



Biodiversity – economy or ecology? Long-term study of changes in the biodiversity of aphids living in steppe-like grasslands in Central Europe

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Abstract. This paper examines the changes in the species composition of aphids living in dry calcareous grasslands in Central Europe over a 25-year period. To the best of our knowledge, this is the first analysis of this type in the world that takes into account both previous and current data on species richness as well as groups of aphids that are distinguishable on the basis of biological and ecological criteria such as host-alternation and feeding types, life cycle, ecological niche, symbiosis with ants and their ecological functional groups. Over the period of more than 25 years, there has been a significant decrease in aphid α -diversity, from 171 to 105 species. The gain, which is in species not previously recorded, was 17 taxa. The loss of biodiversity occurred despite the fact that these habitats are protected and are valuable regional biodiversity hotspots. The losses are mostly related to intensive human activity in adjacent areas, which, unfortunately, has resulted in the isolation of these small, protected environmental islands by the removal of ecological corridors. Since, as is shown in this study, the frequencies between individual biological and ecological groups of aphids have been retained, it would be possible to restrict this loss of biodiversity if appropriate actions are taken.

INTRODUCTION

The fragments of steppe-like grasslands that still occur in Central Europe are characterized by a high richness of plant and animal species, especially small arthropods. This is why they are also called “regional biodiversity hotspots” (Cremene et al., 2005) and are protected as nature reserves (CRFOP, 2010) or included in the Natura 2000 European network (European Commission, 2013). Unfortunately, strong human interference in recent decades has caused the majority of these fragments of grassland to become smaller and smaller. At present, they exist only as small isolated “habitat islands”, and this may have resulted in biodiversity loss (Burkey, 1989; Collinge, 2000; Krauss et al., 2010).

Therefore, an important question is whether such an unfavourable process really occurs in these protected habitats. It is only possible to answer this question if we have the appropriate comparative data. This is possible for the presented group of insects as we have complete historical data. To fully identify the losses in terms of biodiversity over a period of over 25 years, both the former and current species richness of aphids were analyzed, as well as groups of aphids that were distinguished on the basis of specific biological and ecological criteria. This made it possible to

determine trends in the transformation of the aphid communities in these habitats and the losses or gains in terms of the biodiversity of Aphidoidea, which was the main goal of this study.

MATERIAL AND METHODS

Study areas

This comparative study was carried out in three steppe nature reserves (A – Krzyżanowice, 50°27'13"N, 20°33'36"E; B – Skowronno, 50°32'32.58"N, 20°29'10.76"E; C – Winiary Zagojskie, 50°25'52"N, 20°39'43"E), all of which are situated in lowland in the Nida Basin in southern Poland and two sites that are included in the NATURA 2000 programme (D – Góra Brodło, 50°43'36"N, 19°17'01"E; E – Wzgórze Zamkowe, 50°44'58"N, 19°16'26"E) in the Częstochowa Upland in southern Poland.

All of these sites are of the same phytosociological type, dry calcareous grassland assigned to the Festuco-Brometea class.

Biodiversity data

Historical data

Nida Basin; the data are from the 1980s (Szelegiewicz, 1981; Czyłok & Wojciechowski, 1987), which were supplemented at the beginning of the 1990s (Hałaj, 1996a, b).

Częstochowa Upland; the complete material comes from the years 1988–1990 (Hałaj, 1996c; Hałaj & Wojciechowski, 1996).

Current data

Material from all five sites was collected in 2011–2012 (Osiadacz & Hałaj, 2015) and supplemented by the authors in 2015–2016.

Insects collected

In all cases (in both the historical and present study), aphids were collected using standard methods (by visual inspection of all host plants in an area of approx. 50 m², at approximately two-week intervals during the entire vegetative seasons); next, the aphids were prepared (Hałaj & Osiadacz, 2016) and identified using specialist keys, a list of which is presented in the paper by Blackman & Eastop (2016). Historical specimens are deposited in the collection of the Museum and Institute of Zoology of Polish Academy of Sciences in Warsaw and the Department of Zoology of the University of Silesia in Katowice, while more recently collected specimens are deposited in the collection of the Department of Entomology and Environmental Protection of Poznan University of Life Sciences.

Analyses

Biological and ecological criteria

In addition to the strictly qualitative comparisons (species composition), the aphids were also compared in terms of biological and ecological criteria.

