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From species traits to community gradients: Validation of Borhidi-like naturalness indicators in steppe vegetation

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Naturalness is a key ecological concept reflecting the extent to which plant communities correspond to their natural state under minimal anthropogenic influence. The Borhidi system provides a widely used framework for assigning species-level naturalness indicator values based on ecological behaviour; however, its application at the community level remains insufficiently validated. This study aimed to assess whether species-level naturalness indicators correspond to empirically observed patterns in vegetation and to develop a reproducible, community-calibrated naturalness scale for the steppe ecosystems of Ukraine. The analysis was based on a large vegetation dataset encompassing a broad gradient of naturalness and anthropogenic transformation, including natural, semi-natural, urban, agricultural, and technogenic habitats. A modified Borhidi-like classification was developed by integrating functional traits, ecological niche breadth, synanthropic status, and conservation information into a unified species-level index. Relationships between species traits, environmental gradients, and community composition were analysed using RLQ ordination. A curvilinear naturalness trajectory was derived from the ordination space and used to construct a continuous community-level indicator scale. The results show that species-level naturalness categories exhibit non-random patterns in community composition and are related to environmental gradients. They do not form a single linear gradient; instead, naturalness emerges as a multidimensional property structured by multiple ecological processes. The most consistent dimension corresponds to the contrast between stress-tolerant and ruderal strategies, which approximates a functional naturalness gradient. Functional traits, particularly stress tolerance and ecological niche breadth, significantly contribute to explaining variation along this gradient, although they do not fully determine species positions. The proposed approach allows the transformation of discrete Borhidi-like categories into a continuous, empirically calibrated naturalness scale. This scale reflects community-level organisation and provides a more robust basis for ecological interpretation than purely expert-based classifications. At the same time, the results highlight that the transfer of species-level indicators to the community level is only partially valid, as many categories exhibit context-dependent behaviour. The study demonstrates that naturalness can be operationalised as a continuous, community-derived indicator when species' ecological properties are integrated with empirical vegetation data. The proposed framework offers a reproducible tool for assessing vegetation naturalness and analysing ecosystem transformation across heterogeneous landscapes.

Keywords: biotic homogenization; CSR strategies; ecological niche breadth; RLQ analysis; plant community structure; functional traits; synanthropisation; invasion ecology; steppe ecosystems; vegetation gradients.

Introduction

Naturalness refers to the extent to which the current state of an ecosystem or plant community corresponds to its natural, historically established condition that existed, or could have existed, before significant anthropogenic impact (Erdős et al., 2022). It reflects the reduction of characteristics associated with degradation, artificiality, synanthropization, and the dominance of species linked to disturbed or transformed environments (Winter, 2012). The assignment of naturalness indicator values to species is based on the presence of a naturalness–degradation gradient along which species are non-randomly distributed (Anderson, 1991). Because species differ in their realised ecological niches, ecological optima, and tolerance ranges to anthropogenic disturbance, their positions along this gradient can be quantified (Fanelli et al., 2006). Such quantitative positioning of a species along the naturalness gradient is interpreted as its indicator value of naturalness (Borhidi, 1995; Pinke et al., 2011). In the Borhidi system (Borhidi, 1995), species' naturalness indicator values are derived from a combination of ecological and biogeographical characteristics. These include, in particular, plant CSR strategies according to Grime (Fanelli et al., 2006; Kilinç et al., 2010), the breadth of ecological amplitude across environmental gradients, and nominal status categories reflecting conservation importance or the role of a species as an adventive, weed, or invasive element of the flora. Borhidi explicitly links the system of social behaviour types to naturalness values through species' ecological behaviour in plant communities and their responses to disturbance, competition, stress, and anthropogenic habitat transformation. The Borhidi system has a regional scope, as it was originally developed for Hungary's flora. More broadly, it can serve as a reference framework for the Pannonian region and adjacent parts of Central Europe, though with caution, as species' indicator values may vary across regions. A separate system has been proposed for Ukraine by Goncharenko (Goncharenko, 2017; Yorkina et al., 2022). Although Borhidi's naturalness indicator values are region-specific (Borhidi, 1995), the underlying principles of their construction are general and can be applied to other regions. This is because they are based on fundamental ecological patterns, including the existence of anthropogenic disturbance gradients, differentiation of species according to their realised niches, CSR strategies, ecological amplitude, and their association with natural or disturbed habitats. At the same time, specific indicator values must be calibrated separately for each region, taking into account local flora, biogeographical context, and the history of anthropogenic impacts.

In Borhidi's system (Borhidi, 1995), a species' CSR strategy is determined by expert assessment based on its ecological behaviour, coenotic role, and response to stress and disturbance. It is integrated into the system of social behaviour types and serves as one of the foundations for assigning naturalness indicator values to species (Minarchenko et al., 2025). By contrast, modern approaches to CSR classification are based on plant functional traits, particularly leaf area (LA), specific leaf area (SLA), and leaf dry matter content (LDMC), which enable the position of a species within CSR space to be quantified (Pierce et al., 2017). This allows Borhidi's conceptual framework to be adapted to regional floras using measurable ecological properties of species rather than relying solely on expert judgement. In Borhidi's approach, the breadth of a species' ecological niche is also assessed by experts, based on its coenotic behaviour: the degree of specialisation to particular natural communities or, conversely, its ability to occur across a wide range of environmental conditions, including disturbed and anthropogenically transformed habitats. Thus, it represents a categorical expert-based estimate of ecological amplitude rather than a direct quantitative measure of niche breadth. For the flora of Ukraine, Didukh's phytoindication scales provide a methodological basis for quantifying ecological amplitude (Didukh, 2011). Their main advantage lies in their range-based structure: They characterise both the ecological optimum (or preference) of a species along a given environmental gradient and the width of its ecological tolerance. Therefore, these scales can serve as a quantitative foundation for estimating species' ecological niche breadth when adapting Borhidi's principles to the regional conditions of Ukraine.

According to Borhidi's approach (Borhidi, 1995), conservation significance is not treated as a separate, formalised attribute but is incorporated integratively through a species' assignment to a particular social behaviour type. Species associated with natural, climax, or minimally disturbed communities are assigned higher naturalness values, whereas ruderal, weed, adventive, and invasive species receive lower values (Ridder, 2007). Thus, in classical phytoindication and coenotic approaches, conservation value is inferred from an integrated assessment of species' ecological behaviour, habitat affiliation, and sensitivity to anthropogenic disturbance (Tobias & Pigot, 2019). Modern functional ecology, however, offers a range of approaches that formalise and express such assessments in quantitative, reproducible terms (Pierce et al., 2017). One major direction involves using rarity and distribution metrics, including species frequency, range size, and degree of endemism, which are directly related to vulnerability and conservation importance (Crisfield et al., 2024). Another approach is based on species' responses along environmental gradients, where phytoindication scales play a key role by capturing both ecological preferences and tolerance ranges (Diekmann, 2003). A conceptually related framework is provided by coefficients of conservatism (C-values), which quantify species' tolerance to environmental transformation and are widely used in ecosystem quality assessment (Spyreas, 2019). More recently, trait-based approaches have gained prominence, particularly those based on CSR strategies, where species' positions in functional trait space (e.g., SLA, LDMC, leaf area) reflect their adaptation to competition, stress, and disturbance (Pierce et al., 2017). Such approaches enable objective comparisons across species and communities, largely independent of regional floristic context (McGill et al., 2006). Another important direction is the quantitative assessment of ecological niche breadth, which can be derived from variation in species' responses along environmental gradients or from specific indices of ecological amplitude (Violle & Jiang, 2009). Narrow specialisation is generally associated with higher conservation value, whereas broader tolerance reflects greater ecological plasticity and resilience to disturbance (Devictor et al., 2010). In addition, species' affiliation with natural, semi-natural, or anthropogenically transformed habitats provides a direct measure of their position along the naturalness gradient (Knapp et al., 2008). Taken together, contemporary approaches to assessing conservation value integrate measures of ecological specialisation, niche position and breadth, functional traits, and distribution patterns. This integration facilitates a transition from expert-based classifications to quantitative, reproducible indices that describe species' positions along a naturalness gradient and can be adapted to regional ecological contexts.

Borhidi assessed species adventiveness and invasiveness through expert classification into specific social behaviour types, such as adventives, weeds, alien competitors, and others (Borhidi, 1995). These categories reflect species origin, degree of naturalisation, dispersal ability, and impact on plant communities. This constitutes a categorical evaluation integrated into the overall naturalness framework, where adventive and invasive species correspond to lower levels of naturalness. In turn, modern approaches to the quantitative assessment of species adventiveness and invasiveness integrate several complementary tools that treat invasiveness as a multidimensional, measurable property (Roy et al., 2018). A key component is the stage of the invasion process, ranging from introduction to full naturalisation and invasion, reflecting a species' ability to overcome successive ecological barriers (Blackburn et al., 2011). Spatial distribution is another important indicator, typically quantified according to species frequency in communities, the number of localities, range size, and the diversity of occupied habitats (Gaston, 1996). The temporal dynamics of spread are also considered, particularly the rate of range expansion or increase in frequency over time, which allows stable adventive species to be distinguished from actively expanding invasive ones (Aikio et al., 2010). Habitat breadth is a further critical dimension, describing a species' ability to occupy a wide range of biotopes, including natural communities, thereby indicating its ecological plasticity and invasion potential (Fristoe et al., 2021). At the community level, the role of a species is assessed through measures of local dominance, such as cover, biomass, or abundance, since invasive species often form dominant stands. A key aspect is also the impact on native ecosystem components, which can be quantitatively classified using frameworks such as the Environmental Impact Classification for Alien Taxa (EICAT), reflecting the degree of change in community structure and ecosystem functioning (Hawkins et al., 2015). All these metrics can be integrated into composite indices of invasiveness that combine information on distribution, ecological amplitude, spread dynamics, dominance, and ecological impact. Unlike categorical expert-based classifications, such approaches allow adventiveness and invasiveness to be described as continuous, quantitatively measurable characteristics, suitable for comparative analyses across species, communities, and regions.

A key methodological assumption of the species-indicator approach is that the autecological properties of individual species can be extrapolated to the level of plant communities (Diekmann, 2003). This assumption underpins the widely accepted notion that species composition can be used to assess the naturalness or degradation of a habitat: If species differ in their optima along a naturalness–degradation gradient, their presence within a community is interpreted as an indicator of its condition (Erdős et al., 2017). Within this framework, species' ecological properties, expressed in terms of naturalness, effectively serve as indicator values, and mean or cover-weighted values of these indicators are used to characterise community-level naturalness (Käfer & Witte, 2004). However, such a transfer from the species level to the community level is not straightforward. Species naturalness, as an autecological property, reflects a species' typical position, tolerance, or preference along gradients of anthropogenic impact. By contrast, community naturalness emerges from the interaction of multiple species, their abundances, competitive relationships, historical development, local environmental conditions, and disturbance regimes. Therefore, the transfer of species-level indicator values to the community level cannot be assumed to be automatically valid without explicit validation. In many approaches, this assumption is taken for granted: Species are treated as carriers of a certain level of naturalness, and communities are interpreted as aggregated sums or averages of these species-level values. Yet, the validity of this transfer between autecological and synecological levels remains insufficiently examined. For this reason, it is essential to distinguish between two levels of analysis: species-level naturalness, i.e., naturalness as a property of individual species, and community-level naturalness, i.e., naturalness as a property of plant communities. The latter can be defined in terms of CSR strategies, ecological amplitude, synanthropic status, invasiveness, or the conservation value of species. The latter must be empirically evaluated based on community structure, species composition, and their relationships with actual environmental gradients. Such an approach allows testing whether species-level indicators truly capture naturalness within plant communities.

This study is based on the assumption that Borhidi's naturalness scales generally reflect a genuine gradient of naturalness to degradation in vegetation (Borhidi, 1995). Accordingly, the numerical scores assigned to species are interpreted as their positions along this gradient. The study aims to assess the extent to which variation in species' naturalness indicator values, as defined by Borhidi, corresponds to observed patterns of variation in plant communities along environmental gradients. In other words, the validity of transferring species-level indicator values to the synecological level is evaluated. If naturalness scales indeed reflect the state of naturalness and can be considered indicators of this state at the community level, then naturalness categories, treated as discrete species traits, should exhibit consistent, non-random patterns within community composition. In this case, changes in the representation of these categories along environmental gradients should form a coherent and interpretable pattern corresponding to the naturalness gradient. Under these conditions, species' positions along an empirically derived naturalness gradient, based on community structure, can be interpreted as their indicator values. Thus, naturalness indicator values acquire an operational meaning as a species property that holds informational value at the community level, reflecting the species' contribution to the formation of a synecological naturalness gradient.

