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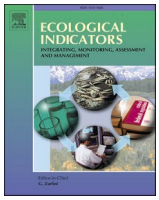

Self-sustainability status indicators of vegetation stands and types utilising Potential Natural Vegetation estimations

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ABSTRACT

Optimising conservation and restoration efforts calls for detailed assessment on the potential self-sustainability of vegetation types. We propose an indicator framework relying on matches and mismatches between predicted distributions of vegetation types and observed distributions. We examined the utility of all combinations of predicted and observed values, however, we introduced a five-rank scale to categorise predictions rather than simple presence/absence outputs. This yielded 10 possible indicator combinations, out of which nine was present in the dataset. We tested the indicators' applicability using countrywide observed vegetation data and potential natural vegetation estimates for Hungary. Indicators were subjected to Principal Component Analysis (PCA) to examine the interrelationships as well as mapped in space habitat-wise and as aggregated (synthetic) maps across vegetation types. Indicators were identified in relation to levels of unsuitability, uncertain presence, levels of potentiality, extinction debt and levels of self-sustainability in existing stands. Each indicator was found to correspond to an individual interpretation in terms of ecological insight (including potentiality and vegetation inertia), conservation and restoration optimisation. PCA results reinforced the finding with the first three components explaining 90% and 80% of the variation for the absolute count and relative count based indices respectively. Map representations proved to be informative on conservation and restoration priorities habitat-wise. Furthermore, our indices supported identification of conservation and restoration hotspots, as well as provided insights about the vulnerability of individual vegetation types. Identification of localities and spatial concentration of areas with predominantly self-sustaining or threatened vegetation has potential to support for conservation and restoration decisions.

1. Introduction

Natural and semi-natural vegetation is increasingly fragmented due to human land use, such as agriculture and urbanisation (Gonçalves-Souza et al., 2020; Lawrence et al., 2021). For the effective restoration and protection of the remaining stands, it is essential to know their survival chances at the specific location (Török et al., 2018; Sabatini et al., 2020). Conservation budgets are typically limited, thus optimising conservation efforts is central to conservation science (Reynolds and Hessburg, 2005; Hoffmann, 2022). Indicators reflecting survival chances, i.e. the self-sustainability of vegetation types, can become a decision support tool to optimise conservation effort. Self-sustaining stands are good candidates of protection in their contemporary state, while stands in an unstable situation can be supported in natural dynamics either passively (Prach et al., 2020; Ladouceur et al., 2023) or by active interventions (Chazdon et al., 2021; Hartup et al., 2022). Furthermore, restoration can benefit from indicators of potential presence even in the absence of the target habitats (Török et al., 2018).

Ecological phenomena connected to self-sustainability of vegetation with conservation relevance are wide-ranging including further suitable locations, identifying restoration targets, survival chances of protected stands. Finding further suitable locations is the most frequent target of species distribution (McCune, 2016; Fois et al., 2018) and predictive vegetation models (Franklin, 1995; Somodi et al., 2017). From an application perspective, these sites are important for restoration as they point to the most cost-effectively maintainable target habitat for

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restorations (Řehounková et al., 2018; Török et al., 2018; Somodi et al., 2021; Vörös et al., 2025). Less attention has been given to the significance of indication on the fate of a stand stemming from different levels of survival chances. The two extremes in this aspect are complete coincidence with the environmental conditions and thus predictable survival without active human interventions (including management), and decoupling of site conditions with occurrences. The former has particular significance for conservation by pointing out self-sustaining stands that can be preserved cost-effectively (Batllori et al., 2017; Tang et al., 2022). The latter has been termed vegetation inertia for vegetation stands (Lewin, 1985; Eriksson, 1996). Vegetation inertia is the community-level scale-up of local inertia, characteristic of plant species able to persist under long periods of unfavourable conditions due their longevity and reproductive strategies (large seed banks, clonal propagation). This phenomenon is conceptually similar to the the extinction debt of metapopulations (Tilman et al., 1994; Kuussaari et al., 2009). However, while extinction debt often refers to the number of species in a community that are present in a seeming surplus compared to the habitat extent available, vegetation inertia refers to the presence of a specific community/vegetation type in the face of unsuitable environmental conditions. In case of vegetation inertia, dominant plant species also create and maintain an environment for the rest of species with favourable microsite conditions, despite the change in the environmental background (Lewin, 1985; Keuper et al., 2011). However, without a return of site conditions to favourable, this situation inevitably leads to collapse or transition into another vegetation type (Berdugo et al., 2022; Orbán et al., 2023).

Besides considering self-sustainability of individual habitat types, characterisation of the landscape regarding ecological restoration has also gained momentum (von Holle et al., 2020; Helm, 2021). This perspective change calls for new ways to assess restoration chances, such as restoration potential of habitat complexes (Gilby et al., 2020), identification of hotspots of restoration per se (Gilby et al., 2020) or, where existing stands have significant survival chances enhanceable with additional restoration of gaps between the stands (Brancalion et al., 2019; Chazdon, 2019).