Host-feeding types (Heie, 1980; Hałaj & Osiadacz, 2016):

FT- α (monophagous and narrow oligophagous), species with a narrow host range that are trophically connected with one species or one genus of host plants;

FT- β (oligophagous and polyphagous), species with a broad host range, which includes the remaining aphids.

Life cycle (Heie, 1980; Blackman & Eastop, 2016; Hałaj & Osiadacz, 2016):

LC- α (anholocyclic), aphids with an incomplete life cycle, which reproduce only by parthenogenesis;

LC- β (holocyclic), aphids with a complete life cycle with a sexual generation and overwintering fertilized eggs.

Host-alternating (Heie, 1980; Blackman & Eastop, 2016; Hałaj & Osiadacz, 2016):

HA- α (monoecious), aphids that do not change their host during their life cycle;

HA- β (heteroecious), aphids that change their host during their life cycle.

Ecological niche (Blackman & Eastop, 2016):

EN- α : aphids that feed on the aboveground parts of plants, i.e. stalks, leaves, inflorescences;

EN- β : aphids that feed on ground level and underground parts of plants, i.e. root collars and roots.

Symbiosis type (Blackman & Eastop, 2016; Depa & Wojciechowski, 2008):

SA- α : aphids obligatorily attended by ants;

SA- β : aphids that are not attended by ants or only rarely.

Ecological functional groups (Osiadacz & Hałaj, 2016):

EFG- α : specialized species (S) that are monophagous and narrowly oligophagous (FT- α), mainly monoecious (HA- α) and holocyclic (LC- β) species of aphids living in forest-free areas covered by a dense growth of grass and herbaceous plants;

EFG- β : generalist opportunists (G) that are polyphagous and oligophagous (FT- β), mainly heteroecious (HA- β) and holocyclic or anholocyclic (LC- α or LC- β) species of aphids.

Statistical analysis

Since the data was binary, we applied an indirect nonlinear ordination method, i.e. non-metric multi-dimensional scaling (NMDS), to determine the community composition at the sites studied (Minchin, 1987; Oksanen et al., 2016). Bray-Curtis distance measures were used to construct the dissimilarity matrix.

In order to determine whether there are significant differences in species richness between the historical and current data, a Paired Sample T-test (data was normal, Shapiro-Test: $p > 0.05$) was used.

In order to determine differences in the frequencies in the functional groups between historical and current data, contingency tables (G test) were used.

All statistics were performed using the R Language and Environment (R Core Team, 2015, package *vegan*).

RESULTS

Losses and gains in species diversity

The data includes 188 species of aphids that occur in calcareous grasslands (Table 1), which constitutes as much as 12.5% of the aphid fauna in Europe. Of these, 171 taxa were found previously and only 105 currently. Thus, 66 species have been lost. Losses were also recorded in different regions in this study, a loss of 54 species (from 106 to 52) in the Nida Basin and 38 (from 120 to 82) in the Częstochowa Upland. The greatest increase was recorded at Góra Brodło (site D – as many as 43 species) and the lowest at Krzyżanowice (site A – only 4) (Table 1). During the current research, a slight gain of 17 species was recorded, which were not previously recorded in the calcareous grasslands at these sites. More species were recorded in the Częstochowa Upland (12 – out of which only eight here) and fewer in the Nida Valley (seven – out of which only three here). The largest number of new species (12) was recorded at Wzgórze Zamkowe (site E) and the lowest at Krzyżanowice (site A) and Skowronno (site B), with five species at each site (Table 1).

The losses of species were recorded for all the groups of aphid species distinguished and analyzed. The greatest losses were recorded for the holocyclic species (group LC- β – 76 species) and monoecious species (HA- α – 70), which live above ground (EN- α – 55) and are not attended by ants or only sometimes visited by ants (SA- β – 50), which, at the same time, are specialists with a narrow host range (SE- α – 46) (Table 1).

Changes in species richness and composition

The average species richness during the course of this study decreased significantly at the sites studied ($t = -3.8197$, $p = 0.01878$) from 65.6 ± 23 to 41.4 ± 16.2 . The NMDS analysis revealed that these sites varied over time and the gradient in species richness and differences in species compositions changed along the NMDS2 axis (Fig. 1). Considering the functional structure, there were no significant differences in the frequency of the different biological and ecological groups of species in the histori-

Table 1. Previous and current occurrence of aphids at the sites studied, taking into account biological and ecological groups. † – lost species, * – new species.