Material and methods

Study area and representation of the naturalness–disturbance gradient. The assessment of species naturalness according to the Borhidi concept was performed for the entire vascular plant flora of Dnipropetrovsk and Zaporizhzhia regions of Ukraine, based on the regional flora by Tarasov (2012) and supplemented by the authors' own field observations (Fig. 1). The vegetation database spanned a broad gradient of naturalness and anthropogenic transformation and comprised 10,665 *relevés*. The natural and near-natural pole was represented mainly by the Dnipro–Oril Nature Reserve, which contributed the largest subset of *relevés* (4,139 *relevés*; 38.8%; here and below, values in parentheses indicate the number of *relevés* and their percentage of the total dataset) (Lisovets et al., 2025a; Tutova et al., 2025), together with 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 Biogeocoenotic Station of Oles Honchar Dnipro National University near Andriivka (235 in total; 2.2%). Semi-natural vegetation was represented by Balka Kamenysta near Dnipro (525; 4.9%). A separate part of the natural gradient was represented by Khortytsia Island (729; 6.8%) (Lisovets et al., 2025b; Zhukov et al., 2025), which was treated as a natural area affected by military disturbance. The anthropogenically transformed pole of the gradient was represented by urbanised habitats from the city of Dnipro (1,220; 11.4%), Studentskyi Park (670; 6.3%) (Zhukov et al., 2025), and Ivan Starov Garden Square (150; 1.4%) (O. Lisovets et al., 2024). Technogenically transformed habitats included the reclamation research station near Pokrov (1,976; 18.5%) (Zhukov et al., 2025), electric substations in Dnipropetrovsk Oblast (175; 1.6%), and the quarry near Voloske (30; 0.3%). Agrarian habitats were represented by fallows (36; 0.3%) and *Robinia pseudoacacia* plantations near Dnipro (40; 0.4%). Overall, the dataset included both natural and semi-natural vegetation and strongly transformed urban, agrarian, and technogenic habitats. Natural localities formed the largest part of the sample, while urbanised and technogenically transformed sites provided substantial representation of the disturbed end of the gradient. This structure supports the use of the dataset for analysing changes in species composition, functional traits, and naturalness indicators along a broad gradient from natural to anthropogenically transformed vegetation.

Identification of competitors. Competitor species were identified using the CSR strategy scores available for each taxon. In the modified Borhidi-like classification, a species was assigned to the competitor group when the competitive component C was clearly dominant over both the stress-tolerant S and ruderal R components. Two conditions were applied simultaneously to avoid assigning weakly differentiated CSR profiles to competitors: The C score had to be at least 40 and exceed both S and R by at least 5 units. Species with C as the maximum CSR component, but without strict dominance, were also assigned to the competitor group as weak or mixed competitors. This allowed the procedure to retain the original Borhidi concept of competitors as species with a pronounced competitive strategy while also classifying intermediate CSR types in a reproducible way. Competitors were assigned +6 points in the modified Borhidi-like scoring system.

Identification of stress-tolerant specialists and generalists. Stress-tolerant species were identified using CSR strategy scores. A species was first assigned to the stress-tolerant group when the stress-tolerant component S was dominant in its CSR profile. Strict stress-tolerant plants were defined as species with $S \geq 40$ and with S exceeding both C and R by at least 5 units. Species with mixed CSR profiles that did not satisfy this strict rule but had S as the largest CSR component were also assigned to the stress-tolerant group at the fallback stage. The stress-tolerant group was then subdivided according to ecological breadth. Ecological breadth was estimated from Didukh's paired lower and upper ecological indicator values. For each ecological gradient, the breadth was calculated as the difference between the upper and lower margin values and standardised by the empirical range of the corresponding scale. The mean of these standardised breadths across all available gradients was used as the species-level ecological breadth index. The distribution of the ecological breadth index was analysed using a normal probability plot. Species located in the lower tail of the distribution were interpreted as having narrow ecological spectra and were classified as stress-tolerant specialists (S). Species located in the upper tail were interpreted as having broad ecological spectra and were classified as stress-tolerant generalists (G). Species in the central part of the distribution were classified as intermediate stress-tolerant species (ST). In the modified Borhidi-like scoring system, stress-tolerant specialists received +7 points, intermediate stress-tolerant species were given +5 points, and stress-tolerant generalists were assigned +4 points.

Identification and classification of ruderal species. Ruderal species were identified using the ruderal component R of the CSR strategy profile. Species were classified as strict ruderals at $R \geq 40$, provided their values exceeded both C and S by at least 5 units. Species with mixed CSR profiles but with R as the largest CSR component were assigned to the ruderal direction at the fallback stage. This ruderal pool was subsequently refined by status-based and functional rules: Invasive or quarantine species were assigned to AC, escaped cultivated or ornamental plants to I, species with high ruderal and competitive components to RC, adventive species to A, and weed species to W. Remaining ruderals were classified as disturbance tolerants (DT). A subset of DT species with $R \geq 50$ and nutrient availability not exceeding the median was further reassigned to natural pioneers (NP). Alien status was used to identify adventive alien species. Archaeophytes, defined as alien plants introduced before approximately 1500 CE, and neophytes, defined as alien plants introduced after approximately 1500 CE, were both treated as adventive alien taxa (Vynokurov et al., 2024). In the modified Borhidi-like classification, adventive species were assigned to the A category unless they were captured by a higher-priority rule, such as invasive or quarantine status, escape from cultivation status, or ruderal competitor status. Adventive alien species received −2 points in the final scoring system. Alien type was used to refine the treatment of alien taxa according to their degree of naturalisation and habitat infiltration (Vynokurov et al., 2024). Ephemerophytes, colonophytes, hemiepoecophytes, and epoecophytes were treated as adventive alien species and assigned to category A. Ergasiophyophytes, representing escapes from cultivation, were assigned to the category I. Agriophytes, defined as alien species fully established in natural or semi-natural communities and capable of invading near-natural habitats, were treated as aggressive alien or invasive taxa and assigned to category AC. These rules were applied as status-based overrides before the CSR-based assignment of native or semi-natural species. The negative part of the scoring scale was extended to account for the degree of alien species naturalisation. Casual aliens and species that escaped cultivation received weak negative scores, whereas colonophytes, hemiepoecophytes, epoecophytes, ruderal competitors, and agriophytes received progressively stronger negative scores. The field "cultivated plant" (Mosyakin & Fedoronchuk, 1999) was used as an additional indicator of cultivated or decorative origin. Species marked in this checklist were treated as species that escaped cultivation and assigned to the I category, unless a higher-priority invasive or quarantine rule captured them. This criterion was combined with Tarasov's cultural/decorative flag and the alien type category ergo to identify taxa associated with cultivation or escape from cultivation. In the final scoring system, the I category received −1 point. Information on adventive origin, weed status, cultivated or decorative origin, invasiveness, and quarantine status was used as a set of high-priority status-based rules (Tarasov, 2012). These rules were applied before the CSR-based assignment, because such species represent anthropogenic, alien, or disturbance-related elements whose behaviour cannot be adequately inferred from CSR scores alone—species identified as invasive or quarantine taxa were assigned to AC. Cultivated or decorative taxa and species that escaped from cultivation were assigned to category I. Adventive alien taxa were assigned to A unless they met a higher-priority rule. Native weed species were assigned to W, while species combining ruderal behaviour with a substantial competitive component were assigned to RC. Thus, status-based information was used to separate anthropogenic and alien elements from the native semi-natural pool before applying the remaining Borhidi-like functional classification.

Natural conservation bonus. Conservation value was incorporated as an additional bonus in the modified Borhidi-like naturalness assessment. Conservation statuses from regional, national, European, and international sources were recoded into a unified ordinal bonus scale (Table 1). The purpose of this step was to account for the conservation importance of species independently of their social behaviour type. The following conservation sources were used: the official list of regionally rare plants of Dnipropetrovsk Oblast (RLD) (Baranovsky & Tarasov, 2010); RLZ, the project of the list of regionally rare plants of Zaporizhzhia Oblast; the *Ukrainian Red Book* (URB); the *European Red List* (ERL); the *IUCN Red List of Threatened Species* (IUCN); and Resolution 6 of the Bern Convention, which lists species of European conservation concern. All conservation statuses were converted to six unified categories. Data-deficient or insufficiently studied taxa were assigned the lowest positive bonus. Rare or regionally rare species received a moderate bonus. Vulnerable and near-threatened taxa received higher values, while disappearing, endangered, critically endangered, extinct in the wild, or extinct taxa received the highest bonuses. Species with no conservation status, non-listed species, and taxa evaluated as Least Concern received no bonus. For the regional lists, RLD was treated as a differentiated source because it contains ordered categories ranging from 'insufficiently studied' to 'extinct'. By contrast, RLZ was treated as a non-differentiated regional rarity list. Therefore, species listed only in RLZ were assigned to the 'rare/regionally rare' category. If a species occurred in both RLD and RLZ, the differentiated RLD category was used to determine the bonus. The final conservation bonus was calculated as the maximum bonus value across all available conservation sources, not as a sum. This avoided artificially inflating the score for species listed in multiple conservation sources.

Table 1
Unified recoding scheme for conservation-status bonuses used in the modified Borhidi-like naturalness assessment

Unified category	Conservation meaning and source categories	Conservation bonus
1	Insufficiently studied / Data Deficient / Indeterminate: insufficiently studied (RLD), DD (URB), Indeterminate (ERL), DD (IUCN)	2
2	Rare / regionally rare: rare (RLD), listed in RLZ without differentiated status, RR (URB), Rare (ERL)	3
3	Near threatened / Vulnerable: vulnerable (RLD), VU (URB), Vulnerable (ERL), NT or VU (IUCN), Resolution 6 of the Bern Convention	4
4	Disappearing / Vanishing / Endangered: disappearing (RLD), UV or EN (URB), EN (IUCN)	5
5	Critically endangered / extinct in the wild/extinct: EW (URB), CR (IUCN), extinct (RLD)	6
6	No conservation status or Least Concern: not listed, empty status, LC (IUCN), NE / not evaluated	0

The modified naturalness assessment retained the general logic of Borhidi's classification of plant species into social behaviour types reflecting different degrees of naturalness and anthropogenic disturbance. However, instead of assigning categories solely on expert judgement, the procedure operationalised classification using available quantitative and categorical species-level information. Grime's CSR strategy scores were used to identify competitors, stress-tolerant species, and ruderals. The ecological breadth of species was estimated from Didukh's range-based ecological indicator scales and used to distinguish stress-tolerant specialists, intermediate stress-tolerant species, and stress-tolerant generalists. Additional regional and international information on conservation status was incorporated as a conservation bonus. By contrast, data on adventive origin, alien status, alien type, cultivated or decorative origin, weed status, invasiveness, and quarantine status were used to identify anthropogenic and alien elements of the flora. Thus, the original Borhidi framework was preserved as a conceptual structure, but its implementation was adapted to the available data and made reproducible. The scoring system was also expanded to better differentiate among levels of naturalness and anthropogenic transformation. Positive scores were assigned to natural and semi-natural social behaviour types, with the highest values given to narrow stress-tolerant specialists, competitors, and intermediate stress-tolerant species. Negative scores were extended to alien, ruderal-competitive, and invasive groups to distinguish weakly established adventive species from naturalised, semi-naturalised, and aggressive alien taxa. Conservation bonuses were added separately to account for the regional, national, European, or international conservation value of species. As a result, the final score integrates Borhidi-like social behaviour type, ecological strategy, ecological breadth, conservation value, and anthropogenic or alien status into a unified species-level naturalness index.

