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From expert-based scores to community-derived indicator values: Reconstruction of species hemeroby scales from vegetation composition

H. Tutova*, O. Lisovets**, O. Kunakh**, O. Zhukov*

**Bogdan Khmelnitsky Melitopol State Pedagogical University, Melitopol, Ukraine*
***Oles Honchar Dnipro National University, Dnipro, Ukraine*

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Bogdan Khmelnitsky Melitopol State Pedagogical University, Hetmanska st., 20, Melitopol, 72318, Ukraine. Tel.: +38-098-507-96-82. E-mail: zhukov_dnipro@ukr.net

Oles Honchar Dnipro National University, Gagarin av., 72, Dnipro, 49000, Ukraine. Tel.: +38-098-507-96-82. E-mail: kunah_olga@ukr.net

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Hemeroby is widely used as an integral indicator of the anthropogenic transformation of ecosystems and vegetation. In most existing approaches, community-level hemeroby is estimated by averaging expert-based species indicator values. However, this procedure implicitly assumes that species-level autecological characteristics can be directly aggregated into synecological properties of plant communities. Such an assumption is rarely explicitly evaluated and may become especially problematic when hemeroby scales are transferred to regions with different environmental conditions, land-use histories, and species pools. The present study aimed to reconstruct and calibrate a regional hemeroby indicator system for the Steppe zone of Ukraine by linking species indicator values to the compositional structure of plant communities. The analysis was based on 10,665 vegetation relevés representing a broad gradient of anthropogenic transformation across Dnipropetrovsk and Zaporizhzhia regions, including natural, semi-natural, urban, agrarian, and technogenic habitats. Species hemeroby values were initially derived from the expert-based system of Frank and Klotz, adapted for Ukraine by Goncharenko. Community composition was analysed using canonical correspondence analysis and partial constrained ordination. Ecological gradients estimated using Didukh phytoindication scales were included as conditioning variables to separate the anthropogenic component of floristic variation from natural environmental differentiation. Species positions along the extracted hemeroby-related gradient were subsequently used to reconstruct regional indicator values. The results demonstrated that anthropogenic transformation represents an independent and ecologically interpretable component of regional vegetation differentiation. The extracted hemeroby gradient was associated primarily with disturbance severity, mowing frequency, species abundance structure, and the occurrence of adventive and cultivated species. The reconstructed scale substantially reduced the within-community inconsistency of species hemeroby values compared with the original expert-based system. Communities with high hemeroby showed pronounced compositional convergence and lower internal heterogeneity of species indicator values. The study demonstrates that species hemeroby values can be directly reconstructed from the compositional organisation of vegetation communities. Unlike traditional expert-based systems, the proposed approach derives both species scores and community positions from the same latent ordination space. Consequently, the abundance-weighted aggregation of species values constitutes an internally coherent reconstruction of community position along the anthropogenic transformation gradient, rather than an arbitrary averaging procedure. The developed framework provides a theoretically grounded, regionally calibrated basis for assessing ecosystem transformation in the Steppe zone of Ukraine and can be applied to studies of vegetation naturalness, restoration dynamics, biodiversity monitoring, and landscape assessment.

Keywords: anthropogenic transformation; vegetation ordination; canonical correspondence analysis; indicator values; plant communities; regional calibration; Steppe zone of Ukraine.

Introduction

Anthropogenic transformation of vegetation is one of the principal processes determining contemporary changes in ecosystem structure, biodiversity, and ecological functioning (Szyszko-Podgórska et al., 2025; Kunakh et al., 2026). Urbanisation, agricultural intensification, industrial activity, infrastructure development, recreation, and technogenic disturbance substantially modify environmental conditions and alter the composition and organisation of plant communities (Williams et al., 2015). The assessment of the degree of anthropogenic transformation has become an important task in vegetation ecology, conservation biology, landscape monitoring, and restoration ecology (Casanelles-Abella & Egerer, 2025). One of the most widely used concepts for describing anthropogenic transformation of ecosystems is hemeroby (Walz & Stein, 2014; Battisti & Fanelli, 2016; Erdős et al., 2022). The term “hemeroby” was introduced to characterise the degree of deviation of ecosystems from natural conditions due to human activity. In its broad ecological interpretation, hemeroby reflects the extent to which species, communities, or ecosystems are associated with anthropogenically transformed environments and tolerate or depend on human-induced disturbance. Unlike purely floristic measures of synanthropization or alien species richness, hemeroby aims to integrate multiple aspects of ecosystem transformation into a single conceptual framework (Jalas, 1955; Sukopp, 1972). The hemeroby concept has been applied at different organisational levels. At the ecosystem and landscape levels, hemeroby is used to classify habitats according to their degree of naturalness or anthropogenic alteration (Steinhardt et al., 1999; Walz & Stein, 2014). At the species level, hemeroby reflects species' ecological optima along gradients of disturbance and habitat transformation. Species associated with natural or weakly disturbed habitats are considered low-hemerobic taxa, whereas ruderal, urban, agricultural, and invasive species are considered highly hemerobic. Because plant communities represent structured combinations of species with different ecological properties, community-level hemeroby is commonly estimated by aggregating species-level indicator values.

Several systems of species hemeroby indicators have been proposed in Central and Eastern European vegetation science. Among the most influential approaches is the indicator system developed by Frank & Klotz (1990), which classifies vascular plant species according to their affinity to anthropogenically transformed habitats. In Ukraine, Goncharenko adapted this approach for the forest and forest-steppe zones, providing one of the first regionally adjusted hemeroby scales for Eastern European vegetation (Goncharenko, 2017). Such systems are conceptually related to broader traditions of ecological indicator values, including the Ellenberg approach and the phytoindi-

cation framework of Didukh (Didukh, 2011), where species ecological preferences are used to characterise environmental conditions of plant communities. Despite their broad practical use, species-based hemeroby systems involve an important methodological problem. Species indicator values are autecological properties describing the typical ecological position of individual taxa, whereas hemeroby of vegetation communities represents a synecological property emerging from the structure of species assemblages (Diekmann, 2003). In most studies, the transition from the species level to the community level is performed through arithmetic or abundance-weighted averaging of species scores (Doležal et al., 2004; Liu et al., 2026). However, the transfer from species-level indicator values to community-level estimates through averaging remains methodologically non-trivial, because the ordinal nature of such scales means that arithmetic operations on them require additional justification rather than being automatically valid (Tölgyesi et al., 2014). This creates a conceptual gap between species-level ecological interpretation and community-level assessment of anthropogenic transformation. An additional limitation of traditional hemeroby scales is their dependence on expert-based classifications (Tichý et al., 2023). Although expert systems provide ecologically meaningful interpretations, they may contain inconsistencies arising from regional differences in vegetation composition, habitat conditions, and anthropogenic regimes (Tyler et al., 2021; Midolo et al., 2023; Tichý et al., 2023). Species occupying similar positions within real vegetation gradients may receive substantially different indicator values, whereas species assigned to similar hemeroby categories may exhibit contrasting co-occurrence patterns in vegetation data (Tutova et al., 2026). Consequently, expert-based scales do not always fully reflect the actual organisation of plant communities along anthropogenic transformation gradients.

