Tuexenia 40: 459–478. Göttingen 2020.
doi: 10.14471/2020.40.015, available online at www.zobodat.at

Ancient settlements in Southern Ukraine: how do local and landscape factors shape vascular plant diversity patterns in the last remnants of grass steppe vegetation?

Antike Siedlungen in der Südukraine: Wie prägen die lokalen und landschaftlichen Faktoren die Diversitätsmuster der Gefäßpflanzen in den letzten Überresten der Steppenvegetation?

Polina Dayneko[1, *], Ivan Moysiyenko[1], Iwona Dembicz[2], Maria Zachwatowicz[3] & Barbara Sudnik-Wójcikowska[2]

[1]Department of Botany, Kherson State University, ul. Universytetska 27, 73000 Kherson, Ukraine;
[2]Institute of Environmental Biology, Faculty of Biology, University of Warsaw, ul. Żwirki i Wigury 101, 02-089 Warsaw, Poland;
[3]Department of Geoecology, Faculty of Geography and Regional Studies, University of Warsaw, ul. Krakowskie Przedmieście 30, 00-927 Warsaw, Poland
**Corresponding author, e-mail: daynekopm@gmail.com*

Abstract

Agricultural intensification in the last century resulted in a significant loss and fragmentation of steppe habitats. As a result, steppes are scattered and rarely preserved in highly transformed landscapes. Steppe patches have often remained on sites with cultural importance, such as ancient burial mounds (kurgans), old cemeteries or ancient settlements (earthworks). Thus, not only natural but also cultural objects could show a high conservation value. We hypothesised that ancient settlements (3rd – 2nd century BC) may act as steppe habitat islands, equally important as e.g. burial mounds for steppe plant protection. The aim of this study was to examine the local and landscape factors affecting vascular plants' richness patterns in ancient settlements and to check the importance of such ancient settlements for nature conservation. We asked the following questions: 1) How high is the species richness of vascular plants on ancient settlements? 2) Do ancient settlements have a nature conservation value comparable to other steppe enclaves of the studied zone? 3) Which factors are the most important for the species richness and species composition in ancient settlements? We analysed total richness and its separate categories as dependent variables in simple regressions against seven environmental variables such as ancient settlement's area, microhabitat variety index, afforestation degree, steppe cover in 1 km buffer around an ancient settlement, distance to the closest settlements, area of settlements in 1 km buffer around an ancient settlement and mean annual precipitation. In 18 studied ancient settlements located in the Lower Dnipro basin (Southern Ukraine), we recorded a considerable number of native (396 species, 75.6%), steppe (239 species, 45.6%) and non-synanthropic plants (225 species, 42.9%), which indicated a good state of preservation of the steppe on these objects. The microhabitat variety index, as a measure of habitat heterogeneity, appeared to be the most significant positive predictor of total species richness, followed by ancient settlement's area, afforestation degree and steppe cover around the ancient settlements. The same factors were significant for the richness of non-synanthropic plants. Distance to settlements was a significant negative predictor for established alien species richness. Our study confirmed that ancient settlements are valuable enclaves of steppe flora, surprisingly species-rich and of relatively

Manuscript received 15 March 2020, accepted 29 May 2020
Co-ordinating Editor: Balázs Deák

high ratio of steppe and non-synanthropic plants compared to the flora of nature reserves and kurgans. Our results could help to better plan active protection of plant diversity on ancient settlements, e.g. through steppe restoration around the ancient settlements, maintenance of small-scale disturbance and microhabitat diversity (pastures, mown areas, burnt areas, loess or limestone extraction sites etc.) and limiting afforestation to a certain degree.

Keywords: ancient settlements, biodiversity drivers, Lower Dnipro basin, nature conservation, vascular plant richness patterns

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

The steppes are among the most transformed biomes in Europe (VALKÓ et al. 2016). Within the contemporary borders of Ukraine, the forest cover has decreased almost three times (from 50% to 17% of the area) from the 1st century AD to present, while the steppe area has diminished nearly forty times, presently covering only 1% of today's territory of the country (BURKOVSKYI et al. 2013). This dramatic and nearly total destruction of Ukrainian steppes was primarily induced by the availability of fertile chernozems and chestnut soils and the fact that extensive steppe areas were located in favourable topographic conditions, and secondly resulted from exceptionally easy terms for agricultural exploitation with no need of drainage or uprooting of trees.

The Soviet Union actively developed a utilitarian attitude towards nature; therefore, the unfavourable attitude towards the steppes was aggravated in Soviet times (CHIBILYOV 2002, MOON 2016). "Empty places", being in fact the virgin steppes, were converted to "useful" land in every possible way: mostly by ploughing, but also by afforestation, urbanisation and mining activities. As a result, the steppes have been almost completely destroyed, are preserved today only in small steppe reserve enclaves or in areas that are not suitable for agricultural use (e.g. steep slopes of river valleys, loess ravines, rocky outcrops etc.) and therefore require careful protection. Steppe patches surrounded by adverse environmental conditions are often considered habitat islands.

Such habitat islands are supposed to function in consistence with the equilibrium theory of island biogeography by MACARTHUR & WILSON (1967). The theory, being a mainstay of biogeography, has been the subject of a broad debate in scientific literature (ANDRZEJEWSKI 2002, HAILA 2002, AKATOV 2013, MENDENHALL et al. 2014). One should bear in mind that the species richness in continental habitat islands depends, apart from patch size and isolation, on other important factors such as patch heterogeneity, edge effects, specifics of landscape matrix and habitat amount in the surrounding landscape (e.g. FAHRIG 2003, EWERS & DIDHAM 2006).

Recent studies have demonstrated the high importance of habitat islands of anthropogenic origin, such as burial mounds and kurgans (MOYSIYENKO & SUDNIK-WÓJCIKOWSKA 2006, SUDNIK-WÓJCIKOWSKA et al. 2011, MOYSIYENKO et al. 2015, DEÁK et al. 2016, 2018; VALKÓ et al. 2018), sacred groves and forest enclaves (BHAGWAT & RUTTE 2006, BRANDT et al. 2013) or cemeteries and graveyards (BARRETT & BARRETT 2001, LÖKI et al. 2019) for biodiversity conservation. Prehistoric and historic ancient settlements (known also as earthworks and in some regions as castle hills or hillforts) can play the role of habitat islands and function as a "reservoir" of species introduced by humans in former centuries (WYRWA 2003, CELKA 2007, 2011; SUDER 2011, MOYSIYENKO et al. 2018, 2020). They have been studied relatively extensively in Central Europe in terms of relationships between the contemporary distribution of weed species and historic human settlements (HERBICH 1996) and were found to be enclaves for many rare species typical for dry and mesic grasslands in the nemoral zone (CELKA 2007, SUDER 2011) as well as the sites where relics of cultivation were revealed (CELKA 2011). Though the role of ancient settlements in the steppe zone in preserving many rare steppe plant species was confirmed only recently (MOYSIYENKO et al. 2018, DAYNEKO 2019, MOYSIYENKO et al. 2020), there has neither been any research on diversity patterns of these objects nor on environmental factors affecting their species richness and vegetation composition. A better understanding of such factors seems to be essential to develop conservation measures for the protection of steppe plants and the vegetation of steppe patches on ancient settlements. Therefore, in this study we asked: (1) How high is the species richness of vascular plants on ancient settlements located in the grass steppe zone of Southern Ukraine? (2) Do ancient settlements have a nature conservation value comparable to other steppe enclaves of the studied zone? (3) Which factors are the most important for the species richness and species composition in ancient settlements?

2. Materials and methods

2.1 Study area

The research was conducted in the Lower Dnipro region (Southern Ukraine), 40–100 m a.s.l. (ZAMORYI 1961), in the provinces Kherson and Mykolayiv (46.48–47.37° N, 32.00–33.97° E). The Lower Dnipro region is located in the West Pontic grass steppe zone of the Eastern European Plain (BOHN et al. 2000). The climate is continental, with a mean annual temperature of 9–10 °C (MARYNYCH & SHYSHCHENKO 2005). Loess is the most common geological surface formation in the region, reaching a thickness of several tens of meters. Under the loess lay Neogene deposits (limestone, sands, sandstones, marls and clays) in the whole territory along the Lower Dnipro. A dominating undulating topography sets it significantly apart from surrounding steppe plains. The soil types represented within the study area are: low-humus chernozem, dark chestnut, sod and clay sand and meadow-swamp soils (MARYNYCH & SHYSHCHENKO 2005).

According to the geobotanical division of the Eurasian Steppe Zone, the Lower Dnipro region is located in the Black Sea and Azov sub-province of the Pontic steppe province (ANDRIENKO et al. 1977). The steppe physiognomy in the region is determined by tussock grasses of the genera *Stipa*, *Festuca*, *Koeleria* and *Agropyron* (LAVRENKO et al. 1991, BOHN et al. 2000). Depending on the types of soils, the steppe vegetation is represented by three classes: *Festuco-Brometea* Br.-Bl. et Tx.ex Soó (meadow steppes, especially spread on the border with the steppe zone, and fescue-needle grass steppes) on chernozem soils, *Helianthemo-Thymetea* Romaschenko, Didukh et V. Sl. (steppe calciphilous communities located in the southeastern part of Southern Ukraine) on carbonate rendzinas and *Festucetea vaginatae* Soó ex Vičherek (steppe psammophytic communities, scattered in river valleys) on sandy deposits.

Historically, the territory of the Lower Dnipro region was inhabited, visited or invaded by many different ethnic cultures, which succeeded one another from the middle of the Bronze to the Iron Age. Their cultural heritage such as the ancient settlements and kurgans are essential elements of the interior of Southern Ukraine to this day. Most of the ancient settlements were created from the 3rd to the 2nd century BC; however, some of the ancient settlements were used for many subsequent centuries by different ancient cultures. Due to defensive and economic reasons (mostly trade), basically all post-Scythian settlements were constructed on the steep banks of the Dnipro river, usually between two closely located ravines (locally called *balkas*) (GAVRYLYUK 2001, GAVRYLYUK & MATERA 2016).

