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Vegetation diversity and ecological factor assessment via phytoindication on the arena terrace of the Dnipro valley

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The floodplain terraces of rivers in Europe's temperate zone play a crucial ecological role by supporting unique biodiversity and ensuring landscape stability. This study focused on the vegetation diversity and ecological assessment of the arena terrace, specifically the first above-floodplain terrace of the Dnipro River valley within the Dnipro-Orilsky Nature Reserve. The terrace represents a complex geomorphological feature shaped initially by fluvial processes in the Late Pleistocene and subsequently modified by aeolian activities, resulting in sandy soils and psammophytic vegetation. The research aimed to assess the floristic composition, biodiversity levels, and ecological conditions of plant communities, identifying the primary abiotic factors influencing vegetation structure. Geobotanical surveys conducted between 2013 and 2024 documented 297 vascular plant species across 1079 sample plots, classified into 24 associations representing 14 vegetation classes. Results indicated significant variability in vegetation richness and ecological characteristics among different associations. Species richness ranged notably, with the highest diversity observed in meadow and pioneer psammophytic communities, such as *Veronica dillenii-Secaletum sylvestris*, while the lowest occurred in communities such as *Secaletum sylvestre*. Shannon diversity indices confirmed these findings, highlighting meadow associations like *Limonio meyeri-Festucetum pseudodalmaticae* among the most diverse. The phytoindication method revealed critical abiotic gradients influencing vegetation patterns, primarily moisture, nutrient availability, soil acidity, salt content, carbonate levels, nitrogen content, and soil aeration. The moisture regime showed extensive variability, significantly affecting community differentiation. Meadow communities demonstrated high moisture availability, whereas psammophytic communities experienced moisture deficits. Soil nitrogen content sharply contrasted between ecosystems, with meadow and forest ecosystems exhibiting significantly higher nitrogen levels compared to psammophytic steppe ecosystems. Climatic regimes, especially thermal and moisture-related indicators, also displayed pronounced variability influencing the ecological niches of plant associations. The thermal radiation balance and continentality indices were relatively stable, whereas ombroclimate and cryoclimate demonstrated significant spatial variation. The study underscored the ecological importance of the first above-floodplain terrace as a biodiversity hotspot, emphasizing its role in maintaining ecosystem stability amid anthropogenic pressures and climate change. Findings offer valuable insights for conservation management, restoration practices, and ecological monitoring, addressing a critical gap in understanding floodplain terraces' ecological functions and their responses to environmental gradients.

Keywords: floodplain terrace; vegetation diversity; phytoindication; species richness; psammophytic vegetation; soil moisture; abiotic gradients; biodiversity hotspot; ecological assessment; Dnipro river valley.

Introduction

The river floodplains that are located within the temperate zone of Europe play a pivotal ecological role in ensuring the structural and functional integrity of natural landscapes (Havrdová et al., 2023). Floodplains represent transition zones between aquatic and terrestrial ecosystems, and as such, they form a unique environment characterised by high spatial and temporal dynamics (Thoms, 2003). These dynamics are a result of periodic flooding, changes in groundwater levels and the deposition of alluvial material (Devitt et al., 2023). This phenomenon contributes to the formation of a mosaic of habitats, encompassing marshy meadows, floodplain forests and shrubbery, as well as sandy shoals and oxbows (Janssen et al., 2020). Each of these habitats supports unique communities of organisms (Janssen et al., 2020). The biodiversity of floodplain ecosystems is exceptionally high in comparison to surrounding areas (Tockner & Stanford, 2002). This ecological zone is of particular significance as a refuge for rare and endangered species, with a rich variety of flora and fauna, including numerous endemic and relict elements (Glińska-Lewczuk et al., 2016). Floodplain meadows and forests play an important role as a food source, nesting sites and migration routes for waterbirds, amphibians and mammals (Cheng et al., 2012). In the waters of the littoral zoone and temporary water bodies, aquatic insect larvae develop, fish spawn and organic matter is actively filtered by invertebrates (Lisovets et al., 2024). In addition to preserving biodiversity, floodplains perform a number of important ecosystem services (Zurbrügg et al., 2012). It has been demonstrated that they function as natural regulators of the hydrological regime (Xue et al., 2024). This is evidenced by their ability to retain floodwaters, thereby reducing the risk of flooding in lower reaches. Furthermore, they contribute to the replenishment of groundwater and the purification of surface runoff. Due to the large area of soil contact with water and active biogeochemical cycling, floodplains are effective areas for purifying water from excess nitrogen, phosphorus, pesticides and other pollutants. Alluvial soils are highly fertile and capable of rapid recovery, which has historically led to their active use in agriculture (Yorkina et al., 2020). Intensive ploughing, land reclamation, construction and hydraulic engineering have led to the degradation of many floodplain ecosystems in Europe, significantly reducing their ecological potential and fragmenting natural habitats. In the context of climate change and increasing anthropogenic pressure, the conservation and restoration of floodplains is of strategic importance (Zhukov et al., 2022). This includes the implementation of nature-based water management approaches, rewilding, restoration of flood dynamics and renaturalisation of river valleys (Virdana et al., 2025). In this context, floodplains are not only nature conservation areas, but also active elements of adaptation to global change, capable of maintaining ecosystem stability and environmental security across entire regions.

The formation of above-floodplain terraces is of significant ecological importance within the broader framework of river valley structures, emerging at the interface between the dynamic processes of the floodplain and the more stable topographical features that prevail in the surrounding landscape (Gao et al., 2020). These deltas are situated above the level of regular floods but maintain geomorphological and hydrological connections with the river system. This results in the formation of unique ecosystems that differ from floodplain and dryland biotopes (Brinkmann et al., 2000). The ecological significance of the floodplain terrace is attributable to its transitional nature, whereby it combines features of alluvial and eolian landscapes, often forming a mosaic of soil and hydrological conditions, ranging from well-drained sandy areas to local depressions with close groundwater levels (Baker & Barnes, 1998). This phenomenon contributes to the high spatial heterogeneity of the environment, which, in turn, creates conditions conducive to the existence of a wide range of plant formations, including pioneer communities on dry sands, as well as mixed grass and cereal communities on sandy loam or peaty soils. Psammophytic steppes, boreal pine forests, light oak forests, as well as sparse forests and shrub formations can develop on such terraces, which often have conservation value due to the presence of rare, endemic and relict species (Nykytiuk et al., 2025). The river valley terraces, being of a high mosaic nature, function as centres of structural and functional biodiversity. This supports a variety of life forms, trophic levels and adaptive strategies. Above-floodplain terraces are also important for the ecological stabilisation of river valleys (Didukh et al., 2015). The elevated position of these features renders them comparatively resistant to the impacts of flooding and erosion. In addition to their primary function, they also act as a physical and biological divide between the river floodplain and surrounding agricultural or urbanised areas. This ecological function also serves to foster connectivity between natural habitats throughout the landscape. In the current context of floodplain degradation and active land use, floodplain terraces are becoming even more important as reservoirs for the conservation of natural flora and fauna (Chetvertak et al., 2025), sites for the restoration of natural ecosystems and the formation of ecological networks (Ponomarenko et al., 2024). They are promising areas for nature-oriented land use, redevelopment and conservation, especially in regions where floodplain ecosystems have already lost their natural dynamics.

The first above-floodplain terrace of the Dnipro River represents a geomorphological feature that reflects a complex interplay between ancient fluvial deposition and subsequent aeolian modification. Initially, this terrace originated during the Late Pleistocene as a result of fluvial processes associated with channel migration, sediment accumulation, and lateral aggradation (Matoshko, 2004). The terrace surface was constructed by the river through the deposition of alluvial sands and silts during a high-energy phase of fluvial activity. These sediments typically formed broad sandy floodplains and channel bars, which over time became vertically and laterally stabilised. Following the stabilisation of the Dnipro River course and a marked decline in fluvial dynamics, aeolian processes became the dominant agents reshaping the terrace surface. This transformation occurred under periglacial conditions, where limited vegetation cover and dry climatic conditions facilitated the wind-driven reworking of previously fluvial sands. As a result, large portions of the terrace acquired typical aeolian features, such as sand sheets and low dunes, forming the geomorphological structure locally referred to as the arena (Zelenova et al., 2024). These aeolian deposits are now clearly separated from the active floodplain, both geomorphologically and ecologically, as they support well-drained sandy soils and psammophytic vegetation. The first above-floodplain terrace of the Dnipro River was initially shaped by fluvial deposition but was later transformed by extensive aeolian processes. The current morphology and ecological characteristics of this terrace are a testament to the dominance of wind-driven sedimentation after the cessation of fluvial influence. This dual genesis highlights the terrace as a key geomorphological archive of Late Pleistocene landscape evolution in the Dnipro valley (Matoshko, 2004).

Floodplain terraces are unique elements of river landscapes that combine features of both floodplain and terrestrial ecosystems (Ward et al., 2002). The area's unique ecological mosaic, shaped by a combination of geomorphology, moisture regime, soil conditions and light regime, fosters a conducive environment for the proliferation of diverse plant communities and elevated species diversity (Nakamura et al., 2020). Nevertheless, despite their potential ecological value, the biological diversity of floodplain terraces and the factors that determine it remain the subject of only a modicum of study in the temperate zone of Europe (Tutova et al., 2023). The following text is intended to provide a comprehensive overview of the subject matter. In many cases, such terraces are considered to be merely transitional geomorphological forms, with insufficient attention being paid to their ecological functioning, species composition, phytocenosis structure and response to abiotic gradients. A paucity of studies has been identified which have comprehensively assessed the relationship between species richness, structural diversity of vegetation cover and abiotic factors such as moisture, light, aeration and soil fertility. This poses a significant challenge to the development of scientifically sound measures for the conservation and restoration of floodplain terraces, which are under increasing pressure from land reclamation, agricultural use and climate change. The primary objective of this study is to assess the species composition and level of biological diversity of plant communities on floodplain terraces within the designated nature conservation area. The second objective is to identify the abiotic environmental factors that exert the greatest influence on species abundance and the structural characteristics of phytocenoses. Thirdly, the spatial patterns of ecological differentiation of communities within terraces with differing moisture regimes, light conditions and soil types are to be analysed. Fourthly, the formulation of recommendations for the protection, monitoring and potential restoration of floodplain terrace ecosystems is to be based on the identified ecological relationships. The present study contributes to the scientific corpus by addressing knowledge gaps and establishing a foundation for the effective management of the valuable components of natural ecosystems of river valleys in the context of landscape change.

Material and methods

Geobotanical surveys of the first floodplain terrace of the Dnipro River within the Dnipro-Orilsky Nature Reserve were conducted between 2013 and 2024. We recorded the presence of all vascular plant species on 1079 sample plots measuring 4 × 4 m (Fig. 1). Projective species coverage was determined as a percentage. For the purposes of this study, we generally accepted infraspecific taxa as species (Mykhailyuk et al., 2023). Critical samples were collected and identified using microscopy. The sample plots were distributed across the entire study area and their exact location was determined using GPS (Garmin eTrex, ± 5 m). We tried to select samples that represented the entire variation of community types and plot sizes within the grid system. Plant taxonomy was based on Euro+Med Plantbase (http://ww2.bgbm.org/EuroPlusMed). Vegetation classification was performed using the TWINSPAN programme. The precision of the diagnostic species for clusters is determined by the Phi coefficient, with a 25% accuracy threshold (for highly diagnostic species, this rises to 50%). Species exhibiting a frequency of occurrence greater than 25% are deemed constant (for highly constant species, this rises to 50%), while dominant species are identified as those with a projective cover greater than 10% (Lavrinenko et al., 2023).