The analysis of community-level responses to environmental and anthropogenic drivers can be facilitated by identifying the key patterns expressed in species composition (Ter Braak, 1986). Such patterns can be detected using ordination methods, which arrange vegetation plots and species in a reduced multidimensional space and provide both a visual representation and a formal statistical framework for analysing compositional gradients (ter Braak & Prentice, 1988). Modern ordination methods offer opportunities to address these limitations by reconstructing ecological gradients directly from vegetation composition (van der Veen et al., 2023; Budka et al., 2024). In community ecology, constrained ordination techniques such as canonical correspondence analysis (CCA) are widely used to identify latent gradients associated with environmental factors and disturbance regimes (ter Braak & Prentice, 1988; ter Braak & Verdonschot, 1995; Tutova et al., 2026). From this perspective, anthropogenic transformation can be interpreted as a compositional gradient expressed through changes in species co-occurrence structure. Species positions along such gradients may therefore provide an empirical basis for reconstruction and calibration of regional hemeroby scales. In the constrained ordination procedure, community-level indicator estimates of ecological conditions derived from biological assemblage composition were used as conditioning variables. This approach follows the general bioindication logic that ecological gradients can be inferred from community structure itself, because assemblage composition reflects the joint response of species to habitat conditions and disturbance. The possibility of reconstructing ecological gradients and species indicator values directly from community composition has long been recognised in ordination-based vegetation analysis. Early studies demonstrated that ordination methods can extract meaningful gradients of community composition. In contrast, weighted averages of species indicator values can be used to interpret these gradients in ecological terms and even to estimate unknown indicator values for species from their position in ordination space (Persson, 1981). If hemeroby is considered one of the ecological factors structuring community composition alongside natural environmental gradients, its assessment requires separating the anthropogenic component from variation caused by natural habitat conditions. Otherwise, the hemeroby signal may be confounded with gradients of soil moisture, nutrient availability, carbonate content, light conditions, or climate. This separation can be achieved using constrained ordination, particularly CCA, in which hemeroby is treated as the focal explanatory variable and natural ecological factors are included as conditioning variables. In this framework, the extracted constrained axis represents the component of floristic variation specifically associated with anthropogenic transformation, after accounting for the effects of natural ecological gradients.

In this study, a regional hemeroby indicator system was reconstructed for the Steppe zone of Ukraine using vegetation data from Dnipropetrovsk and Zaporizhzhia regions. The study aimed to evaluate the relationship between expert-based species hemeroby values and observed community-level patterns of vegetation differentiation along anthropogenic gradients. Specifically, the objectives were: (i) to extract the independent floristic gradient associated with anthropogenic transformation while accounting for natural ecological variation; (ii) to reconstruct species hemeroby values from ordination-derived community structure; (iii) to evaluate the consistency between expert-based and ordination-derived species positions; and (iv) to develop a regionally calibrated hemeroby indicator system applicable to natural, semi-natural, urban, agrarian, and technogenic habitats of the Ukrainian Steppe zone.

Material and methods

Study area and representation of the hemeroby gradient. The evaluation of species hemeroby was conducted for the entire vascular plant flora of the Dnipropetrovsk and Zaporizhzhia regions of Ukraine, using the regional flora compiled by Tarasov (2012) and augmented by the authors' field observations. The vegetation database encompassed a wide range of naturalness and anthropogenic alteration, comprising 10,665 relevés. The natural and near-natural end of the gradient was predominantly represented by the Dnipro–Oril Nature Reserve, which contributed the largest subset of relevés (4,139 relevés; 38.8%; hereafter, values in parentheses denote the number of relevés and their percentage of the total dataset) (Lisovets et al., 2025a; Tutova et al., 2025). Additional natural and near-natural sites included Balka Mayorka (289; 2.7%) (Lisovets et al., 2024), Biryuchyi Island (250; 2.3%), the "Kamyani Mohyly" section of the Ukrainian Steppe Nature Reserve (174; 1.6%) (Podpriatov, 2025), the Kilchenskyi Reserve (15; 0.1%), and the Biogeocenotic Station of Oles Honchar Dnipro National University near Andriivka (235 in total; 2.2%). Semi-natural vegetation was represented by Balka Kamenystaya near Dnipro (525; 4.9%). Khortytsia Island (729; 6.8%) (Lisovets et al., 2025b; Zhukov et al., 2025) constituted a distinct segment of the natural gradient, characterised as a natural area influenced by military disturbance. The anthropogenically transformed end of the gradient included urban habitats within the city of Dnipro, represented by sites differing in their degree of hemeroby, from relatively natural urban vegetation to industrial zones (1,220; 11.4%). Additional surveys of urban park areas included Studentskyi Park (670; 6.3%) (Zhukov et al., 2025) and Ivan Starov Square (150; 1.4%), which comprise park plantations subject to recreational pressure. Technogenically altered habitats comprised the reclamation research station near Pokrov (1,976; 18.5%) (Zhukov et al., 2025), electric substations within Dnipropetrovsk Oblast (175; 1.6%), and a quarry near Voloske (30; 0.3%). Agrarian habitats were represented by fallows (36; 0.3%) and *Robinia pseudoacacia* plantations near Dnipro (40; 0.4%). Collectively, the dataset incorporated natural and semi-natural vegetation alongside heavily transformed urban, agrarian, and technogenic habitats. Natural localities constituted the majority of the sample, whereas urbanised and technogenically modified sites provided substantial representation of the disturbed extremity of the gradient. This composition renders the dataset suitable for analysing variations in species composition, functional traits, and indicators of naturalness across a comprehensive gradient ranging from natural to anthropogenically altered vegetation.

Species-level ecological, functional, and disturbance indicators. Species hemeroby was evaluated according to the indicator system of Frank & Klotz (1990) and subsequently adapted by Goncharenko for the forest and forest-steppe zones of Ukraine (Goncharenko, 2017). In the present study, this adapted scale was used as the initial expert-

based framework for regional calibration in the Steppe zone of Ukraine, within the Dnipropetrovsk and Zaporizhzhia regions. The scale reflects species optima along a gradient of anthropogenic transformation, with higher values corresponding to species associated with strongly transformed habitats and lower values indicating species typical of natural or weakly disturbed ecosystems. The original ordinal seven-grade scale was rescaled to a continuous 100-point scale to increase discriminatory resolution and comparability among species (Yorkina et al., 2022). Interval indicator values were converted into optimum values as the half-sum of the lower- and upper-class limits. Higher indicator values correspond to species associated with strongly transformed habitats, whereas lower values characterise species typical of natural or weakly disturbed ecosystems. Community-level hemeroby was estimated as the projective-cover-weighted mean of species indicator values. This approach follows the conceptual interpretation of hemeroby as a latent compositional gradient expressed through vegetation structure. The ecological conditions of plant communities were assessed using the phytoindication scales of Didukh (2011), based on vegetation relevés. The Didukh indicator system includes both edaphic and climatic scales. The edaphic indicators comprise soil water regime (Hd), variability of soil moisture (fH), soil aeration (Ae), soil acidity (Rc), total salt regime (Sl), carbonate content (Ca), and soil nitrogen availability (Nt). The climatic indicators include the thermal regime (Tm), ombroregime (Om), cryoregime (Cr), and continentality (Kn). Weighted mean indicator values were calculated for each vegetation plot based on species composition and projective cover. Species-level functional strategies were characterised according to Grime's CSR scheme, which distinguishes among competitive (C), stress-tolerant (S), and ruderal (R) strategies (Grime, 2001). Species CSR scores were obtained from the global CSR database and classification framework, where plant strategies are quantified from leaf functional traits and expressed as relative C, S, and R components (Pierce et al., 2017). For each relevé, community-weighted mean CSR values were calculated using species projective cover as weights. These values were included in the environmental table to characterise the relative contribution of competitive, stress-tolerant, and ruderal strategies to the functional structure of each plant community. Plant species were also characterized by their disturbance indicator values according (Midolo et al., 2023). These indicators describe species optima along several disturbance gradients, including disturbance severity, disturbance frequency, mowing frequency, grazing pressure, and soil disturbance. Disturbance severity and frequency were considered for both the whole community and the herb layer, whereas soil disturbance was defined as biomass loss from soil turning or furrowing. Community-weighted mean values of these indicators were calculated for each relevé, using species-projected cover as weights, and used to characterise the sensitivity of plant communities to different disturbance regimes. Information on adventive origin, invasive species status, weed status, quarantine status, and cultivated or decorative origin was used as a system of high-priority status-based criteria (Vynokurov et al., 2024).