RLQ analysis linking community composition, environmental gradients, and species naturalness traits. RLQ analysis was used to relate community composition to environmental gradients and species-level naturalness traits (Dray & Legendre, 2008; ter Braak et al., 2012). The analysis was based on three linked tables: the site-by-species abundance matrix L, the site-level environmental table R, and the species-level trait table Q. The initial vegetation matrix contained 10,665 *relevés* and 972 species. Before the analysis, empty *relevés* and species absent from all *relevés* were removed, and the species lists were harmonised across the abundance matrix, Didukh indicator table, CSR table, and Borhidi-like naturalness table. The R table represented environmental predictors at the *relevé* level. We measured soil water regime (Hd), variability of damping/flooding (fH), soil acidity (Rc), soil salt regime (Sl), carbonate content (Ca), nitrogen availability (Nt), soil aeration (Ae), thermal regime (Tm), ombroregime or humidity/aridity of climate (Om), continentality of climate (Kn), cryoregime or winter severity (Cr), and light regime (Lc). For each species, the midpoint between the lower and upper indicator limits was used as the species score for the corresponding gradient. In addition, two composite predictors were calculated: edaphic, the mean of Hd, fH, Rc, Sl, Ca, Nt, and Ae; and climatic, the mean of Tm, Om, Kn, Cr, and Lc. The environmental table also included community-weighted mean CSR strategy values, which described the relative contribution of competitive, stress-tolerant, and ruderal strategies to each *relevé* (Grime, 2001). Species-level CSR scores were obtained from the global CSR database and classification framework in which plant strategies are quantified from leaf functional traits and expressed as relative C, S, and R components (Pierce et al., 2017). Because these three components are compositional variables and sum to a constant, a log-ratio transformation was applied to avoid artefacts associated with the direct analysis of closed compositional data (Egozcue et al., 2003). The two log-ratio contrasts were added to account for the compositional structure of CSR scores: the contrast between competitiveness and the combined stress-tolerant–ruderal component, and the contrast between stress tolerance and ruderality. The environmental table combined site-level ecological conditions and functional-strategy composition. The Q table contained the trait variable used in the RLQ analysis. This trait was the ordered Borhidi-like naturalness score of each species, calculated from the modified Borhidi-like classification. The score integrated social behaviour type, CSR strategy, ecological breadth, synanthropic and alien status, and conservation bonus. In the RLQ analysis, the score was treated as an ordered categorical trait, ranging from negative anthropogenic categories to positive high-naturalness categories. The RLQ analysis was performed with the ade4 package. Correspondence analysis was first applied to the species abundance table L. Principal component analysis was then applied to the environmental predictor table R, using the row weights from the correspondence analysis. Multiple Correspondence Analysis was applied to the ordered naturalness trait table Q, using the species weights from the correspondence analysis. The final RLQ ordination linked environmental gradients, community composition, and species naturalness traits in a common ordination space.

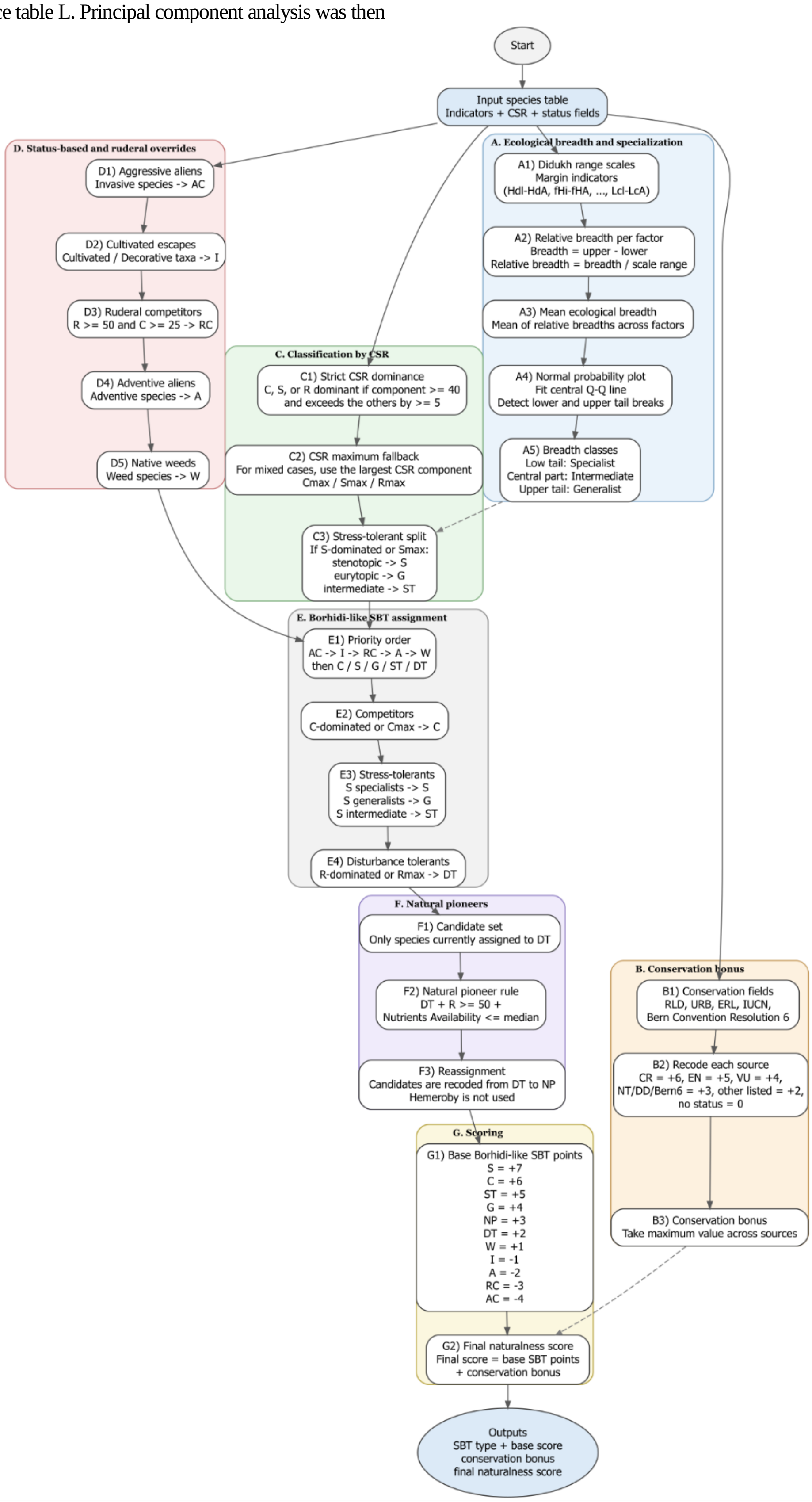


Fig. 1. Workflow for calculating the modified Borhidi-like naturalness score of plant species based on ecological breadth, CSR strategy, synanthropic status, conservation value, and functional reassignment of natural pioneers

Derivation of the RLQ-based curvilinear naturalness gradient. The curvilinear arrangement of Borhidi-like naturalness groups in the RLQ space was derived from the ordination of trait states along the first RLQ axis. For each naturalness category, centroid positions were calculated in the multidimensional RLQ space based on their coordinates across the retained axes. A smooth curve was then fitted through these points using a non-linear smoothing procedure (e.g., LOESS), capturing the main trajectory of variation across categories. The position of each category along this curve was subsequently projected onto a one-dimensional scale, which was rescaled to a 1–100 range to represent a continuous naturalness gradient. The purpose of this procedure was to extract an empirical, community-level naturalness gradient from the multidimensional RLQ ordination. Because the Borhidi-like categories did not align linearly along any single RLQ axis, the fitted curvilinear trajectory allowed integration of their positions across multiple axes into a single synthetic gradient. This provided (i) a continuous representation of naturalness at the community level, (ii) a basis for comparing species and categories along a common scale, and (iii) a response variable for subsequent modelling of naturalness using functional traits.

Recoding and ordination of conservation-status variables. Conservation-status data from multiple sources (regional, national, European, and global red lists) were first harmonised and recoded into a unified ordinal scale. Original categorical statuses (e.g., Data Deficient, Rare, Vulnerable, Endangered, Critically Endangered, Extinct) from different systems were mapped onto a common six-level ranking reflecting increasing conservation concern. Non-listed species and taxa classified as Least Concern were assigned a value of zero, whereas categories of increasing rarity and threat received progressively higher scores. This recoding ensured comparability among heterogeneous conservation systems and avoided inconsistencies arising from differences in classification schemes across sources. The recoded variables were then used as input to principal component analysis (PCA), yielding a set of orthogonal components that summarise the main dimensions of conservation information. The purpose of this procedure was to reduce dimensionality, remove collinearity among overlapping red-list variables, and extract independent gradients of conservation significance (e.g., overall conservation importance, regional specificity, and global conservation context). This allowed conservation information to be incorporated into subsequent analyses in a compact, statistically robust, and interpretable form.

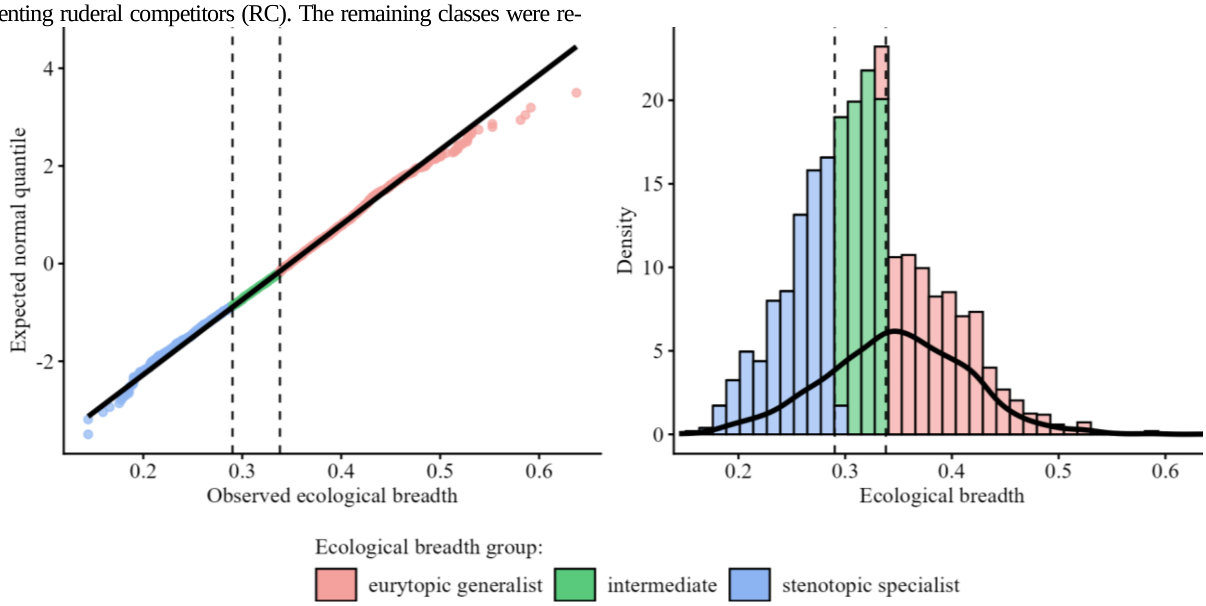
Generalised additive model (GAM) and elastic net modelling of species naturalness. The relationship between functional traits and the RLQ-derived naturalness gradient was analysed using a generalised additive model (GAM). The response variable was the position of species along the RLQ-based naturalness trajectory, rescaled to a 1–100 continuous scale. Predictor variables included CSR strategy components (C, S, and R), the log-ratio CSR contrasts, and indices of climatic and edaphic ecological breadth. Smooth terms were fitted for each predictor using penalised regression splines, with a Gaussian error distribution and smoothing parameter selection by Restricted Maximum Likelihood (REML). The purpose of this analysis was to evaluate whether functional traits can explain variation along the empirically derived naturalness gradient. The use of GAM allowed modelling of potentially non-linear relationships between predictors and naturalness, avoiding restrictive linear assumptions. Partial effect plots were then used to visualise the independent contribution of each predictor while holding other variables constant. This approach enabled the identification of which functional dimensions (e.g., stress tolerance, competitiveness, ecological breadth) are most strongly associated with increases or decreases in naturalness, and the assessment of whether these relationships are monotonic or non-linear. An elastic net regression model was used to predict species positions along the RLQ-derived naturalness gradient. The response variable was the projected position of species on the curvilinear RLQ trajectory, interpreted as a continuous naturalness gradient. Predictor variables included CSR strategy components, indices of ecological niche breadth (climatic and edaphic), conservation-related principal components derived from red-list data, and categorical variables describing alien and synanthropic status. Model calibration was performed using a training dataset of species, and regularisation parameters were optimised through cross-validation. The elastic net approach, combining L_1 (lasso) and L_2 (ridge) penalties, was used to control model complexity, reduce multicollinearity among predictors, and perform variable selection by shrinking less informative coefficients towards zero. The purpose of this analysis was to identify the most important ecological and conservation predictors associated with the naturalness gradient and to construct a predictive model linking species functional properties to their position along this gradient. The model performance (cross-validated error curves) was used to determine the optimal level of regularisation. At the same time, standardised coefficients were interpreted to assess the direction and relative strength of each predictor's effect. This allowed quantification of the relative importance of functional traits, conservation status, and synanthropic characteristics in shaping species-level naturalness.