Aphid species	Biodiversity data (-1 – historical; -2 – current)										Biological and ecological criteria												
	Krzyżanowice		Skowronno		Winiary Zagojskie		Góra Brodno		Wzgórze Zamkowe		Host-feeding		Life cycle		Host-alternating		Ecological niche		Symbiosis with ants		Functional groups		
	A-1	A-2	B-1	B-2	C-1	C-2	D-1	D-2	E-1	E-2	FT-α	FT-β	LC-α	LC-β	HA-α	HA-β	EN-α	EN-β	SA-α	SA-β	EFG-α	EFG-β	
<i>Acaudinum centaureae</i> (Koch)	-	-	+	-	+	+	-	-	+	+	+	-	-	+	+	-	+	+	-	+	+	-	-
<i>Acyrtosiphon chelidonii</i> (Kaltenbach)	-	-	-	-	-	-	-	-	-	-	+	-	-	+	+	-	+	-	-	+	+	-	-
<i>Acyrtosiphon cyparissiae</i> (Koch) †	+	-	-	-	-	-	-	-	-	-	+	-	-	+	+	-	+	-	-	+	+	-	-
<i>Acyrtosiphon malvae malvae</i> (Mosley)	-	-	-	-	-	-	+	-	+	+	+	-	-	+	+	-	+	-	-	+	+	-	+
<i>Acyrtosiphon pisum pisum</i> (Harris)	+	+	+	+	-	+	-	+	-	+	-	+	-	+	+	-	+	-	-	+	+	-	+
<i>Ammiaphis sii</i> (Koch)	-	+	+	+	-	+	-	-	-	-	+	-	-	+	+	-	+	-	-	+	+	-	+
<i>Anoecia corni</i> (F.)	-	-	+	-	+	+	+	-	+	+	-	+	-	+	-	+	-	+	+	-	+	-	+
<i>Anoecia furcata</i> (Theobald) †	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Anoecia stipae</i> Mamontova	-	+	-	+	+	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Anoecia vagans</i> (Koch) †	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Anoecia zimnitsi</i> Mordvilko †	-	-	-	-	-	-	+	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Anuraphis catonii</i> Hille Ris Lambers †	-	-	+	-	+	-	+	-	+	-	-	+	-	+	-	+	-	+	+	-	+	-	+
<i>Anuraphis subterranea</i> (Walker) †	+	-	+	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis acetosae</i> L.	-	-	-	-	-	-	-	-	+	+	-	+	-	+	+	-	+	-	+	-	+	-	+
<i>Aphis antherici</i> Holman	-	-	-	-	-	-	-	+	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis austriaca</i> Hille Ris Lambers	-	-	-	-	+	+	+	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-	-
<i>Aphis breviseta</i> Holman †	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	-
<i>Aphis calaminthae</i> (Börner) †	-	-	-	-	-	+	+	-	+	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis chloris</i> Koch	-	+	+	+	+	+	+	+	+	+	+	-	+	+	-	+	-	+	+	-	+	-	+
<i>Aphis confusa</i> Walker	-	-	-	+	+	+	+	-	+	-	-	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis coronillae</i> Ferrari	+	+	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis craccae</i> L. *	-	+	-	+	-	+	-	-	+	+	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis craccivora</i> Koch	+	-	+	-	+	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis eryngiglomerata</i> Bozhko *	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis euphorbiae</i> Kaltenbach	+	-	-	-	+	+	+	+	+	+	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis fabae</i> Scopoli †	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis galiiscabri</i> Schrank	-	+	-	+	-	-	+	+	+	+	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis helianthemii</i> Ferrari	-	-	-	+	+	+	+	+	+	+	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis hieracii</i> Schrank †	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis jacobaeae</i> Schrank	-	-	+	+	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis klimeschi</i> (Börner)	-	+	-	-	+	+	+	+	+	+	+	-	+	+	-	+	-	+	-	+	-	+	-
<i>Aphis korshunovi</i> Ivanovskaja	-	-	-	-	-	-	+	+	+	+	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis lambersi</i> (Börner)	-	-	-	+	+	-	-	-	+	+	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis leontodontis</i> (Börner) †	-	-	-	-	-	-	-	-	+	+	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis molluginis</i> (Börner)	-	-	-	-	-	-	+	-	+	+	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis nasturtii</i> Kaltenbach	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis picridis</i> (Börner)	-	-	+	-	+	+	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis pilosellae</i> (Börner) †	-	-	-	-	+	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Aphis plantaginis</i> Goetze	+	-	-	-	-	-	+	+	+	+	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis polygonata</i> Nevsky *	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis pomi</i> de Geer	-	-	-	-	-	-	-	-	+	+	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis proffii</i> (Börner) †	+	-	-	+	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis psammophila</i> Szelegiewicz	-	-	-	-	-	-	-	-	+	+	-	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis roepkei</i> (Hille Ris Lambers) †	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis salviae</i> Walker *	-	+	-	+	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis sanguisorbae poterii</i> (Börner)	-	+	-	+	+	+	-	+	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis schilderi</i> (Börner)	-	+	+	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis sedi</i> Kaltenbach	-	-	-	-	+	+	+	+	+	+	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis selini</i> (Börner) †	-	-	+	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis serpylli</i> Koch	-	+	-	+	+	+	+	+	+	+	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis seseli</i> (Bozhko)	-	-	-	-	+	+	+	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis stachydis</i> Mordvilko	-	-	-	-	-	-	+	+	+	+	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis subnitida</i> (Börner) †	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis subviridis</i> (Börner)	-	-	-	-	-	-	+	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis tacita</i> Huculak †	-	-	-	-	+	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis taraxacicola</i> (Börner) *	-	-	-	-	-	-	-	-	+	+	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis teucriti</i> (Börner)	-	-	-	-	-	+	+	+	+	+	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis thesi</i> Holman	-	-	-	-	+	+	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis thomasi</i> (Börner) †	+	-	+	-	-	-	+	-	+	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis triglochis</i> Theobald †	-	-	-	-	+	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis umbrella</i> (Börner) †	+	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis urticata</i> J.F. Gmelin *	-	+	-	-	-	-	-	-	-	+	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis verbasci</i> Schrank	-	-	+	-	-	-	-	+	+	+	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Aphis verticillatae</i> (Börner) †	+	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis (Bursaphis) holiotherae</i> Rakauskas	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aphis (Pseudoprotaphis) erigerontis</i> (Holman) †	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aspidaphis adjuvans</i> (Walker) *	-	-	-	-	-	-	-	-	-	+	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Atheroides serrulatus</i> Haliday	-	-	-	-	+	-	-	-	+	+	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aulacorthum knautiae</i> Heie †	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Aulacorthum solani</i> (Kaltenbach)	-	-	+	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Brachycaudus (Acaudus) cardui</i> (L.)	+	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Brachycaudus (A.) linariae</i> Stroyan	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Brachycaudus (A.) mordvilkoii</i> Hille Ris Lambers	-	-	+	-	+	-	+	+	+	+	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Brachycaudus (A.) populi</i> (del Guercio)	-	-	-	-	-	-	-	+	+	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Brachycaudus (Appelia) prunicola</i> (Kaltenbach)	-	-	+	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Brachycaudus (A.) tragopogonis</i> (Kaltenbach) *	-	-	-	-	-	-	-	+	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Brachycaudus (Brachycaudus) helichrysi</i> (Kaltenbach)	-	-	-	-	-	-	-	+	+	+	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Brachycaudus (B.) salicinae</i> Börner	-	+	+	-	+	+	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Brachycaudus (Scrophulaphis) mimeuri</i> (Remaudière) †	-	-	+	-	+	-	+	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Brachycolus cucubali</i> (Passerini) †	-	-	-	-	-	-	-	-	+	+	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Brevicoryne brassicae</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Cavariella aegopodii</i> (Scopoli)	-	-	-	-	-	-	-	-	+	+	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Cavariella theobaldi</i> (Gillette et Bragg)	-	-	-	-	-	-	+	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Chaetosiphella stipae</i> Hille Ris Lambers †	-	-	-	-	+	-	-	-	-	-	-	+	-	+	-	+	-</						