Ordination, calibration, and reconstruction of regional hemeroby indicators. The reconstruction and calibration of regional hemeroby indicators were based on the assumption that anthropogenic transformation is primarily expressed at the level of plant community organisation and species co-occurrence structure. Therefore, regional species hemeroby values were not treated solely as fixed, expert-based autecological characteristics, but were also evaluated against observed compositional patterns of vegetation along gradients of anthropogenic transformation. The calibration procedure aimed to identify the component of floristic variation specifically associated with hemeroby after accounting for major natural ecological gradients and to reconstruct species positions within this latent compositional space. In this framework, plant communities represent the synecological expression of anthropogenic transformation, whereas species hemeroby values correspond to the positions of species along the reconstructed community-level gradient. The overall analytical approach, therefore, combined constrained ordination, rank-based association analysis, and regression calibration to derive a regionally adjusted hemeroby indicator system consistent with the observed vegetation structure in the Steppe zone of Ukraine.

Plant community ordination was performed using canonical correspondence analysis (CCA), with the species composition matrix of vegetation relevés used as the response table (ter Braak & Verdonschot, 1995). Hemeroby and ecological indicator values based on Didukh phytoindication scales were included as explanatory variables. This analysis was used to identify the main gradients of floristic differentiation and to evaluate the position of the hemeroby gradient within the overall structure of vegetation variation. The partial CCA was additionally applied to separate the component of community variation specifically associated with anthropogenic transformation from variation induced by natural ecological gradients. In this model, hemeroby was used as the constraining variable, whereas the Didukh ecological indicator values were included as conditioning variables. Thus, the ordination extracted the independent hemeroby-related component of species composition after accounting for soil moisture, soil reaction, salinity, carbonate content, nutrient availability, aeration, thermal regime, ombroregime, cryoregime, continentality, and light conditions. The constrained axis obtained from the partial CCA was interpreted as a latent floristic gradient associated with anthropogenic transformation. Species scores along this axis were subsequently used to reconstruct regional hemeroby indicator values, whereas site scores represented the position of vegetation plots along the independent hemeroby gradient. Scatter plots were used as a diagnostic tool to compare the initial expert-based species hemeroby values with species scores derived from the ordination space. This visual comparison enabled assessment of whether the ordination-derived gradient preserved the expected ordering of species from natural or weakly disturbed habitats to strongly anthropogenically transformed habitats.

The strength of this relationship was evaluated using Spearman's rank correlation coefficient. This choice was justified by the ordinal nature of the hemeroby scale and the study's analytical design. The linear component of variation associated with ecological gradients had already been extracted at the previous stage through conditioning variables in the partial CCA. Therefore, the remaining hemeroby-related component was expected to reflect primarily the consistency of rank ordering along the anthropogenic transformation gradient rather than a strictly linear metric relationship.

Several alternative regression approaches were evaluated to describe the relationship between the initial expert-based hemeroby values and the ordination-derived species scores. Linear, polynomial, generalised additive, quantile, and nonparametric local regression models were considered candidate approaches because the relationship was expected to be potentially non-linear and heteroscedastic. Model selection was based on a combination of statistical and ecological criteria, including the strength and significance of the relationship, the explained variance, the residual structure, the preservation of the expected ecological ordering of species along the anthropogenic transformation gradient, and robustness to deviations from normality and homoscedasticity. Particular attention was paid to whether the fitted model preserved the monotonic ordering of species along the hemeroby gradient and produced ecologically interpretable transformations of the original expert-based scale. The final approach was selected as the model that provided the most stable and ecologically coherent reconstruction of species positions along the ordination-derived anthropogenic transformation gradient.

A capped log-transformed mean abundance value was calculated as an additional species-level predictor, reflecting a species' tendency to attain local dominance within plant communities. For each species, the mean projective cover was calculated across all relevés in which the species was present. These values were log-transformed to reduce the disproportionate influence of extremely high abundance values. Subsequently, a capping procedure was applied so that increases above a selected threshold no longer produced proportional increases in the predictor value. The purpose of this transformation was to represent the ecological assumption that strongly anthropogenically transformed communities are often characterised by reduced species diversity and local expansion of a limited number of disturbance-tolerant species. Therefore, the relationship between species abundance

and hemeroby was expected to be saturating rather than strictly linear. The optimal capping threshold was selected by comparing alternative models using the Akaike Information Criterion (AIC) in regressions relating species abundance characteristics to ordination-derived hemeroby scores. The resulting capped log-transformed abundance variable was subsequently included as a predictor in the reconstruction of regional species hemeroby values.

Results

Hemeroby and the set of ecological factors together explained 8.9% of the total community inertia in the CCA model. The CCA biplot revealed several complementary ecological gradients (Fig. 1).

In the CCA1–CCA2 plane, the main pattern contrasted soil moisture with carbonate content, indicating differentiation of communities along a hydrological-edaphic gradient. A second trend was associated with nutrient availability and light conditions, reflecting variation in community composition along a productivity–illumination gradient. The CCA3–CCA4 plane further separated communities along a hemeroby-related gradient, with CCA3 largely reflecting variation in anthropogenic transformation.

A partial constrained ordination was performed to extract the component of plant communities' variation specifically associated with hemeroby. In this model, hemeroby was used as the constraining variable, whereas the ecological indicator values were included as conditioning variables. This approach allowed the hemeroby-related trend to be separated from variation in vegetation composition induced by natural environmental gradients. After accounting for the effects of soil moisture, soil reaction, salinity, carbonate content, nutrient availability, aeration, thermal regime, ombroregime, continentality, cryoregime, and light conditions, hemeroby explained 0.65% of the total community inertia. The corresponding constrained axis, therefore, represents the independent component of compositional variation associated with anthropogenic transformation of plant communities.