Ancient settlements where surrounded by steppes during the period of their existence. Over time they have been left abandoned for many centuries, which allowed spontaneous steppe recovery on their surfaces. Therefore, ancient settlements have a specific role as nature refuge for biodiversity and especially for the flora in today's intensively used agricultural landscapes.

2.2 Selected ancient settlements and vascular plant richness data

In our study we used complete species lists of vascular plants from 18 ancient settlements located on the Dnipro river banks (Fig. 1, 2), which were surveyed at least three times during the growth seasons from 2015 to 2019 (MOYSIYENKO et al. 2020). We included all ancient settlements in the Lower Dnipro region that have survived to the present. Due to the construction of the Kakhovka reservoir in the 1950s, a significant number of archaeological sites, especially on the left bank of the Dnipro river, have been destroyed (i.e. ancient settlements in Bilozerka, Kairy and Hornostaivka; GAVRYLYUK & MATERA 2016). For details on the studied ancient settlements, i.e. coordinates, area, age, culture that built and/or used the ancient settlement and distance from existing settlements, see Supplement E1.

We classified each species as a "steppe" or "non-steppe" species and assigned it to the appropriate group of the historical-geographical classification scheme according to KORNAŚ (1977): native species including non-synanthropic species – natives occurring exclusively in natural or semi-natural vegetation; apophytes – natives associated with anthropogenic habitats; hemiapophytes – natives associated with natural and anthropogenic (mostly semi-natural) habitats; alien species including archaeophytes – arrived in Europe before the year 1500; kenophytes – introduced after the year 1500. Both groups are permanently established, in contrast to ergasiophygophytes – cultivated aliens escaping from cultivation and appearing temporarily.

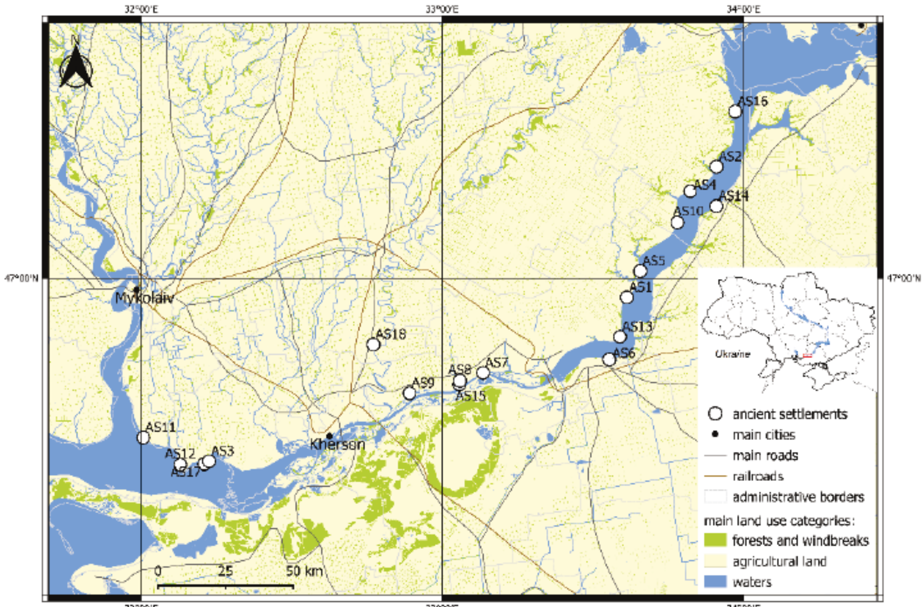

Fig. 1. Location of 18 studied ancient settlements within the Lower Dnipro (Southern Ukraine). Explanation: AS1 – Chervonomaiatske, AS2 – Gavrylivske, AS3 - Glyboka Prystan, AS4 – Hannivske, AS5 – Konsulivske, AS6 – Liubymivske, AS7 – Lvivske, AS8 – Male Tiagynske, AS9 – Poniativske, AS10 – Sablukivske, AS11 – Skelka, AS12 – Stanislavske, AS13 – Staroshvedske, AS14 – Velykolepetykhske, AS15 – Velyke Tiagynske, AS16 – Zolotabalkivske, AS17 – Zolotyi Mys, AS18 – Oleksandrivka-Roksanivka. Map was created in QGIS 3.10.1 (QGIS Development Team 2019), Open Street Map (© OpenStreetMap contributors), Natural Earth (https://www.naturalearthdata.com) and Wikimedia Commons (https://commons.wikimedia.org/wiki/File:Map_of_Ukraine_political_simple_blank.png).

Abb. 1. Lage von 18 untersuchten antiken Siedlungen am Ufer des Unteren Dnepr (Südukraine).

The abundance of each species on each ancient settlement was assessed using a 3-point scale: 1 – sporadic, 2 – infrequent, 3 – common species.

Additionally, we used data published by MOSYAKIN & FEDORONCHUK (1999), MOYSIYENKO (2007, 2013), BOIKO (2010), SUDNIK-WÓJCIKOWSKA et al. (2011, 2012), SHAPOVAL (2012), and MOYSIYENKO et al. (2014, 2019) in order to link the flora of ancient settlements to other steppe enclaves.

2.3 Environmental data

To test for a relationship between the ancient settlement's area and the species richness, we measured the area of each ancient settlement using QGIS software (QGIS DEVELOPMENT TEAM 2019). With the same software and Google and Bing satellite images (as a complementary source) available in the Open Layers Plugin, we mapped steppe areas and current settlement areas in 1 km radius around each ancient settlement. The steppe cover in this 1 km buffer was used to determine the connectivity of the remaining steppe patches on the ancient settlements with other steppe patches in the surrounding landscape, while the settlement areas in the 1 km buffer were analysed in order to assess the potential pressure of human activities on the species richness of the studied objects. Additionally, we measured the distance to the nearest settlement in order to estimate the level of human disturbance.

Many steppe areas are subject to man-made afforestation or woody encroachment, both of which leads to a destruction of steppe vegetation. Thus, we assessed the percentage of the total area of an ancient settlement affected by afforestation or encroachment of trees or shrubs as a factor called afforestation degree using a six-grade scale: 0.5 – less than 1% of the area covered by trees and shrubs, 1 – (1–5%), 2 – (6–25%), 3 – (26–50%), 4 – (51–75%), 5 – (75–100%).

Ancient settlements in the studied region are often used or managed by people, and there are a number of natural and human disturbances creating "microhabitats" like: pastures, mown areas, afforested areas, burnt areas, loess or limestone extraction sites, roads, inner gullies, excavations, military and electrical supports, dumps and wellsprings. In order to reflect the microhabitat diversity (i.e. the amount of natural and human-induced impact on ancient settlements), we calculated a microhabitat variety index as a sum of all microhabitat types present at a given ancient settlement.

As annual precipitation is one of the strongest environmental factors shaping diversity patterns in the steppe zone of Ukraine (MARYNYCH & SHYSHCHENKO 2005) and our ancient settlements were located in large geographical distance, we also used mean annual precipitation data obtained from the WorldClim 2 database (FICK & HIJMANS 2017) in the analyses.

2.4 Data analysis

In order to check for the influence of environmental factors on species richness of the ancient settlements, we subjected four variables, i.e. total richness (the number of all vascular plant species recorded), number of non-synanthropic species, number of established alien species and ratio of non-synanthropic species in total richness, to a regression analysis performed in R software (R CORE TEAM 2017). We analysed these groups and the ratio as dependent variables against seven environmental variables as predictors (ancient settlement's area, microhabitat variety index, afforestation degree, steppe cover in 1 km buffer around an ancient settlement, distance to the closest settlements, area of settlements in 1 km buffer around an ancient settlement and annual mean precipitation) (Table 1). Because of the limited number of studied ancient settlements, we decided to use several univariate regressions instead of single multiple regression models to avoid model overfitting. In all univariate models we additionally tested the inclusion of a quadratic term of the given environmental variable using t-test. If the quadratic term was significant ($p < 0.05$), it was included in the regression together with the linear term of the given variable. The regression models' overall significance and fit were assessed using F-test and R^2, respectively. Additionally, we checked for correlations between the environmental variables used in our analyses to enable more accurate interpretation of the results. The Pearson correlation coefficients are presented in Supplement E2.

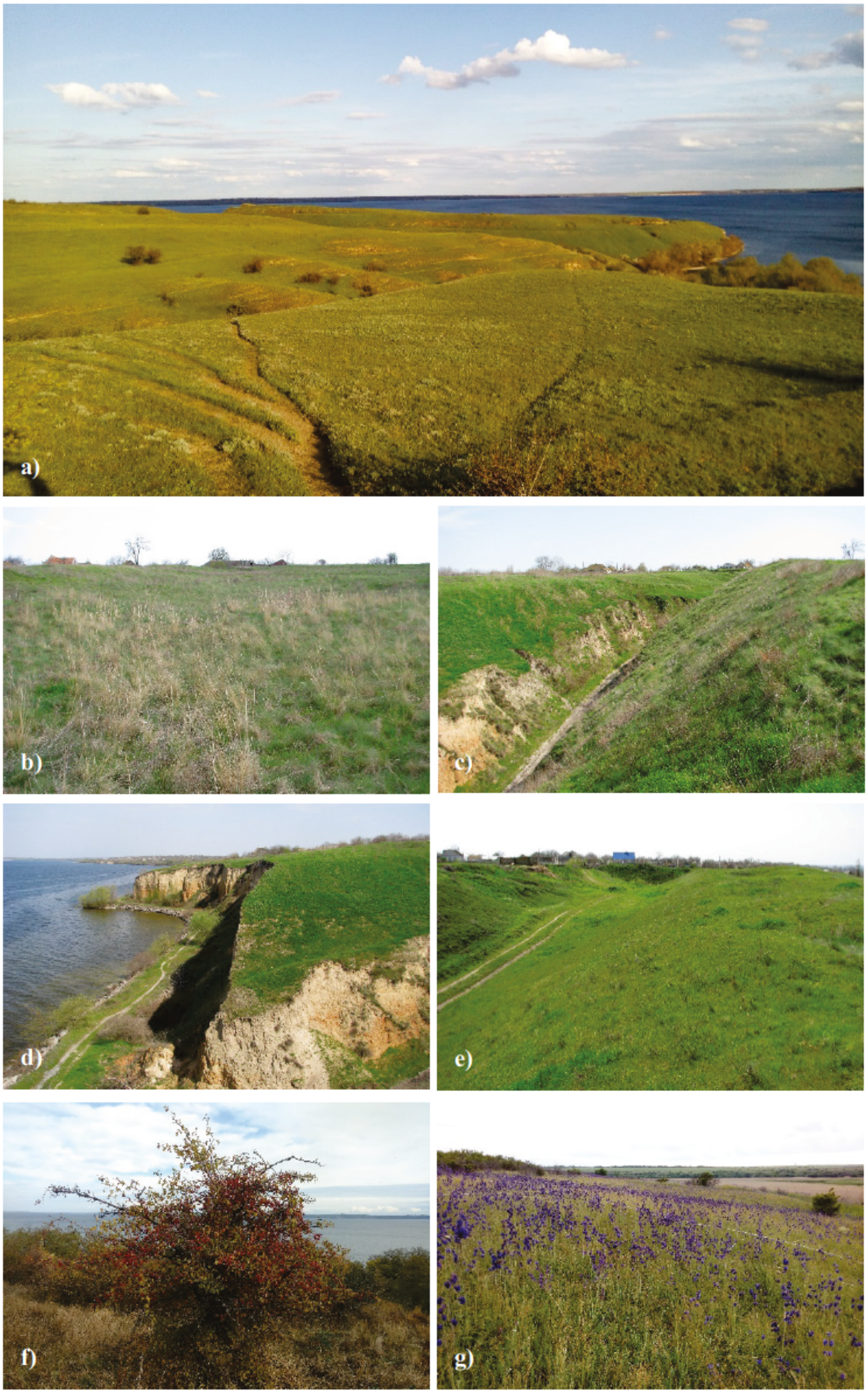
a)
b)
c)
d)
e)
f)
g)