The phi coefficient was calculated using the indicspecies library (Cáceres, M. D. 2013. How to use the indicspecies package (ver. 1.7.1). R Project, 29). Syntaxes were identified to the association level; syntax names are given according to the pan-European Vegetation of Europe (Mucina et al., 2016) and the Prodromus of the Vegetation of Ukraine (Dubina et al., 2019). The phytoindication assessment of ecological factors was carried out in accordance with the synphytoindication methodology of Didukh (2011), and calculations were made using the ideal indicator method (Buzuk, 2017; Zhukov & Kunakh, 2025). For clarity, the scores were converted into equivalent physical values (Zhukov & Kunakh, 2025). The botanical database is freely available in the Global Biodiversity Information Facility (GBIF) database (Lisovets et al., 2025). A complete syntaxonomic table and the prodromus of the vegetation are available in the Mendeley Data repository (Zhukov et al., 2025).

Results

Syntaxonomic diversity of plant cover. Within the studied area (Fig. 2), 297 plant species representing 24 plant associations were identified. In turn, the associations represent 14 vegetation classes. The *Festuco-Puccinellietea* class unites moist, fresh and dry inland communities on saline soils. It is represented within the studied area by two associations: *Limonio meyeri-Festucetum pseudodalmaticae* and *Junco gerardii-Agrostietum stoloniferae*. The leading factors in the formation of coenotic diversity and its ecotopic differentiation are the relief of the habitat, the duration of flooding, the type and density of the soil, and the degree of salinisation.

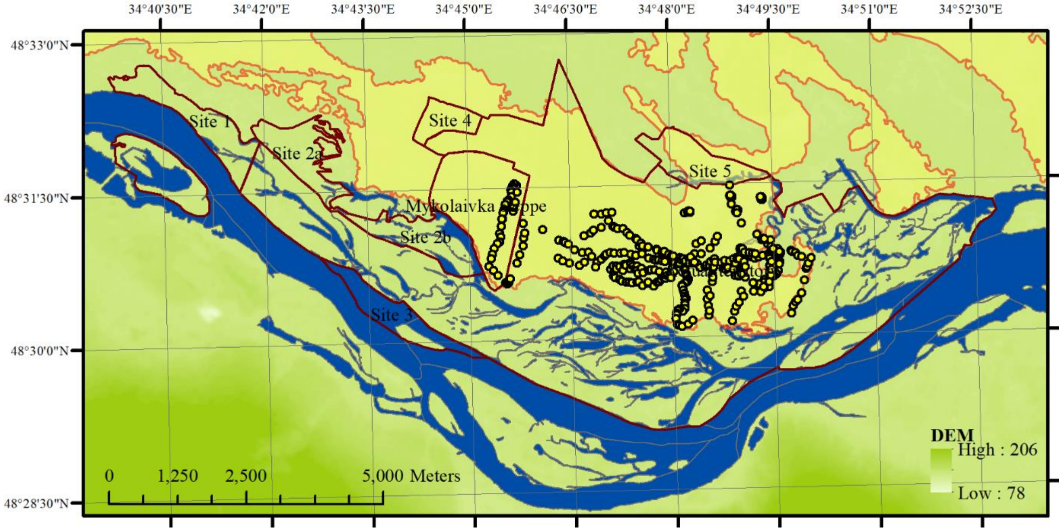

Fig. 1. Configuration of the first above-floodplain terrace of the Dnipro River valley (red boundary) and the locations of vegetation releves: the burgundy line indicates the boundary of the Dnipro-Oril Nature Reserve; sites 1–5 and the Mykolaivka Steppe represent proposed areas for inclusion into the reserve due to their conservation value; the boundary of the first above-floodplain terrace is delineated by the 78-meter contour line above sea level, which clearly outlines the area of sandy soils and psammophytic vegetation that characterises the terrace (arena) zone

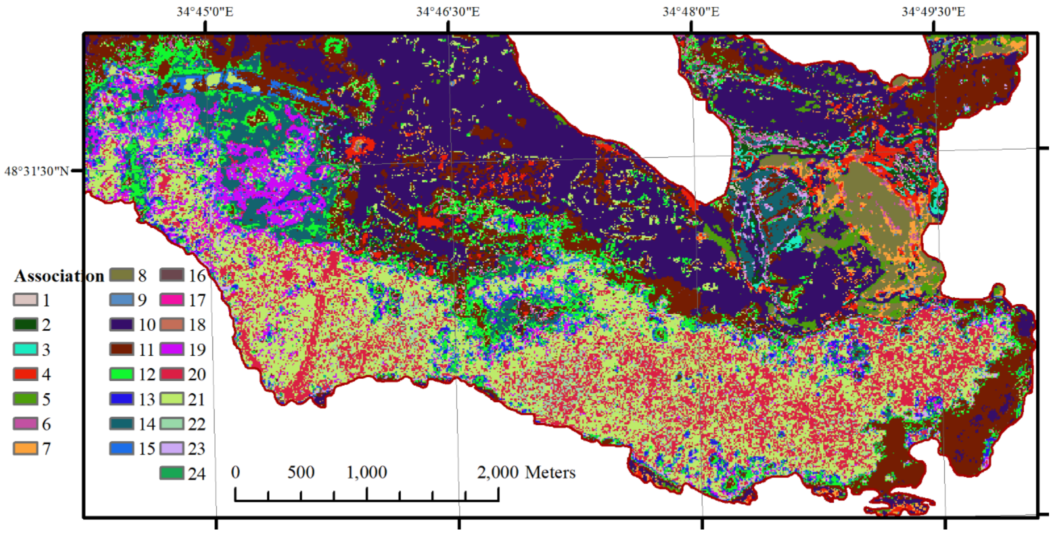

Fig. 2. Spatial distribution of plant associations on the first above-floodplain terrace of the Dnipro River within the boundaries of the "Dnipro-Orilskyi" Nature Reserve and adjacent areas: the classification model was developed using a random forest algorithm with Sentinel-derived spectral indices as predictors; syntaxons: 1 refers to the association *Limonio meyeri-Festucetum pseudodalmaticae* Umanets et I. Solomakha in Dubyna, Dziuba et Iemelianova 2013, 2 refers to the association *Poetum pratensis* Ravarut et al. 1956, 3 refers to the association *Junco gerardii-Agrostietum stoloniferae* Grigoriev et al. 2002, 4 refers to the association *Caricetum gracilis* Savič 1926, 5 refers to the association *Populetum nigro-albae* Slavnić 1952, 6 refers to the association *Salicetum albae* Issler 1926, 7 refers to the association *Alliario officinalis-Chaerophylletum temuli* (Kreh 1935) Lohmeyer 1949, 8 refers to the association *Ficario-Ulmetum minoris* Knapp 1942, 9 refers to the association *Melico nutantis-Quercetum roboris* Shevchyk et Solomakha in Shevchyk, Solomakha et Voityuk 1996, 10 refers to the association *Symphyto officinalis-Anthriscetum sylvestris* Passarge 1975, 11 refers to the association *Salici rosmarinifoliae-Holoschoenetum vulgaris* Mititelu et al. 1973, 12 refers to the association *Calamagrostietum epigei* Juraszek 1928, 13 refers to the association *Aceri tatarici–Quercetum roboris* Zólyomi 1957, 14 refers to the association *Melico transsilvanicae-Agropyretum* T. Müller in Görs 1966, 15 refers to the association *Chamaecytiso borysthenici-Agropyretum dasyanthi* Karnatovska 2006, 16 refers to the association *Veronico dillenii-Secaletum sylvestris* Shevchyk et Solomakha 1996, 17 refers to the association *Artemisio dniproicae-Salicetum acutifoliae* Shevchyk et Solomakha 1996, 18 refers to the association *Hieracio pilosellae-Pinetum* Polishko 2005, 19 refers to the association *Centaureo borysthenicae-Festucetum beckeri* Vicherek 1972, 20 refers to the association *Secali sylvestri-Caricetum colchicae* Davydova 2019, 21 refers to the association *Centaureo brevicipiti-Festucetum beckeri* Vicherek 1972, 22 refers to the association *Eragrostietum minoris-pilosae* Paschkevich 2024, 23 refers to the association *Festucetum beckeri* Ad. Oprea 1998, 24 refers to the association *Secaletum sylvestre* Popescu et Sanda 1973

The *Molinio-Arrhenatheretea* class is represented by the *Poëtum pratensis* association. This association is found in low-lying areas of watersheds, in the bottoms of shallow flowing valleys and other depressions where groundwater does not stagnate, as well as in the lower parts of the slopes of pine terraces. The group is confined to areas with soddy, soddy-meadow and meadow sandy loam, less frequently loamy soils, sometimes with carbonate-saline groundwater at a depth of 0.7–1.0 m. The prerequisite for their formation is a floodplain regime. The leading factor in spatial differentiation is the moisture regime and the richness of the soils in nutrients. The *Phragmito-Magnocaricetea* class is represented by the *Caricetum gracilis* association. This is a group of plants of wet, marshy and boggy meadows, marshes on soddy, peaty, silty and meadow-bog soils. They are characteristic of periodically flooded ecotopes in the floodplains of the Protich River. They are resistant to water level fluctuations during the growing season. The *Salicetea purpureae* class is represented by three associations. These are floodplain wooded willow and poplar, as well as shrub communities and plantations on moist silty-marshy, soddy, sandy and gravelly alluvial soils. The *Populetum nigro-albae* association usually occupies elevated areas with soddy-sandy and meadow-marsh soils under conditions of periodic flooding. The *Salicetum albae* association is typical for lowland habitats in the transition zone from the floodplain to the central part of the floodplain, where alluvial-erosion processes are significantly weakened and sandy loam meadow soils are formed. The *Artemisio dniproicae-Salicetum acutifoliae* association occurs in floodplain areas with soddy, poorly formed, layered, light loamy soils and atmospheric moisture supply. *Galio-Urticetea* covers semi-natural communities formed by tall and medium-sized grass species on nitrogen-enriched marginal habitats: mesophytic forest edges and along linear watercourses. The class is represented by the associations *Alliario officinalis-Chaerophylletum temuli* and *Symphyto officinalis-Anthriscetum sylvestris*. The association *Alliario officinalis-Chaerophylletum temuli* occurs on nitrified edges of broad-leaved forests on soils without mechanical damage. The *Symphyto officinalis-Anthriscetum sylvestris* association occurs on nitrified forest edges with fresh, loose soils.

The *Carpino-Fagetea Sylvaticae* class is zonal for forest and forest-steppe zones and covers nemoral forests. This class is represented by the *Ficario-Ulmetum minoris* association, which occurs on well-formed, rich, fresh soils, in the talweg of deep forest ravines and along streams. The *Quercetea robori-petraeae* class covers acidophilic oak forests on poor soils and is represented by the *Melico nutantis-Quercetum roboris* association. These communities occur on interhill depressions of river terraces on light sandy soils. The *Quercetea pubescentis* class covers thermophilic, xerophilic and mesoxerophilic forests and is represented by the *Aceri tatarici–Quercetum roboris* association. These are mainly shrubby communities on hills in the arena. The *Pyrolo-Pinetea sylvestris* class represents Euro-Siberian thermophilic forests on sandy soils. Within the studied area, the class is represented by the *Hieracio pilosellae-Pinetum* association. These communities are the result of the naturalisation of artificial pine plantations over 40 years old, which grow on the tops and gentle slopes of local elevations in the form of hilly ridges with sandy dry soils. The *Epilobietea angustifolii* class includes nitrophilic herbaceous and shrubby communities, which are the first stage in the secondary succession process of forest coniferous vegetation restoration after windbreaks and fires. It is represented by the association *Calamagrostietum epigei*, which is typical of sandy and sandy loam soils in pine forests after fires or windbreaks. The *Artemisietea vulgaris* class includes ruderal communities of tall biennial and perennial plants, common in nitrified ecotopes with varying moisture and light regimes. It is represented by the *Melico transsilvanicae-Agropyretum* association, which occurs on disturbed soils.