Table 1 (continued).

Aphid species	Biodiversity data (-1 – historical; -2 – current)								Biological and ecological criteria														
	Krzyżanowice		Skowronno		Winiary Zagojskie		Góra Brodno		Wzgórze Zamkowe		Host-feeding	Life cycle	Host-alternating	Ecological niche	Symbiosis with ants	Functional groups							
	A-1	A-2	B-1	B-2	C-1	C-2	D-1	D-2	E-1	E-2	FT-α	FT-β	LC-α	LC-β	HA-α	HA-β	EN-α	EN-β	SA-α	SA-β	EFG-α	EFG-β	
<i>Diuraphis (Diuraphis) noxia</i> (Kurdjumov) *	-	+	-	+	-	+	-	-	-	-	+	-	+	+	-	+	-	-	+	-	+	-	+
<i>Dysaphis aereselini</i> Szelegiewicz †	-	-	+	-	-	-	-	-	-	-	+	-	+	+	-	+	-	+	+	-	+	-	+
<i>Dysaphis sorbi</i> (Kaltenbach) †	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-	+	-	+	+	-	-	-	+
<i>Forda formicaria</i> von Heyden †	-	-	-	-	-	+	-	-	+	-	-	+	+	-	+	-	+	+	-	-	-	-	+
<i>Forda marginata</i> Koch	-	-	-	-	+	-	-	-	+	+	-	+	-	+	-	-	+	+	-	-	-	-	+
<i>Geoica urticularia</i> (Passerini) †	-	-	-	-	+	-	+	-	+	-	-	+	+	-	+	-	+	+	-	-	-	-	+
<i>Hayhurstia atriplicis</i> (L.) *	-	-	-	-	+	-	+	-	+	-	-	+	-	+	-	+	-	+	-	-	-	-	+
<i>Hyadaphis hofmanni</i> (Börner)	-	+	-	-	-	-	-	-	+	-	+	-	-	+	-	+	-	+	-	+	+	-	-
<i>Hyadaphis molluginis</i> Börner †	-	-	-	-	+	-	+	-	-	-	+	-	-	+	-	+	-	+	-	+	+	-	-
<i>Hyadaphis mosana</i> Hille Ris Lambers †	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+	+	-	+	-	-	-
<i>Hyalopteroides humilis</i> (Walker) †	-	-	-	-	+	-	+	-	-	-	-	+	-	+	-	+	-	+	-	+	-	-	+
<i>Hyperomyzus (Hyperomyzus) lactucae</i> (L.) *	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	-	+
<i>Hyperomyzus (Neonasonovia) picridis</i> (Börner & Blunck) †	+	-	+	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	-	+
<i>Hyperomyzus (N.) zimitsi</i> Hille Ris Lambers †	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	-	+
<i>Izzypha bufo</i> (Walker) †	+	-	-	-	+	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	-	+
<i>Laingia psammae</i> Theobald	-	-	-	-	-	-	-	-	+	+	-	+	-	+	-	+	-	+	-	+	-	-	+
<i>Linosophon galiophagum</i> (Wimshurst)	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Liosomaphis berberidis</i> (Kaltenbach) †	-	-	+	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	-	+
<i>Lipaphis erysimi</i> (Kaltenbach)	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Lipaphis turitella</i> (Wahlgren) †	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Longicaudus trirhodus</i> (Walker) †	-	-	+	-	+	-	-	-	-	-	+	-	-	+	-	+	-	+	-	+	-	-	+
<i>Macrosiphoniella artemisiae</i> (Boyer de Fonscolombe)	+	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-	-	+
<i>Macrosiphoniella dimidiata</i> Börner	+	-	-	-	-	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-	-	+
<i>Macrosiphoniella millefolii</i> (de Geer)	+	+	-	+	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Macrosiphoniella subaequalis</i> Börner	+	-	-	-	+	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Macrosiphoniella subterranea</i> (Koch) †	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	+	-	-	+	-	-	+
<i>Macrosiphoniella usquetensis</i> Hille Ris Lambers	+	-	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Macrosiphoniella (Phalangomyzus) oblonga</i> (Mordvilko)	-	-	-	-	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Macrosiphoniella (Ramitrichophorus) medvedevi</i> Bozh. †	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-	+
<i>Macrosiphum euphorbiae</i> (Thomas)	-	-	+	-	+	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Macrosiphum rosae</i> (L.)	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Maculolachnus submacula</i> (Walker)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Megoura viciae</i> Buckton	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-
<i>Metopolophium festucae</i> (Theobald) †	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-	-	+	-	-	+	-	-	+
<i>Metopolophium fasciatum</i> Stroyan †	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	+	-	-	+	-	-	+
<i>Microlophium carnosum</i> (Buckton) *	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Myzaphis rosarum</i> (Kaltenbach)	-	-	-	-	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Myzus cerasi</i> (F.)	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	+	-	-	+	-	-	+
