, Gemmill-Herren B, LeBuhn G, Minckley R, et al. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol Lett.* 2007;10(4):299–314. <http://dx.doi.org/10.1111/j.1461-0248.2007.01018.x>
9. Öckinger E, Smith HG. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *J Appl Ecol.* 2006;44(1):50–59. <http://dx.doi.org/10.1111/j.1365-2664.2006.01250.x>
10. Taki H, Kevan PG, Ascher JS. Landscape effects of forest loss in a pollination system. *Landsc Ecol.* 2007;22(10):1575–1587. <http://dx.doi.org/10.1007/s10980-007-9153-z>
11. Lopes LE, Buzato S. Variation in pollinator assemblages in a fragmented landscape and its effects on reproductive stages of a self-incompatible treelet, *Psychotria suterella* (Rubiaceae). *Oecologia.* 2007;154(2):305–314. <http://dx.doi.org/10.1007/s00442-007-0830-z>
12. Thomas JA, Bourn N. D, Clarke RT, Stewart KE, Simcox DJ, Pearman GS, et al. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proc R Soc Lond B Biol Sci.* 2001;268(1478):1791–1796. <http://dx.doi.org/10.1098/rspb.2001.1693>
13. Johnson SD, Steiner KE. Generalization versus specialization in plant pollination systems. *Trends Ecol Evol.* 2000;15(4):140–143. [http://dx.doi.org/10.1016/S0169-5347\(99\)01811-X](http://dx.doi.org/10.1016/S0169-5347(99)01811-X)
14. Zych M. On flower visitors and true pollinators: the case of protandrous *Heracleum sphondylium* L. (Apiaceae). *Plant Syst Evol.* 2006;263(3–4):159–179. <http://dx.doi.org/10.1007/s00606-006-0493-y>
15. Watts S, Ovalle DH, Herrera MM, Ollerton J. Pollinator effectiveness of native and non-native flower visitors to an apparently generalist Andean shrub, *Duranta mandonii* (Verbenaceae). *Plant Species Biol.* 2012;27(2):147–158. <http://dx.doi.org/10.1111/j.1442-1984.2011.00337.x>
16. ter Braak CJE, Schaffers AP. Co-correspondence analysis: a new ordination method to relate two community compositions. *Ecology.* 2004;85(3):834–846. <http://dx.doi.org/10.1890/03-0021>
17. Chmura D, Adamski P, Denisiuk Z. The plant-pollinator interactions in xerothermic habitats using phytosociological data. In: Chytrý M, editor. 17th International Workshop European Vegetation Survey. Using phytosociological data to address ecological questions, 1–5 May 2008, Brno, Czech Republic. Brno: Masaryk University; 2008. p. 25.
18. Denisiuk Z, Chmura D, Adamski P. Flowering and generative reproduction in small, isolated populations of endangered monocarpic perennial *Carlina onopordifolia* Besser (Asteraceae) in Poland. *Pol J Ecol.* 2009;57(1):89–97.
19. Westhoff V, van der Maarel E. The Braun-Blanquet approach. In: Whitaker RH, editor. Classification of plant communities. Hague: Junk; 1978. p. 287–399.
20. Pollard E. A method for assessing changes in the abundance of butterflies. *Biol Conserv.* 1977;12(2):115–134. [http://dx.doi.org/10.1016/0006-3207\(77\)90065-9](http://dx.doi.org/10.1016/0006-3207(77)90065-9)
21. Pollard E, Yates TJ. Monitoring butterflies for ecology and conservation: the British butterfly monitoring scheme. London: Chapman and Hall; 1993.
22. Tolman T. Butterflies of Europe. Princeton NJ: Princeton University Press; 2001.
23. De la Barrera E, Nobel PS. Nectar: properties, floral aspects, and speculations on origin. *Trends Plant Sci.* 2004;9(2):65–69. <http://dx.doi.org/10.1016/j.tplants.2003.12.003>
24. Hill MO. Diversity and evenness: a unifying notation and its consequences. *Ecology.* 1973;54:427–432.
25. The R project for statistical computing [Internet]. 2008 [cited 2012 Sep 27]; Available from: <http://www.R-project.org>
26. ter Braak CJE, Šmilauer P. CANOCO reference manual and CanoDraw for Windows user's guide: software for Canonical Community Ordination (version 4.5). New York NY: Microcomputer Power; 2002.
27. Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulißen D. Zeigerwerte der Pflanzen in Mitteleuropa. *Scr Geobot.* 1992;18:1–248.
28. Matuszkiewicz W. Przewodnik do oznaczania zbiorowisk roślinnych Polski. Warsaw: Polish Scientific Publishers PWN; 2001.