Construction of the community-level naturalness indicator scale. The continuous naturalness indicator was derived from the position of species and naturalness categories along the RLQ-based curvilinear trajectory. This trajectory represents the main direction of variation in community composition associated with the naturalness–disturbance gradient, extracted from the multidimensional RLQ ordination. For each species, its position along the fitted trajectory was obtained by projection onto the one-dimensional curvilinear path. This projection yields a continuous variable describing the relative location of the species along the empirically derived naturalness gradient. The projected values were transformed to a 1–100 range using rank-based rescaling to obtain an evenly distributed indicator scale that provides relatively uniform coverage of the full range of naturalness conditions. Species were ordered according to their position along the trajectory, and ranks were linearly transformed so that the minimum value corresponded to 1 and the maximum to 100, with intermediate values distributed proportionally according to their rank. This rank-based transformation was applied instead of direct linear rescaling of the raw projection values. The rationale for this choice is that distances in the RLQ space are not strictly metric with respect to naturalness, and the curvilinear trajectory may exhibit non-uniform spacing of categories. Rank rescaling preserves the ordinal structure of the gradient while avoiding distortions caused by local irregularities in the geometry of the RLQ space. As a result, the final 1–100 scale represents a monotonic, community-derived naturalness gradient that is robust to non-linearity and heteroscedasticity in the underlying ordination space. The scale can be interpreted as an indicator of community-level naturalness, reflecting the relative position of species along the main trajectory of variation in plant community composition.

Results

The distribution of species ecological breadth was clearly structured along a narrow-to-broad ecological gradient (Fig. 2). In the normal probability plot, most observations followed the central fitted line, indicating that the central part of the distribution was approximately consistent with the expected normal trend. Deviations were mainly observed in the lower and upper tails, which justified separating species with unusually narrow and unusually broad ecological spectra. The lower breakpoint separated stenotopic specialists, whereas the upper breakpoint separated eurytopic generalists; species located between these two thresholds were classified as intermediate in ecological breadth. The histogram confirmed the same pattern. Most species were concentrated in the central part of the ecological breadth distribution, whereas stenotopic specialists occupied the lower-value tail and eurytopic generalists occupied the upper-value tail. The density curve showed a unimodal distribution with an extended right tail, indicating that species with broader ecological spectra were less frequent but formed a distinct upper-tail group. The combined diagnostic plots supported the use of quantile-based tail separation for distinguishing stenotopic specialists, intermediate species, and eurytopic generalists.

The regional flora comprised 2,130 species. The distribution of the final modified Borhidi–like naturalness score with conservation bonus was clearly shifted towards the positive part of the scale (Fig. 3). In total, 1,464 species (68.7%) had positive scores, whereas 666 species (31.3%) were assigned to negative–score categories; no species had a score of 0. The largest proportion of species was concentrated at score 8 (418 species; 19.6%), representing taxa in the high–naturalness part of the scale that also received a conservation bonus. A second major peak occurred at score 2 (387 species; 18.2%), corresponding to disturbance–tolerant species (DT). Among the negative categories, the most frequent class was score -5 (251 species; 11.8%), representing ruderal competitors (RC). The remaining classes were represented less strongly. Among positive scores, competitors (C; score 6) accounted for 157 species (7.37%), whereas weeds (W; score 1), natural pioneers (NP; score 3), and stress–tolerant generalists (G; score 4) each comprised 139 species (6.53%). Stress–tolerant specialists (S; score 7) included 49 species (2.30%), and intermediate stress–tolerant species (ST; score 5) were least frequent among the positive classes, with only 36 species (1.69%).



a *b*

Fig. 2. Distribution and normal probability diagnostics of species ecological breadth: *a* – normal probability plot of observed species ecological breadth values against expected normal quantiles (the solid black line represents the fitted central trend, and dashed vertical lines indicate the lower and upper breakpoints used to separate ecological breadth groups); *b* – density-scaled histogram of ecological breadth values with the same breakpoints; species were classified as stenotopic specialists, intermediate species, or eurytopic generalists according to their position in the lower tail, central part, or upper tail of the ecological breadth distribution, respectively

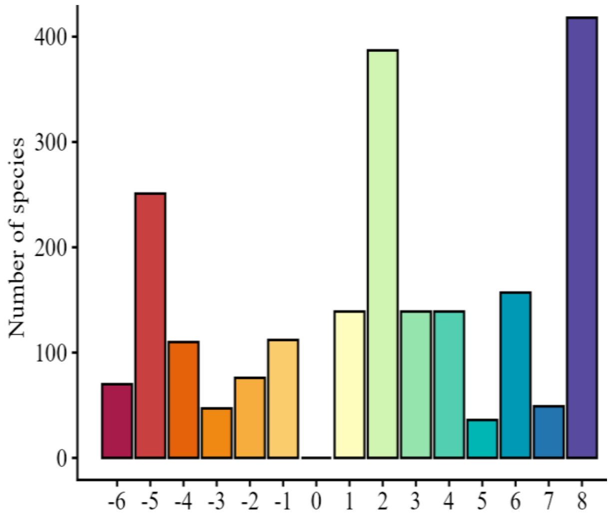


Fig. 3. Frequency distribution of the final Borhidi–like naturalness score with conservation bonus across species: the histogram shows the frequency distribution of species along the final modified Borhidi–like naturalness scale. In this system, negative scores represent alien and ruderal categories of decreasing naturalness: –6 – aggressive alien competitors (AC) and the most strongly naturalised adventive taxa (agriophytes), –5 – ruderal competitors (RC), –4 – epoecophytes, –3 – ephemerophytes, colonophytes, and hemiepoecophytes, –2 – adventive species (A), and –1 – introduced species or species that escaped cultivation (I). Positive scores represent increasing naturalness: 1 – weeds (W), 2 – disturbance tolerants (DT), 3 – natural pioneers (NP), 4 – stress–tolerant generalists (G), 5 – intermediate stress tolerants (ST), 6 – competitors (C), and 7 – stress–tolerant specialists (S). The value 8 indicates species from the high–naturalness part of the scale that additionally received a conservation bonus

In the negative part of the scale, introduced or cultivated escape species (I; score –1) accounted for 112 species (5.26%), adventive species (A; score –2) for 76 species (3.57%), ephemerophytes, colonophytes, and hemiepoecophytes (score –3) for 47 species (2.21%), epoecophytes (score –4) for 110 species (5.16%), and the most strongly transformed alien–related categories, i.e. aggressive alien competitors (AC) and agriophytes (score –6), for 70 species (3.29%). The score distribution indicates that the regional flora was dominated by species assigned to the more natural segments of the modified Borhidi–like scale, particularly taxa with conservation significance (score 8), while synanthropic, ruderal, and alien–related categories formed a substantial but clearly smaller fraction of the flora.

The RLQ coordinates of environmental variables and Borhidi–like naturalness trait states indicate that the response of plant communities to environmental gradients was not organised as a single coherent gradient of naturalness (Table 2). Instead, the ordination revealed a complex, multidimensional structure in which different naturalness–related trait states were associated with distinct RLQ axes and, therefore, with distinct combinations of environmental factors. The first RLQ axis was mainly associated with variation in light, salinity, moisture–related, and climatic components. Positive values were observed for Lc, Sl, fH, Kn, and the climatic composite variable, whereas negative values were associated with Nt, Hd, Om, Ae, and the edaphic composite variable. However, the Borhidi–like trait states did not form a simple monotonic sequence along this axis. Several negative or anthropogenic categories, such as adventive species (–2) and introduced plants or plants that escaped cultivation (–1), had high positive coordinates, but high–naturalness categories such as intermediate stress-tolerant species (5) and stress–tolerant specialists (7) were also strongly positive. Conversely, disturbance tolerant species (2), competitors (6), and conservation–bonus high–naturalness species (8) were positioned on the negative side. Thus, RLQ1 separated contrasting ecological and functional responses, but not a continuous transition from low to high naturalness.

Table 2
RLQ coordinates of environmental factors and Borhidi-like naturalness trait states along the first ten RLQ axes

Block	Variable	RLQ1	RLQ2	RLQ3	RLQ4	RLQ5	RLQ6	RLQ7	RLQ8	RLQ9	RLQ10
Environ-mental factor	Hd	–0.31	0.06	0.02	–	–0.12	–0.18	0.20	0.09	0.28	0.06
	fH	0.31	–0.18	0.20	0.14	–0.49	0.17	–0.04	0.25	0.09	–0.44
	Rc	0.23	–0.08	0.03	–0.41	0.07	–0.63	–	0.29	–0.47	–0.04
	Sl	0.34	–0.08	–0.08	0.08	–0.26	–0.20	–0.15	–0.37	0.30	0.04
	Ca	0.12	0.12	–0.40	–0.19	0.25	0.02	–0.15	–0.20	0.19	0.23
	Nt	–0.33	–0.16	0.03	0.07	–0.36	–	–0.44	–0.06	–0.23	0.45
	Ae	–0.27	0.10	0.03	0.07	0.06	–0.27	0.50	–	0.19	–0.12
	Tm	0.10	0.04	0.61	0.13	0.05	0.11	0.27	0.06	–0.08	0.41
	Om	–0.27	–0.03	–0.16	0.13	0.28	0.08	–0.28	0.52	0.21	–0.14
	Kn	0.26	0.10	–	–0.13	0.13	0.17	0.20	–0.30	–	0.02
	Cr	–0.06	–0.15	0.37	0.30	0.33	–0.41	–0.38	–0.32	0.08	–0.20
	Lc	0.37	–0.03	–0.10	–0.13	–0.09	–0.10	–0.08	0.31	0.36	0.24
	Edaphic niche breadth	–0.17	–	–0.05	–	–0.34	–0.41	0.12	–0.03	0.33	0.10
	Climatic niche breadth	0.25	–	0.27	0.08	0.34	–0.03	–0.12	0.22	0.33	0.19
	Competitive component (C)	–0.15	–0.20	0.21	–0.49	0.04	0.13	–0.10	–0.17	0.16	–0.33
	Stress-tolerant component (S)	0.04	0.55	0.04	0.09	–0.12	–0.08	–0.13	0.04	–0.05	0.04
	Ruderal component (R)	0.08	–0.45	–0.20	0.28	0.10	–	0.22	0.08	–0.07	0.21
	Competitiveness vs stress tolerance–ruderal contrast	–0.17	–0.22	0.25	–0.50	–0.04	0.13	–	0.03	0.20	0.23
	Stress tolerance vs ruderality contrast	–0.03	0.52	0.16	–0.10	–0.08	0.02	–0.17	0.09	0.04	–
Trait	–6 – AC / agriophytes	0.89	–0.44	1.57	0.36	–0.21	0.54	0.41	0.04	–0.13	–0.22
	–5 – ruderal competitors	0.58	–0.77	–0.30	–0.21	0.97	–2.45	1.96	1.17	2.85	2.55
	–4 – epoecophytes	–	–0.82	0.49	0.20	1.08	–1.90	–3.99	2.76	–1.22	–1.17
	–3 – ephemerophytes / colonophytes / hemiephemerophytes	0.90	–0.91	0.12	–0.37	0.67	–1.02	–2.12	1.45	1.67	–0.74
	–2 – adventive species	1.89	–1.26	–0.20	–1.53	1.38	–1.63	–1.56	–3.10	2.55	–
	–1 – introduced species or plants that escaped from cultivation	1.79	0.15	–0.51	–0.89	2.42	0.33	–0.84	–1.53	–4.36	4.52
	1 – weeds	0.24	–0.67	–1.13	–0.80	–1.45	0.69	–0.39	–0.05	–0.03	–
	2 – disturbance tolerants	–1.31	–0.62	–0.18	1.27	–0.07	–0.45	0.04	–0.73	–0.27	0.26
	3 – natural pioneers	0.87	–0.74	–2.00	0.99	1.39	0.98	1.35	2.57	0.18	0.30
	4 – stress–tolerant generalists	0.68	1.85	–0.25	–	–1.16	–1.88	0.64	0.20	–0.59	–0.32
	5 – intermediate stress tolerants	1.89	2.03	–1.55	–0.47	2.58	0.90	0.18	–1.79	–3.26	0.56
	6 – competitors	–1.07	–	0.02	–1.61	1.24	–	0.99	–0.11	–0.38	–1.42
	7 – stress–tolerant specialists	2.20	2.51	–2.42	3.70	1.92	1.70	–1.01	–1.94	1.63	–3.24
	8 – high–naturalness species	–0.90	1.55	0.49	–0.34	0.16	0.97	–0.79	0.35	0.97	0.95