Table 1. Explanatory variables used in simple linear and quadratic regressions performed for plant species richness on the ancient settlements ($n = 18$) studied in Southern Ukraine.

Tabelle 1. Erklärende Variablen für den Pflanzenartenreichtum der 18 in der Südukraine untersuchten antiken Siedlungen, die in einfachen linearen und quadratischen Regressionen verwendet wurden.

Explanatory variables	Mean ± SD	Min.	Max.
Numerical			
Area (ha)	6.3 ± 4.3	1.3	20.6
Steppe cover in 1 km buffer (ha)	37.5 ± 25.4	6.8	107.1
Area of settlements in 1 km buffer (ha)	70.7 ± 54.8	0	175
Distance to settlements (km)	0.8 ± 1.1	0	3.4
Mean annual precipitation (mm)	430.6 ± 9.2	410	448
Ordinal			
Afforestation degree	"0.5" – six ancient settlements; "1" – three ancient settlements; "2" – four ancient settlements; "3" – two ancient settlements; "4" – two ancient settlements; "5" – one ancient settlement		
Microhabitat variety index	"1" – one ancient settlement; "2" – four ancient settlements; "3" – five ancient settlements; "4" – three ancient settlements; "6" – five ancient settlements		

To check for patterns in the species composition of ancient settlements and to assess the role of environmental variables in shaping these patterns, we used the data on species abundance (in 1–3 scale) and environmental variables of the studied ancient settlements for a redundancy analysis (RDA) performed in Canoco version 5.0 (BRAAK & ŠMILAUER 2012). As environmental variables we used the same set as in the regression analysis (Table 1). Since the species lists were rather long and the number of studied objects limited, we decided to exclude very rare species from the analysis, i.e. those occurring on three or less ancient settlements.

---

vorherige Seite (previous page):

Fig. 2. General views of some ancient settlements of the Lower Dnipro: **a)** panorama of the Chervonomaiatske ancient settlement, **b)** spatial structures of the Liubymivske ancient settlement (plain part), **c)** natural defensive moat (Liubymivske ancient settlement), **d)** cliff (Liubymivske ancient settlement), **e)** artificial defensive moat (Liubymivske ancient settlement), **f)** Gavrylivske ancient settlement with the highest afforestation degree (*Rosa corymbifera*), **g)** Velyke Tiagynske ancient settlement with the vascular plant diversity (*Salvia nutans* aspect) (Photos: I. Moysiyenko, 2017 and 2018).

Abb. 2. Ansichten einiger antiker Siedlungen am Unteren Dnepr: **a)** Panorama der antiken Siedlung Chervonomaiatske, **b)** räumliche Strukturen der antiken Siedlung Liubymivske (ebener Teil), **c)** natürlicher Verteidigungsgraben (antike Siedlung Liubymivske), **d)** Klippe (antike Siedlung Liubymivske), **e)** künstlicher Verteidigungsgraben (antike Siedlung Liubymivske), **f)** die antike Siedlung Gavrylivske mit dem höchsten Aufforstungsgrad (*Rosa corymbifera*), **g)** die antike Siedlung Velyke Tiagynske mit der höchsten Arrtenvielfalt (*Salvia nutans*-Aspekt) (Fotos: I. Moysiyenko, 2017 und 2018).

3. Results

Overall, we found 524 species belonging to 283 genera, 74 families, 3 classes and 2 divisions. A full list of the flora of vascular plants in the ancient settlements of the Lower Dnipro is available in previous studies (DAYNEKO 2019, MOYSIYENKO et al. 2020). Total species richness ranged from 125 (Gavrylivske) to 290 (Velyke Tiagynske). The mean number of vascular plant species per archaeological site was 178. The flora of the investigated ancient settlements represents 10.3% of the flora of Ukraine, which includes 5100 species (MOSYAKIN & FEDORONCHUK 1999).

A majority of 75.6% (396 species) of all species that occurred on the ancient settlements were native plants. The share of native species in total species richness varied much from 62.1% (Liubymivske) to 81.7% (Velyke Tiagynske). More than half of this group (i.e. 225 species) and 42.9% of the total number of species were non-synanthropic plants, represented on the ancient settlements mostly by steppe plants and halophytes. It should be noted that non-synanthropic species include not only steppe species, but also those originating from moist and forest habitats (these species were sometimes noted on ancient settlements). Non-synanthropic plants occurring with the highest frequency were: *Kochia prostrata* (L.) Schrad., *Potentilla recta* L., *Teucrium polium* L., *Thymus dimorphus* Klokov & Des.-Shost., *Koeleria cristata* Pers., *Festuca valesiaca* Schleich. ex Gaudin and *Verbascum phoeniceum* L. Worth noting separately are steppe non-synanthropes like *Amygdalus nana* L., *Carduus uncinatus* M.Bieb., *Carex melanostachya* Willd., *Carex supina* Wahlenb., *Festuca rupicola* Heuff., *Gagea bulbifera* Salisb., *Hylotelephium stepposum* (Boriss.) Tzvelev, *Kochia prostrata* (L.) Schrad., *Stipa capillata* L., *Stipa lessingiana* Trin. & Rupr. and *Veronica steppacea* Kotov. Although the maximum and mean numbers of non-synanthropic species on the ancient settlements were higher than the maximum and mean numbers of established alien species, their average contribution to the total species richness was only 35% (see Supplement E3). The most frequently encountered established alien species were: *Anisantha tectorum* (L.) Nevski, *Amaranthus albus* L., *Amaranthus retroflexus* L., *Ambrosia artemisiifolia* L., *Ballota nigra* L., *Bromus squarrosus* L., *Buglossoides arvensis* (L.) I.M.Johnst., *Capsella bursa-pastoris* L., *Centaurea diffusa* Lam., *Chenopodium strictum* Roth, *Conyza canadensis* (L.) Cronquist, *Descurainia sophia* (L.) Webb ex Prantl, *Digitaria sanguinalis* (L.) Scop., *Galium spurium* L., *Geranium pusillum* L., *Lactuca serriola* L., *Onopordum acanthium* L., *Polygonum aviculare* L., *Reseda lutea* L., *Sedum reflexum* L., *Setaria viridis* (L.) P.Beauv., *Solanum nigrum* L., *Sonchus oleraceus* L. and *Ulmus pumila* L.

The total number of vascular plant species of the ancient settlements far exceeded the flora of the "Staroshvedskyi" (263 ha) and "Lesovyi Canyon" (35 ha) reserves (located on the slopes of the Dnipro River in similar environmental conditions) as well as the flora of kurgans of the grass steppe (Table 2). Furthermore, the total species richness of the ancient settlements was even higher than the total number of species in the Askania-Nova Biosphere Reserve, despite the fact that the area of this reserve is 100 times larger (11,054 ha). The percentage of non-synanthropic species in the flora of settlements was higher than in all objects mentioned above, with the exception of Askania-Nova. The proportion of native species in the flora of ancient settlements was similar to and within the range of values of the nature reserves' and kurgan floras, but the proportion of steppe species was lower than in other objects (Table 2).

Regression results indicated that the main drivers of vascular plant richness were microhabitat variety index (positive relationship), area (positive relationship), afforestation degree (unimodal relationship) and steppe cover in 1 km buffer (positive relationship) (Table 3,

Table 2. Number and percentage of particular groups of vascular plant species of ancient settlements and kurgans and three nature reserves situated in the grass steppe zone (percentage values given in relation to the total species richness of each of the reserves investigated or to the total species richness of 18 ancient settlements and 26 kurgans).

Tabelle 2. Anzahl und prozentualer Anteil bestimmter Gruppen von Gefäßpflanzenarten der antiken Siedlungen und Grabhügel (Kurgane) sowie der drei Steppenschutzgebiete (Prozentangaben im Verhältnis zum Gesamtartenreichtum jedes der untersuchten Schutzgebiete bzw. zum Gesamtartenreichtum der 18 antiken Siedlungen und 26 Grabhügel).