Groups of sandy, loosely consolidated sands are represented by the classes *Koelerio-Corynephoretea canescentis* and *Festucetea vaginatae*. These classes have many common features and differ in that *Koelerio-Corynephoretea canescentis* communities usually form on more acidic soils, while Festucetea vaginatae communities form on more alkaline soils. The *Koelerio-Corynephoretea canescentis* class includes pioneer communities on sandy, shallow soils that are mostly dry and low in nutrients. It is represented by the association *Veronico dillenii-Secaletum sylvestris*, which occurs on soddy soils formed on alluvial deposits on islands and in the floodplain of the Dnipro River, or on eluvial sandy deposits. The *Festucetea vaginatae* class covers sandy steppe and psammophytic meadow communities. It is represented by seven associations within the studied area. The *Salici rosmarinifoliae-Holoschoenetum vulgaris* association occupies interdune depressions with a groundwater level relatively close to the surface. The *Festucetum beckeri* association is usually found on the slopes of sand dunes. The *Secaletum sylvestre* association occupies the levelled tops of dunes that are subject to significant wind erosion. The *Chamaecytiso borysthenici-Agropyretum dasyanthi* association is a pioneer in wind-blown depressions, which usually form from small depressions several centimetres deep and wide, which later turn into hollows. The most represented phytocenoses of the association are found in deflation depressions on the first floodplain terrace in the Dnipro River valley, where eolian processes are still ongoing. The *Centaureo borysthenicae-Festucetum beckeri* association is widespread on sandy humus soils. The *Centaureo brevicipiti-Festucetum beckeri* association is found in flat areas of sandy steppe and on the slopes of wind-blown hollows with moderately and poorly developed sandy soils. The *Secali sylvestri-Caricetum colchicae* association is found on gentle dune slopes.

The *Stellarietea mediae* class includes Segetal communities that form along roads. This class is represented by the *Eragrostietum minoris-pilosae* association. This community is often found along sandy roads and is represented by species that tolerate trampling well.

Prodomus of plants of the first floodplain terrace (arena) of the Dnipro River valley within the Dnipro-Orilsky Nature Reserve:

Festuco-puccinellietea Soó ex Vicherek 1973
- *Festuco valesiacae-Limonietalia gmelinii* Mirkin in Golub et Solomakha 1988
  - *Diantho guttati-Milion vernalis* Umanets et I. Solomakha 1998
    - *Limonio meyeri-Festucetum pseudodalmaticae* Umanets et I. Solomakha in Dubyna, Dziuba et Iemelianova 2013
- *Scorzonero-Juncetalia gerardii* Vicherek 1973
  - *Carici dilutae-Juncion gerardii* Lysenko and Mucina 2015
    - *Junco gerardii-Agrostietum stoloniferae* Grigoriev et al. 2002

Molinio-Arrhenatheretea Tx. 1937
- *Arrhenatheretalia elatioris* Tx. 1931
  - *Arrhenatherion elatioris* Luquet 1926
    - *Poëtum pratensis* Ravarut et al. 1956

Phragmito-Magnocaricetea Klika in Klika et Novák 1941
- *Magnocaricetalia* Pignatti 1953
  - *Magnocaricion gracilis* Géhu 1961
    - *Caricetum gracilis* Savič 1926

Salicetea purpureae Moor 1958
- *Salicetalia purpureae* Moor 1958
  - *Salicion albae* Soó 1951
    - *Populetum nigro-albae* Slavnić 1952
    - *Salicetum albae* Issler 1926
  - *Artemisio dniproicae-Salicion acutifoliae* Shevchyk et Solomakha in Shevchyk et al. 1996
    - *Artemisio dniproicae-Salicetum acutifoliae* Shevchyk et Solomakha 1996

Galio-Urticetea Passarge ex Kopecký 1969
- *Galio-Alliarietalia* Oberd. in Görs et T. Müller 1969
  - *Geo urbani-Alliarion officinalis* Lohmeyer et Oberd. in Görs et T. Müller 1969
    - *Alliario officinalis-Chaerophylletum temuli* (Kreh 1935) Lohmeyer 1949
- *Aegopodium podagrariae* Tx. 1967
    - *Symphyto officinalis-Anthriscetum sylvestris* Passarge 1975

Carpino-Fagetea Sylvaticae Jakucs ex Passarge 1968
- *Alno-Fraxinetalia excelsioris* Passarge 1968
  - *Alnion incanae* Pawłowski et al. 1928
    - *Ficario-Ulmetum minoris* Knapp 1942

Quercetea robori-petraeae Br.-Bl. et Tx. ex Oberd. 1957

Quercetalia roboris Tx. 1931
  Convallario majalis-Quercion roboris Shevchyk et Solomakha in Shevchyk, Solomakha et Voityuk 1996
    Melico nutantis-Quercetum roboris Shevchyk et Solomakha in Shevchyk, Solomakha et Voityuk 1996
Quercetea pubescentis Doing-Kraft ex Scamoni et Passarge 1959
  Quercetalia pubescenti-petraeae Klika 1933
    Aceri tatarici-Quercion Zólyomi 1957
      Aceri tatarici–Quercetum roboris Zólyomi 1957
Pyrolo-Pinetea sylvestris Korneck 1974
  Koelerio glaucae-Pinetalia sylvestris Ermakov 1999
    Koelerio glaucae-Pinion sylvestris Ermakov 1999
      Hieracio pilosellae-Pinetum Polishko 2005
Epilobietea angustifolii Tx. et Preising ex von Rochow 1951
  Galeopsio-Senecionetalia sylvatici Passarge 1981
    Epilobion angustifolii Oberd. 1957
      Calamagrostietum epigei Juraszek 1928
Artemisietea vulgaris Lohmeyer et al. in TX. ex von Rochow 1951
  Agropyretalia intermedio-repentis T. Müller et Görs 1969
    Convolvulo arvensis-Agropyrion repentis Görs 1967
      Melico transsilvanicae-Agropyretum T. Müller in Görs 1966
Koelerio-Corynephoretea canescentis Klika in Klika et Novák 1941
  Corynephoretalia canescentis Klika 1934
    Koelerion glaucae Volk 1931
      Veronico dillenii-Secaletum sylvestris Shevchyk et Solomakha 1996
Festucetea vaginatae Soó ex Vicherek 1972
  Festucetalia vaginatae Soó 1957
    Artemisio arenariae-Festucion beckeri Dubyna et Dziuba 2019
      Salici rosmarinifoliae-Holoschoenetum vulgaris Mititelu et al. 1973
      Festucetum beckeri Ad. Oprea 1998
      Secaletum sylvestre Popescu et Sanda 1973
    Festucion beckeri Vicherek 1972
      Chamaecytiso borysthenici-Agropyretum dasyanthi Karnatovska 2006
      Centaureo borysthenicae-Festucetum beckeri Vicherek 1972
      Centaureo brevicipiti-Festucetum beckeri Vicherek 1972
      Secali sylvestri-Caricetum colchicae Davydova 2019
Stellarietea mediae Tx. et al. in Tx. 1950
  Eragrostietalia J. Tx. ex Poli 1966
    Eragrostion Tx. in Oberd. 1954
      Eragrostietum minoris-pilosae Paschkevich 2024

Ecological characteristics of plant associations. The affiliation of a community to a particular association was able to explain 37.4% of the variability in species richness of communities (F = 29.0, P < 0.001). The lowest number of species was found in the associations *Secaletum sylvestre* (7.8 ± 1.7 species/relevé) and *Ficario-Ulmetum minoris* (8.2 ± 2.4 species/relevé) (Table 1). The largest number of species was found in the associations *Veronico dillenii-Secaletum sylvestris* (17.4 ± 4.6 species/relevé) and *Chamaecytiso borysthenici-Agropyretum dasyanthi* (16.4 ± 5.4 species/relevé). The association of a community with a particular association was able to explain 37.7% of the species richness variability according to Shannon (F = 29.4, P < 0.001).

Table 1
Descriptive statistics (mean ± standard deviation) of species richness, Shannon diversity, and canopy, shrub, and herb layer cover by association (significant differences between associations were identified using Tukey HSD: different letters indicate significant differences)

Syntaxon*	Species richness	Shannon diversity, bit	Canopy layer, %	Shrub layer, %	Herb layer, %
1 (N = 40)	15.9 ± 2.4^{ab}	3.6 ± 0.3^{a}	1.3 ± 1.5^{f}	3.7 ± 4.8^{de}	52.1 ± 9.0^{ab}
2 (N = 40)	15.0 ± 3.3^{ab}	3.5 ± 0.3^{a}	1.0 ± 2.1^{f}	1.6 ± 2.8^{e}	48.9 ± 14.7^{abc}
3 (N = 29)	14.4 ± 3.2^{ab}	3.5 ± 0.4^{a}	0.9 ± 1.8^{f}	0.7 ± 2.0^{e}	47.8 ± 11.5^{abcd}
4 (N = 39)	10.3 ± 3.9^{defg}	2.9 ± 0.5^{cd}	3.1 ± 6.1^{f}	15.3 ± 12.6^{abc}	40.0 ± 9.8^{cdef}
5 (N = 106)	11.0 ± 2.1^{def}	2.5 ± 0.3^{f}	57.5 ± 15.4^{a}	12.3 ± 9.7^{bcd}	11.7 ± 6.5^{k}
6 (N = 35)	11.0 ± 2.5^{cdef}	3.0 ± 0.4^{bcd}	31.6 ± 13.8^{bc}	23.8 ± 23.5^{a}	34.6 ± 12.3^{defgh}
7 (N = 80)	10.7 ± 2.2^{def}	2.9 ± 0.3^{cd}	30.6 ± 13.2^{c}	13.2 ± 11.6^{bcd}	29.3 ± 11.4^{gh}
8 (N = 116)	8.2 ± 2.4^{g}	2.3 ± 0.5^{f}	25.0 ± 11.6^{cd}	11.7 ± 7.3^{bcd}	15.1 ± 12.9^{jk}
9 (N = 53)	10.6 ± 2.3^{defg}	2.8 ± 0.3^{de}	36.8 ± 9.9^{b}	11.7 ± 9.0^{bcd}	27.5 ± 9.4^{ghi}
10 (N = 123)	9.2 ± 3.4^{fg}	2.6 ± 0.5^{ef}	24.9 ± 9.0^{d}	20.9 ± 13.3^{a}	19.9 ± 12.1^{ij}
11 (N = 33)	13.3 ± 5.0^{bc}	2.6 ± 0.8^{def}	14.4 ± 12.8^{e}	10.2 ± 13.3^{bcde}	34.1 ± 22.8^{efgh}
12 (N = 27)	14.7 ± 4.3^{ab}	3.2 ± 0.5^{abc}	7.8 ± 8.1^{ef}	17.7 ± 19.1^{ab}	45.3 ± 11.8^{bcde}
13 (N = 21)	15.8 ± 5.8^{ab}	3.0 ± 0.7^{bcd}	27.4 ± 12.6^{cd}	13.5 ± 14.0^{abcd}	27.5 ± 18.0^{ghi}
14 (N = 12)	15.4 ± 5.1^{ab}	2.7 ± 0.8^{def}	0.7 ± 2.3^{f}	26.2 ± 33.6^{a}	44.4 ± 13.3^{bcdef}
15 (N = 20)	16.4 ± 5.4^{ab}	3.3 ± 0.6^{abc}	7.4 ± 9.9^{ef}	18.6 ± 18.6^{ab}	55.1 ± 14.9^{ab}
16 (N = 18)	17.4 ± 4.6^{a}	3.3 ± 0.4^{ab}	7.6 ± 11.3^{ef}	9.6 ± 13.3^{bcde}	48.3 ± 17.2^{abcd}
17 (N = 17)	10.6 ± 4.8^{defg}	2.6 ± 0.6^{def}	0.3 ± 0.8^{f}	10.3 ± 14.8^{bcde}	34.7 ± 24.1^{defgh}
18 (N = 21)	13.0 ± 3.8^{bcd}	3.0 ± 0.3^{bcd}	6.6 ± 5.8^{ef}	2.0 ± 2.4^{de}	36.8 ± 24.9^{cdefg}
19 (N = 29)	13.8 ± 2.2^{bc}	2.8 ± 0.4^{cde}	0.1 ± 0.2^{f}	0.9 ± 1.4^{e}	45.9 ± 8.0^{bcde}
20 (N = 57)	11.4 ± 2.6^{cde}	2.5 ± 0.4^{ef}	0.0 ± 0.2^{f}	1.3 ± 2.7^{e}	45.8 ± 10.8^{bcde}
21 (N = 71)	11.6 ± 3.0^{cde}	2.8 ± 0.4^{de}	1.8 ± 4.9^{f}	3.5 ± 7.5^{de}	51.8 ± 18.6^{ab}
22 (N = 22)	11.3 ± 2.0^{cdef}	2.9 ± 0.4^{cde}	1.8 ± 6.0^{f}	6.2 ± 11.0^{bcde}	59.7 ± 18.9^{a}
23 (N = 32)	9.7 ± 1.8^{efg}	2.6 ± 0.3^{def}	1.2 ± 3.2^{f}	6.1 ± 5.7^{cde}	32.1 ± 12.8^{fgh}
24 (N = 38)	7.8 ± 1.7^{g}	2.4 ± 0.4^{f}	0.0 ± 0.0^{f}	2.9 ± 3.6^{de}	22.6 ± 6.1^{hij}