The second RLQ axis showed the clearest association with CSR composition. It was positively related to the mean proportion of stress–tolerant species (S) and to the contrast between stress–tolerant species (S) and ruderals (R), while being negatively related to the mean proportion of ruderals (R). This indicates a contrast between stress–tolerant and ruderal components of community structure. This axis was also the one on which several naturalness–related categories behaved in a more intuitively ordered way: Stress–tolerant generalists (4), intermediate stress–tolerant species (5), stress–tolerant specialists (7), and conservation–bonus high–naturalness species (8) had positive coordinates, whereas ruderal and alien–related categories such as ruderal competitors (–5), epoecophytes (–4), adventive species (–2), weeds (1), and disturbance tolerants (2) had negative coordinates. Nevertheless, even here the pattern was not fully linear. For example, introduced plants or plants that escaped cultivation (–1) were close to the positive side, while competitors (6) were near zero. This suggests that RLQ2 partly reflected a stress–tolerance versus ruderalization gradient, but it did not fully represent a naturalness gradient. Higher RLQ axes further emphasised the independent behaviour of individual naturalness–related trait states. For example, RLQ3 contrasted high positive coordinates of aggressive alien competitors/agriophytes (–6) with strongly negative coordinates of natural pioneers (3), intermediate stress tolerants (5), and stress–tolerant specialists (7). RLQ4 was strongly positive for stress–tolerant specialists (7) and disturbance tolerants (2), but negative for competitors (6) and adventive species (–2). RLQ5, RLQ6, RLQ7, and subsequent axes also showed high coordinate values for particular categories rather than a stable ordering across the whole naturalness scale. This indicates that the Borhidi–like categories acted as partially independent functional states, each responding to different combinations of environmental conditions and community composition. Overall, the RLQ results show that trait states associated with naturalness at the species level did not behave as markers of a single integrated community–level naturalness gradient. Although some axes captured interpretable contrasts, particularly the opposition between stress–tolerant species (S) and ruderals (R) on RLQ2, the full pattern was multidimensional. Categories that are expected to represent increasing naturalness at the species level were not consistently ordered across the RLQ space. Instead, they formed distinct response groups, suggesting that community–level naturalness emerges from multiple independent ecological processes rather than a single universal gradient. The Borhidi–like naturalness categories can be informative descriptors of species–level ecological status, but their expression at the community level depends strongly on the environmental context and on the particular functional pathway through which community composition changes.

Importantly, only two RLQ axes showed a statistically significant nominal association with the ordered naturalness gradient. RLQ2 had the most robust relationship with the numerical order of Borhidi-like naturalness groups (Spearman's ρ – 0.71, P – 0.005, BH-adjusted P – 0.048), whereas RLQ6 showed a weaker nominal correlation (ρ – 0.60, P – 0.022) that did not remain significant after Benjamini–Hochberg correction (BH-adjusted P – 0.110). All other RLQ axes were not significantly associated with the naturalness order. This result indicates that the community-level expression of naturalness was restricted to a limited part of the RLQ space and did not form a dominant, integrated gradient across the whole ordination structure.

The configuration of the extreme naturalness states in the RLQ space made it possible to identify a general naturalness gradient (Fig. 4). In particular, the most transformed alien and ruderal groups were positioned towards one end of the trajectory. By contrast, high-naturalness and conservation-related groups tended to occur towards the opposite end. This pattern indicates that the RLQ ordination retained a meaningful ecological signal associated with naturalness.

At the same time, the arrangement of the canonical Borhidi-like groups along this trajectory did not fully follow the expected ordinal sequence. Several intermediate and positive naturalness groups deviated from the smoothed curve or occupied positions that were not strictly consecutive along the gradient. Therefore, the inferred RLQ naturalness trajectory should be interpreted as a broad community-level tendency rather than as a direct reproduction of the species-level Borhidi-like scale. This result supports the view that naturalness-related trait states can help identify the main direction of community response. Still, their behaviour at the community level remains multidimensional and partly independent of one another.

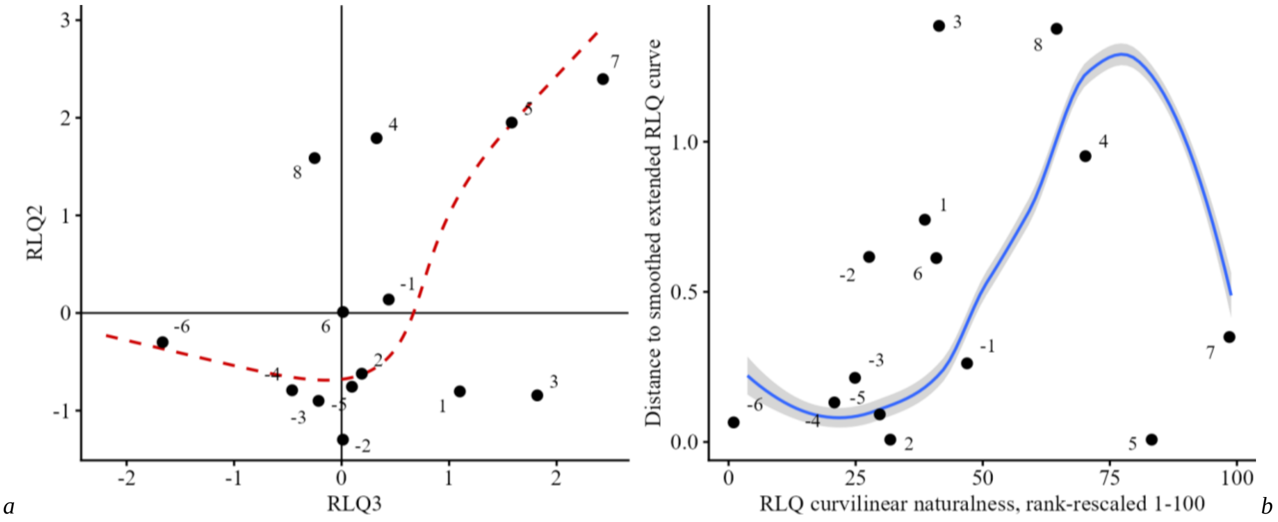


Fig. 4. Curvilinear arrangement of Borhidi–like naturalness groups in RLQ space and their deviation from the fitted naturalness curve: a) the labelled points represent Borhidi–like naturalness groups positioned in the RLQ ordination space, and the dashed red line shows the smoothed extended curvilinear naturalness trajectory; b) the same groups are plotted according to their position along the rank–rescaled RLQ curvilinear naturalness gradient (1–100) and their distance to the fitted curve, illustrating how closely each group follows the inferred community–level naturalness trajectory. Group labels are as follows: –6 – aggressive alien competitors/agriophytes, –5 – ruderal competitors, –4 – epoecophytes, –3 – ephemerophytes, colonophytes, and hemiepoecophytes, –2 – adventive species, –1 – introduced species or species that escaped cultivation, 1 – weeds, 2 – disturbance tolerants, 3 – natural pioneers, 4 – stress–tolerant generalists, 5 – intermediate stress tolerants, 6 – competitors, 7 – stress–tolerant specialists, and 8 – high–naturalness species with an additional conservation bonus

The first three principal components summarised complementary dimensions of conservation status. PC1 represented a general conservation trend, as all red-list variables had positive loadings on this component (Table 3). The strongest contributions were associated with the *Ukrainian Red Book*, the *European Red List*, the proposed regional rare-plant list for Zaporizhzhia Oblast, and Resolution 6 of the Bern Convention. Therefore, PC1 can be interpreted as an overall gradient of conservation significance shared by regional, national, European, and international sources. PC2 reflected a regional specificity component. It contrasted the two regional lists with the broader conservation sources: The proposed list for Zaporizhzhia Oblast and the official list for Dnipropetrovsk Oblast had negative loadings, whereas the *Ukrainian Red Book*, *IUCN Red List*, *European Red List*, and Bern Convention variables had positive or near-positive loadings. This indicates that PC2 captured differences between region-specific conservation assessments and broader-scale conservation frameworks. PC3 was mainly associated with the global conservation context. The *IUCN Red List* had the strongest positive loading on this component, followed by Resolution 6 of the Bern Convention, whereas the *European Red List* had a negative loading. Thus, PC3 primarily distinguished species emphasised by global or international conservation criteria from those more strongly represented in European-scale assessments.

Table 3
Principal component loadings of red-list conservation variables

Red–list variable	PC1, 25.32%	PC2, 19.74%	PC3, 17.20%
Official list of regionally rare plants in Zaporizhzhia Oblast, proposal	0.46	–0.48	0.10
Official list of regionally rare plants in Dnipropetrovsk Oblast	0.17	–0.74	0.20
Ukrainian Red Book	0.54	0.27	–0.24
European Red List	0.51	0.07	–0.44
IUCN Red List	0.20	0.26	0.78
Resolution 6 of the Bern Convention	0.40	0.28	0.31

Alternative nominal markers of naturalness (alien status and inclusion in red lists) were used to define the poles of the gradient rather than as direct predictors of species naturalness. This approach avoids circular reasoning: Status variables establish the extreme reference points but do not explain species positions between them. To test whether independent functional traits can serve as a linking mechanism between these poles, a generalised additive model (GAM) was constructed in which species positions along the RLQ-derived naturalness gradient were predicted using CSR strategies and ecological niche breadth measures. The model included the CSR components (C, S, R), the log-ratio CSR (S vs R), and the mean climatic and edaphic niche breadths. Interactions between competitive, stress-tolerant, and ruderal strategies with climatic and edaphic breadth were also incorporated. Importantly, status variables (alien categories and conservation status) were deliberately excluded from the model.

The GAM results demonstrate that functional predictors are indeed related to the RLQ-derived naturalness gradient. The strongest non-linear effect was associated with stress tolerance (S), which showed a clear positive relationship with increasing naturalness (Fig. 5). Competitive strategy (C) and climatic niche breadth also had significant effects, with the latter showing a predominantly negative association. By contrast, ruderal strategy (R), the CSR balance, and edaphic niche breadth did not exhibit significant smooth effects in this model. The model explained 25.7% of deviance and showed a moderate correspondence between predicted values and the RLQ-derived gradient (Pearson's r – 0.507; Spearman's ρ – 0.495; MAE – 20.0 on a 1–100 scale). Thus, the regression is informative but not exhaustive. This indicates that CSR strategies and ecological breadth do not fully determine species naturalness, but rather define a functional predisposition or probability structure. On the one hand, this represents a limitation: Species positions along the naturalness gradient cannot be fully reconstructed from CSR strategies and niche breadth alone. On the other hand, it is an important positive result. Functional strategy does not determine the outcome. High stress tolerance may increase the likelihood of conservation relevance, but does not guarantee Red List inclusion. Similarly, ruderal strategies or broad ecological amplitudes may increase the likelihood of synanthropic behaviour, but do not inevitably lead to weediness or alien status. In summary, functional traits confirm the existence of a meaningful ecological linkage between the two nominal poles, but do not fully account for the naturalness gradient. Therefore, for practical indication purposes, it is appropriate to use a synthetic index that combines functional information with nominal markers of alien status and conservation value. Such an index should not be interpreted as an absolute measure of "true" naturalness, but rather as an operational, calibrated indicator of species position along the naturalness gradient.

An elastic net regression model was fitted using the projections of species onto the most probable RLQ trajectory of naturalness as the response variable for modelling the community-level naturalness gradient (Fig. 6). This projected position was interpreted as a hypothetical ideal naturalness gradient, derived from the curvilinear arrangement of Borhidi-like naturalness states in the RLQ space. The model included CSR components, ecological breadth indices, alien and synanthropic status variables, and synthetic red-list components as predictors, because these species properties were expected to be the most probable determinants of naturalness. The model was calibrated using 968 training species. Cross-validation showed a clear minimum in prediction error at low to moderate regularisation strength, followed by a rapid increase in error at stronger penalisation. This indicates that excessive shrinkage removed informative predictors and reduced model performance. The selected model retained a limited set of predictors with non-zero coefficients. Model performance was high. The predicted values strongly correlated with the RLQ-calibrated naturalness gradient (Spearman ρ – 0.82; Pearson r – 0.82), with RMSE – 16.8 and MAE – 14.1. The association remained strong after rank rescaling (Spearman ρ – 0.82; Pearson r – 0.82), with RMSE – 17.1 and MAE – 12.4. The model captured the main structure of the RLQ-derived naturalness gradient while retaining interpretable ecological and conservation-related predictors.