<i>Myzus langei</i> (Börner)	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Nasonovia compositellae nigra</i> (Hille Ris Lambers) †	+	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	+	-	-	+	-	-	+
<i>Nasonovia pilosellae</i> (Börner) †	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Nasonovia ribisnigri</i> (Moseley)	-	-	+	-	-	-	-	-	-	+	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Nevskya fungifera</i> (Ossiannilsson) †	+	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Phorodon humuli</i> (Shrank) †	-	-	+	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Plectrochophorus duponti</i> Hille Ris Lambers †	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	+	-	-	+	-	-	+
<i>Plectrochophorus glandulosus</i> (Kaltenbach) †	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Plectrochophorus persimilis</i> Börner †	-	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Protaphis carlinae</i> (Börner)	-	+	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Protaphis elongata</i> (Nevsky) †	-	-	+	-	+	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Protaphis hartigi</i> (Hille Ris Lambers) †	-	-	+	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Protrama flavescens</i> (Koch) †	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Protrama longitarsus</i> (Ferrari) †	-	-	+	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Pseudobrevicoryne erysimi</i> Holman	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Rhopalomyzus (Judenkoa) loniceriae</i> (Siebold) *	-	-	+	-	+	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Rhopalosiphum oxyacanthae</i> (Schrank)	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Rhopalosiphum maidis</i> (Fitch)	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Rhopalosiphum padi</i> (L.)	-	-	-	-	-	+	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+
<i>Schizaphis graminum</i> (Rondani) †	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-	-	+	-	-	+	-	-	+
<i>Schizaphis jaroslavi</i> (Mordvilko) †	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Semiaphis dauci</i> (F.)	+	-	-	-	+	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Semiaphis pimpinellae</i> (Kaltenbach)	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Sipha (Rungisia) elegans</i> del Guercio	-	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Sipha (R.) maydis</i> Passerini	-	+	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Sipha (Sipha) glyceriae</i> (Kaltenbach) †	-	-	-	-	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Sitobion avenae</i> (F.)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Sitobion fragariae</i> (Walker) †	-	-	-	-	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Smiela fusca</i> Mordvilko †	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Staegegeriella necopinata</i> (Börner)	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Taiwanomyzus alpicola</i> (Hille Ris Lambers)	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	+	-	-	-	+	-	-	+
<i>Therioaphis (Pterocallidium) luteola</i> (Börner)	-	+	+	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Therioaphis (P.) trifolii</i> (Monell)	+	-	+	-	+	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Therioaphis (Therioaphis) ononidis</i> (Kaltenbach) †	+	-	+	-	+	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Tetraneura ulmi</i> (L.)	+	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Titanosiphon artemisiae</i> (Koch)	-	-	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Toxoptera vandergootii</i> (Börner)	-	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Trama centaureae</i> Börner	-	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Trama troglodytes</i> von Heyden †	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Uroleucon (Uroleucon) achillaeae</i> (Koch)	-	-	-	-	-	-	+	+	-	+	+	-	+	+	-	+	+	-	+	+	-	+	+
<i>Uroleucon (U.) cichorii</i> (Koch)	+	-	+	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Uroleucon (U.) cirsi</i> (L.)	-	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Uroleucon (U.) grossum</i> (Hille Ris Lambers) †	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Uroleucon (U.) hypochoeridis</i> (F.)	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+	-	-	+	-	-	+
<i>Uroleucon (U.) leontodontis</i> (Hille Ris Lambers) *	-	-	-	-	-	-	+	-	-	-	+	-	-	+	-								