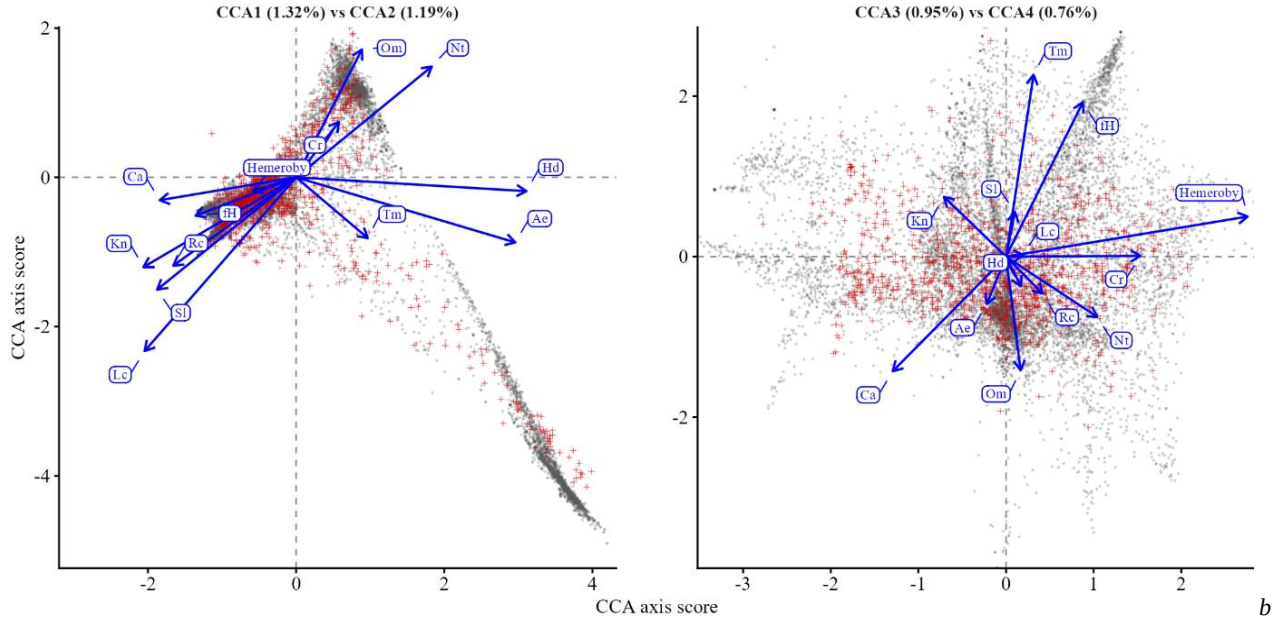

Fig. 1. Canonical correspondence analysis (CCA) ordination biplots showing relationships between vegetation composition, hemeroby, and ecological factors according to Didukh indicator values: *a* – CCA1 vs CCA2; *b* – CCA3 vs CCA4; grey dots represent vegetation plots, red crosses indicate species scores, and blue arrows denote environmental gradients; hemeroby and ecological factors together explained 8.9% of the total community inertia

The first axis of the partial canonical correspondence analysis represented the independent hemeroby gradient after extraction of the compositional variation explained by Didukh ecological indicator values. Relationships between species scores along this axis and the predictor variables revealed several ecologically interpretable trends (Fig. 2). Species associated with higher hemeroby values tended to occur under stronger disturbance severity, higher mowing frequency, and greater nutrient availability. In contrast, grazing pressure showed a negative relationship with the hemeroby gradient. Among the Didukh ecological indicator values, humidity (Hd), continentality (Kn), carbonate content (Ca), and ombroregime (Om) were positively associated with the gradient. At the same time, variability of damping (fH) and soil reaction (Rc) showed negative relationships.

The CSR strategy components displayed only weak relationships with the partial hemeroby gradient. Stress tolerance (S), ruderality (R), and competitiveness (C) all showed slight negative trends, indicating that none of the major CSR dimensions alone strongly structured the independent anthropogenic component of species turnover after accounting for natural ecological gradients. Species abundance-related predictors showed contrasting effects: capped log mean abundance showed a weak positive relationship with the hemeroby gradient, whereas log frequency showed a slight negative relationship. Occurrence-based disturbance indicators also differed in their responses: disturbance severity was positively associated with hemeroby, whereas herb-layer disturbance metrics and disturbance frequency variables showed comparatively weak relationships. Overall, the strongest responses along the extracted hemeroby gradient were associated with disturbance intensity and management-related variables rather than with the major natural ecological gradients represented by the Didukh indicator system.

The mean abundance, when present, was transformed into a capped predictor to account for the expected threshold-like response of species hemeroby to quantitative occurrence. The optimal threshold was selected by testing a sequence of candidate cut-off values across the empirical distribution of log-transformed mean abundance and choosing the value that minimised AIC in a simple regression with the partial CCA1 hemeroby score. The resulting variable, capped log-transformed mean abundance, increased with mean abundance only up to the selected threshold and then remained constant, reflecting the expectation that anthropogenic transformation promotes dominance by a limited set of tolerant species rather than unlimited linear increases in abundance. This capped abundance predictor was then included, along with the ecological indicator values, CSR strategy components, disturbance-sensitivity indicators, and species status variables, in all subsequent regression models. Thus, the comparison among modelling approaches was based on the same predictor set and the same response variable, namely the species scores on the first axis of the partial CCA hemeroby gradient. Among the tested models, the linear model performed best overall. It had the lowest RMSE (0.651) and MAE (0.48), and the highest explained variance (R^2 = 0.31).

The random forest model performed almost identically (R^2 = 0.31), whereas the elastic net model was weaker (R^2 = 0.25). Because the linear model combined the highest predictive performance with direct ecological interpretability, it was selected as the primary modelling framework.

The linear model was used to identify which species-level ecological, functional, status-related, and disturbance-related characteristics were most closely associated with the hemeroby gradient extracted by partial CCA (Table 1). Because this gradient represents the component of species turnover remaining after the variation explained by Didukh's ecological indicator values had been partialled out, the model describes predictors related specifically to the independent anthropogenic component of community differentiation. In this context, the clearest signals were associated with abundance-related responses and disturbance-related variables. The strongest positive effect was observed for capped log-transformed mean abundance. This pattern suggests that, under more hemerobic conditions, species richness declines, and the remaining tolerant species can expand into the released ecological space, leading to higher local abundance. Disturbance severity and mowing frequency also showed significant positive relationships with the hemeroby gradient, whereas grazing pressure was negatively associated with it. Among the Didukh ecological indicator values, soil moisture (Hd), damping variability (fH), continentality (Kn), and carbonate content (Ca) were associated with the hemeroby gradient. Soil moisture, continentality, and carbonate content showed positive effects, whereas damping variability showed a negative effect. Other ecological indicators had weaker or statistically non-significant relationships after BH correction. Species status variables also contributed to the model. Adventive species status and cultivated or decorative species status were positively associated with the hemeroby gradient, whereas invasive and quarantine species did not show statistically significant effects after BH correction. In contrast, the CSR strategy components, including stress tolerance (S), ruderality (R), and competitiveness (C), did not show statistically significant relationships with the partial CCA hemeroby gradient after BH correction. Thus, the extracted independent hemeroby component was determined mainly by abundance-related responses, disturbance intensity, and management-related factors, rather than by primary CSR strategy components.