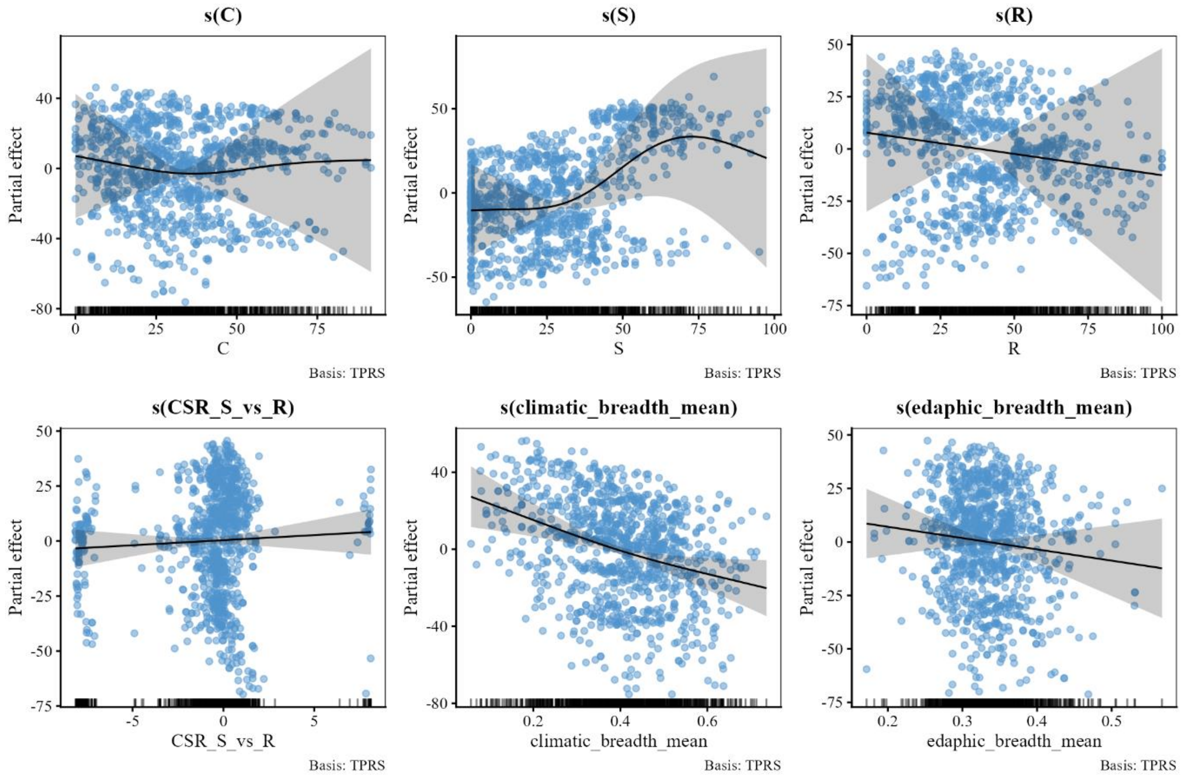


Fig. 5. Partial effects of functional predictors on the RLQ-derived naturalness gradient: smooth terms were estimated using a generalised additive model with a Gaussian error distribution and REML smoothing parameter selection; the response variable was the RLQ-derived naturalness score, rank-rescaled to a 1–100 scale; solid black curves show fitted partial effects; grey bands indicate approximate 95% confidence intervals; points are partial residuals; rug marks show the distribution of predictor values; the strongest non-linear effect was associated with stress tolerance, S (edf – 3.75, P < 0.001), followed by competitive strategy, C (edf – 2.82, P – 0.016), and climatic niche breadth (edf – 1.82, P – 0.003); ruderal strategy, CSR S-vs-R balance, and edaphic niche breadth did not show significant smooth effects; the model explained 25.7% of deviance and showed a moderate correspondence with the RLQ-derived gradient (r – 0.51; Spearman's ρ – 0.49; MAE – 20.0; n – 96)

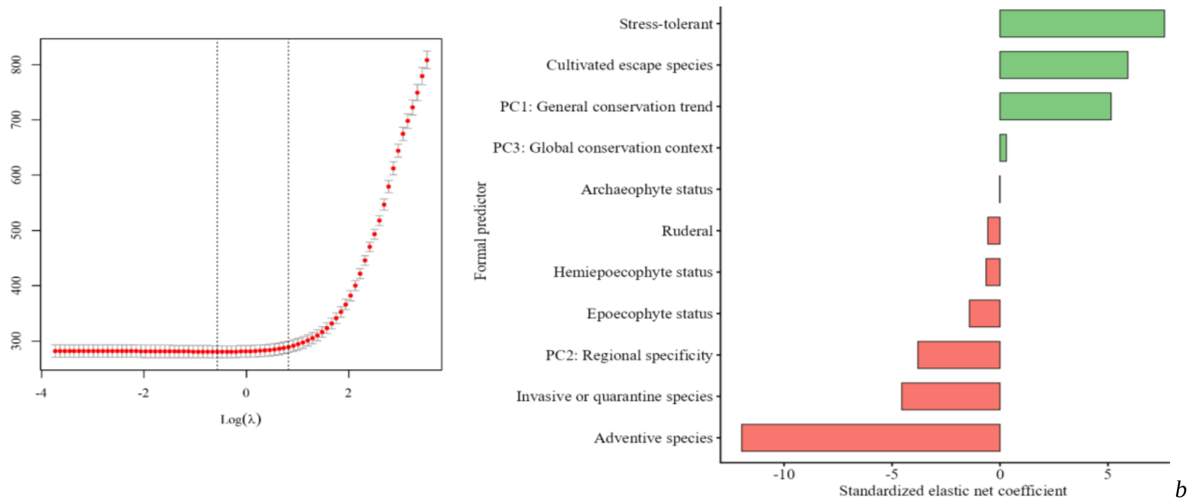


Fig. 6. Elastic net model performance and relative importance of ecological and conservation predictors: *a* – cross-validated mean squared error across the regularisation path; *b* – the standardised coefficients of predictors, indicating their direction and strength of association with the response variable

The strongest positive coefficients were associated with the stress-tolerant component, plants that escaped cultivation, and the general conservation trend. A weaker positive contribution was also observed for the global conservation context. By contrast, the strongest negative coefficient was associated with adventive species, followed by invasive or quarantine species, regional conservation specificity, and several alien-status categories, including epoecophytes and hemiepoecophytes.

The boxplot generally confirms the relevance of the proposed modelling approach, because the predicted naturalness scores broadly follow the expected ordering of the initial Borhidi-like categories (Fig. 7). Negative categories tend to have lower predicted values, while higher positive categories are usually associated with higher scores on the 1–100 naturalness scale. At the same time, several important deviations from the expected sequence are evident. Species of category 5 tend to occur under relatively more natural conditions than expected, indicating that this strategy cannot be interpreted unambiguously as a marker of exclusively unnatural or disturbed habitats. For categories 1 and 2, the Borhidi–like classification appears less adequate, as these groups show considerable internal variation and overlap in predicted naturalness. Category –1, in particular, demonstrates a wide range of naturalness values, suggesting that introduced plants or plants that escaped cultivation may occur across very different ecological contexts. Conversely, species of category 6 often occur under relatively unnatural conditions, despite their positive position in the initial scale. Therefore, competitors cannot be treated as unequivocal indicators of high naturalness. Overall, the figure shows that the initial Borhidi–like categories retain a meaningful general trend, but several categories behave context–dependently and do not function as strict markers of community–level naturalness.

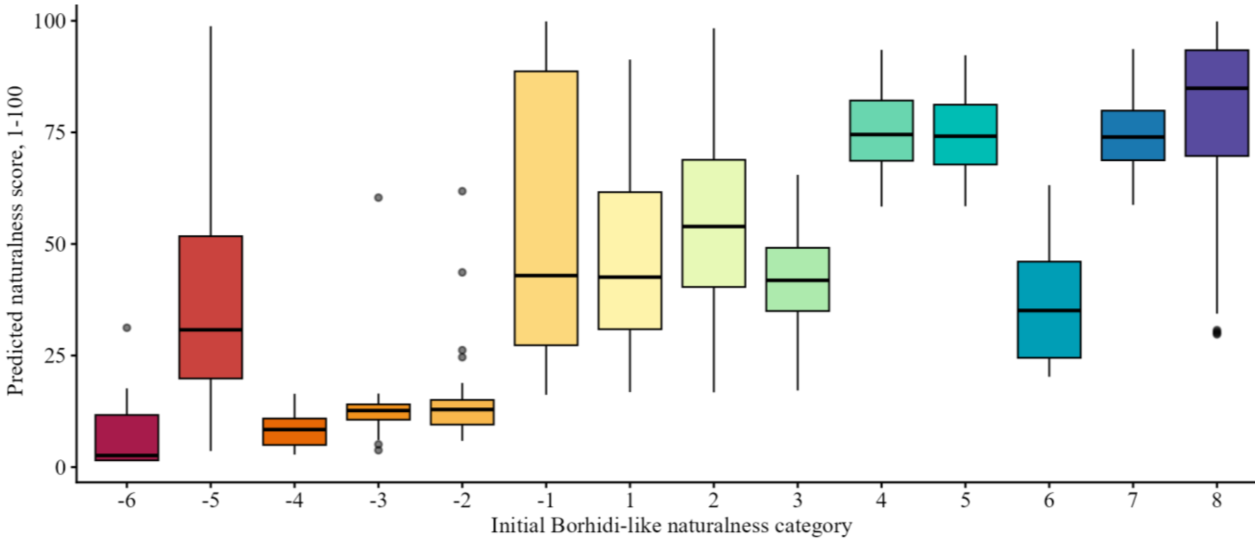


Fig. 7. Distribution of predicted naturalness scores (1–100 scale) across initial Borhidi-like naturalness categories: the x-axis represents the initial Borhidi-like naturalness categories treated as a categorical variable; at the same time, the y-axis shows the predicted naturalness scores on a 1–100 scale derived from the RLQ-based model; boxplots illustrate the median, interquartile range, and variability within each category: –6 – aggressive alien competitors/agriophytes, –5 – ruderal competitors, –4 – epoecophytes, –3 – ephemerophytes, colonophytes, and hemiepoecophytes, –2 – adventive species, –1 – introduced species or species that escaped cultivation, 1 – weeds, 2 – disturbance tolerants, 3 – natural pioneers, 4 – stress–tolerant generalists, 5 – intermediate stress tolerants, 6 – competitors, 7 – stress–tolerant specialists, and 8 – high–naturalness species with an additional conservation bonus

The distribution of species naturalness scores differed systematically across Red List categories and data sources (Fig. 8). In most cases, categories associated with higher conservation concern were shifted towards higher values on the naturalness gradient. However, the degree of separation varied among the lists. In the regional lists (e.g., *Dnipropetrovsk Oblast Red List*), categories such as Dissapearing and Extinct tended to occupy the upper part of the naturalness gradient, whereas Insufficiently Studied and Rare species showed broader and more overlapping distributions. This indicates that regional conservation categories partly reflect variation along the naturalness gradient, but with substantial within-category heterogeneity. In the *Ukrainian Red Book*, categories such as Endangered and Rare were generally associated with relatively high naturalness scores, although their distributions still overlapped considerably. The category Data Deficient showed a wide spread across the gradient, suggesting that insufficient knowledge does not correspond to a consistent position in ecological space. The *European Red List* and IUCN categories showed clearer structuring, with Vulnerable, Endangered, and Near Threatened species tending to occupy intermediate to high portions of the gradient. However, the separation between categories remained incomplete, and some lower-concern categories extended into high naturalness values. This pattern reflects the fact that conservation status is influenced not only by ecological characteristics but also by population trends, geographic range, and external pressures. Across all lists, the distributions were continuous and strongly overlapping. Even categories representing the highest conservation concern did not form isolated clusters but rather corresponded to the upper tail of a broader gradient. Conversely, categories associated with lower conservation concern or uncertain status frequently spanned a wide range of naturalness values. These results indicate that Red List categories align with the RLQ-derived naturalness gradient but do not partition it into clearly distinct classes. Instead, they represent probabilistic segments of a continuous ecological gradient, with substantial within-category variability.