Group of species	Total of 18 ancient settlements (103.7 ha)		Total of 26 kurgans (5.5 ha)		Lesovyi Canyon reserve (35 ha)		Staroshvedskyi projected reserve (263 ha)		Askania Nova biosphere reserve (11,054 ha)	
	MOYSIYENKO et al. 2020		SUDNIK-WÓJCIKOWSKA & MOYSIYENKO 2006		MOYSIYENKO 2007		MOYSIYENKO et al. 2019		MOYSIYENKO et al. 2014	
	No.	%	No.	%	No.	%	No.	%	No.	%
Total number of species	524	100.0	352	100.0	222	100.0	359	100.0	495	100.0
Steppe species	239	45.6	197	56.0	132	60.0	171	44.8	226	46.0
Native species	396	75.6	248	70.5	168	75.7	279	77.7	389	78.6
Non-synanthropic species	225	42.9	137	39.0	87	39.0	123	34.2	239	48.0
Protected species	31	5.9	18	5.1	13	5.9	21	5.8	31	6.3

Fig. 3). Analogue results were obtained for the number of non-synanthropic species (Table 3). Distance to settlements was a significant negative predictor only for established alien species richness, while the other significant factors for this group were also microhabitat diversity index (positive), afforestation degree (unimodal) and area of the settlements in 1 km buffer (positive) (Table 3, Fig. 3).

There was no strong differentiation of the vegetation composition of studied ancient settlements along the RDA axes (Fig. 4). The most important environmental variable for species composition was afforestation degree, followed by two other significant variables – steppe cover in 1 km buffer and distance to settlements. All explanatory variables explained 26.1% of the total variation.

4. Discussion

4.1 General characteristics of ancient settlements' flora compared to the flora of the reserves and kurgans

The flora of the ancient settlements may be considered typical of the Pontic grass steppe zone, representing more than 26% of the flora of the Northern Black Sea region (MOYSIYENKO 2013). The ancient settlements are an example of small habitat islands, enormously species-rich and preserving considerable numbers of non-synanthropic and steppe

Table 3. Results of simple linear and quadratic regressions for total richness, non-synanthropic species, established alien species and the ratio of non-synanthropic species to total species richness of vascular plants on the ancient settlements (n = 18) studied in Southern Ukraine against selected local and landscape environmental variables. *b1* – regression coefficient of a linear term, *b2* – regression coefficient of a quadratic term. Bold font indicates significant results.

Abb. 3. Ergebnisse einfacher linearer und quadratischer Regressionen für den Gesamtartenreichtum, nicht-synanthrope Arten, etablierte gebietsfremde Arten und das Verhältnis von nicht-synanthropen Arten zum Gesamtartenreichtum von Gefäßpflanzen in den in der Südukraine untersuchten alten Siedlungen (n = 18) gegen ausgewählte lokale und Landschafts-Umweltvariablen. *b1* - Regressionskoeffizient eines linearen Terms, *b2* - Regressionskoeffizient eines quadratischen Terms. Fettdruck zeigt signifikante Ergebnisse an.

	Total richness				Non-synanthropic species				Established alien species				Ratio non-synanthropic/ total richness		
	b1	*b2*	*p*	R^2	*b1*	*b2*	*p*	R^2	*b1*	*b2*	*p*	R^2	*b1*	*p*	R^2
Area	6,21	-	**<0.001**	**0,43**	4,3	-	**<0.001**	**0,43**	0,29	-	0,542	0,02	0,009	**0,043**	**0,23**
Microhabitat variety index	21,47	-	**<0.001**	**0,74**	13,52	-	**<0.001**	**0,6**	2,83	-	**0,016**	**0,31**	0,026	**0,027**	**0,27**
Afforestation degree	-0,001	-	0,337	0,06	3,79	-	0,462	0,03	-1,59	-	0,283	0,07	0,021	0,153	0,12
Afforestation degree + (Afforestation degree)^2	72,45	-15,1	**0,015**	**0,43**	45,68	-8,75	**0,05**	**0,33**	10,98	-2,62	**0,025**	**0,31**	-	-	-
Steppe cover in 1 km buffer	0,89	-	**0,017**	**0,31**	0,6	-	**0,021**	**0,29**	0,02	-	0,801	0	0,001	0,059	0,21
Distance to settlements	-6,2	-	0,511	0,03	1,71	-	0,796	0	-4,42	-	**0,011**	**0,34**	0,025	0,175	0,11
Area of settlements in 1 km buffer	-0,12	-	0,538	0,02	-0,2	-	0,11	0,15	0,07	-	**0,041**	**0,24**	-0,001	**0,014**	**0,32**
Mean annual precipitation	-0,94	-	0,397	0,05	-0,24	-	0,765	0,01	-0,37	-	0,09	0,17	0,002	0,453	0,04

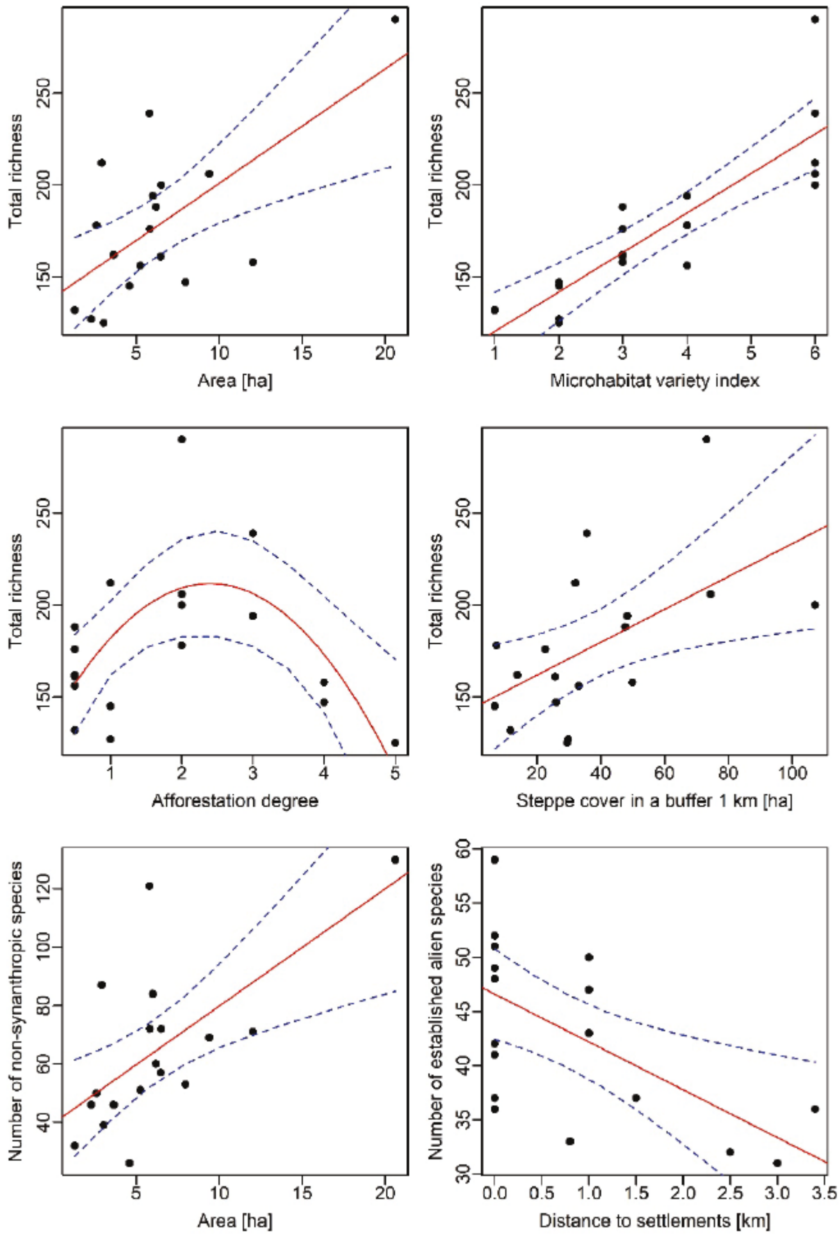

Fig. 3. Relationships between total species richness (four upper plots), number of non-synanthropic species (bottom left), number of established alien species (bottom right) and selected predictors on ancient settlements (n = 18) of the Lower Dnipro region. Red solid lines indicate significant relationships (t-test, $p < 0.05$), blue dashed lines the corresponding 95% confidence intervals.

Abb. 3. Beziehungen zwischen dem Gesamtartenreichtum (vier obere Diagramme), der Anzahl nicht-synanthroper Arten (unten links), der Anzahl etablierter gebietsfremder Arten (unten rechts) und ausgewählten Prädiktoren auf alten Siedlungen des Unteren Dnepr-Gebiets (n = 18). Rote durchgezogene Linien zeigen signifikante Beziehungen (t-Test, $p < 0{,}05$), blau gestrichelte Linien die entsprechenden 95 %-Konfidenzintervalle.

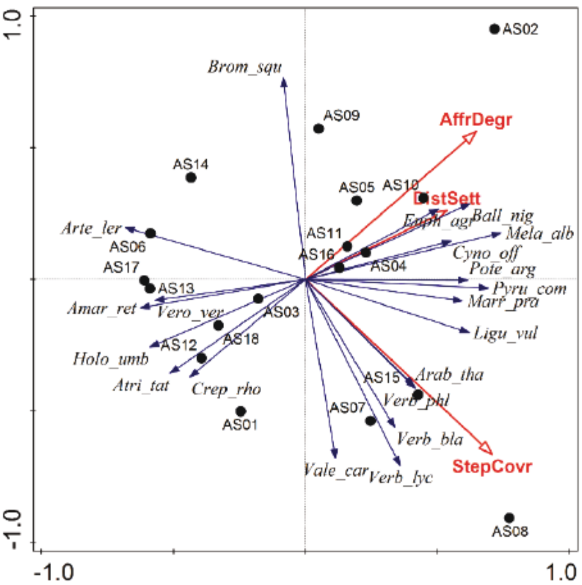

Fig. 4. Redundancy Analysis (RDA) of vegetation data of 18 ancient settlements studied in Southern Ukraine. The obtained eigenvalues for the first two RDA axes were 0.1036 and 0.0854. Significant environmental variables are shown as red arrows and species best fitting the ordination as blue arrows. The analysis included species in abundance scale 1–3 and only species that occurred on at least four ancient settlements.