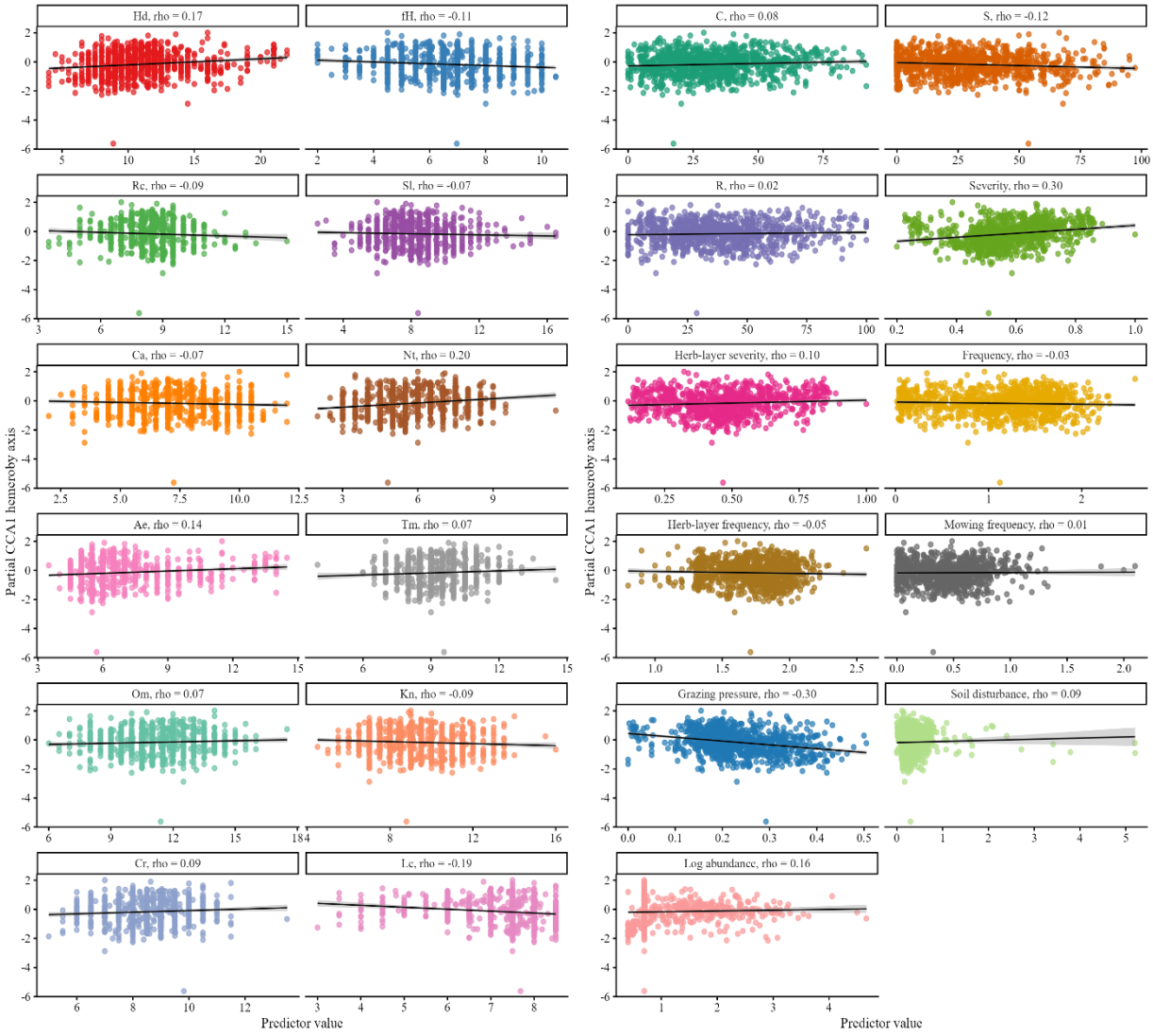

Fig. 2. Relationships between species scores on the first axis of the partial CCA hemeroby gradient and individual predictor variables used in the regression analysis: panels show Didukh ecological indicator values, CSR strategy components, disturbance-related variables, capped log mean abundance, and occurrence-based disturbance indicators; solid lines indicate fitted trends, and grey ribbons show 95% confidence intervals; Spearman's rank correlation coefficients (ρ) are shown in the panel headers; the Y-axis represents species scores on the first axis of the partial canonical correspondence analysis after accounting for natural environmental gradients

Prediction quality for species with observed partial CCA1 scores was moderate but consistent across evaluation metrics. The predicted and observed values showed Pearson and Spearman correlations of 0.56 and 0.55, respectively, indicating that the model reproduced both the magnitude and the rank structure of the hemeroby gradient reasonably well. The model explained 31.7% of the variance in the par-

tial CCA1 scores ($R^2 = 0.31$), with an RMSE of 0.651 and an MAE of 0.487. These results indicate that, although a substantial proportion of species-level hemeroby variation remains unexplained, the model captures a biologically meaningful component of the gradient and provides sufficiently robust predictions for species lacking direct hemeroby estimates.

The newly derived partial CCA-based hemeroby scale produced substantially lower within-site variability than the initial species hemeroby scores. The mean weighted variance of species hemeroby within vegetation plots decreased from 371 in the original scale to 55 in the new scale, representing an approximately 6.7-fold reduction. The same pattern was observed for median variance values. Paired Wilcoxon tests confirmed that the reduction in within-site variance was highly significant ($P < 0.001$). These results indicate that the partial CCA-based hemeroby estimates are considerably more internally consistent within plant communities and therefore more closely aligned with the compositional structure of the observed vegetation.

Table 1

Standardised regression coefficients for predictors of species scores on the first axis of the partial canonical correspondence analysis (CCA) hemeroby gradient after accounting for ecological variation explained by Didukh indicator values

Predictor	Standardised β ± SE	*P*-value	BH-adjusted *P*
Stress tolerance (S)	–0.38 ± 0.26	0.145	0.245
Ruderality (R)	–0.29 ± 0.25	0.244	0.321
Competitiveness (C)	–0.29 ± 0.22	0.188	0.273
Capped log-transformed mean abundance	0.27 ± 0.02	< 0.001	< 0.001
Disturbance severity	0.16 ± 0.05	< 0.001	0.002
Soil moisture (Hd)	0.13 ± 0.05	0.008	0.023
Mowing frequency	0.11 ± 0.03	0.001	0.004
Grazing pressure	–0.11 ± 0.03	< 0.001	0.004
Adventive species status	0.10 ± 0.02	< 0.001	< 0.001
Variability of damping (fH)	–0.10 ± 0.03	< 0.001	0.001
Cultivated or decorative species status	0.08 ± 0.02	< 0.001	0.002
Continentality (Kn)	0.08 ± 0.03	0.003	0.010
Carbonate content (Ca)	0.06 ± 0.03	0.021	0.055
Soil reaction (Rc)	–0.05 ± 0.03	0.059	0.143
Herb-layer disturbance severity	–0.05 ± 0.06	0.415	0.481
Ombroregime (Om)	0.05 ± 0.03	0.065	0.145
Salinity (Sl)	0.05 ± 0.03	0.090	0.174
Cryoregime (Cr)	0.04 ± 0.03	0.110	0.199
Invasive species status	0.04 ± 0.02	0.081	0.168
Nutrient availability (Nt)	–0.04 ± 0.03	0.152	0.245
Weed species status	0.03 ± 0.03	0.209	0.288
Light conditions (Lc)	–0.03 ± 0.03	0.356	0.449
Quarantine species status	–0.03 ± 0.02	0.182	0.273
Soil disturbance	–0.02 ± 0.02	0.375	0.453
Disturbance frequency	0.01 ± 0.06	0.849	0.912
Thermal regime (Tm)	0.01 ± 0.03	0.776	0.865
Herb-layer disturbance frequency	0.01 ± 0.05	0.912	0.934
Aeration (Ae)	0.00 ± 0.05	0.934	0.934

The relationship between mean site hemeroby and within-site hemeroby variance differed substantially between the original and the newly derived scales (Fig. 3). Under the initial hemeroby scale, within-site variance showed only a very weak positive relationship with mean hemeroby (Spearman's $\rho = 0.07$, $P < 0.001$). The overall structure of the relationship remained diffuse and poorly organised across the gradient. In contrast, the new partial CCA-based hemeroby scale revealed a strong negative relationship between mean hemeroby and within-site variance (Spearman's $\rho = -0.44$, $P < 0.001$). Specifically, highly hemerobic communities were characterised by markedly lower internal heterogeneity in species hemeroby values. The GAM-smoothed trends also showed that the new scale produced a much more coherent ecological structure, with variance decreasing progressively toward the highly transformed end of the gradient. This pattern indicates increasing compositional convergence among vegetation transformed by anthropogenic activities. It suggests that the partial CCA-based scale captures the ecological organisation of plant communities along the hemeroby gradient more effectively.