Notes: * – syntaxons: 1 refers to the association *Limonio meyeri-Festucetum pseudodalmaticae*, 2 refers to the association *Poëtum pratensis*, 3 refers to the association *Junco gerardii-Agrostietum stoloniferae*, 4 refers to the association *Caricetum gracilis*, 5 refers to the association *Populetum nigro-albae*, 6 refers to the association *Salicetum albae*, 7 refers to the association *Alliario officinalis-Chaerophylletum temuli*, 8 refers to the association *Ficario-Ulmetum minoris*, 9 refers to the association *Melico nutantis-Quercetum roboris*, 10 refers to the association *Symphyto officinalis-Anthriscetum sylvestris*, 11 refers to the association *Salici rosmarinifoliae-Holoschoenetum vulgaris*, 12 refers to the association *Calamagrostietum epigei*, 13 refers to the association *Aceri tatarici–Quercetum roboris*, 14 refers to the association *Melico transsilvanicae-Agropyretum*, 15 refers to the association *Chamaecytiso borysthenici-Agropyretum dasyanthi*, 16 refers to the association *Veronico dillenii-Secaletum sylvestris*, 17 refers to the association *Artemisio dniproicae-Salicetum acutifoliae*, 18 refers to the association *Hieracio pilosellae-Pinetum*, 19 refers to the association *Centaureo borysthenicae-Festucetum beckeri*, 20 refers to the association *Secali sylvestri-Caricetum colchicae*, 21 refers to the association *Centaureo brevicipiti-Festucetum beckeri*, 22 refers to the association *Eragrostietum minoris-pilosae*, 23 refers to the association *Festucetum beckeri*, 24 refers to the association *Secaletum sylvestre*.

The greatest diversity was characteristic of meadow communities with associations *Limonio meyeri-Festucetum pseudodalmaticae* (3.6 ± 0.3 bits), *Poëtum pratensis* (3.5 ± 0.3 bits), *Junco gerardii-Agrostietum stoloniferae* (3.5 ± 0.4 bits). The lowest diversity was found in associations such as *Ficario-Ulmetum minoris* (2.3 ± 0.5 bits) and *Secaletum sylvestre* (2.4 ± 0.4 bits). As expected, the densest canopy layer was characteristic of forest communities. *Populetum nigro-albae* associations had the most closed canopy layer (57.5 ± 15.4%), while *Ficario-Ulmetum minoris* associations had the most sparse canopy layer (25.0 ± 11.6%). The densest shrub layer was characteristic of *Salicetum albae* (23.8 ± 23.5%) and *Melico transsilvanicae-Agropyretum* (26.2 ± 33.6%) associations. For the latter association, this is due to the significant role of the semi-shrub *Chamaecytisus ruthenicus* in the community. The community's membership in a particular association was able to explain 80.1% of the variability in the grass layer cover (F = 189.4, P < 0.001). The densest herbaceous cover was characteristic of meadow associations: *Limonio meyeri-Festucetum pseudodalmaticae* (52.1 ± 9.0%), *Poëtum pratensis* (48.9 ± 14.7%), *Junco gerardii-Agrostietum stoloniferae* (47.8 ± 11.5), as well as for some psammophytic associations such as *Chamaecytiso borysthenici-Agropyretum dasyanthi* (48.3 ± 17.2%) and *Eragrostietum minoris-pilosae* (59.7 ± 18.9%).

Phytoindication assessment of edaphic regimes. The most variable edaphic regimes were the conditions of plant nutrient supply (CV = 75.9%) and carbonate content (CV = 53.1%), while the most stable regime was acidity (CV = 2.8%). Phytoindication assessments indicate that the available moisture for plants in the soil ranged from 33.1 to 148.2 mm in 95% of cases. The affiliation of the community to a particular association was able to explain 90.5% of the variability in the range of available moisture for plants in the soil (F = 445.9, P < 0.001). The *Caricetum gracilis* association demonstrated the highest level of moisture supply (156.77 ± 32.84 mm), while a wide range of psammophytic vegetation exhibited the lowest level (Table 2). In spatial terms, communities with the highest moisture supply are widespread in the northeast, east and north of the study area, while the eastern and, to a greater extent, southern areas are characterised by moisture deficiency (Fig. 2).

Table 2
Descriptive statistics (mean ± standard deviation) of phytoindication estimates of edaphic regimes by association
(significant differences between associations were identified using Tukey HSD: different letters indicate significant differences)

Syntaxon*	Hd (mm)	fH (unitless)	Rc (pH)	Sl (µg/l)	Ca (CaO+MgO %)	Nt (g/kg)	Ae (%)
1 (N = 40)	77.23 ± 11.36^{f}	0.29 ± 0.02^{def}	6.79 ± 0.11^{a}	51.24 ± 13.05^{a}	2.97 ± 0.66^{a}	2.37 ± 0.38^{f}	60.27 ± 4.71^{d}
2 (N = 40)	89.93 ± 17.54^{e}	0.28 ± 0.02^{ef}	6.71 ± 0.13^{ab}	40.66 ± 11.95^{bc}	2.47 ± 0.82^{abc}	2.47 ± 0.50^{f}	57.96 ± 6.93^{d}
3 (N = 29)	120.89 ± 24.93^{b}	0.31 ± 0.03^{bcdef}	6.66 ± 0.09^{abc}	40.23 ± 11.04^{bc}	2.00 ± 0.75^{bcde}	3.13 ± 0.44^{e}	35.73 ± 9.66^{g}
4 (N = 39)	156.77 ± 32.84^{a}	0.20 ± 0.03^{g}	6.48 ± 0.11^{def}	23.17 ± 3.55^{fgh}	1.14 ± 0.65^{g}	3.63 ± 0.56^{d}	23.19 ± 8.34^{h}
5 (N = 106)	110.29 ± 9.66^{c}	0.20 ± 0.02^{g}	6.63 ± 0.12^{bc}	23.91 ± 2.77^{fgh}	1.20 ± 0.43^{fg}	4.04 ± 0.39^{bc}	49.40 ± 5.15^{e}
6 (N = 35)	119.42 ± 11.08^{b}	0.20 ± 0.03^{g}	6.48 ± 0.21^{def}	19.95 ± 3.33^{gh}	1.18 ± 0.48^{g}	3.75 ± 0.63^{cd}	40.96 ± 8.36^{fg}
7 (N = 80)	113.42 ± 10.11^{bc}	0.17 ± 0.03^{h}	6.59 ± 0.11^{cd}	22.90 ± 3.40^{fgh}	1.42 ± 0.44^{fg}	3.98 ± 0.48^{bc}	43.72 ± 6.19^{f}
8 (N = 116)	117.49 ± 9.14^{b}	0.16 ± 0.02^{i}	6.58 ± 0.11^{cd}	22.02 ± 2.44^{gh}	1.52 ± 0.48^{efg}	4.31 ± 0.31^{a}	44.09 ± 5.47^{f}
9 (N = 53)	112.13 ± 8.71^{bc}	0.18 ± 0.02^{gh}	6.55 ± 0.09^{cd}	19.91 ± 2.90^{h}	1.71 ± 0.49^{def}	3.92 ± 0.42^{bcd}	45.35 ± 5.80^{f}
10 (N = 123)	104.08 ± 13.00^{d}	0.19 ± 0.04^{g}	6.51 ± 0.19^{def}	19.42 ± 3.23^{h}	1.19 ± 0.50^{g}	4.11 ± 0.83^{ab}	50.65 ± 8.23^{e}
11 (N = 33)	58.25 ± 11.61^{g}	0.32 ± 0.03^{bcd}	6.24 ± 0.24^{g}	20.24 ± 8.26^{gh}	1.02 ± 0.69^{g}	0.60 ± 0.51^{gh}	75.01 ± 6.35^{c}
12 (N = 27)	51.21 ± 7.69^{ghi}	0.33 ± 0.03^{abc}	6.38 ± 0.17^{fg}	20.93 ± 6.30^{gh}	1.44 ± 1.05^{efg}	0.50 ± 0.40^{ghi}	80.52 ± 3.90^{ab}
13 (N = 21)	56.52 ± 7.86^{gh}	0.28 ± 0.03^{f}	6.48 ± 0.24^{def}	22.42 ± 6.69^{fgh}	2.54 ± 1.27^{abc}	0.91 ± 0.51^{g}	75.01 ± 3.19^{c}
14 (N = 12)	49.26 ± 7.84^{ghij}	0.29 ± 0.03^{def}	6.62 ± 0.12^{bcd}	29.86 ± 9.31^{defg}	3.18 ± 0.95^{a}	0.67 ± 0.30^{gh}	75.90 ± 4.30^{bc}
15 (N = 20)	43.01 ± 2.89^{ijk}	0.31 ± 0.03^{bcdef}	6.37 ± 0.17^{fg}	25.16 ± 10.20^{efgh}	1.84 ± 0.89^{cdef}	0.27 ± 0.26^{hij}	80.99 ± 3.91^{ab}
16 (N = 18)	43.60 ± 4.18^{hijk}	0.33 ± 0.03^{abc}	6.45 ± 0.18^{def}	28.74 ± 6.81^{defg}	1.64 ± 0.61^{defg}	0.23 ± 0.15^{hij}	81.54 ± 2.99^{ab}
17 (N = 17)	40.96 ± 6.01^{ijk}	0.35 ± 0.03^{a}	6.51 ± 0.19^{def}	30.67 ± 11.47^{def}	1.03 ± 0.89^{g}	0.17 ± 0.08^{hij}	83.28 ± 4.57^{ab}
18 (N = 21)	40.55 ± 6.02^{ijk}	0.31 ± 0.03^{bcde}	6.27 ± 0.20^{g}	24.72 ± 9.29^{efgh}	1.21 ± 0.63^{fg}	0.15 ± 0.10^{hij}	83.12 ± 3.80^{ab}
19 (N = 29)	37.89 ± 2.79^{jk}	0.31 ± 0.03^{bcdef}	6.59 ± 0.14^{bcd}	39.73 ± 10.30^{bc}	2.49 ± 1.10^{abc}	0.21 ± 0.12^{hij}	80.80 ± 2.82^{ab}
20 (N = 57)	34.85 ± 2.76^{k}	0.30 ± 0.04^{cdef}	6.50 ± 0.11^{def}	36.46 ± 10.53^{cd}	2.55 ± 1.01^{ab}	0.12 ± 0.05^{ij}	80.95 ± 2.28^{ab}
21 (N = 71)	39.39 ± 4.28^{jk}	0.30 ± 0.04^{def}	6.42 ± 0.16^{ef}	32.27 ± 13.33^{de}	2.16 ± 1.02^{bcd}	0.11 ± 0.08^{j}	83.36 ± 2.81^{a}
22 (N = 22)	38.80 ± 3.39^{jk}	0.33 ± 0.03^{ab}	6.46 ± 0.22^{def}	46.01 ± 24.70^{ab}	1.68 ± 0.72^{defg}	0.12 ± 0.05^{ij}	84.32 ± 1.95^{a}
23 (N = 32)	39.49 ± 2.98^{jk}	0.30 ± 0.03^{cdef}	6.47 ± 0.15^{def}	28.63 ± 5.92^{efg}	1.73 ± 0.74^{def}	0.11 ± 0.07^{j}	82.00 ± 3.77^{ab}
24 (N = 38)	38.44 ± 3.51^{jk}	0.33 ± 0.03^{ab}	6.52 ± 0.12^{de}	42.59 ± 13.11^{bc}	1.69 ± 0.80^{def}	0.11 ± 0.07^{ij}	81.63 ± 2.91^{ab}