Abbreviations of species names: *Amar_ret* – *Amaranthus retroflexus*, *Arab_tha* – *Arabidopsis thaliana*, *Arte_ler* – *Artemisia lerchiana*, *Atri_tat* – *Atriplex tatarica*, *Ball_nig* – *Ballota nigra*, *Brom_squ* – *Bromus squarrosus*, *Crep_rho* – *Crepis rhoeadifolia*, *Cyno_off* – *Cynoglossum officinale*, *Euph_agr* – *Euphorbia agraria*, *Holo_umb* – *Holosteum umbellatum*, *Ligu_vul* – *Ligustrum vulgare*, *Marr_pra* – *Marrubium praecox*, *Mela_alb* – *Melandrium album*, *Pote_arg* – *Potentilla argentea*, *Pyru_com* – *Pyrus communis*, *Vale_car* – *Valerianella carinata*, *Verb_bla* – *Verbascum blattaria*, *Verb_lyc* – *V. lychnitis*, *Verb_phl* – *V. phlomoides*, *Vero_ver* – *Veronica verna*.

Abb. 4. Redundanzanalyse (RDA) der Vegetationsdaten der 18 in der Südukraine untersuchten antiken Siedlungen. Die erhaltenen Eigenwerte für die ersten beiden RDA-Achsen waren 0,1036 und 0,0854. Signifikante Umweltvariablen sind als rote Pfeile und Arten, die am besten zur Ordination passen, als blaue Pfeile dargestellt. Es wurde alle Arten in die Analyse einbezogen, die eine Abundanz von 1–3 aufwiesen und mindestens auf vier antiken Siedlungen vorkamen.

species. Previously, such conclusions have been formulated for ancient kurgans (SUDNIK-WÓJCIKOWSKA et al. 2011, 2012). The flora of ancient settlements is comparable to the flora of kurgans in terms of the shares of non-synanthropic and native species and somewhat poorer in terms of the shares of steppe species (MOYSIYENKO et al. 2014). Still, the overall species richness of ancient settlements exceeds the values noted for zonal nature reserves, which are much more extensive in area, e.g. "Lesovyi Canyon" (MOYSIYENKO 2007) and the projected nature reserve "Staroshvedskyi" (MOYSIYENKO et al. 2019). The ancient settlements' flora is structurally most similar to the flora of the Askania Nova Biosphere Reserve, known as one of the largest and most valuable enclaves of remaining virgin grass steppe in Europe (MOYSIYENKO et al. 2014, SHAPOVAL 2012). It is obvious that the dimensions of these comparison objects are very different: burial mounds are much smaller, and the Askania-Nova reserve is much larger in area than the ancient settlements. However, the main point is to show that such small objects as ancient settlements provide habitat for such a high number of valuable species (and that is why they are compared to much bigger steppe enclaves).

4.2 Local and landscape factors shaping the patterns of ancient settlements' flora

The patch size (i.e. the area of an ancient settlement) was found to be one of the most important explanatory variables of vascular plant species richness on ancient settlements. This result corresponds to the well-known ecological pattern of species-area relationship (CONNOR & MCCOY 1979). Since a positive correlation with ancient settlement's area has been confirmed not only for total vascular plant species richness, but also for non-synanthropic species (and not for the established alien species), we can conclude that the ancient settlement's area significantly contributes to the preservation of the grass steppe habitats.

The size of habitat patch has been recognised as important factor for species preservation also for other habitat islands in the grass steppe zone (DEMBICZ et al. 2016) as well as for the patches of extrazonal semi-natural grasslands (e.g. BRUUN 2000, KRAUSS et al. 2004, ÖSTER et al. 2007, D'ANTRACCOLI et al. 2019) and other non-grassland communities (e.g. HONNAY et al. 1999). However, there are also studies not confirming such a relationship (e.g. LINDBORG & ERIKSSON 2004, COUSINS et al. 2007). These inconsistencies are reported to be caused mainly by differences in management type and intensity and other forms of human impact affecting the habitat islands (COUSINS et al. 2007). Thus, we tested for such effects and expressed them by means of the "microhabitat variety index". The microhabitat diversity within ancient settlement patches showed to be the most significant predictor of species richness patterns among all the groups analysed (total species richness, non-synanthropic species, established alien species and the ratio of non-synanthropic species to total species richness). The microhabitat variety index was also correlated to the ancient settlement's area, which was an expected effect. Human pressure is usually perceived as adversely affecting biodiversity of zonal ecosystems; however, in this case the management practices were of limited range and applied only to some parts of ancient settlements, while the predominant area was covered by relatively intact steppe habitats. Favourable conditions for the conservation of steppe species were assured particularly by the steep slopes of ancient settlements (the potential of slopes for biodiversity conservation of other steppe cultural monuments – kurgans – has been confirmed before, e.g. SUDNIK-WÓJCIKOWSKA & MOYSIYENKO 2006, SUDNIK-WÓJCIKOWSKA et al. 2011, DEÁK et al. 2016, DEMBICZ et al. 2016).

In such circumstances, small-scale natural and human-induced disturbances affecting the ancient settlements (e.g. mowing, grazing, burning, spontaneous succession and afforestation, inner gullies, roads, archaeological excavations, small industrial facilities, dumps, etc.) may on the one hand have facilitated the establishment of non-synanthropic species characteristic of steppe habitats. One the other hand, it may have created some new anthropogenic niches for synanthropic species. In consequence, disturbance and maintenance factors acted in combination and contributed to the overall increase of the species richness on ancient settlements.

Among local factors, the "afforestation degree" showed an especially interesting, unimodal relationship. It appears that up to a certain point, the species diversity increases with afforestation, shows the highest values for small to medium-scale tree cover and tends to decrease with a further increasing share of trees and shrubs. This observed pattern is most probably associated with the strong modelling impact of forests on natural steppe ecosystems. The natural grass steppe is zonally not associated with woody species (PACHOSKY 1915, BELGARD 1971, ANDRIENKO et al. 1977), and their appearance with high coverage significantly changes habitat and light conditions, leading to the decline of steppe plants. However, low or moderate but scattered covers of woody species do not induce the decay of the steppe and additionally may facilitate the occurrence of some non-synanthropic and synanthropic shade-tolerant plants. In consequence, the presence of small clumps of trees and shrubs does not hinder the preservation of zonal steppe plant diversity and at the same time enables the occurrence of extrazonal shade plants typical for forests.

Woody encroachments were generally reported in the literature as negatively influencing species diversity within other cultural enclaves of zonal steppe vegetation (DEÁK et al. 2016). DEÁK et al. (2018) reported also that some clonal plants cope well with increasing woody encroachment and are yet unable to cope with high disturbances. Extensive grazing was found to be a potentially positive disturbance, which can increase the cover and species richness of specialist species (DEÁK et al. 2017).

We claim that in the case of ancient settlements, which were used for centuries as human settlements and defensive objects and in modern times for small-scale management practices, recreational reasons etc., the interplay of natural and anthropogenic disturbances is historically well established and balanced, as long as the impact remains marginal and infrequent.

Concerning landscape factors, the available habitat amount in the surroundings, the area of settlements in 1 km buffer and the distance to contemporary human settlements acted as significant predictors of species richness patterns on the ancient settlements, indicating the state of habitat isolation and fragmentation. Both the total species richness and the number of non-synanthropic species increased with the amount of steppe habitats in the surroundings, which confirms the importance of landscape connectivity for effective propagule dispersal and for immigration success of steppe species. Due to their defensive role, many ancient settlements were historically located between loess ravines (so-called balkas) and have thus been able to assure the local species pool for centuries. Balkas are among the most species-rich habitats in the studied region (BOIKO 2010, BURKOVSKYI et al. 2013). They may still act as valuable sources of diaspores for steppe habitats that have persisted on ancient settlements. Moreover, the elongated shape of balkas may facilitate connections with other steppe remnants (e.g. kurgans or river terraces), which is of high importance since grassland specialist species disperse slower than generalists and in a step-wise manner (COUSINS & LINDBORG 2008).

Our findings are consistent with the model of species-isolation relationship (SIR), which states that the species richness declines with an increasing degree of fragment isolation (WHITTAKER & FERNANDEZ-PALACIOS 2007), and with the findings of other authors conducting research on steppe cultural monuments (DEMBICZ et al. 2016, DEÁK et al. 2018). Similar isolation effects were reported for species groups characterised by low dispersal capabilities also in non-grassland communities (GRASHOF-BOKDAM 1997, RUREMONDE & KALKHOVEN 2009); still, there are numerous studies reporting no relationship or weak isolation effects (e.g. HONNAY et. al. 1999, BRUUN 2000, KRAUSS 2004), indicating that the matter is more complex in nature and may depend on the interplay of factors (e.g. the degree of payment of the extinction debt).

Simultaneously, we observed the adverse landscape level effects of anthropogenic impact on ancient settlement's flora. It was expressed by the increase of the shares of established alien species on ancient settlements located close to human settlements. Also, the ratio of non-synanthropic species to total species richness was negatively correlated with the amount of human settlements in the neighbourhood. These findings indicate that human settlements act as a proxy of human disturbances. The proceeding urbanisation, the increase of human population density and the intensity of present and past agricultural activities can be considered to be the most important factors negatively affecting the success of preservation of steppe remnants on ancient settlements.

5. Conclusions and implications for conservation

Our study confirmed that ancient settlements preserve valuable remnants of steppe habitats and have the potential of being local hotspots of plant diversity. Despite their relatively small size, they appeared to be enormously species-rich enclaves of steppe flora located beyond the ecological networks. The ancient settlements, compared to other cultural monuments (kurgans) and to nature reserves created to protect the zonal grass steppe ecosystems, harbour high ratios of steppe and non-synanthropic plants. They are valuable for both culture and nature and should therefore be actively protected. At present Ukrainian ancient settlements are preserved as archaeological monuments, but the natural value of these sites is not taken into account by law.

Habitat area and connectivity act jointly with microhabitat diversity as the most important factors in conserving the natural values of ancient settlements. Thus, both local and landscape factors should be taken into account in protection planning. The preservation of the ancient settlements' flora can be obtained by creating surrounding buffers of natural steppe habitats, preserving the existing remnants of steppe patches in the surrounding, limiting woody encroachments to a degree not exceeding small clumps of trees and shrubs and implementing moderate grazing, if necessary. The diverse small-scale natural and human-induced disturbances may be maintained since they were shown to increase the overall species richness without prejudice to the steppe flora. Given the great conservation value of the ancient settlements, it is also necessary to amend the archaeological survey procedures in such a way that the nature conservation aims can be achieved.