Discussion

Hemeroby is considered here as the degree of anthropogenic transformation of ecosystems. Such transformation forms a gradient that can be operationally identified only through the response patterns of living organisms (Hill et al., 2002). This is because anthropogenic impacts are highly diverse and differ in their spatial configuration, temporal rhythm, intensity, and duration (Walz & Stein, 2014). As a result, it is practically impossible to use a universal set of directly measurable physical or chemical variables to assess ecosystem transformation consistently (Fehrenbach et al., 2015). Species indicator values for hemeroby, therefore, represent an attempt to construct an analytical tool analogous to ecological indicator scales for environmental factors. However, these scales are expert-based, which substantially complicates their transfer across geographical regions. A more general limitation is also inherent in all indicator-value systems: autecological properties of species are often directly converted, through simple algebraic operations, into assessments of the state of whole ecosystems. This creates a methodological gap between species-level indicator values and community-level ecosystem transformation. Therefore, the transfer of hemeroby indicator systems to new geographical conditions is further complicated by this methodological limitation, because species-level autecological characteristics may not retain the same relationships with ecosystem-level transformations across different regional environmental and land-use contexts.

Our approach assumes that an adopted hemeroby scale contains relevant information about species sensitivity to anthropogenic pressure and can therefore be applied, at least in a broad sense, under geographically different but ecologically comparable conditions. Such a transfer may provide adequate general estimates of anthropogenic transformation. However, accurate point estimates of species hemeroby require regional calibration, because local environmental settings, land-use history, and the regional species pool mediate species responses to anthropogenic pressure (Tyler et al., 2021; Tichý et al., 2023). For this reason, two criteria can be used to evaluate the updated hemeroby scale. The first is a comparison with independent hemeroby estimates obtained by an alternative method. The second is the reduction of within-site variation in species hemeroby values. The latter criterion is based on the expectation that species co-occurring within the same vegetation plot should be more similar in their hemeroby values if the scale adequately reflects the compositional organisation of communities along the anthropogenic transformation gradient. An independent alternative estimate of hemeroby may be obtained using landscape-based approaches to hemeroby assessment. The conceptual and methodological foundations of such an approach require separate investigation and therefore represent an important direction for future research. In the present study, emphasis was placed on the second criterion, namely the reduction of within-site variance in species hemeroby values. Based on these assumptions, the present study aimed to use the hemeroby scale as a predictor to extract a gradient of variation in community composition. This approach more closely aligns with the original interpretation of hemeroby as a measure of ecosystem transformation rather than an isolated species property. Within this framework, a species' position along the hemeroby gradient can serve as the basis for defining its hemeroby indicator value.

The proposed procedure changes the conceptual status of species hemeroby values. In the original expert-based approach, species indicator values represent autecological properties that are subsequently averaged to characterise entire communities (Scherrer & Guisan, 2019). However, the additivity of such values is largely assumed rather than formally justified. In contrast, the present approach first extracts a hemeroby-related gradient directly from community composition and only then derives species indicator values from species optima along this gradient. As a result, species hemeroby values become coordinates within a community-level compositional space rather than isolated species attributes. Under this framework, additivity emerges naturally from the weighted-averaging properties of correspondence-based ordination methods. Because species scores are derived from the structure of communities themselves, abun-

dance-weighted averaging of species values reconstructs the position of communities along the same hemeroby gradient from which the species scores were originally obtained. Consequently, the resulting indicator values possess an internally consistent community-level interpretation and can be meaningfully applied to estimate the hemeroby of vegetation plots and ecosystems.

The ordination results indicate that hemeroby constitutes an important component of regional floristic differentiation, although it does not dominate the first two axes of community variation. The first four CCA axes captured several complementary dimensions of vegetation structure, among which the hemeroby-related component emerged as a distinct and ecologically interpretable gradient. This is important because anthropogenic transformation was not simply superimposed on a single environmental axis, but appeared as one of the major directions of floristic variation alongside hydrological, edaphic, productivity-related, and light-related gradients. A key point is that hemeroby became especially evident in the higher-order ordination structure, particularly in the CCA3–CCA4 plane. This suggests that the anthropogenic component of regional floristic differentiation is partly independent of the dominant natural ecological gradients. In other words, hemeroby does not merely duplicate variation in soil moisture, carbonate content, nutrient availability, or light conditions. Instead, it represents a separate dimension of vegetation organisation that becomes visible after the main environmental gradients are accounted for. This result supports the interpretation of hemeroby as a synthetic ecological characteristic of plant communities. It integrates the consequences of disturbance, land-use intensity, management regime, and species replacement under anthropogenic pressure. Therefore, even though the total explained inertia of the CCA model was moderate, the position of hemeroby among the first four leading trends of variation shows that anthropogenic transformation is a structurally important factor in the regional flora rather than a marginal or secondary attribute.