Notes: * syntaxons: 1 refers to the association *Limonio meyeri-Festucetum pseudodalmaticae*, 2 refers to the association *Poëtum pratensis*, 3 refers to the association *Junco gerardii-Agrostietum stoloniferae*, 4 refers to the association *Caricetum gracilis*, 5 refers to the association *Populetum nigro-albae*, 6 refers to the association *Salicetum albae*, 7 refers to the association *Alliario officinalis-Chaerophylletum temuli*, 8 refers to the association *Ficario-Ulmetum minoris*, 9 refers to the association *Melico nutantis-Quercetum roboris*, 10 refers to the association *Symphyto officinalis-Anthriscetum sylvestris*, 11 refers to the association *Salici rosmarinifoliae-Holoschoenetum vulgaris*, 12 refers to the association *Calamagrostietum epigei*, 13 refers to the association *Aceri tatarici–Quercetum roboris*, 14 refers to the association *Melico transsilvanicae-Agropyretum*, 15 refers to the association *Chamaecytiso borysthenici-Agropyretum dasyanthi*, 16 refers to the association *Veronico dillenii-Secaletum sylvestris*, 17 refers to the association *Artemisio dniproicae-Salicetum acutifoliae*, 18 refers to the association *Hieracio pilosellae-Pinetum*, 19 refers to the association *Centaureo borysthenicae-Festucetum beckeri*, 20 refers to the association *Secali sylvestri-Caricetum colchicae*, 21 refers to the association *Centaureo brevicipiti-Festucetum beckeri*, 22 refers to the association *Eragrostietum minoris-pilosae*, 23 refers to the association *Festucetum beckeri*, 24 refers to the association *Secaletum sylvestre*.

Moisture variability ranged from 0.14 to 0.37. The group's affiliation to a particular association explained 82.6% of the variability in moisture contrast (F = 222.8, P < 0.001). The highest contrast in moisture conditions was characteristic of the *Artemisio dniproicae-Salicetum acutifoliae* association (0.35 ± 0.03), while the *Ficario-Ulmetum minoris* association demonstrated the least variability (0.16 ± 0.02). Soil acidity in 95% of cases ranged from pH = 6.1 to pH = 6.8. The affiliation of a community to a particular association was able to explain 34.4% of the variability in soil acidity (F = 25.6, P < 0.001). The highest pH was characteristic of the *Limonio meyeri-Festucetum pseudodalmaticae* association (6.79 ± 0.11), and the lowest for the *Salici rosmarinifoliae-Holoschoenetum vulgaris* (6.24 ± 0.24) and *Hieracio pilosellae-Pinetum* (6.27 ± 0.20) associations. Salt content in the soil solution varied in the range from 14.7 to 61.6 µg/l in 95% of cases. The belonging of a group to a particular association was able to explain 52.4% of the variability of salt content in the soil solution (F = 52.7, P < 0.001).

The highest salt content in the soil solution was found in the associations *Limonio meyeri-Festucetum pseudodalmaticae* (51.24 ± 13.05 µg/L) and *Eragrostietum minoris-pilosae* (46.01 ± 24.70 µg/L). The carbonate content ranged from 0.46% to 3.89% in 95% of cases. The affiliation of a community to a particular association was able to explain 36.6% of the variability in the carbonate content in the soil (F = 28.1, P < 0.001). The highest carbonate content was typical for *Limonio meyeri-Festucetum pseudodalmaticae* (2.97 ± 0.66%) and *Melico transsilvanicae-Agropyretum* (3.18 ± 0.95%), and the lowest for *Salici rosmarinifoliae-Holoschoenetum vulgaris* (1.02 ± 0.69%) and *Artemisio dniproicae-Salicetum acutifoliae* (1.03 ± 0.89%). Soil nitrogen content varied in the range from 0.06 to 4.52 g/kg in 95% of cases. The affiliation of a community to a particular association was able to explain 94.2% of the variability in soil nitrogen content (F = 766.8, P < 0.001). Meadow and forest ecosystems differ significantly from psammophytic steppe ecosystems in terms of higher soil nitrogen content. In grassland and forest ecosystems, soil nitrogen content usually exceeds 2 g/kg, while in psammophytic steppe ecosystems, this indicator is less than 1 g/kg. The percentage of air-filled porosity relative to the total porosity volume varied in the range from 22.8% to 86.3% in 95.0% of cases. The affiliation of a community to a particular association was able to explain 90.8% of the variability in soil aeration (F = 467.9, P < 0.001). Soil aeration in psammophytic communities usually exceeds 70%, while soil aeration in meadow or forest communities was less than 60%.

Phytoindication assessment of edaphic regimes. Among the climatic indicators, ombroclimate and cryoclimate scores changed the most (CV = 66.4% and 68.5%, respectively). The most stable indicators were thermoclimatic (CV = 8.7%) and continentality (CV = 22.7%). The phytoindication assessment of the thermoclimatic regime indicates that the surface radiation balance varied in the range from 1.56 to 2.32 gJ/(m^2 year) (Table 3). The spatial variability of the thermal climate regime demonstrates small-scale patterns, which are likely due to the influence of relief on this ecological regime (Fig. 3).

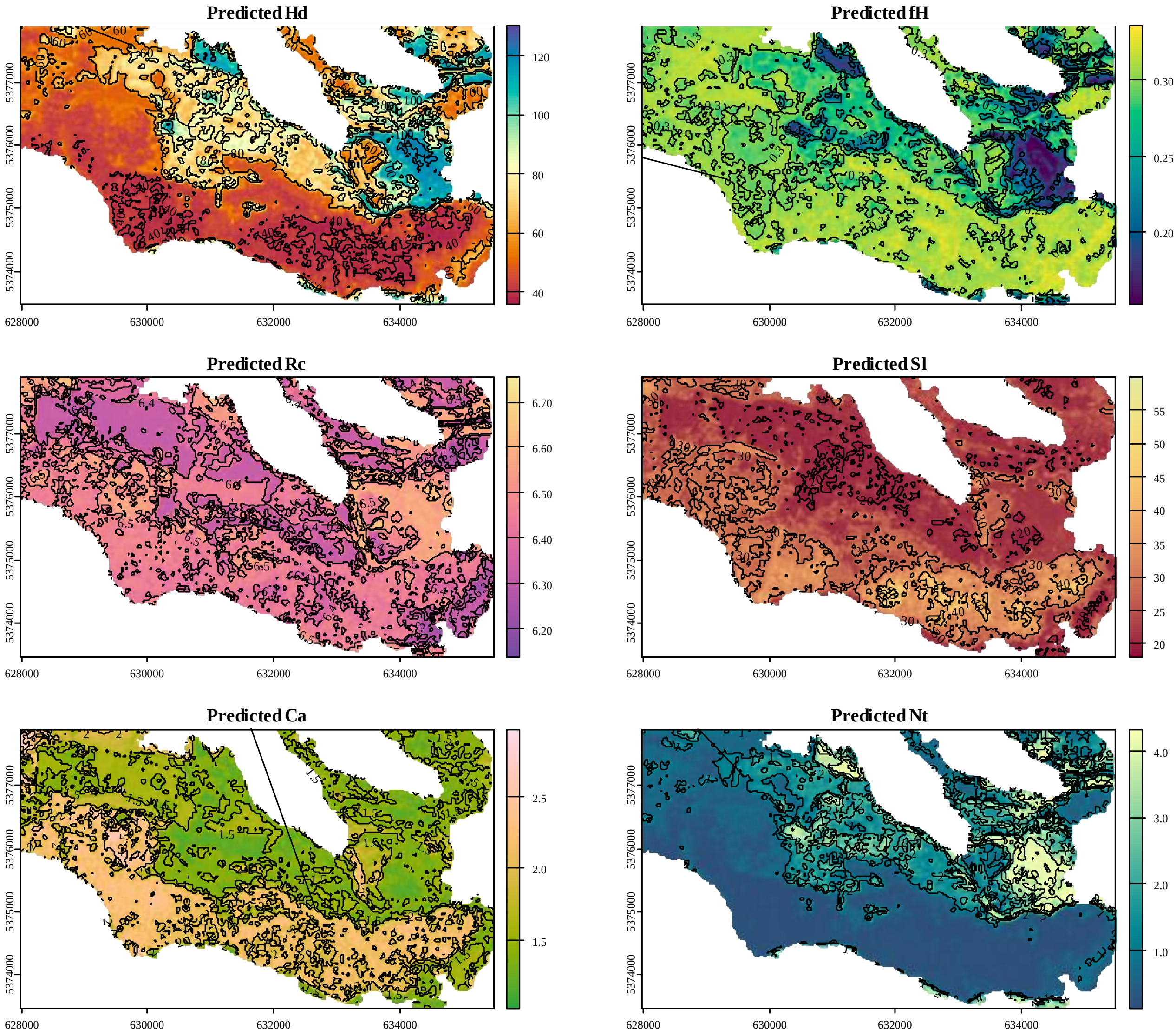

Fig. 3. Spatial variability of predicted assessments of environmental factors based on plant bioindication: the regression model was developed using a random forest algorithm with Sentinel-derived spectral indices as predictors: Hd represents the content of productive moisture in the one-meter layer of soil (mm), fH represents the coefficient of irregularity of soil moisture ω (unitless), Rc represents the negative logarithm of the concentration of hydrogen ions in the soil solution (pH), Sl represents the salt content in the soil solution, measured in micrograms per litre (µg/L), Ca represents the carbonate content, expressed in terms of calcium and magnesium oxides (CaO+MgO %), Nt represents the soil's nitrogen content, measured in grams per kilogram (g/kg)

Table 3
Descriptive statistics (mean ± standard deviation) of phytoindication estimates of climate regimes by association
(significant differences between associations were identified using Tukey HSD: different letters indicate significant differences)