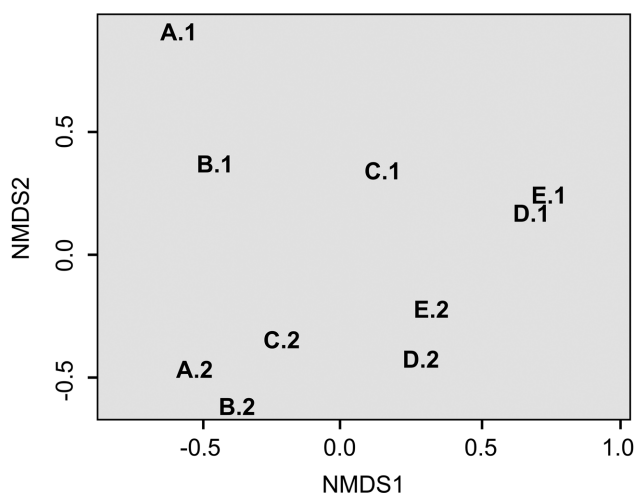


Fig. 1. Non-metric multi-dimensional scaling (NMDS) ordination of the results for all of the sites studied in two-dimensional space. Explanations: A–E – sites; 1 – historical data, 2 – current data.

cal and current records (Table 2). A significant increase at Wzgórze Zamkowe (site E) was recorded in group FT-β (oligophagous and polyphagous) compared to that in FT-α (monophagous and narrow oligophagous), and in SE-β (generalists) compared to that in SE-α (specialists) (Table 2).

DISCUSSION

Changes in biodiversity

Studies in recent years have shown that there have been dramatic decreases in biodiversity (e.g. Butchart et al., 2010; Boyle & Boyle, 2013; Burns et al., 2014; Kunz, 2016). Our study reveals that this happens not only in well-studied groups of insects, e.g. butterflies, beetles and Hymenoptera etc. (e.g. Stewart et al., 2007; Nowacki & Wąsala, 2008; Banaszak & Ratyńska, 2014; Senapathi et al., 2015; Pozsgai et al., 2016), but also in *suctorial phytophagous* insects, which are rarely thought of in terms of biodiversity. Our analyses have shown a decrease in the α-diversity of aphids over a period of more than 25 years at all the sites studied. Although this applies to aphids in all of the distinguished biological and ecological groups, the most worrying is the decrease in the number of specialists (SE-α) along with a simultaneous increase in the number of generalists (SE-β), which leads to “biotic homogenisation” (Fig. 1). Similar changes are reported in other dry grass-

lands studied (Osiadacz & Hałaj, 2016), which result in the “synanthropisation” of communities. This is most marked at Wzgórze Zamkowe (site E). Many specialist species are no longer recorded there, e.g. those of the genera *Aphis* and *Uroleucon*. *Coloradoa* spp., *Pleotrichophorus* spp. and *Xerobion judenkoi* also no longer occur there although their host plant (*Artemisia campestris*) is as abundant as previously (Urbisz, 2008). This confirms the thesis put forward by Osiadacz & Hałaj (2015). It is also reported in other types of habitats, e.g. bogs (Hałaj, 1991, 1993) and coniferous and broad-leaved forests (Hałaj & Wojciechowski, 1997; Durak & Wojciechowski, 2005) that the presence of host plants is not a sufficient condition for the occurrence of a specific species of aphid. The number of generalists, on the other hand, is associated with the increase in synanthropic plants that colonize these habitats. This also confirms another thesis that changes in the composition of an aphid community are closely related to changes in the composition of plant assemblages (which is also recorded for other invertebrates: Schaffers et al., 2008), which indicate important changes in the habitat (Osiadacz & Hałaj, 2016). On a much smaller scale, such a phenomenon was recorded at Wzgórze Zamkowe (sites E) and Góra Brodło (site D). As both sites are currently situated in a strongly developing tourist area in the Częstochowa Upland area, it is concluded that the changes in biodiversity are associated with tourism (Hall, 2010). However, despite the fact that a general loss in diversity was recorded at the sites analyzed, the frequencies of the occurrence of aphids in different biological and ecological groups remained the same (except at Wzgórze Zamkowe – site E). This indicates that there have not been similar changes in the habitats there and that it is possible to limit further losses if modern methods of protecting natural resources, which take into account the contemporary achievements of science, were used (Forman, 1995; Kunz, 2016). Therefore, one should consider actively protecting these sites, especially in respect to regaining and restoring ecological corridors. Perhaps, it will be necessary to limit tourism in order to avoid losing these precious dry calcareous grasslands (even the relic ones at Góra Brodło – site D: Wika, 1986).