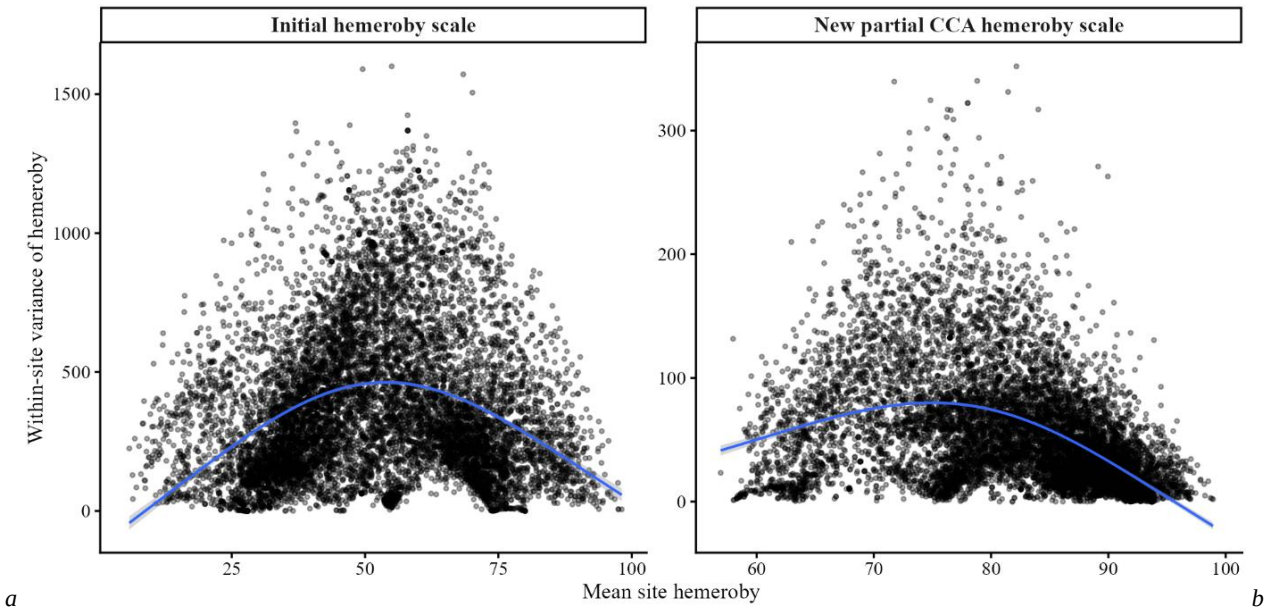

Fig. 3. Relationship between mean site hemeroby and within-site variance of species hemeroby under the initial and newly derived hemeroby scales: points represent individual vegetation plots; blue curves show GAM-fitted trends: *a* – initial hemeroby scale based on original species indicator values; the relationship between mean hemeroby and within-site variance was weak and poorly structured; *b* – new partial CCA-based hemeroby scale derived from species scores along the first axis of partial canonical correspondence analysis; the new scale revealed a pronounced decline in within-site hemeroby variance with increasing mean site hemeroby, indicating increasing compositional convergence of highly anthropogenically transformed communities

The main gradient of plant community variation contrasted more humid habitats with habitats characterised by higher carbonate content and greater light availability. Ecologically, this gradient corresponds to the opposition between mesic or wet depressions and open upland habitats occupied by steppe vegetation. Steppe communities are typically herbaceous, highly illuminated, and formed under moisture-deficient conditions, often on carbonate-rich soils. By contrast, the opposite end of the gradient represents communities in lower-relief positions, primarily river floodplains and the thalwegs of ravines, where increased soil moisture is the dominant ecological condition. The hemeroby indicator further shows that upland steppe habitats are more frequently exposed to anthropogenic pressure. This pattern is consistent with the high level of agricultural transformation in the region, as well-drained interfluve areas are most suitable for cultivation and have therefore undergone long-term land-use intensification. Consequently, the hemeroby gradient partly reflects the spatial coincidence between steppe vegetation and the main agroecosystem development zone. The same gradient also indicates that communities of upland habitats are associated with greater tolerance to continental climatic conditions, stronger moisture contrast, and more alkaline soil reaction. These features are ecologically consistent with open steppe habitats, where seasonal water deficit, high irradiation, and carbonate-rich parent materials jointly shape plant community composition.

Hemeroby was the dominant marker of CCA3, which allows this axis to be interpreted primarily as a hemeroby-related gradient. However, hemeroby was not the only predictor associated with this axis. This indicates that anthropogenic impact is superimposed on specific ecological conditions rather than acting independently of the environmental background. Therefore, separating the effect of ecological factors was essential for obtaining a more refined hemeroby gradient. The partial CCA approach enabled the extraction of the component of community variation most directly induced by anthropogenic transformation, rather than by environmental factors correlated with it.

Although hemeroby accounted for only 0.65% of the total community inertia after accounting for Didukh ecological indicator values, this component represented approximately 7.3% of the inertia jointly explained by hemeroby and ecological factors. Therefore, the independent hemeroby effect should not be regarded as negligible. Rather, it represents a distinct anthropogenic component within the constrained ecological structure of regional vegetation. This result is especially important because hemeroby was extracted after removing the variation attributable to major natural environmental gradients, indicating that anthropogenic transformation contributes an additional, non-redundant dimension to floristic differentiation. The canonical

axis obtained from the partial CCA was interpreted as a marker of hemeroby reflected in the compositional structure of plant communities.

The reconstructed hemeroby scale was represented as a rank-rescaled distribution. This transformation provides an analytical advantage, because species indicator values cover the full hemeroby range more evenly. As a result, the scale has improved information properties as a measurement tool: different parts of the anthropogenic transformation gradient are represented by comparable numbers of species, reducing the concentration of indicator values in only a limited part of the scale. The rank-rescaled representation of the reconstructed hemeroby scale improves its measurement properties by more evenly distributing species indicator values across the full gradient range. From the perspective of measurement theory, this increases the effective resolution of the scale, because different segments of the hemeroby gradient are represented by comparable numbers of indicator species. In this sense, the transformation is analogous to the use of evenly spaced units on a ruler: it does not imply that the measured phenomenon is uniformly distributed, but it ensures that the measurement instrument provides comparable discrimination across the entire range. Thus, rank rescaling enhances the analytical utility of the species indicator system for estimating community-level hemeroby.

A critical methodological consequence of this approach is that the aggregation procedure used to estimate community-level hemeroby cannot be regarded as automatically valid (Diekmann, 2003). In traditional indicator-value systems, species scores are commonly combined using simple arithmetic or abundance-weighted averaging, often without explicit consideration of the measurement properties of the scale itself (Zelený & Schaffers, 2012). Such procedures implicitly assume that the indicator values form an interval-like measurement system in which distances between adjacent values are comparable across the entire gradient (Nykytiuk et al., 2025). However, this assumption is rarely examined explicitly. In expert-based hemeroby scales, species values are often unevenly distributed along the gradient. As a result, some sections of the scale may contain many species with very similar indicator values, whereas only a few taxa represent other sections. Under these conditions, arithmetic averaging becomes problematic because different parts of the gradient contribute unequally to the resulting community estimate. In effect, the measurement system possesses variable informational density along the gradient, meaning that some ranges are measured with substantially higher resolution than others. The reconstructed hemeroby scale proposed here attempts to reduce this problem by rank-rescaling species values into a more even distribution across the gradient. This transformation does not imply that ecological reality itself is uniformly distributed. Rather, it improves the scale's discriminatory properties as a measurement instrument, in much the same way that evenly spaced units on a ruler provide comparable resolution across the entire measurement range. Consequently, community-level estimates derived from weighted averaging become more internally consistent because the indicator system itself possesses a more balanced distribution of measurement resolution.