29. Gotelli NJ, Entsminger GL. EcoSim: null models software for ecology. Version 7 [Internet]. 2008 [cited 2012 Mar 31]; Available from: <http://www.garyentsminger.com/ecosim/index.htm>
30. Stone L, Roberts A. The checkerboard score and species distributions. *Oecologia.* 1990;85(1):74–79. <http://dx.doi.org/10.1007/BF00317345>
31. Gotelli NJ, McCabe DJ. Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. *Ecology.* 2002;83(8):2091–2096. [http://dx.doi.org/10.1890/0012-9658\(2002\)083\[2091:SCOAMA\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2002)083[2091:SCOAMA]2.0.CO;2)
32. van Der Werf W, Woldewahid G, Van Huis A, Butrous M, Sykora K. Plant communities can predict the distribution of solitary desert locust *Schistocerca gregaria*. *J Appl Ecol.* 2005;42(5):989–997. <http://dx.doi.org/10.1111/j.1365-2664.2005.01073.x>
33. Agrawal AA, Lau JA, Hambäck PA. Community heterogeneity and the evolution of interactions between plants and insect herbivores. *Q Rev Biol.* 2006;81(4):349–376.
34. Siemann E, Tilman D, Haarstad J, Ritchie R. Experimental tests of the dependence of arthropod diversity on plant diversity. *Am Nat.* 1998;152(5):738–750. <http://dx.doi.org/10.1086/286204>
35. Knops JMH, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, et al. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecol Lett.* 1999;2(5):286–293. <http://dx.doi.org/10.1046/j.1461-0248.1999.00083.x>
36. Hatfield R, LeBuhn G. Patch and landscape factors shape community assemblage of bumble bees, *Bombus* spp. (Hymenoptera: Apidae), in montane meadows. *Biol Conserv.* 2007;139(1–2):150–158. <http://dx.doi.org/10.1016/j.biocon.2007.06.019>
37. Albrecht M, Duelli P, Müller C, Kleijn D, Schmid B. The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. *J Appl Phycol.* 2007;44(4):813–822. <http://dx.doi.org/10.1111/j.1365-2664.2007.01306.x>
38. Skórka P, Settele J, Woyciechowski M. Effects of management cessation on grassland butterflies in southern Poland. *Agric Ecosyst Env.* 2007;121(4):319–324. <http://dx.doi.org/10.1016/j.agee.2006.11.001>
39. Fontaine C, Dajoz I, Meriguet J, Loreau M. Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *Plos Biol.* 2006;4(1):e1. <http://dx.doi.org/10.1371/journal.pbio.0040001>
40. Ollerton J, Cranmer L. Latitudinal trends in plant-pollinator interactions:

- are tropical plants more specialised? *Oikos*. 2002;98(2):340–350. <http://dx.doi.org/10.1034/j.1600-0706.2002.980215.x>
41. Gioria M, Bacaro G, Feehan J. Evaluating and interpreting cross-taxon congruence: potential pitfalls and solutions. *Acta Oecol*. 2011;37(3):187–194. <http://dx.doi.org/10.1016/j.actao.2011.02.001>
 42. Martinko EA, Hagen RH, Griffith JA. Successional change in the insect community of a fragmented landscape. *Landsc Ecol*. 2006;21(5):711–721. <http://dx.doi.org/10.1007/s10980-005-5322-0>
 43. Lopes LE, Buzato S. Variation in pollinator assemblages in a fragmented landscape and its effects on reproductive stages of a self-incompatible treelet, *Psychotria suterella* (Rubiaceae). *Oecologia*. 2007;154(2):305–314. <http://dx.doi.org/10.1007/s00442-007-0830-z>
 44. Schaffers AP, Raemakers IP, Sýkora KV, ter Braak CJF. Arthropod assemblages are best predicted by plant species composition. *Ecology*. 2008;89(3):782–794. <http://dx.doi.org/10.1890/07-0361.1>
 45. Hopwood JL. The contribution of roadside grassland restorations to native bee conservation. *Biol Conserv*. 2008;141(10):2632–2640. <http://dx.doi.org/10.1016/j.biocon.2008.07.026>
 46. Powell JA, Logan JA. Insect seasonality: circle map analysis of temperature-driven life cycles. *Theor Popul Biol*. 2005;67(3):161–179. <http://dx.doi.org/10.1016/j.tpb.2004.10.001>
 47. Yurk BP, Powell JA. Modeling the evolution of insect phenology. *Bull Math Biol*. 2008;71(4):952–979. <http://dx.doi.org/10.1007/s11538-008-9389-z>
 48. Moroń D, Lenda M, Skórka P, Szentgyörgyi H, Settele J, Woyciechowski M. Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes. *Biol Conserv*. 2009;142(7):1322–1332. <http://dx.doi.org/10.1016/j.biocon.2008.12.036>
 49. Kwaiser KS, Hendrix SD. Diversity and abundance of bees (Hymenoptera: Apiformes) in native and ruderal grasslands of agriculturally dominated landscapes. *Agric Ecosyst Env*. 2008;124(3–4):200–204. <http://dx.doi.org/10.1016/j.agee.2007.09.012>
 50. Tello JS, Stevens RD, Dick CW. Patterns of species co-occurrence and density compensation: a test for interspecific competition in bat ectoparasite infracommunities. *Oikos*. 2008;117(5):693–702. <http://dx.doi.org/10.1111/j.0030-1299.2008.16212.x>