Changes in landscape

Due to intensive human activity in a relatively small area, Europe has been and continues to experience a loss of biodiversity. This applies particularly to Central Eu-

Table 2. The percentage of biological and ecological groups of aphids at the sites studied. 1 – historical data, 2 – current data. Data in bold are significant (G-test) at p < 0.05.

Biological and ecological groups		A-1	A-2	B-1	B-2	C-1	C-2	D-1	D-2	E-1	E-2
Host-feeding types	FT-α	35.3	50.0	45.7	38.5	59.1	56.8	51.8	47.6	54.3	30.6
	FT-β	64.7	46.7	54.3	57.7	40.9	43.2	49.4	50.0	46.7	69.4
Life cycle	LC-α	2.9	10.0	6.5	11.5	12.1	10.8	8.2	4.8	8.7	5.6
	LC-β	97.1	90.0	93.5	88.5	87.9	89.2	91.8	95.2	91.3	94.4
Host-alternating	HA-α	88.2	93.3	78.3	84.6	87.9	86.5	81.2	88.1	88.0	76.4
	HA-β	11.8	6.7	21.7	15.4	12.1	13.5	18.8	11.9	12.0	23.6
Ecological niche	EN-α	82.4	80.0	65.2	84.6	65.2	70.3	72.9	83.3	73.9	83.3
	EN-β	17.6	20.0	34.8	15.4	34.8	29.7	27.1	16.7	26.1	16.7
Symbiosis with ants	SA-α	26.5	43.3	41.3	50.0	48.5	48.6	36.5	31.0	44.6	38.9
	SA-β	73.5	56.7	58.7	50.0	51.5	51.4	63.5	69.0	55.4	61.1
Ecological functional groups	EFG-α	46.7	35.3	47.8	46.2	60.6	59.5	55.3	50.0	56.5	33.3
	EFG-β	63.3	64.7	52.2	53.8	39.4	40.5	44.7	50.0	43.5	66.7

rope. In this region, the character of the economy changed after changes in the political system. As a result, the direct actions that influence nature have intensified. They are especially visible in the transformation of landscapes, especially by their fragmentation (e.g. new traffic routes, housing, tourist accommodation, agrocenoses, bodies of water etc.). The fragmentation of habitats causes a significant loss of biodiversity (Krauss et al., 2010). This process is significantly influenced by the size of the fragments in the habitats that are saved (if their surface area decreases, this process becomes more intense) or the loss of ecological corridors (no connection between local populations of a species within the metapopulation can lead to its extinction) (Burkey, 1989; Moilanen & Hanski, 1998; Collinge, 2000; Wallis De Vries et al., 2002). These phenomena are the main causes of the loss of biodiversity in the habitats studied. Although the sites that were analyzed in this study have been protected since the 1950s, due to changes in the political system and the introduction of a market economy, their surrounding area was heavily transformed, which broke the connections between protected patches and sites. In addition, sheep farming, which was undoubtedly a stabilizing factor, was also abandoned (Fischer et al., 1996; Poschlod & Bonn, 1998). Moreover, the recent intensive development of tourism in these areas is not a factor that promotes the preservation of the status of these areas (Vaughan, 2000).

CONCLUSION

This analysis demonstrates there has been a considerable decrease in the biodiversity of aphids in the entire area studied over a period of a quarter of a century. This process is especially dangerous because it has resulted in the loss of ubiquitous species, which results in the gradual “homogenisation of communities”, which along with a small increase in generalist species leads to the synanthropisation of communities. The main cause of these changes is human activity associated with the economy (development of agriculture and tourism). As a result, the connectivity among local habitat islands no longer exists due to the disappearance of ecological corridors. In addition, such isolated islands gradually become limited territorially (decreased), which reduces the level of connection among the local populations of species within metapopulations, which, along with the decrease in their area, affect the rate of extinction. If we combine these regional factors with global ones (climate change), then the processes of extinction become more dramatic. Obviously, the conflict between “anthropogenization” and biodiversity (since the first human settlements) will continue and its balance will never be equal to zero (as in the natural landscape). However, by applying the principles of sustainable development (taking into account the results of the latest ecological trends), the process can be or even should be mitigated. In the long term, it may turn out that the expected benefits from the infrastructure that is created will only be an insignificant percentage of the losses that are associated with the decrease in biodiversity.

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