The rank-rescaled transformation substantially changes the measurement properties of the hemeroby scale (Lisovets et al., 2025; Tutova et al., 2025). In the original ordination space, distances between species scores have a direct geometrical meaning because they reflect differences in species optima along the extracted compositional gradient (Chetvertak et al., 2025). Neighbouring values, therefore, correspond to relatively similar ecological positions, whereas greater distances indicate stronger differentiation in responses to anthropogenic transformation (Nykytiuk & Kravchenko, 2025). Under this interpretation, the scale retains a metric relationship to the underlying ordination structure. Rank rescaling alters this relationship. After transformation, the distances between adjacent values no longer represent the original ecological distances in compositional space. Instead, the transformed values primarily preserve the ordering of species along the gradient while redistributing them more evenly across the available range. Thus, the scale shifts from a strictly geometrical representation of ordination distances toward a measurement-oriented representation optimised for discriminatory performance. This distinction is important because equal intervals in the transformed scale no longer imply equal ecological differences in the original ordination space. Rather, they correspond to approximately equal informational resolution along the gradient. In this sense, the transformation is analogous to nonlinear calibration procedures used in measurement systems, where raw physical signals are transformed into scales with more uniform sensitivity across the measurement range. The objective is not to preserve the original geometry exactly, but to improve the practical interpretability and analytical stability of the measurement instrument. As a consequence, the reconstructed hemeroby values should not be interpreted as absolute metric quantities. For example, a community with a hemeroby value of 80 cannot be interpreted as experiencing "twice" the anthropogenic transformation of a community with a value of 40. Instead, the transformed values represent ordered positions within a latent compositional space associated with anthropogenic transformation. Their primary function is comparative and discriminatory rather than strictly metric. At the same time, the transformation does not invalidate aggregation procedures based on weighted averaging. Because both species scores and community estimates are derived from the same ordination-based compositional framework, the transformed scale preserves internal consistency between species-level and community-level representations. The aggregation procedure, therefore, remains meaningful, although the resulting estimates should be interpreted as positions along a calibrated latent gradient rather than as direct physical measurements of anthropogenic impact.

In the proposed framework, abundance-weighted averaging is theoretically justified primarily by the origin of the hemeroby scale. In conventional indicator-value systems, species scores are usually assigned independently of community structure and are only subsequently aggregated to characterise vegetation plots or ecosystems. Under such conditions, the validity of weighted averaging is largely assumed rather than formally derived from the properties of the indicator system. In contrast, the reconstructed hemeroby values proposed here originate directly from community composition. The hemeroby gradient was first extracted as a latent axis of floristic differentiation using ordination methods, and species scores were then derived from their positions along this gradient. Consequently, species indicator values are not externally derived expert-based attributes imposed on vegetation data, but rather coordinates of species within the compositional space that defines community organisation. This distinction is critical because correspondence-based ordination methods are intrinsically based on reciprocal relationships between species scores and site scores. Species positions are estimated from their occurrence structure across communities, whereas the weighted contribution of species simultaneously determines community positions. Therefore, abundance-weighted averaging is not an arbitrary post hoc operation, but a natural property of the ordination geometry itself. Under this interpretation, aggregation of species hemeroby values reconstructs the position of a community within the same latent compositional space from which the species scores were originally obtained. The resulting community-level estimates are therefore internally coherent with the structure of the indicator system. In this sense, additivity is not imposed externally through algebraic manipulation but rather emerges from the dual structure of the ordination framework, which links species composition and community differentiation. This property substantially distinguishes the proposed approach from traditional expert-based hemeroby scales. The latter often rely on implicit assumptions that species indicator values can be averaged meaningfully across communities. In contrast, in the present framework, this operation is directly supported by the mathematical structure of the underlying compositional model.

Although median-based aggregation could provide a more robust summary for ordinal indicator systems, such an approach would be less consistent with the ordination-derived nature of the reconstructed hemeroby scale. In the present framework, species scores originate from a compositional gradient in which community positions are intrinsically linked to abundance-weighted species distributions. Therefore, weighted averaging is not merely a convenient statistical summary but a direct reconstruction of community position within the same latent ordination space. Importantly, dominance structure itself

represents an ecologically meaningful component of anthropogenic transformation, because highly transformed communities are often characterised by the expansion of a limited set of tolerant species. Median-based aggregation would suppress this structural signal, thereby weakening the correspondence between species-level and community-level representations of hemeroby. An additional argument supporting the proposed reconstruction of the hemeroby scale is the substantial reduction in within-site variability of species hemeroby values. Under the original expert-based scale, co-occurring species within the same vegetation plot often exhibited highly contrasting hemeroby scores. Such heterogeneity implies that the scale only partially reflects the actual compositional organisation of communities along the anthropogenic transformation gradient. If hemeroby is interpreted as a property of ecosystem transformation at the community level, then species within the same plant community would be expected to occupy relatively similar positions along the hemeroby gradient. The reconstructed scale markedly reduced this internal inconsistency. Mean within-site variance decreased approximately 6.7-fold, indicating that species co-occurring within the same vegetation plots became substantially more coherent in their hemeroby estimates. This result is theoretically important because the reconstructed species scores were derived directly from community compositional structure rather than assigned independently through expert interpretation. Consequently, the scale became more consistent with the actual geometry of species co-occurrence patterns in vegetation space. Importantly, this reduction in within-site variability should not be interpreted merely as a statistical smoothing effect. Excessive variance reduction could theoretically arise from trivial compression of the scale itself. However, in the present case, the reconstructed hemeroby values retained clear differentiation along the gradient while simultaneously improving internal consistency within communities. Thus, the decrease in within-site variance indicates that the updated scale more accurately captures the shared anthropogenic context structuring species assemblages. The observed relationship between mean site hemeroby and within-site variance additionally supports the ecological significance of this result. Under the reconstructed scale, highly hemerobic communities displayed lower internal heterogeneity of species hemeroby values. This pattern suggests increasing compositional convergence under strong anthropogenic transformation, where communities become dominated by a more restricted set of disturbance-tolerant species. Therefore, the reduced within-site variance reflects not only improved measurement consistency but also a biologically meaningful property of transformed vegetation systems.

Conclusion

The present study developed a regionally calibrated hemeroby indicator system for the Steppe zone of Ukraine, based on the compositional structure of plant communities across a broad gradient of anthropogenic transformation. The proposed framework combines expert-based species indicator values with ordination-derived community patterns, thereby linking autecological species properties with the synecological organisation of vegetation. A key methodological outcome of the study is the resolution of the long-standing problem of scale aggregation – namely, the transfer of species-level ecological properties into integrated community-level estimates of anthropogenic transformation. In conventional hemeroby systems, this transfer is usually assumed implicitly through averaging procedures, although the theoretical justification of such aggregation remains insufficient. In the proposed approach, this problem was addressed by extracting an independent hemeroby gradient from vegetation composition using constrained and partial ordination methods. Species hemeroby values were subsequently reconstructed from their positions within the ordination-derived compositional space associated with anthropogenic transformation. The calibration procedure developed in this study provides a bridge between species-level indicator values and community-level assessment of anthropogenic transformation. By deriving the hemeroby gradient from observed vegetation structure, the study shows how species properties can be integrated into a coherent estimate of community hemeroby without relying solely on untested averaging assumptions. This makes the regional hemeroby scale more suitable for comparative assessment of vegetation transformation across natural, semi-natural, urban, agrarian, and technogenic habitats. The reconstructed regional hemeroby scale demonstrated improved discriminatory properties and substantially reduced within-community inconsistency of species indicator values. The calibrated system, therefore, more accurately reflects the actual organisation of plant communities under different levels of anthropogenic disturbance and provides a more coherent basis for estimating vegetation transformation at the regional scale. The study also demonstrated that anthropogenic transformation represents a distinct component of vegetation differentiation that cannot be reduced solely to natural environmental gradients. After accounting for ecological variation using Didukh phytoindication scales, hemeroby retained an independent and ecologically interpretable component of floristic variation. This confirms that anthropogenic transformation acts as an additional structuring factor in the vegetation organisation of the Steppe zone of Ukraine. The proposed framework provides a theoretically grounded and empirically calibrated basis for regional hemeroby assessment. It may serve as a methodological foundation for future studies of vegetation naturalness, ecosystem transformation, restoration dynamics, and biodiversity monitoring.

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