Erweiterte deutsche Zusammenfassung

Einleitung – In der Ukraine führte die Intensivierung der Landwirtschaft im 20. Jahrhundert zu einem erheblichen Verlust und der Fragmentierung von Steppenlebensräumen. In der stark veränderten Landschaft sind infolgedessen Steppenlebensräume nur noch selten zu finden. Überreste der Steppenvegetation sind jedoch oft an Orten von kultureller Bedeutung erhalten geblieben, wie auf alten Grabhügeln (Kurgane), alten Friedhöfen oder antiken Siedlungen. Wir stellten die Hypothese auf, dass antike Siedlungen (3.–2. Jh. v. Chr.) als steppenartige Lebensrauminseln fungieren und somit ebenso wichtig für den Steppenpflanzenschutz sein könnten wie Grabhügel. Ziel dieser Studie war es, die lokalen und landschaftlichen Faktoren zu untersuchen, die den Artenreichtum von Gefäßpflanzen in antiken Siedlungen beeinflussen, und den Wert von antiken Siedlungen für den Naturschutz zu überprüfen. Wir fragten: 1) Wie hoch ist der Artenreichtum von Gefäßpflanzen auf antiken Siedlungen? 2) Haben antike Siedlungen einen vergleichbaren Naturschutzwert wie andere Steppenenklaven der untersuchten Zone? 3) Welche Faktoren sind für den Artenreichtum und die Artenzusammensetzung auf antiken Siedlungen am wichtigsten?

Materialien und Methoden – Von 2015 bis 2019 erstellten wir von 18 antiken Siedlungen am Ufer des Dnepr in mindestens drei Begehungen pro Siedlung zur Vegetationszeit vollständige Artenlisten von Gefäßpflanzen. Mittels einfacher Regressionen analysierten wir wie der Gesamtartenreichtum, die Anzahl nicht-synanthroper Arten, die Anzahl etablierter fremder Arten und der Anteil nicht-synanthroper Arten am Gesamtartenreichtum von sieben Umweltvariablen (Fläche der antiken Siedlung, Mikrohabitat-Varietäts-Index, Aufforstungsgrad, Steppenbedeckung in einem 1-km Puffer um eine antike Siedlung herum, Entfernung zu den nächstgelegenen Siedlungen, Siedlungsfläche in einem 1-km Puffer um eine antike Siedlung herum, mittlerer Jahresniederschlag) beeinflusst wurde. Wir verwendeten außerdem multivariate Methoden (Redundanzanalyse; RDA), um anhand der Artenhäufigkeit und den Umweltvariablen die Muster der Artenzusammensetzung und die Rolle der Umweltvariablen zu untersuchen.

Ergebnisse – Wir fanden eine beträchtliche Anzahl von einheimischen (396 Arten; 75,6 %), Steppen- (239; 45,6 %) und nicht-synanthropen Pflanzenarten (225; 42,9 %), was auf einen guten Erhaltungszustand der Steppe der untersuchten antiken Siedlungen hindeutet. Die Gesamtzahl der Gefäßpflanzenarten der antiken Siedlungen überstieg damit jene der meisten Schutzgebiete ("Staroshvedskyi" [359 Arten], "Lesovyi Canyon" [222], Askania-Nova [495]), sowie der Grabhügel (352). Der Anteil der einheimischen Arten an der Gesamtartenzahl war vergleichbar mit jenem der Schutzgebiete und der Grabhügel, aber der Anteil der Steppenarten an der Gesamtartenzahl war geringer als in anderen Objekten. Der Gesamtartenreichtum zeigte eine positive Beziehung zum Mikrohabitat-Varietäts-Index als Maß für die Habitat-Heterogenität, sowie der Fläche der antiken Siedlung und der Steppenbedeckung um eine antike Siedlung herum, als Maß für Habitatkonnektivität. Gesamtartenreichtum und Aufforstungsgrad zeigten hingegen eine unimodale Beziehung. Dieselben Faktoren waren auch für den Artenreichtum an nicht-synanthropen Pflanzen von Bedeutung. Je weiter eine Siedlung entfernt war, desto geringer war die Anzahl an gebietsfremden Arten.

Schlussfolgerungen – Unsere Studie bestätigte, dass antike Siedlungen trotz ihrer geringen Größe eine enorm artenreiche Steppenflora aufweisen und sie somit die wertvollen Überreste der Steppenlebensräume erhalten können. Im Vergleich zu anderen Kulturdenkmälern (Kurgane) und Steppenschutzgebieten, ist in antiken Siedlungen die Gesamtartenzahl sowie der Anteil von nicht-synanthropen Pflanzenarten sehr hoch. Da die Flächengröße und die Habitatkonnektivität zusammen mit der Mikrohabitatvielfalt eine wichtige Rolle für Artenzahl und -zusammensetzung der Steppen auf antiken Siedlungen spielen, sollten bei der Planung von Schutzmaßnahmen sowohl lokale als auch landschaftliche Faktoren berücksichtigt werden. Unsere Ergebnisse verdeutlichen, dass zum Beispiel die Erhaltung kleinräumiger Störungen und der Habitatvielfalt (Weiden, gemähte Flächen, Brandflächen, usw.) und die Offenhaltung durch Entbuschungsmaßnahmen einen wichtigen Beitrag zum Schutz dieser Lebensräume leisten können. Die vielfältigen, kleinräumigen natürlichen und vom Menschen verursachten Störungen können beibehalten werden, da sie den Artenreichtum insgesamt erhöhen, ohne die Steppenflora zu beeinträchtigen. Die antiken Siedlungen wurden jahrhundertelang als menschliche Siedlungen und Verteidigungsobjekte genutzt und in der Neuzeit auch von Menschen betreten, so dass das Zusammenspiel von natürlichen und anthropogenen Einwirkungen historisch gut belegt und ausgewogen ist, solange die Einwirkungen marginal und selten bleiben. Antike Siedlungen sind somit sowohl für die Kultur als auch für die Natur wertvolle Objekte, die als solche aktiv geschützt werden sollten.

Acknowledgements

We would like to express our gratitude to Serhii Niemtsev and Denys Sikoza for inestimable help with data concerning location, age and area of ancient settlements and comments from archaeologists' point of view. We also thank Łukasz Kozub for help in producing and correcting the RDA ordination plots in Canoco. We further thank Aiko Huckauf for the linguistic edition of the text.

This research is supported by the Swedish Science Council (Vetenskapsrådet) project N 2012-06112.

Author contribution

P.D. and I.M. conceived the ideas leading to this research and prepared the data for analyses. I.D. carried out the statistical analyses. I.D., I.M. and M.Z. prepared illustrations. B.S.-W. and I.M. critically checked the nomenclature used and assessed the assignments of the species to the list of the flora and to the species groups. All authors participated in field sampling, methodological discussions, interpretation of the results and writing the manuscript.

ORCIDs

Polina Dayneko https://orcid.org/0000-0002-8680-9809
Ivan Moysiyenko https://orcid.org/0000-0002-0689-6392
Iwona Dembicz https://orcid.org/0000-0002-6162-1519
Maria Zachwatowicz https://orcid.org/0000-0001-7651-2211
Barbara Sudnik-Wójcikowska https://orcid.org/0000-0001-6022-9235

Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Description of the studied ancient settlements of the Lower Dnipro, Southern Ukraine.

Anhang E1. Beschreibung der untersuchten antiken Siedlungen am unteren Dnepr in der Südukraine.

Supplement E2. Correlation matrix of environmental variables used in the analyses of the species richness of vascular plants in the ancient settlements (n = 18) studied in Southern Ukraine.

Anhang E2. Korrelationsmatrix von Umgebungsvariablen, die bei der Analyse des Artenreichtums von Gefäßpflanzen in den in der Südukraine untersuchten antiken Siedlungen (n = 18) verwendet wurden.

Supplement E3. Species richness of vascular plants on the studied ancient settlements (n = 18) of the Lower Dnipro, Southern Ukraine.

Anhang E3. Artenreichtum von Gefäßpflanzen in den untersuchten antiken Siedlungen (n = 18) des unteren Dnepr in der Südukraine.

References

AKATOV, V.V. (2013): The 60th anniversary of the equilibrium theory in island biogeography: Problems of testing, results of field studies, and applied importance. – Biol. Bull. Rev. 3: 1–16.

ANDRIENKO, T.L., BILYK, G.I., BRADIS, E.M. & BARBARYCH, A.I. (1977): Geobotanichne raionuvannia Ukrainskoyi RSR (Geobotanical zoning of Ukrainian RSR) [in Ukranian]. – Naukova Dumka, Kyiv: 301 pp.

ANDRZEJEWSKI, R. (2002): Wyspy środowiskowe - kilka pojęć i zagadnień (Environmental islands - several concepts and issues) [in Polish]. – In: BANASZAK, J. (Ed.): Wyspy środowiskowe. Bioróżnorodność i próby typologii: 291–302. Wydaw. ABydg., Bydgoszcz.

BARRETT, G.W. & BARRETT, T.L. (2001): Cemeteries as repositories of natural and cultural diversity. – Conserv. Biol. 15: 1820–1824.

BELGARD, A.L. (1971): Stepnoe lesovedenie (Steppe forestry) [in Russian]. – Lesnaya promyishlennost, Moscow: 321 pp.

BHAGWAT, S.A. & RUTTE C. (2006): Sacred groves: potential for biodiversity management. – Front. Ecol. Environ. 4: 519–524.

BOHN, U., NEUHÄUSL, R., GOLLUB, G., HETTWER, C., NEUHÄUSLOVÁ, Z., SCHLÜTER, H. & WEBER, H. (Eds.) (2000): Karte der natürlichen Vegetation Europas. Maßstab 1:2 500 000. Teil 1–3. Münster: Landwirtschaftsverlag.

BOIKO, P.M. (2010): Lower Dnipro Ecocorridor of National Econet of the Ukraine. – Ailant, Kherson: 204 pp.