Syntaxon*	Tm, *gJ* / (m^2 year)	Om, mm	Kn, %	Cr, °C	Lc, %
1 (N = 40)	1.79 ± 0.15^{hi}	–0.78 ± 0.14^{defg}	144.28 ± 14.64^{d}	–13.93 ± 2.39^{g}	88.95 ± 2.80^{ab}
2 (N = 40)	1.78 ± 0.16^{i}	–0.68 ± 0.24^{de}	123.43 ± 19.57^{e}	–12.79 ± 3.03^{fg}	87.32 ± 3.20^{ab}
3 (N = 29)	1.85 ± 0.22^{fghi}	–0.59 ± 0.39^{bcd}	103.18 ± 15.82^{gh}	–16.82 ± 3.76^{h}	87.37 ± 3.59^{ab}
4 (N = 39)	1.60 ± 0.20^{j}	–0.69 ± 0.46^{def}	120.00 ± 15.52^{ef}	–19.73 ± 4.22^{i}	82.80 ± 6.71^{b}
5 (N = 106)	2.18 ± 0.12^{a}	–0.77 ± 0.22^{def}	110.44 ± 10.67^{g}	–3.42 ± 2.88^{a}	37.00 ± 9.43^{f}
6 (N = 35)	2.05 ± 0.09^{bc}	–0.94 ± 0.30^{fgh}	120.59 ± 8.81^{ef}	–6.22 ± 4.26^{bc}	51.65 ± 12.49^{d}
7 (N = 80)	2.08 ± 0.12^{b}	–0.61 ± 0.28^{cd}	112.49 ± 11.80^{fg}	–4.90 ± 3.96^{ab}	41.61 ± 11.26^{e}
8 (N = 116)	2.01 ± 0.08^{cd}	–0.47 ± 0.43^{bc}	107.73 ± 16.42^{g}	–3.52 ± 2.86^{a}	39.43 ± 10.17^{ef}
9 (N = 53)	2.08 ± 0.13^{b}	–0.33 ± 0.24^{b}	108.08 ± 10.86^{g}	–4.44 ± 2.76^{ab}	40.37 ± 10.73^{ef}
10 (N = 123)	1.99 ± 0.12^{cde}	–0.06 ± 0.35^{a}	95.38 ± 21.94^{h}	–4.61 ± 4.42^{ab}	57.81 ± 10.39^{c}
11 (N = 33)	1.84 ± 0.13^{ghi}	–0.90 ± 0.36^{efgh}	150.52 ± 13.64^{cd}	–10.87 ± 3.14^{ef}	91.64 ± 2.07^{a}
12 (N = 27)	1.97 ± 0.17^{cdef}	–1.04 ± 0.32^{ghi}	154.99 ± 14.42^{bcd}	–10.99 ± 3.07^{ef}	91.57 ± 1.95^{a}
13 (N = 21)	1.94 ± 0.07^{cdefg}	–0.91 ± 0.17^{efgh}	155.92 ± 11.77^{bcd}	–7.06 ± 2.88^{bcd}	84.93 ± 7.53^{ab}

Syntaxon*	Tm, *gJ* / (m^2 year)	Om, mm	Kn, %	Cr, °C	Lc, %
14 (N = 12)	1.93 ± 0.11^{defg}	–0.86 ± 0.23^{defgh}	153.46 ± 12.15^{bcd}	–7.97 ± 2.88^{cde}	92.80 ± 0.17^{a}
15 (N = 20)	1.90 ± 0.07^{efgh}	–1.13 ± 0.21^{hi}	155.62 ± 7.06^{bcd}	–8.74 ± 2.33^{cde}	92.89 ± 0.85^{a}
16 (N = 18)	2.00 ± 0.08^{cde}	–1.36 ± 0.18^{ijkl}	159.99 ± 5.11^{abc}	–7.49 ± 2.09^{bcde}	91.20 ± 2.94^{a}
17 (N = 17)	1.98 ± 0.06^{cdef}	–1.63 ± 0.24^{lm}	162.16 ± 10.99^{abc}	–7.49 ± 2.33^{bcde}	92.27 ± 1.57^{a}
18 (N = 21)	1.90 ± 0.05^{efgh}	–1.20 ± 0.26^{hij}	163.83 ± 6.54^{abc}	–8.85 ± 2.01^{cde}	92.70 ± 0.41^{a}
19 (N = 29)	1.93 ± 0.04^{defg}	–1.53 ± 0.24^{klm}	161.91 ± 7.19^{abc}	–6.62 ± 1.05^{bcd}	92.78 ± 0.06^{a}
20 (N = 57)	1.89 ± 0.06^{efgh}	–1.44 ± 0.20^{jkl}	162.34 ± 6.76^{abc}	–8.92 ± 2.01^{de}	92.77 ± 0.42^{a}
21 (N = 71)	1.90 ± 0.08^{efgh}	–1.42 ± 0.27^{jkl}	164.98 ± 9.26^{ab}	–8.91 ± 2.30^{de}	92.79 ± 0.54^{a}
22 (N = 22)	1.93 ± 0.05^{defg}	–1.75 ± 0.34^{m}	172.40 ± 9.49^{a}	–8.59 ± 2.01^{cde}	92.89 ± 0.05^{a}
23 (N = 32)	1.89 ± 0.07^{efgh}	–1.28 ± 0.20^{ijk}	159.21 ± 7.56^{abc}	–7.70 ± 1.76^{cde}	92.76 ± 0.41^{a}
24 (N = 38)	1.93 ± 0.06^{defg}	–1.47 ± 0.21^{jklm}	164.81 ± 8.07^{ab}	–6.65 ± 2.08^{bcd}	92.80 ± 0.07^{a}

Notes: * – syntaxons: 1 refers to the association *Limonio meyeri-Festucetum pseudodalmaticae*, 2 refers to the association *Poëtum pratensis*, 3 refers to the association *Junco gerardii-Agrostietum stoloniferae*, 4 refers to the association *Caricetum gracilis*, 5 refers to the association *Populetum nigro-albae*, 6 refers to the association *Salicetum albae*, 7 refers to the association *Alliario officinalis-Chaerophylletum temuli*, 8 refers to the association *Ficario-Ulmetum minoris*, 9 refers to the association *Melico nutantis-Quercetum roboris*, 10 refers to the association *Symphyto officinalis-Anthriscetum sylvestris*, 11 refers to the association *Salici rosmarinifoliae-Holoschoenetum vulgaris*, 12 refers to the association *Calamagrostietum epigei*, 13 refers to the association *Aceri tatarici–Quercetum roboris*, 14 refers to the association *Melico transsilvanicae-Agropyretum*, 15 refers to the association *Chamaecytiso borysthenici-Agropyretum dasyanthi*, 16 refers to the association *Veronico dillenii-Secaletum sylvestris*, 17 refers to the association *Artemisio dniproicae-Salicetum acutifoliae*, 18 refers to the association *Hieracio pilosellae-Pinetum*, 19 refers to the association *Centaureo borysthenicae-Festucetum beckeri*, 20 refers to the association *Secali sylvestri-Caricetum colchicae*, 21 refers to the association *Centaureo brevicipiti-Festucetum beckeri*, 22 refers to the association *Eragrostietum minoris-pilosae*, 23 refers to the association *Festucetum beckeri*, 24 refers to the association *Secaletum sylvestre*.

The assosiation membership in a particular association was able to explain 54.6% of the variability in thermoclimatic assessments (F = 57.4, P < 0.001). The highest thermal climate rating was established for the *Populetum nigro-albae association* (2.18 ± 0.12 gJ / (m^2 year)), and the lowest for the *Caricetum gracilis* association (1.60 ± 0.20 gJ / (m^2 year)). Meadow communities differed in the lowest thermoclimatic indicators (usually less than 1.9 gJ / (m^2 year)), while forest communities were characterised by the highest thermoclimatic indicators (usually more than 2 gJ / (m^2 year)). Intermediate values were typical for psammophytic communities. The ombroclimate ranged from –1.85 to 0.29 mm in 95% of cases. The affiliation of a community to a particular association was able to explain 70.3% of the variability in ombroclimate estimates (F = 112.0, P < 0.001).

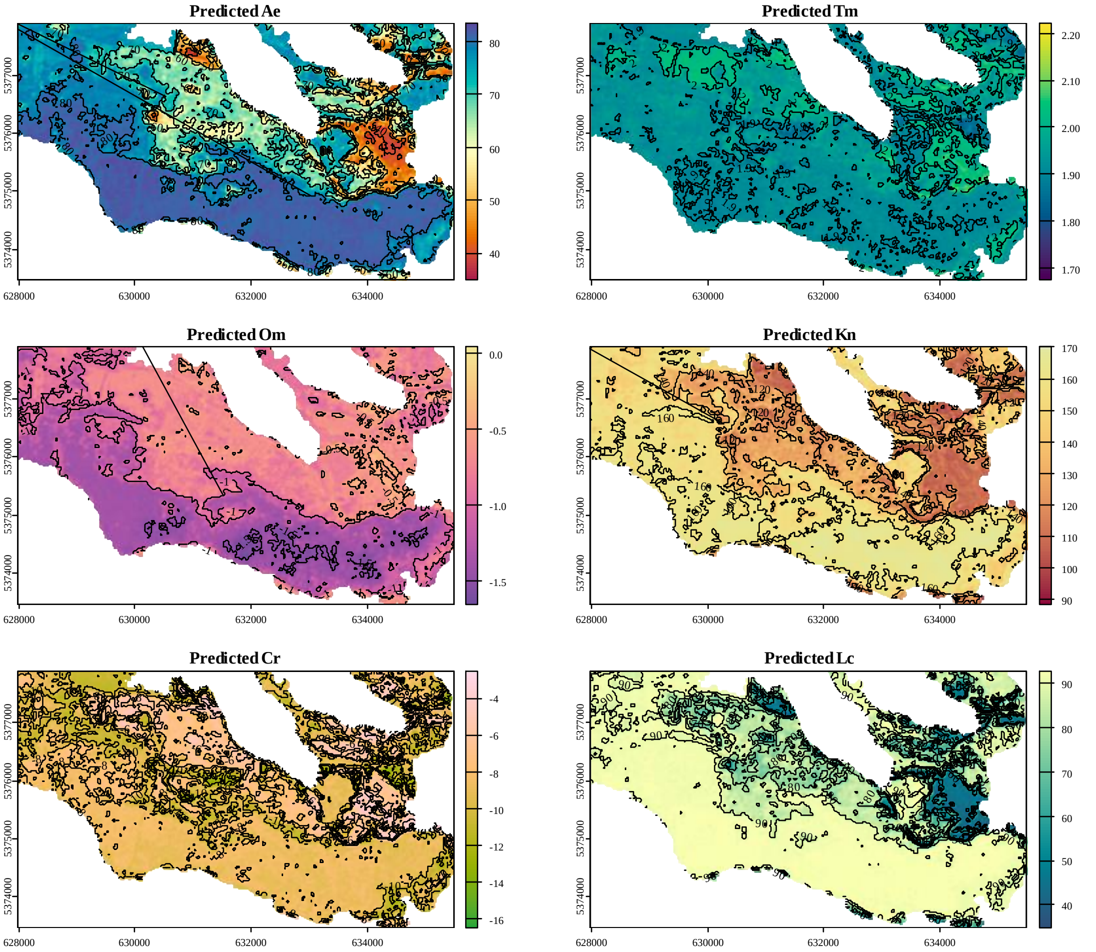

Fig. 4. Spatial variability of predicted assessments of environmental factors based on plant bioindication: the regression model was developed using a random forest algorithm with Sentinel-derived spectral indices as predictors: Ae represents the air-filled porosity percentage, which is the percentage of the total volume of pore space in the soil (%), Tm represents the radiation balance (gJ / (m^2 year)), Om represents the difference between the average daily precipitation and the evaporation from the open water surface over the same period, measured in millimetres (mm), Kn represents the Ivanov continentality scale (%), Cr represents the average temperature of the coldest month of the year, measured in degrees Celsius (° C), Lc represents the relative light level (%)

The highest ombroclimate values were characteristic of the *Symphyto officinalis-Anthriscetum sylvestris* association (–0.06 ± 0.35 mm), and the lowest for the associations *Artemisio dniproicae-Salicetum acutifoliae* (–1.63 ± 0.24 mm) and *Eragrostietum minoris-pilosae* (172.40 ± 9.49 mm). Continentality estimates ranged from 78.8 to 177.5% in 95% of cases. The membership of a community in a particular association was able to explain 78.6% of the variability in continentality estimates (F = 173.4, P < 0.001). The *Limonio meyeri-Festucetum pseudodalmaticae* association and all psammophytic communities were characterised by relatively higher continentality estimates, which usually exceeded 140%. Meadow and forest communities were characterised by a continentality index that was usually less than 130%. Cryogenic regime scores ranged from –19.4 to +1.2 °C. The association of a community with a particular association was able to explain 62.9% of the variability in cryogenic regime scores (F = 80.5, P < 0.001). Meadow communities were usually characterised by cryo-regime estimates below –12 °C, while forest and psammophytic communities had cryo-regime indices above this threshold value. The light regime varied in the range from 26.3% to 92.9% in 95% of cases. The affiliation of a community to a particular association was able to explain 90.9% of the variability in light regime estimates (F = 466.4, P < 0.001). In forest communities, the light level was usually less than 60%, while in meadow and psammophytic communities, the light level was higher than 80%.