Discussion

The development of a naturalness scale is particularly relevant for regions where vegetation is shaped by a combination of natural gradients, long-term anthropogenic transformation, and acute disturbance events (Brackhane et al., 2021). The steppe zone of Ukraine represents such a system, where natural, semi-natural, and strongly transformed communities coexist within a relatively narrow geographical space (Borovyk et al., 2024; Buzhdygan et al., 2026). The region is characterised by a high level of urbanisation and industrial transformation, a large proportion of ploughed land, extensive infrastructure development, and a high degree of river flow regulation (Buzhdygan et al., 2025; Langraf et al., 2025). These factors are associated with habitat fragmentation, soil degradation, altered hydrological regimes, salinisation, synanthropisation of vegetation, and the spread of alien and ruderal species (Kunakh et al., 2023; Zelenova et al., 2024). Additional pressure is caused by changes in fire regimes, degradation of steppe remnants, transformation of river valleys, and the loss of connectivity between natural habitats (Olexander Zhukov et al., 2022; Nykytiuk et al., 2025). In recent years, a significant additional driver of ecosystem change has been the impact of military disturbance associated with the ongoing armed aggression of Russian occupying forces (Didukh et al., 2024; Tutova et al., 2026), including direct habitat destruction, fires, pollution, soil disturbance, infrastructure damage, and the disruption of protected and semi-natural areas (Didukh et al., 2024; Kuzemko et al., 2026). Under these conditions, the assessment of naturalness becomes not only a descriptive task but a necessary analytical tool for distinguishing different states of vegetation organisation, identifying trajectories of transformation, and interpreting relationships between community composition and environmental gradients (Lisovets et al., 2025; Tutova et al., 2025). Existing approaches, often based on coarse categorical classifications or regionally generalised indices, provide limited resolution for such analyses (Chetvertak et al., 2025; Nykytiuk & Kravchenko, 2025). Therefore, there is a need for a quantitative, reproducible scale that reflects variation in plant communities and operates at the level of community structure rather than solely at the level of individual species.

Ecological niche breadth emerges as a key functional predictor of species naturalness (Tutova et al., 2025). This finding aligns with both theoretical concepts of plant community organisation and the empirical results obtained in this study. Traditionally, naturalness is associated with climax or quasi-climax communities, which are characterised by relatively stable environmental conditions and a dominant role of interspecific competition. In such systems, species success largely depends on their ability to occupy narrow ecological niches and to compete effectively within a limited range of environmental conditions. In this context, stenotopy can be considered a functional marker of naturalness. Species with narrow ecological amplitudes are typically associated with stable and specific environmental conditions characteristic of minimally disturbed ecosystems. Their presence in communities reflects not only current environmental conditions but also the historical development of the system and the degree of preservation of ecological processes. By contrast, species with broad ecological amplitudes are characterised by high tolerance to environmental variability and the ability to persist across a wide range of conditions, including those transformed by anthropogenic activity. Ecological strategies oriented towards rapid spread and colonisation rely precisely on such tolerance and plasticity. Ruderal and invasive species efficiently exploit disturbances, rapidly occupy available niches, and persist under highly variable environmental conditions. In this case, eurytopy represents not only a measure of ecological amplitude but also a functional trait associated with anthropogenic transformation of environments. Thus, ecological niche breadth can be interpreted as one of the fundamental functional dimensions of naturalness, reflecting the balance between specialisation and tolerance to environmental change. However, its indicative value is realised only in combination with other characteristics, such as CSR strategies, synanthropic status, and the history of anthropogenic impact, which together shape the complex structure of naturalness at the level of plant communities.

Range-based phytoindication scales developed by Didukh were utilised to assess ecological niche breadth as an alternative to direct expert classification. These scales account for both a species' position along an environmental gradient and the breadth of its tolerance to a given factor. However, they do not represent purely instrumental measurements of niche breadth, as they are based on expert synthesis of phytocoenotic and ecological data. Their advantage lies in the extensive empirical validation they have undergone in subsequent studies, making them one of the most suitable tools for the quantitative characterisation of ecological amplitude in the flora of Ukraine. Nevertheless, the regional context remains critically important. Ecological amplitude is not an entirely fixed species trait; it may vary depending on the climatic, edaphic, coenotic, and historical–floristic conditions of a given region. Therefore, applying nationwide phytoindication scales to a specific regional flora requires validation against local data. Such verification enables more reliable estimates of species' ecological plasticity and provides a more accurate interpretation of their position within the system of naturalness indicator values. The use of transparent, reproducible sources for assessing CSR strategies significantly enhances the methodological rigour of naturalness scales. In this study, results from a global synthesis of CSR strategies based on plant morphological and functional traits were employed. This approach offers a notable advantage in that it minimises the reliance on subjective expert judgement and permits species' positions within CSR space to be treated as quantitatively defined characteristics. However, this procedure also has certain limitations. Grime's original concept encompasses a broader range of traits and ecological criteria, including growth patterns, competitive ability, stress tolerance, responses to disturbance, and reproductive strategies. Consequently, assessing CSR strategies solely based on morphological traits does not fully capture the conceptual breadth of this framework. In addition, substantial gaps persist in trait data for regional floras, complicating the precise estimation of species' positions within CSR space. Consequently, the CSR values employed in this study should be regarded as reproducible and methodologically transparent approximations of plant ecological strategies, rather than definitive representations of their coenotic behaviour.

Information on the conservation status of species is also heterogeneous. The *Dnipropetrovsk Oblast Red List* provides detailed and differentiated information on plant species requiring protection, including their status and degree of threat. By contrast, the current official *Zaporizhzhia Oblast Red List* is methodologically limited and does not offer sufficient resolution for quantitative analysis. Therefore, this study relied on a recommended list of rare plant species for Zaporizhzhia Oblast, which is more suitable for analytical purposes but also requires further refinement and validation. Given the heterogeneity of regional data sources, an operational simplification was applied to harmonise conservation-related information. Species shared between the floras of the Dnipropetrovsk and Zaporizhzhia oblasts were considered to have comparable conservation status within the regional steppe context. Species unique to Zaporizhzhia Oblast and included in the recommended list were interpreted as having the highest level of regional conservation importance. This approach allowed the Zaporizhzhia component of the flora to be incorporated into the integrated assessment. However, it should be regarded as a provisional methodological assumption. Further refinement of this component requires more comprehensive, differentiated, and officially validated information on the conservation status of species in Zaporizhzhia Oblast.

Information on the adventive and invasive status of species is relatively more reproducible than assessments of their conservation status (Blackburn et al., 2011). This is largely because anthropogenically transformed environments often undergo ecological homogenisation, leading to adventive, ruderal, and invasive species exhibiting similar ecological profiles across regions (Smart et al., 2006). Such species are typically associated with disturbed, urban, agricultural, or technogenic habitats and are characterised by broad ecological amplitude and high dispersal ability (McKinney, 2006). An additional advantage is that many harmful, invasive, or widespread adventive species occur in high abundance and have broad distributions. This provides a substantially larger pool of observations than is available for rare or localized species of conservation concern. Consequently, data on their frequency, habitat affiliation, degree of naturalisation, and ability to infiltrate natural communities are statistically more robust and better suited to formalised analysis. The integration of these data sources enabled the reconstruction of a naturalness scale consistent with Borhidi's general conceptual framework, but founded on more formalised and reproducible criteria. The resulting spectrum of categories provides valuable information for assessing the overall naturalness of the regional flora. Its structure reflects the combination of three principal components: a substantial proportion of ruderal competitors, indicating anthropogenic transformation; disturbance tolerants, representing a broad transitional segment between natural and disturbed habitats; and species belonging to the high-naturalness end of the scale, which additionally received a conservation bonus and constitute the conservation-relevant core of the flora. Consequently, the regional flora is not homogeneous in terms of naturalness. It comprises a pronounced synanthropic–ruderal component, a broad group of disturbance tolerants, and simultaneously a significant fraction of species with high natural and conservation value. This distribution reflects the mosaic character of steppe-region floras, where natural and semi-natural habitats coexist with urban, agricultural, and technogenically transformed environments.

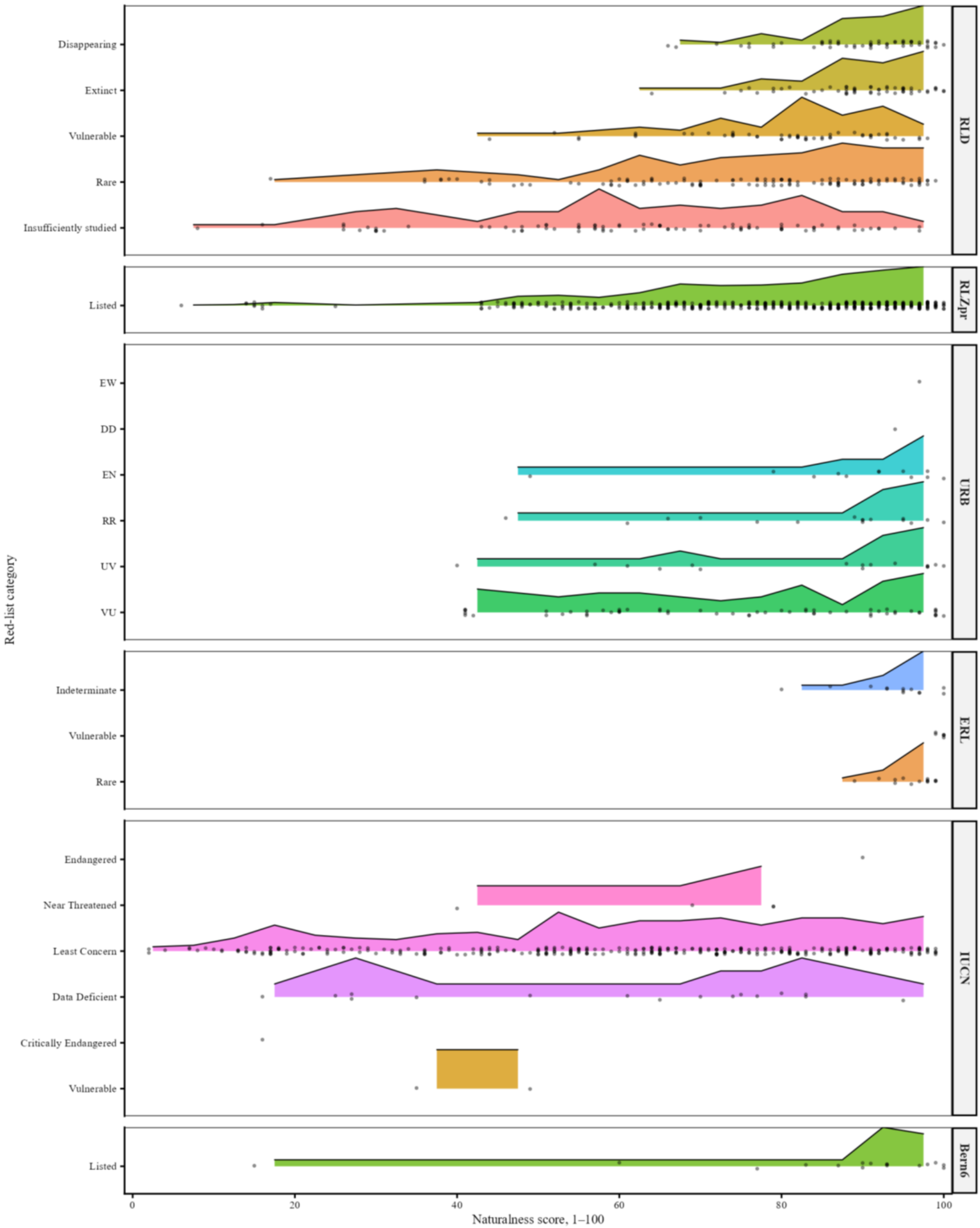


Fig. 8. Distribution of species naturalness scores across Red List categories from different sources: ridgeline histograms show the distribution of predicted naturalness scores (1–100) for species belonging to different conservation status categories; within each category, histogram heights are normalised to the local maximum to allow comparison of distribution shapes irrespective of sample size; black points represent individual species; panels correspond to different Red List sources: RLD – *Dnipropetrovsk Oblast Red List*; RLZpr – *Zaporizhzhia Oblast Red List*; URB – *Ukrainian Red Book*; ERL – *European Red List*; IUCN – *International Union for Conservation of Nature Red List*; Bern6 – Resolution 6 of the Bern Convention; category abbreviations: CR – Critically Endangered; EN – Endangered; VU – Vulnerable; NT – Near Threatened; LC – Least Concern; DD – Data Deficient; EW – Extinct in the Wild; RR – Rare; UV – Unvalued (insufficiently evaluated); Listed – species included in the corresponding list without further categorization

RLQ analysis enabled the examination of species traits that Borhidi's system identifies as indicators of naturalness, from a neutral ordination perspective. In this approach, these traits were analysed not as predefined assessments of naturalness or degradation, but as discrete, quantitative characteristics associated with community structure and environmental gradients. The results demonstrated their significant relevance: Borhidi-like categories, CSR components, and measures of ecological amplitude provided a meaningful interpretation of the principal gradients that structure vegetation. In the steppe zone, the dominant influence of the moisture gradient is expected and is most clearly represented by RLQ1 in our analysis. Along this gradient, increasing moisture correlates with an expansion in edaphic niche breadth—that is, a wider range of soil-related conditions occupied by communities—while climatic niche breadth decreases. This suggests that under more humid conditions, species can exploit a broader range of edaphic environments, whereas their climatic tolerance becomes more constrained. This pattern aligns with the spatial heterogeneity of steppe ecosystems, where water availability is a key driver of species distribution and determines the accessibility of different edaphic microhabitats. The competitive component (C) exhibits a pronounced response along this gradient, whereas other CSR components do not show a comparable pattern. This indicates that increased moisture primarily enhances the role of competitive strategies, likely due to higher productivity, greater vegetation density, and greater importance of interspecific competition. By contrast, stress-tolerant and ruderal components are not major drivers along RLQ1, emphasising the specific link between competitiveness and the moisture gradient. Conversely, decreasing moisture is associated with an increasing contribution of agriophytes and adventive species. This can be interpreted as a strengthening of the synanthropic and adventive component under more xeric or environmentally constrained conditions, where disturbance, openness of vegetation cover, and instability of resource availability create opportunities for the establishment of alien and naturalised species. Thus, RLQ1 integrates the natural moisture gradient characteristic of steppe ecosystems with a functional reorganisation of communities, in which competitive strategies are reinforced under more humid conditions. Meanwhile, the adventive–agriophytic component becomes more prominent under drier conditions.