BRAAK, C. & ŠMILAUER, P. (2012): Canoco Reference manual and User's guide: Software for Canonical Community Ordination (version 5.0). – Microcomputer Power, Ithaca, NY, USA

BRANDT, J.S., WOOD, E.M., PIDGEON, A.M., HAN, L.X., FANG, Z. & RADELOFF, V.C. (2013): Sacred forests are keystone structures for forest bird conservation in southwest China's Himalayan Mountains. – Biol. Conserv. 16: 34–42.

BRUUN, H.H. (2000): Patterns of species richness in dry grassland patches in an agricultural landscape. – Ecography 23: 641–650.

BURKOVSKYI, O.P., VASYLIUK, O.V., YENA, A.V., KUZEMKO, A.A., MOVCHAN, Y.I., MOYSIYENKO, I.I. & SIRENKO, I.P. (2013): Ostanni stepy Ukrayiny: buty chy ne buty? (The last steppes of Ukraine: to be or not to be?) [in Ukrainian]. –Geoprint, Kyiv: 38 pp.

CELKA, Z. (2007): The vascular plants of earthworks in the Wielkopolska region (western Poland). – Stowarzyszenie Archeologii Środowiskowej Sas (Eurasian Perspectives on Environmental Archaeology) 6: 156–157.

CELKA, Z. (2011): Relics of cultivation in the vascular flora of medieval West Slavic settlements and castles. – Biodiv. Res. Conserv. 22: 1–110.

CHIBILYOV, A. (2002): Step i lesostep (Steppe and forest-steppe) [in Russian]. – In: SHAHGEDANOVA, M. (Ed.): The physical geography of northern Eurasia: 248–266. Oxford University Press, Oxford.

CONNOR, E.F. & MCCOY, E.D. (1979): The statistics and biology of the species-area relationship. – Am. Nat. 113: 791–833.

COUSINS, S.A.O. & LINDBORG, R. (2008): Remnant grassland habitats as source communities for plant diversification in agricultural landscapes. – Biol. Conserv. 141: 233–240.

COUSINS, S.A.O., OHLSON, H. & ERIKSSON, O. (2007): Effects of historical and present fragmentation on plant species diversity in semi-natural grasslands in Swedish rural landscapes. – Landsc. Ecol. 22: 723–730.

D'ANTRACCOLI, M., ·ROMA-MARZIO, F., CARTA, A., LANDI, S., BEDINI,G., CHIARUCCI, A. & PERUZZI, L. (2019): Drivers of floristic richness in the Mediterranean: a case study from Tuscany. – Biodiver. Conserv. 28: 1411–1429.

DAYNEKO, P.M. (2019): Species richness of vascular plants on the ancient settlements of the Lower Dnieper. Biology: from a molecule up to the biosphere. Materials of the XIV International Young Scientists Conference, Kharkiv, 27–29 November, 2019: 147–149.

DEÁK, B., TÖLGYESI, C., KELEMEN, A., BÁTORI, Z., GALLÉ, R., BRAGINA, T.M., ABIL, Y.A. & VALKÓ, O. (2017): Vegetation of steppic cultural heritage sites in Kazakhstan – Effects of micro-habitats and grazing intensity. – Plant Ecol. Divers. 10: 509–520.

DEÁK, B., VALKÓ, O., TÖRÖK, P., KELEMEN, A., BEDE, Á., CSATHÓ, A.I. & TÓTHMÉRÉSZ, B. (2018): Landscape and habitat and filters jointly drive richness and abundance of grassland specialist plants in terrestrial habitat islands. – Landsc. Ecol. 33: 1117–1132.

DEÁK, B., VALKÓ, O., TÖRÖK, P. & TÓTHMÉRÉSZ, B. (2016): Factors threatening grassland specialist plants – A multi-proxy study on the vegetation of isolated grasslands. – Biol. Conserv. 204: 255–262.

DEMBICZ, I., MOYSIYENKO, I.I., SHAPOSHNIKOVA, A., VYNOKUROV, D., KOZUB, Ł. & SUDNIK-WÓJCIKOWSKA, B. (2016): Isolation and patch size drive specialist plant species density within steppe islands: a case study of kurgans in southern Ukraine. – Biodiver. Conserv. 25: 2289–2307.

EWERS, R.M. & DIDHAM, R.K. (2006): Confounding factors in the detection of species responses to habitat fragmentation. – Biol. Rev. 81: 117–142.

FAHRIG, L. (2003): Effects of habitat fragmentation on biodiversity. – Annu. Rev. Ecol. Evol. Syst. 34: 487–515.

FICK, S.E. & HIJMANS, R.J. (2017): WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. – Int. J. Climatol. 37: 4302–4315.

GAVRYLYUK, N.A. (2001): Slave trade and wine trade as the basic branches of Olbia-Barbaric Export-Import in Nothern Black Sea Area (VI—III cc. BC). Olviia ta antychnyi svit. Materialy naukovykh chytan prysviachenykh 75-richchiu utvorennia istoryko-arkheolohichnoho zapovidnyka «Olviia», Kyiv, 19–22 November, 2001: 151–152.
GAVRYLYUK, N.A. & MATERA, M. (2016): «Piznoskifski» abo «postskifski» gorodischa Nizhnogo Podniprovya («Late Scythian» or «Post-Scythian» sites of the lower Dnipro region) [in Ukrainian]. – Archeology 14: 121–135.
GRASHOF-BOKDAM, C. (1997): Forest species in an agricultural landscape in the Netherlands: effects of habitat fragmentation. – J. Veg. Sci. 8: 21–28.
HAILA, Y. (2002): A Conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. – Ecol. Appl. 12: 321–334.
HERBICH, J. (1996): Relationships between the contemporary distribution of weed types and earlier settlements along the Lower Vistula banks (Northern Poland). – Archeol. Prospect. 3: 1–11.
HONNAY, O., ENDELS, P., VEREECKEN, H. & HERMY, M. (1999): The role of patch area and habitat diversity in explaining native plant species richness in disturbed suburban forest patches in northern Belgium. – Divers. Distrib. 5: 129–141.
KORNAŚ, J. (1977): Analiza flor synantropijnych (Analysis of a synanthropic flora) [in Polish]. – Wiad. Bot. 21: 85–91.
KRAUSS, J., KLEIN, A.-M., STEFFAN-DEWENTER, I. & TSCHARNTKE, T. (2004): Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands. – Biodivers. Conserv. 13: 1427–1439.
LAVRENKO, E.M., KARAMYSHEVA, Z.V. & NIKULINA, R.I. (1991): Stepi Eurazii (Steppes of Eurasia) [in Ukrainian]. – Izdat. Nauka, Leningrad: 146 pp.
LINDBORG, R. & ERIKSSON, O. (2004): Historical landscape connectivity affects present plant species diversity. – Ecology 85:1840–1845.
LŐKI, V., DEÁK, B., LUKÁCS, A. B. & MOLNÁR, V. A. (2019): Biodiversity potential of burial places – a review on the flora and fauna of cemeteries and churchyards. – Glob. Ecol.Conserv. 18: e00614.
MACARTHUR, R.H. & WILSON, E.O. (1967): The Theory of Island Biogeography. – Princeton University Press, Princeton, N.J: 203 pp.
MARYNYCH, O.M. & SHYSHCHENKO, P.G. (2005): Fizychna heohrafiia Ukrainy (Physical geography of Ukraine) [in Ukrainian]. – Znannya, Kyiv: 511 pp.
MENDENHALL, C.D., KARP, D.S., MEYER, C.F.J., HADLY, E.A. & DAILY, G.C. (2014): Predicting biodiversity change and averting collapse in agricultural landscapes. – Nature 509: 213.
MOON, D.G. (2016): Steppe by steppe: exploring environmental change in Southern Ukraine. – Glob. Environ. 9: 414–439.
MOSYAKIN, S.L. & FEDORONCHUK, M.M. (1999): Vascular plants of Ukraine. A nomenclatural checklist. – National Academy of Sciences of Ukraine, Kyiv: 346 pp.
MOYSIYENKO, I.I. (2007): An annotated list of the vascular plants of the projected landscape reserve «Lesovyi Canyon» (Kherson Region, Ukraine). – Chornomors'k. Bot. Z. 3 (1): 77–84.
MOYSIYENKO, I.I. (2013): Floristic diversity and taxonomic structure of the flora of the Pivnichne Prychornomoria (Northern Black Sea Coastal Plain). – Chornomors'k. Bot. Z. 9 (1): 41–56.
MOYSIYENKO, I.I., DAYNEKO, P.M., SUDNIK-WÓJCIKOWSKA, B., DEMBICZ, I., ZACHWATOWICZ, M. & ZAKHAROVA, M.YA. (2020): Conspectus of old settlements flora of the Lower Dnipro. – Chornomors'k. Bot. Z. 16 (1): 6–39.
MOYSIYENKO, I.I., DAYNEKO, P.M., ZACHWATOWICZ, M., DEMBICZ, I. & SUDNIK-WÓJCIKOWSKA, B. (2019): Anotovaniy spisok flori proektovanogo botanichnogo zapovidnika «Staroshvedskiy» (Hersonska oblast, Ukrayina) (An annotated list of the flora of the projected botanical reserve «Staroshvedsky» (Kherson region, Ukraine)) [in Ukrainian]. – Chornomors'k. Bot. Z. 15 (2): 185–201.
MOYSIYENKO, I.I., DEMBICZ, I., SUDNIK-WÓJCIKOWSKA, B., ZACHWATOWICZ, M., KUNS, B. & ZAKHAROVA, M. (2018): Ancient settlements as refuges for steppe flora in southern Ukraine. Vegetation survey 90 years after the publication of Braun-Blanquet's textbook – new challenges and concepts Materials of the 27th Congress of the European Vegetation Survey, Wrocław (Poland), 23–26 May, 2018: 13.
MOYSIYENKO, I.I. & SUDNIK-WÓJCIKOWSKA, B. (2006): The flora of kurgans in the desert steppe zone of Southern Ukraine. – Chomomors'k. Bot. Z. 2 (1): 5–35.

MOYSIYENKO, I.I., SUDNIK-WÓJCIKOWSKA, B., DEMBICZ, I. & SHAPOSHNIKOVA, A. (2015): Preservation of phytodiversity on the kurgans. – Scriptorium nostrum 1–2: 261–280.