Correlation between vegetation cover properties and phytoindication assessments of environmental factors. To perform correlation analysis, preliminary steps were taken to eliminate multicollinearity between predictors. Species richness was used for analysis without modification. The Shannon index and species number showed a significant positive correlation (r = 0.80, P < 0.001). Therefore, the residuals of the linear regression of the Shannon index from the logarithm of the number of species were used to characterise species diversity. The indicators of projective cover and horizontal layer closure of plant communities also correlated significantly with each other. Canopy and shrub layers showed a significant positive correlation (r = 0.20, P < 0.001). The herb layer correlated negatively with both canopy (r = –0.55, P < 0.001) and shrub layers (r = –0.21, P < 0.001). To eliminate multicollinearity, data on the projective cover of the herb layer and the canopy and shrub layer closure were subjected to principal component analysis. The principal components obtained were orthogonal, i.e. statistically independent. Principal component 1 represented the variability of the vertical structure of the plant community, which is a consequence of opposite changes in the canopy and shrub vs. herb layer. According to this principal component, forest communities (positive scores) are clearly distinguished from herbaceous communities (negative scores). Principal component 2 indicates shrub layer dominance. This dominance was characteristic of the associations *Melico transsilvanicae-Agropyretum*, *Chamaecytiso borysthenici-Agropyretum dasyanthi*, *Caricetum gracilis*, *Salicetum albae*, and *Calamagrostietum epigei*. Main component 3 indicates the overall density of the vegetation cover, which is due to the predominance of canopy and herb layers, which can also be interpreted as coherent variation in canopy and herb layers. The highest scores for this main component were found for associations such as *Populetum nigro-albae*, *Salicetum albae*, *Melico nutantis-Quercetum roboris*, *Chamaecytiso borysthenici-Agropyretum dasyanthi*, and *Eragrostietum minoris-pilosae*. The lowest scores for this main component were found for *Festucetum beckeri* and *Secaletum sylvestre*.

Correlation analysis showed that species richness significantly responded to changes in environmental conditions, which were reflected in phytocenotic assessments (Table 4). A positive correlation was established between species richness and moisture regime variability, soil solution reaction, carbonate content, aeration level, continentality, and light level. A negative correlation of species richness was established with such ecological regimes as moisture level, nutrient content, thermo-, ombro- and cryo-regimes. Species diversity positively correlated with moisture level, soil solution reaction, nutrient content and ombro-regime level.

Table 4

Correlation coefficients ± bootstrap SD with grouping letters based on Tukey HSD applied to bootstrap distributions (identical letters indicate no statistically significant difference (P < 0.05) among correlation coefficients based on 1000 bootstrap resamples)

Ecological factor	Species richness	Shannon index (resid)	PC1 (canopy and shrub vs. herb layer)	PC2 (shrub layer dominance)	PC3 (coherent variation in canopy and herb layers)
Hd	$–0.26 \pm 0.03^{a}$	0.20 ± 0.03^{a}	0.53 ± 0.03^{a}	–	0.11 ± 0.03^{a}
fH	0.41 ± 0.02^{b}	–	$–0.65 \pm 0.01^{b}$	–	–
Rc	0.09 ± 0.03^{c}	0.16 ± 0.03^{b}	–	–	0.12 ± 0.03^{b}
Sl	0.13 ± 0.03^{d}	–	$–0.52 \pm 0.02^{c}$	–	–
Ca	0.26 ± 0.03^{e}	–	$–0.35 \pm 0.02^{c}$	–	–
Nt	$–0.30 \pm 0.03^{f}$	0.16 ± 0.03^{c}	0.65 ± 0.01^{d}	–	0.13 ± 0.03^{c}
Ae	0.25 ± 0.03^{g}	$–0.24 \pm 0.03^{c}$	$–0.49 \pm 0.02^{e}$	–	$–0.10 \pm 0.03^{d}$
Tm	$–0.10 \pm 0.03^{h}$	$–0.18 \pm 0.03^{d}$	0.53 ± 0.02^{f}	–	0.24 ± 0.03^{e}
Om	$–0.14 \pm 0.03^{i}$	0.17 ± 0.03^{e}	0.46 ± 0.02^{g}	–	–
Kn	0.24 ± 0.02^{j}	$–0.17 \pm 0.03^{f}$	$–0.56 \pm 0.02^{h}$	–	–
Cr	$–0.29 \pm 0.03^{k}$	$–0.23 \pm 0.03^{g}$	0.55 ± 0.02^{i}	–	–
Lc	0.39 ± 0.02^{l}	–	$–0.75 \pm 0.01^{j}$	0.16 ± 0.03	$–0.17 \pm 0.03^{f}$

The main component 1 differentiates forest communities on the one hand, and grassy (meadow and psammophytic) communities on the other. Forest communities were characterised by higher moisture content, nutrient content in the soil, and higher levels of thermal, ombrophilic, and cryogenic regimes. In turn, greater contrast in moisture conditions, soil solution mineralisation, aeration, continentality, and illumination were characteristic of herbaceous communities. Shrub layer dominance correlated positively only with light intensity. Coherent variation in canopy and herb layers positively correlated with moisture content, soil solution reaction, nutrient content, and thermal regime. This property of plant communities negatively correlated with aeration and light intensity.

Discussion

The first floodplain terrace of rivers is specific in terms of its properties, spatial location, and formation, which is primarily determined by its genesis. Floodplain terraces form on the left bank of rivers in the northern hemisphere that flow from north to south. The primary factor in the formation of floodplains was the fluvial process, the significance of which was replaced over time by the predominance of the eolian factor. The fluvial factor in the history of floodplains explains the fact that the thickness of floodplains is proportional to the thickness of the river. It is natural that the floodplain terrace of the Dnipro River is the largest in the region compared to the floodplain terraces of smaller rivers. Floodplain terraces are located in strips along the river channel, but have different widths, which is also due to other geomorphological and geological factors. The floodplain terrace is defined by its geographical boundaries, which are delineated on one side by the river floodplain, and on the other by the adjacent terrace in the river valley, known as the solonchak. The floodplain terrace is composed mainly of sandy deposits and has a relative elevation above the surrounding relief. The steppe zone of Ukraine as a whole is characterised by a predominance of soils that have developed from loess or loess-like loamy soils. These rocks are predominantly composed of silt or clay in their granulometric composition. The floodplain terraces of rivers, on the other hand, are "islands" of sandy soils with unique ecological regimes that differ significantly from the typical conditions of the steppe zone. This feature explains the large number of rare endemic species that are attracted to floodplain terraces. The poor capillary properties of sandy soils and low groundwater levels mean that the main source of moisture for plant communities on this terrace is atmospheric precipitation in the form of rain or condensation. The ability of sand to cool quickly contributes to the formation of conditions under which moisture condensation, especially in the morning or evening, is a significant factor in the water regime. The solonchak terrace is composed of soils with a predominance of silty or clayey fractions, which give the soils greater potential for capillary rise of groundwater to the surface. This terrace is also characterised by a high groundwater level close to the soil surface. The combination of a high groundwater level and the soil's high capacity for capillary rise of moisture leads to the salinisation of such soils due to the evaporation of moisture, which constantly pulls dissolved salts upwards along the soil layer. These conditions contrast with those of the first floodplain terrace. However, the boundaries between terraces are variable, and areas with typical features of saline-alkaline terraces may penetrate the boundaries of the first floodplain terrace, which significantly increases the diversity of ecological conditions and regimes. The zone of such penetration within the studied territory is the riverbed of the Protich River, which penetrates the first floodplain terrace. In the floodplain of the Protich River, which is geographically located within the first floodplain terrace, conditions are formed that cause soil salinisation, which is typical for saline-alkaline terraces. The floodplain of the Protich River is a centre for plant communities of the *Festuco-Puccinellietea* class. The most important factor in the differentiation of associations of this class was the level of soil salinisation. This result is consistent with the findings for this class obtained for the Danube floodplain. The ordination of vegetation syntaxons in the coastal sector of the Kiliya estuary of the Danube indicates a direct linear dependence of their mutual location on factors such as changes in soil salinity and moisture, changes in salinity and soil moisture variability, changes in salinity and soil acidity, and changes in nitrogen content and soil acidity. Climatic factors did not reveal significant differences in different associations, since their values remain practically unchanged in a small area (Dubyna et al., 2014).

The floodplain of the Protich River, as well as inter-dune depressions with groundwater levels close to the soil surface, create conditions favourable for meadow communities of the *Molinio-Arrhenatheretea* and *Phragmito-Magnocaricetea* classes. The humid conditions are also favourable for the development of shrub and forest vegetation of the *Salicetea purpureae* class. These communities are typical of floodplain ecosystems, but also show the ability to penetrate the first terrace above the floodplain. Our results coincide with findings according to which the main factors of differentiation of communities of the *Molinio-Arrhenatheretea* class are moisture variability, general soil salinity, hydrological regime, soil aeration, soil carbonate content and lighting (Shyriaieva, 2022). Also, in the work Didukh & Kuzemko (2014) it was noted that the communities of the *Arrhenatherion elatioris* alliance are characterised by the highest cryogenic regime indicators. Our data also indicate that these communities have the highest phytoindication cryogenic regime ratings among all meadow communities. Plant communities of the *Phragmito-Magnocaricetea* class belong to typical marsh and riparian communities that form on permanently or periodically flooded soils with high moisture levels (Dubyna & Dziuba, 2008). The vast majority of these communities are eutrophic. They require an increased supply of nutrients and organic matter, usually on alluvial silty or loamy substrates. Neutral or slightly alkaline soil reactions with sufficient calcium content are optimal for them. In terms of light, they prefer sunny or semi-shaded areas, but the main factor in their stability and distribution is water level fluctuations. Regular flooding alternates with phases of littoral zone exposure, creating unique hydrological microenvironments necessary for the reproduction and growth of reeds, cattails and sedges (Dubyna & Dziuba, 2008).

Salicetea purpureae communities in the Dnipro River valley form on floodplain alluvial soils that are regularly flooded or remain highly moist for long periods of time. They consist of willow forests and shrubs stretching in narrow strips along the banks of rivers, oxbows and watercourses. The tree layer is formed mainly by plants of the genus *Salix,* with both mesophilic and hydrophilic species growing in the undergrowth. These communities play an important role in stabilising the banks, regulating the water regime and creating transitional environments between aquatic and terrestrial ecosystems. They are characterised by their dynamism and ability to quickly renaturalise after disturbances (Dubyna & Dziuba, 2014). The *Populetum nigro-albae* association communities are typical of the floodplain forests of the Dnipro River valley and are also found on the slopes of sandy hills of the first floodplain terrace bordering the floodplain of the Protych River. These communities occupy elevated areas with soddy-sandy soils in the zone of short-term influence of the flood regime (Tsaryk, 2021). *Salicetum albae* communities are widespread in floodplain forests along river banks, in low-lying and marshy areas with periodic flooding (Kyyak et al., 2023). They prefer sandy and meadow-marsh or marshy soils. The *Artemisio dniproicae-Salicetum acutifoliae* association was found in the low-lying areas of the first floodplain terrace near the Obukhiv floodplain of the Dnipro River and in interdune depressions.