The second RLQ axis (RLQ2) represents another significant dimension of vegetation structure, associated with the balance between stress-tolerant and ruderal components. In contrast to RLQ1, this axis has a more direct functional interpretation and aligns closely with the fundamental principles of CSR strategies. Positive values of RLQ2 indicate an increasing contribution of the stress-tolerant component (S) and a greater S versus R contrast, whereas negative values indicate a growing importance of the ruderal component (R). Thus, RLQ2 can be interpreted as a gradient of 'stress tolerance versus ruderality.' Unlike the first axis, Borhidi-like categories exhibit their most consistent and interpretable patterns along RLQ2. Species associated with higher levels of naturalness (such as stress-tolerant generalists, intermediate stress-tolerant species, stress-tolerant specialists, and the group receiving a conservation bonus) are shifted towards the positive end of the axis. Meanwhile, ruderal competitors, epoecophytes, adventive species, weeds, and disturbance tolerants are concentrated on the negative side. This structure corresponds well with the expected contrast between stable, stress-driven environments and disturbed, ruderal conditions. Therefore, RLQ2 provides the closest approximation to a naturalness gradient in the classical sense. It reflects a transition from communities structured by stable environmental constraints, where stress-tolerant strategies dominate, to communities shaped by disturbance and rapid colonisation, where ruderal strategies prevail. At the same time, even along this axis, the ordering of categories is not strictly linear, indicating a context-dependent realisation of these patterns. RLQ2 thus confirms that naturalness is not a direct function of individual species or categories but emerges from the balance between functional strategies. Within this balance, the stress-tolerant component acts as an indicator of stability and ecological constraint, whereas the ruderal component reflects disturbance and environmental dynamism. It is this functional contrast that forms the most consistent and statistically supported dimension of naturalness at the community level. For all RLQ axes, species properties interpreted as markers of naturalness proved to be ecologically meaningful and provided a substantive interpretation of vegetation structure. These markers did not form a single linear gradient along any individual axis. Instead, their role was expressed within a multidimensional space, where different aspects of naturalness were associated with various combinations of environmental factors and functional strategies. In the context of an ordered gradient of naturalness, the most informative representation was the space defined by the combination of the RLQ2 and RLQ3 axes. It is within this two-dimensional space that a more consistent arrangement of categories related to different levels of naturalness can be observed, allowing them to be interpreted as components of a unified, albeit nonlinear, trajectory of change. This approach reflects the fact that naturalness is not a one-dimensional characteristic but rather emerges from the interaction of several independent ecological processes, including the balance between stress tolerance, ruderality, and other functional dimensions. The indicator properties of species embedded in the Borhidi system cannot be reduced to a single dominant gradient; yet they remain relevant as elements of a multidimensional structure. Their interpretation requires consideration of their relative positions within the ordination space, rather than projection onto individual axes alone, allowing a more adequate representation of the complex organisation of plant communities.

The monotonicity of changes in Borhidi's naturalness scores along the empirically derived gradient is not absolute. The polar states are most distinctly differentiated within the ordination space: on one end, groups associated with the highest degree of naturalness, and on the other, the most anthropogenically transformed categories. Importantly, these poles are largely defined by nominal species attributes. For the upper pole, this primarily concerns conservation status (that is, an anthropocentrically defined assessment of species rarity or threat level). For the lower pole, it relates to adventive, invasive, or synanthropic status, which is similarly assigned as an external categorical attribute of the species. In this context, the key methodological concept of the Borhidi approach is that CSR strategies can serve as a transitional bridge between these contrasting poles. Nominal statuses effectively capture the extreme states of the gradient. Still, their informational value diminishes considerably in the intermediate part of the continuum, where most species are neither rare, conservation-relevant taxa nor clearly adventive or invasive elements. It is precisely here that a linking component is required – one that relies not on external classification but on ecological behaviour, life strategy, and functional traits. The CSR approach fulfils this role, as it allows the position of a species between the poles of naturalness to be interpreted through the balance of competitiveness, stress tolerance, and rudeness. Unlike nominal statuses, the CSR strategy does not describe a species's formal status but rather its mode of existence within a community: its capacity to maintain positions in stable assemblages, tolerate environmental constraints, or exploit disturbance. Therefore, CSR components can provide functional continuity between the extreme categories of naturalness and explain transitional states that cannot be adequately described solely by species presence in red lists or within the adventive–invasive pool. The incomplete monotonicity of the Borhidi scale does not necessarily indicate a weakness; rather, it reflects the hybrid nature of naturalness: Its extreme poles are defined by nominal statuses, whereas the middle portion of the gradient requires functional interpretation through species life strategies. It is the integration of these two types of information (status-based and functional) that renders the naturalness scale ecologically meaningful.

The results of the regression analysis demonstrated that CSR strategies and measures of ecological niche breadth do not fully account for species' positions along the naturalness gradient. This suggests that naturalness cannot be reduced solely to functional species traits. Nevertheless, these variables serve an important role as a linking mechanism within the segment of the gradient where nominal markers lose their informativeness. In the central portion of the continuum, where species do not exhibit a clear conservation or adventive–invasive status, CSR components and ecological amplitude enable the characterisation of their position through life strategies and the degree of ecological plasticity. Thus, functional characteristics do not unambiguously determine naturalness, but they form an ecologically meaningful bridge between the extreme states of the gradient, ensuring its continuity and interpretability. These findings also indicate that a single set of biological traits does not determine a species' invasiveness or rarity. Rather, these statuses are shaped by multiple factors, including dispersal history, regional context, habitat structure, disturbance regimes, demographic processes, and stochastic events. At the same time, the species' ecological properties may influence the likelihood of acquiring such a status. For example, broad ecological amplitude, ruderality, and the capacity for rapid colonisation increase the probability of invasive behaviour. By contrast, stenotopy, stress tolerance, and association with stable habitats may be linked to a higher likelihood of rarity or conservation significance.

The comparison of Borhidi-like naturalness scores with those calibrated against responses from real communities revealed an incomplete correspondence. A general relationship between these estimates is maintained, confirming the conceptual validity of the original scale. However, some categories exhibit a much wider range of naturalness than expected given their initial position on the scale. This is particularly evident for ruderal competitors, which display a broad spectrum of naturalness values. This indicates that the ruderal–competitive strategy is not always an unambiguous marker of low naturalness at the community level. A similar pattern is observed for introduced species or species that escaped cultivation and weeds. These groups also show a wide range of naturalness, reflecting their context-dependent behaviour. Some of these species are associated with clearly transformed habitats, whereas others occur in semi-natural or transitional communities without a clear association with the lowest levels of naturalness. Special attention should be given to the competitor category. In the original Borhidi framework, competitive species are considered elements of more natural and stable communities. However, the results suggest that their role as indicators of high naturalness may be overestimated. Competitive ability can increase not only in natural communities but also in productive, eutrophicated, or secondarily transformed habitats. Therefore, competitiveness alone does not guarantee high naturalness. Additional analysis is also required to interpret species assigned a conservation bonus. Their high position on the scale reflects conservation importance but does not always coincide with their position along the community-level naturalness gradient. This further emphasises that conservation status and ecological naturalness are related, yet not identical, characteristics. Overall, the Borhidi-like scale reproduces the main gradient of naturalness, but its individual categories differ in their indicator reliability. The most problematic are groups with broad ecological realisation or those defined by status-based rather than functional criteria. Therefore, calibrating species values based on actual community responses is a necessary step to improve the synecological validity of the scale.

It should also be noted that the naturalness scale can serve as an independent ecological criterion for comparing species statuses across different red lists. As regional, national, and international lists are developed according to varying principles and levels of detail, their categories are not always directly comparable. Projecting these statuses onto a unified naturalness gradient enables an assessment of the extent to which different conservation classification systems align with species' ecological positions within vegetation. This approach does not replace conservation assessments per se. Still, it allows identifying inconsistencies among the lists, evaluating their ecological coherence, and detecting groups of species whose status requires further verification.

The proposed procedure for assessing naturalness scales is based on the assumption that the initial data on the ecological properties of plant species are sufficiently reliable. This assumption represents a methodological advance compared with Borhidi's original approach, which relied largely on expert-based classification. However, it should not be absolutised. The quality of the resulting naturalness scale depends directly on the accuracy, completeness, and regional relevance of the input data used to describe species ecology. A particularly important limitation concerns CSR strategy estimates. Although trait-based CSR assessment provides a more reproducible basis than purely expert judgement, further refinement is needed for regional floras. Species' ecological behaviour, realised niches, and functional roles may differ among regions; therefore, CSR estimates should be progressively calibrated and validated using regional floristic, coenotic, and trait data. Another limitation concerns the numerical resolution of the proposed indicator scale. The 1–100 range used in this study should be regarded as a first iteration in the search for a justified unit of measurement and an optimal number of scale gradations. A maximum of 100 gradations is relatively optimistic, because the empirical distinguishability of such fine divisions remains to be tested. At the same time, the number of gradations should probably exceed that used in existing coarse naturalness or hemeroby scales, because the proposed approach incorporates more detailed regional ecological information. This possibility of increasing scale resolution is directly related to regional calibration. Broad-scale indicator systems that cover large territories inevitably lose resolution because species' ecological behaviour is averaged across wide environmental and biogeographical contexts. By contrast, regionally calibrated scales can potentially provide finer differentiation of species positions along the naturalness gradient. Therefore, further research should focus on testing different levels of scale resolution, evaluating the stability of indicator values across datasets, and determining the number of gradations that is both statistically justified and ecologically interpretable.

Conclusion

The results obtained confirm that naturalness scales constructed in accordance with the Borhidi framework generally reflect the true gradient of naturalness and degradation of vegetation cover; however, their interpretation at the community level is not straightforward. The analysis demonstrated that naturalness categories, considered as discrete species traits, indeed exhibit non-random dynamics in community composition and are associated with the principal environmental gradients. At the same time, this dynamic is multidimensional and partly non-linear, with individual categories displaying context-dependent behaviour, which limits their direct use as unequivocal indicators. Thus, the validity of transferring species-level indicator values to the synecological level is partial: The Borhidi scale captures the general trend. Still, it does not ensure full correspondence between species-based assessments and community structure. The most reliable are the polar categories, whereas the middle section of the gradient requires additional functional interpretation through CSR strategies and ecological niche breadth. The approach proposed in this study, which combines Borhidi criteria with quantitative assessments of CSR strategies, ecological amplitude, synanthropic status, and conservation significance, and is validated against the response of real communities (using RLQ analysis and regression modelling), allows for the derivation of a more consistent and methodologically robust naturalness scale. Unlike purely expert-based evaluations, such a scale reflects not only the autecological properties of species but also their actual role in shaping the synecological gradient. Indicator values of naturalness can be regarded as an operational characteristic of a species only if calibrated at the community level. In this context, the proposed modified naturalness scale, which integrates the conceptual foundations of the Borhidi approach with empirical verification, can serve both as an indicator of vegetation naturalness and as a tool for comparative analysis of ecosystems with varying degrees of anthropogenic transformation.

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