MOYSIYENKO, I.I., ZACHWATOWICZ, M., SUDNIK-WÓJCIKOWSKA, B. & JABŁOŃSKA, E. (2014): Kurgans help to protect endangered steppe species in the Pontic grass steppe zone, Ukraine. – Wulfenia 21: 83–94.

OLENKOVSKY, M. (2004a): Arheologichni pamyatki Bilozerskogo rayonu Hersonskoyi oblasti (Archaeological sites of the Bilozerka district of the Kherson region) [in Ukrainian]. – Ailant, Kherson: 76 pp.

OLENKOVSKY, M. (2004b): Arheologichni pamyatki Kahovskogo rayonu Hersonskoyi oblasti (Archaeological sites of the Kakhovka district of the Kherson region) [in Ukrainian]. – Ailant, Kherson: 72 pp.

OLENKOVSKY, M. (2005): Arheologichni pamyatki Velikolepetihskogo rayonu Hersonskoyi oblasti (Archaeological sites of the Velyka Lepetykha district of the Kherson region) [in Ukrainian]. – Ailant, Kherson: 51 pp.

OLENKOVSKY, M. (2006): Arheologichni pamyatki Novovorontsovskogo rayonu Hersonskoyi oblasti (Archaeological sites of the Novovorontsovka district of the Kherson region) [in Ukrainian]. – Ailant, Kherson: 92 pp.

OLENKOVSKY, M. (2007): Arheologichni pamyatki Berislavskogo rayonu Hersonskoyi oblasti (Archaeological sites of the Beryslav district of the Kherson region) [in Ukrainian]. – Ailant, Kherson: 108 pp.

ÖSTER, M., COUSINS, S.A. & ERIKSSON, O. (2007): Size and heterogeneity rather than landscape context determine plant species richness in semi-natural grasslands. – J. Veg. Sci. 18: 859–868.

PACHOSKY, I.K. (1915): Opisanie rastytelnosti Khersonskoi gubernii. P 1. Lesa (Description of the vegetation of the Kherson province. Part 1. Forests) [in Russian]. – Materials for the study of soils of the Kherson province, Kherson: 203 pp.

QGIS DEVELOPMENT TEAM (2019): QGIS Geographic Information System. Open Source Geospatial Foundation Project. – URL: http://qgis.osgeo.org

R CORE TEAM (2017): R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RUREMONDE, R. & KALKHOVEN, J. (2009): Effects of woodlot isolation on the dispersion of plants with fleshy fruits. – J. Veg. Sci. 2. 377–384.

SHAPOVAL, V.V. (2012): Flora sudynnyh roslyn Askanijs'kogo stepu (Flora of vascular plants of Askania steppe) [in Ukrainian]. – Askanija Nova: FOP Andrjejev O. V.

SUDER, D. (2011): Participation of thermophilous species in plant communities of earthworks and castle ruins in the Western Carpathians. – Ann. UMCS, Biol. 66 (2): 21–31.

SUDNIK-WÓJCIKOWSKA, B. & MOYSIYENKO, I.I. (2006): The Flora of Kurgans in the West Pontic Grass Steppe Zone of Southern Ukraine. – Chornomors'k. Bot. Z. 2 (2): 14–44.

SUDNIK-WÓJCIKOWSKA, B. & MOYSIYENKO, I.I. (Eds) (2012): Kurhany na „Dzikich Polach" – dziedzictwo kultury i ostoja ukraińskiego stepu. (Kurgans in the 'Wild Field' – a cultural heritage and refugium of the Ukrainian steppe) [in Polish]. – Wydawnictwa Uniwersytetu Warszawskiego, Warszawa: 194 pp.

SUDNIK-WÓJCIKOWSKA, B., MOYSIYENKO, I.I., ZACHWATOWICZ, M. & JABŁOŃSKA, E. (2011): The value and need for protection of kurgan flora in the anthropogenic landscape of steppe zone in Ukraine. – Plant Biosyst. 145: 638–653.

VALKÓ, O., TÓTH, K., KELEMEN, A., MIGLÉCZ, T., RADÓCZ, S., SONKOLY, J., TÓTHMÉRÉSZ, B., TÖRÖK, P. & DEÁK, B. (2018): Cultural heritage and biodiversity conservation-plant introduction and practical restoration on ancient burial mounds. – Nat. Conserv. 24: 65–80.

VALKÓ, O., ZMIHORSKI, M., BIURRUN, I., LOOS, J., LABADESSA, R. & VENN, S. (2016): Ecology and conservation of steppes and semi-natural grasslands. – Hacquetia 15: 5–14.

WHITTAKER, R.J. & FERNÁNDEZ-PALACIOS, J.M. (2007): Island biogeography: ecology, evolution, and conservation, 2nd ed. – Oxford University Press, Oxford.

WYRWA, A.M. (2003): The necessity for interdisciplinary approach to a natural environment in prehistory and history. The case of the settlement complex in Lekno, Wągrowiec County, Wielkopolska Province. – Archeozoologia 21: 161–200.

ZAMORYI, P.K. (1961): Chetvertinni vidkladi Ukrayinskoyi RSR (Quaternary deposits of the Ukrainian SSR) [in Ukrainian]. – Kyiv: KSU.

Dayneko et al.: Ancient settlements in Southern Ukraine: how do local and landscape factors shape vascular plant diversity patterns in the last remnants of grass steppe vegetation?

Supplement E1. Description of the studied ancient settlements of the Lower Dnipro, Southern Ukraine. Archaeological data is based on OLENKOVSKY (2004a, 2004b, 2005, 2006, 2007). LSS - Late Scythian settlement

Anhang E1. Beschreibung der untersuchten antiken Siedlungen am unteren Dnepr in der Südukraine. Die Archäologischen Daten basieren auf OLENKOVSKY (2004a, 2004b, 2005, 2006, 2007). LSS – Spätskythische Siedlung

No.	Name	Latitude N (WGS84)	Longitude E (WGS84)	Area (ha)	Age	Culture/ tribe	Distance to settlements
Kherson region, Ukraine							
1.	Chervonomaiatske	46.95784	33.95784	6.11	III c. BC – IV c. AD	LSS of Sarmatian time	vicinity v. Chervonyi Maiak
2.	Gavrylivske	47.24597	33.91051	3.23	IV- III c. BC	Late Bronze LSS	2.5 km to v. Novooleksandrivka
3.	Glyboka Prystan	46.58631	32.23106	2	V c. BC – III c. AD	Ancient settlement	1.5 km to v. Shyroka balka (W) and 1.8 km to v. Sofiivka (E)
4.	Hannivske	47.19798	33.82716	2.24	II c. BC – II c. AD	LSS	3 km to v. Dudchany (E)
5.	Konsulivske	47.01519	33.6585	5.37	I c. BC – II c. AD	LSS of Sarmatian time	1 km to v. Respublikanets (S)
6.	Liubymivske	46.48567	33.33189	4.43	II c. BC – III c. AD, VIII –X, XIV-XV c. AD	LSS	in v. Liumymivka
7.	Lvivske	47.78660	33.13142	9.24	II c. BC – III c. AD	LSS of Sarmatian time	vicinity v. Lvove
8.	Male Tiagynske	46.76770	33.05897	6.3	XIV- XVI c. AD	Iron Age, Scythian settlement	1 km to v. Tiagynka (N)
9.	Poniativske	46.73772	32.88998	8.27	II c. BC – II c. AD	LSS	in v. Poniativka
10.	Sablukivske	47.12828	33.78358	12	I c. AD	LSS	0.8 km ro v. Sablukivka (E)
11.	Skelka	46.63774	32.00866	5.82	V- III c. BC., I c. BC – III c. AD, VI-V c. BC	Scythian settlement	3.4 km to v. Lupareve (W); 7.25 km to v. Oleksandrivka (E)
12.	Stanislavske	46.57587	32.13176	6.35	XII-XI c. BC, VI-V c. BC, IV-II c. BC, I c. BC - II c. AD, III-IV c. AD	settlement Late Bronze Age Bilozerskoy culture; settlement of Chernyakhiv culture	in v. Stanislav
13.	Staroshvedske	46.86793	33.59151	3.6	II c. BC – III c. AD	LSS of Sarmatian time	in v. Zmiivka
14.	Velykolepetykhske	47.09453	33.54375	4.82	II c. BC – II c. AD	LSS	in v. Velyka Lepetykha
15.	Velyke Tiagynske	46.76189	33.05803	18.7	I - XVI c. AD	LSS, Golden Horde period	1 km to v. Tiagynka (N)
16.	Zolotobalkivske	47.37552	33.97328	1.1	II c. BC – III c. AD	LSS	in v. Zolota Balka
17.	Zolotyi Mys	46.5783	32.20975	1.3	III c. BC – III c. AD	Ancient settlement	vicinity v. Shyroka balka
Mykolayiv region, Ukraine							
18.	Oleksandrivka-Roksanivka	46.85046	32.77082	2.83	V-IV c. BC	settlement of Chernyakhiv culture	vicinity v. Oleksandrivka

Dayneko et al.: Ancient settlements in Southern Ukraine: how do local and landscape factors shape vascular plant diversity patterns in the last remnants of grass steppe vegetation?

Supplement E2. Correlation matrix of environmental variables used in the analyses of the species richness of vascular plants in the ancient settlements (*n* = 18) studied in Southern Ukraine. Values indicate Pearson correlation coefficient.

Anhang E2. Korrelationsmatrix von Umgebungsvariablen, die bei der Analyse des Artenreichtums von Gefäßpflanzen in den in der Südukraine untersuchten antiken Siedlungen (*n* = 18) verwendet wurden.

	Area	Steppe cover in 1km buffer	Area of settlements in 1km buffer	Distance to settlements	Microhabitat variety index	Afforestation degree
Steppe cover in 1km buffer	0.57					
Area of settlements in 1km buffer	-0.19	-0.2				
Distance to settlements	-0.03	0	-0.78			
Microhabitat variety index	0.42	0.66	-0.14	-0.19		
Afforestation degree	0.25	0.21	-0.14	0.08	0.04	
Annual precipitation	-0.3	-0.17	-0.18	0.22	-0.15	-0.08