Forest communities on the first floodplain terrace are usually island-like, so the ecotone effect is very significant in them. Ecotone positions are often occupied by communities of the *Galio-Urticetea* class. An unconditional feature of associations of this class, such as *Alliario officinalis-Chaerophylletum temuli* and *Symphyto officinalis-Anthriscetum sylvestris,* is the high level of nitrogen nutrients in the soil. Elm forests on elevated areas of the relief in the floodplain or in the lower parts of sandy dune slopes close to the Protich River valley or on the slopes of ravines are represented by the *Ficario-Ulmetum minoris* association. The *Ficario-Ulmetum minoris* association is a wooded floodplain forest community with a well-developed herbaceous layer. The variation in herbaceous cover is largely explained by the spatial component rather than soil properties or distance to trees. This indicates the special role of unmeasured factors, in particular species distribution limitations, vegetative growth and competition. Soil properties such as density, water content and aggregate structure also influence the herbaceous vegetation of this association. Trees act as an independent and complex factor influencing both the soil and the herbaceous community (Zhukova et al., 2020; Lobachevska & Karpinets, 2024). The communities of the *Melico nutantis-Quercetum roboris* association belong to the *Convallario majalis-Quercion roboris* alliance. This association is part of thermophilic oak forests, which are widespread on sandy first floodplains of rivers. They cover dry to mesophytic oak forests. The floristic composition of these forests indicates their ecotonal nature. The forest flora is formed by a combination of three floristic components: species of the *Carpino-Fagetea* class (the dominant element), as well as representatives of *Quercetea pubescentis* and *Quercetea roboris.* This compositional structure indicates the transitional nature of phytocenoses formed under the influence of both mesophytic and xerophytic conditions (Goncharenko et al., 2020; Vasheka et al., 2025). The *Aceri tatarici–Quercetum roboris* association occurs on the tops of dunes and is represented by shrubs. These shrubs are probably the result of anthropogenic destruction of oak forests on the edges of which the shrubs grew. This is evidenced by some fragmentary oak forests with preserved oak trees aged 120–150 years in the centre of the communities, which are surrounded by shrubs formed by *Acer tataricum. Pyrolo-Pinetea sylvestris* coniferous forests are represented by naturalised artificial forest plantations, the age of which significantly exceeds 40 years. Coniferous forests in some areas have suffered significant fires and windfalls, where *Calamagrostietum epigei* associations have formed. The disturbed areas are also occupied by *Melico transsilvanicae-Agropyretum* associations. Within the reserve, there are roads along which *Eragrostietum minoris-pilosae* associations have formed as a result of soil cover disturbance. The dune hills themselves are occupied by associations of the *Festucetea vaginatae* class. These plant communities are adapted to life on loose sands with low nutrient content and moisture deficiency. The relief of the sand dunes is a significant factor determining the differentiation of plant associations.

The number of species in plant communities depends significantly on the moisture regime (Hd), which is one of the main ecological factors of vegetation differentiation. Moisture affects species richness, forming a clear ecological gradient. In the driest conditions (e.g., sandy arenas, water-deficient dune tops) and the wettest conditions (e.g., marshy areas with prolonged flooding), the lowest number of species is observed, which is explained by the high level of ecological stress that narrows the range of plants capable of adapting to such conditions (Gibtan et al., 2024). In the study, this is represented by associations with low species richness, such as *Secaletum sylvestre* and *Ficario-Ulmetum minoris*. The maximum species richness is characteristic of plant communities with moderate moisture conditions, which are favourable for the existence of a large number of species with diverse ecological strategies (Kunakh et al., 2024). For example, the highest average species richness was recorded in the associations *Veronico dillenii-Secaletum sylvestris* and *Chamaecytiso borysthenici-Agropyretum dasyanthi*. The relationship between species richness and moisture regime is a classic example of the ecological principle of optimum (Shelford, 1931): the greatest plant diversity is observed at intermediate moisture levels, while extreme conditions lead to a decrease in species richness due to increased selective pressure and limitations on the adaptability of plant species (Moravčík et al., 2024).

The positive correlation between the number of species and the moisture contrast regime (fH) can be explained by the fact that high moisture contrast creates heterogeneous environmental conditions in a small area. This means periodic changes in conditions from very wet to moderately dry throughout the season. Such ecological mosaicism contributes to the formation of a wide range of microenvironments (microhabitats), each of which is suitable for different groups of plant species with different adaptive strategies. In areas with high moisture contrast, both hygrophilous (moisture-loving) and mesophilic (adapted to moderate conditions) and even partially xerophilous (resistant to dry periods) species can coexist. As a result, the overall species richness in such areas increases, since no ecological group has an absolute advantage over others, and periodic changes in the moisture regime prevent the complete domination of individual species. This situation corresponds to the classic principle of ecological heterogeneity (heterogeneity-diversity hypothesis) (Lundholm, 2009), according to which an increase in the heterogeneity of ecological conditions contributes to an increase in biodiversity. That is why the moisture contrast regime (fH) positively correlates with the number of species in plant communities.

The negative correlation between species richness and soil fertility (Nt) can be explained by the fact that with increasing fertility (in particular, nitrogen and other nutrient content) in plant communities, competitive interaction between species intensifies. At high fertility, fast-growing, competitive species that are able to efficiently use excess resources and quickly form dense vegetation cover gain an advantage, creating conditions for intense competition for light and space. As a result, less competitive species, which are characteristic of poorer and less productive ecosystems, are displaced. High soil fertility levels lead to a decrease in overall species richness due to the dominance of a few strong competitors that suppress the development and growth of other plant species. This phenomenon corresponds to the classic ecological principle of competitive exclusion (den Boer, 1986), according to which, when certain resources are abundant in the environment, one or more species dominate, reducing the chances of other species to exist and, accordingly, reducing overall biodiversity.

The positive correlation between species richness and soil aeration can be explained by the fact that improved aeration creates more favourable conditions for the root systems of a wide range of plants. Good soil aeration means that the right balance of oxygen and carbon dioxide is maintained, which is key to effective root respiration and nutrient uptake. This, in turn, allows species with different root systems and different adaptive strategies to coexist, including less competitive species that can only survive when there is sufficient oxygen in the soil. Well-aerated soils are usually characterised by lower density and higher permeability, which promotes better seed germination, development of underground plant organs, and also creates favourable conditions for soil organisms (microorganisms, fungi, invertebrates), which further increase the overall heterogeneity of ecological conditions through their activity. As a result, the diversity of microenvironments and, accordingly, the overall species richness of the plant community increases. The positive correlation between species richness and soil aeration is due to the fact that better aeration conditions expand the range of species that can exist and compete in a given area, as well as contribute to the formation of more diverse ecological niches.

The positive correlation between the number of species and the lighting regime can be explained by the fact that improved lighting conditions contribute to an increase in the structural and functional diversity of the plant cover. High light levels allow both light-loving species and species with less pronounced light requirements to coexist. Good lighting creates favourable conditions for the growth of various plant life forms, from low-growing annuals and perennials to tall grasses and shrubs, forming multi-layered, structurally complex communities. This, in turn, increases the number of available ecological niches, allowing many species with different adaptation strategies to coexist. Good light conditions stimulate the germination of many plant seeds, promote more efficient photosynthesis and increase the productivity of communities, leading to an increase in overall biodiversity. The positive correlation between species richness and light regime is explained by the fact that improved lighting creates favourable conditions for the simultaneous growth and development of a large number of species with different ecological and life characteristics, and also promotes the formation of complex, multi-layered communities with a large number of available ecological niches.

The species diversity correlation pattern (i.e., residual diversity that does not depend on the number of species) reflects the influence of ecological factors on the community structure after removing the effect of species diversity itself. The moisture regime shows a positive correlation with residual diversity, indicating that with increasing moisture (even with fewer species), the structure of the plant community becomes more uniform. Under conditions of stable or increased moisture, there is probably no strong dominance of individual species, which contributes to a more even distribution of their contribution to the total biomass of the community. Soil reaction and soil fertility are positively correlated with residual diversity. This indicates that under conditions of reduced acidity or increased fertility, species diversity is more even. This is probably due to the fact that specific soil conditions (alkaline or fertile) limit the strong dominance of individual species, creating conditions for the relatively even coexistence of the few species that are adapted to such conditions. Soil aeration shows a negative correlation with residual diversity, which means that with increased aeration, on the contrary, the dominance of individual species (for example, competitively strong with deep root systems) increases, leading to a decrease in the evenness of species composition. Similarly, thermal regime, continentality and cryogenic regime show a negative correlation with residual diversity. This can be explained by the fact that with a change in these conditions, for example, increased thermal or climatic stresses, certain species begin to dominate, displacing others, which reduces the uniformity of their distribution. The general pattern of residual diversity indicates that under conditions of ecological stress or competitive pressure (aeration, temperature regime, carbonate content, continentality), the structure of the community shifts towards the dominance of individual species. Conversely, in a more stable and less stressful environment, such as moisture or a certain acidity, soil fertility, species coexist more evenly, regardless of their total number.

The results provide a scientifically sound basis for the conservation, restoration and sustainable management of floodplain ecosystems in river valleys, both within and outside protected areas. Establishing links between the species diversity of plant communities and key environmental factors, such as moisture regime, fertility, aeration and light, makes it possible to identify the most valuable and vulnerable habitats that require priority protection. The results obtained can be used to develop nature-oriented approaches to river landscape management, including regulation of the hydrological regime, restriction of economic impact, and introduction of elements of revegetation or adaptive grazing. The study has practical significance for the development of effective environmental monitoring schemes based on indicator species and phytocenoses, as well as for assessing the ecological potential of territories in the context of climate change and increasing anthropogenic pressure. Thus, the work is useful for ecologists, botanists, nature conservation specialists, landscape managers and authorities responsible for environmental assessment and sustainable land use planning.

Prospects for further research lie in an in-depth analysis of the spatial and temporal dynamics of the vegetation cover of floodplain terraces, taking into account seasonal and interannual changes in the hydrological regime, climatic factors and anthropogenic impact. Further research may focus on studying the functional and trophic structure of phytocenoses, in particular through the assessment of life forms, survival strategies and functional characteristics of species. Another important area is modelling the ecological niche and potential distribution of key communities in response to climate change, which will allow prediction of the risks of natural habitat degradation. It is advisable to deepen the analysis of the relationship between biodiversity and soil microbiocenoses, as well as to investigate the role of terraces in maintaining ecosystem services (hydrological regulation, pollination, soil conservation, etc.). Interdisciplinary approaches using geoinformation technologies, remote sensing and multifactorial ecological modelling are promising for the comprehensive assessment of the ecological status of floodplain terraces and the development of strategies for their revitalisation.

Conclusion

As a result of studying plant communities of the first floodplain terrace of the Dnipro river valley, it was possible to comprehensively characterise the species composition, syntaxonomic structure and ecological factors that determine the biological diversity of this key geomorphological zone. It was found that the plant communities of the floodplain terrace are syntactically diverse and represented by three main types of phytocenoses: meadow, forest and psammophytic. This indicates the high ecological mosaicism of the terraces, which is due to a combination of alluvial and eolian processes, local gradients of humidity, light and soil conditions. Within each group of communities, significant variability in both species composition and cover structure were found, confirming the key role of this ecotope zone in maintaining regional biodiversity. Analysis of ecological gradients showed that species richness is highest under moderate moisture conditions (Hd), while in extreme wet or dry conditions, species richness decreases in accordance with the ecological principle of optimum. The positive correlation between species abundance and moisture contrast (fH) reflects the role of microheterogeneity as a factor enriching species composition. It was found that increased soil fertility (Nt) negatively affects diversity through the competitive exclusion effect, while good aeration (Ae) and lighting (Lc) create conditions for the coexistence of a wider range of ecological strategies and life forms. A study of residual Shannon index values showed that individual ecological factors, in particular moisture, acidity and fertility, contribute to an increase in community evenness, while increased aeration and continental climate, on the contrary, lead to increased dominance. Floodplain terraces are not only structurally diverse but also syntactically representative ecosystems formed under the influence of complex ecological gradients. The results of the study emphasise their important role in maintaining biodiversity and provide a scientific basis for the conservation, ecological monitoring and nature-oriented management of these areas in the context of climate change and anthropogenic pressure.

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