Thus, there is a growing need for ecological indicators to express survival chances of existing and potentially occurring habitats stands. Potential distribution models (PDMs, encompassing correlative models targeting potential distributions from species to communities sensu Bede-Fazekas and Somodi, 2020) offer insight into the spatial distribution of survival chances. PDMs in our understanding include habitat suitability and species distribution models (SDM; Guisan and Zimmermann, 2000), predictive vegetation models (PVM; Franklin, 1995) and ecological niche models (ENM; Peterson and Soberón, 2012).

Comparison of estimated survival chances with observations can help to identify status of known stands and currently unoccupied spaces (Barbosa et al., 2013). Co-incidence of PDM predictions and observations has been most widely used to develop indices of model goodness (Hijmans, 2012; Jiménez-Valverde, 2022). However, matches and mismatches of predictions and observations can carry information as well (Barbosa et al., 2013; Bede-Fazekas et al., 2023; Somodi et al., 2024) rather than being interpreted as model error (sensu Araújo et al., 2019, Feng et al., 2019, Sillero and Barbosa, 2021), whether applied to species or vegetation type occurrences. Barbosa et al. (2013) used combinations of matches and mismatches with binarised predictions to characterise species distributions. However, they combined indices primarily from the point of view of potential distribution. Their approach opened a direction of interpreting matches and mismatches of SDMs, leaving a range of match-mismatch combinations, including opportunities for characterisation of actual distribution to be further explored. Furthermore, another branch of PDMs compared to SDMs, models of the potential natural vegetation (PNV, Tüxen, 1956) are specifically designed to reflect survival changes of vegetation types (often also referred to as habitat types; Somodi et al., 2021). Thus are relevant source of information if stand and vegetation type survival is in focus, as it is the case for nature conservation and ecological restorations (Török et al., 2018; Sabatini et al., 2020). The MPNV approach, an extension of the original PNV concept by Tüxen (1956) further facilitates survival assessment by understanding PNV as a probability distribution of vegetation types capable to survive at a location (Somodi et al., 2017, 2021). The MPNV approach allows the assessment of self-sustainability on a 5-level scale rather than a presence/absence prediction, thus allowing finer understanding of survival chances and their representation in prediction matches and mismatches.

Thus, formalising matches and mismatches between MPNV and observed distributions carries enhanced potential for indices useful for conservation and restoration planning. The proposed indicators rely on predictive vegetation modelling and are intended as diagnostic tools for conservation and restoration planning rather than causal explanatory models of vegetation-environment relationships (Araújo et al., 2019; Sillero and Barbosa, 2021). Elaborating the logic of Barbosa et al. (2013), we aim to adapt the interpretation of prediction/observation matches and mismatches to habitat evaluation as well as additionally exploiting the full range of indicators that emerge from the extended contingency table allowed by the 5-level suitability scale introduced with MPNV. Our specific aims were:

- to exploit the range of indicators that make use of the comparison of potential and actual distribution in a complete and structured approach
- to test these indicators using the vegetation distribution of Hungary as a case study
- to identify the different messages indicators can carry for conservation and restoration ecology.

2. Methods

2.1. Indicators

As a basis of indicators, we rely on the contingency table of potential and actual distributions (Table 1) as Barbosa et al. (2013). Observations are coded binary as in Barbosa et al. and as usual (presence/absence). However, in our study predicted probabilities are rescaled into five ranks for each vegetation type separately as introduced by Somodi et al. (2017). Representing predictions ranks optimised per vegetation types rather than binary codes have a range of advantages, including a finer characterisation of predictions, when a threshold for a binary classification is not evident, representation of uncertainty in predictions as well as room for utilisation for model evaluation, too (Somodi et al., 2024).

The rescaling procedure employs basic statistics of the probability distributions within presence and absence observations (Fig. 1).

The resulting 5 categories can be plausibly expressed after Török et al. (2018):

0: lower probabilities than the minimal probability assigned to any location with observed presence
1: higher probabilities than the minimal probability assigned to any location with observed presence, but lower than the average probability assigned to any location with observed absence

Table 1
The contingency table of the ranked probability given by the MPNV model (the potentiality of a vegetation) and the presence/absence (the actual vegetation).

	Observation (presence/absence, act#)	
Potentiality (MPNV rank, pot#)	act0pot0	act1pot0
	act0pot1	act1pot1
	act0pot2	act1pot2
	act0pot3	act1pot3
	act0pot4	act1pot4
Marginal	act0	act1

Fig. 1. Visual representation of the rescaling of predicted probabilities to MPNV ranks.

2: higher probabilities than the average probability assigned to any location with observed absence, but lower than the average probability assigned to any location with observed presence
3: higher probabilities than the average probability assigned to any location with observed presence, but lower than the highest value assigned to any location with observed absence
4: higher probabilities than the highest value assigned to any location with observed absence

The use of ranked suitability values rather than binarised predictions follows current recommendations in potential distribution modelling, which emphasise that continuous or ordinal suitability outputs retain more ecological information and reduce threshold-related artefacts when models are used for diagnostic or comparative purposes (Araújo et al., 2019; Feng et al., 2019). This scale was originally developed to serve the comparability of predicted suitability probabilities within MPNV estimations. Here we exploit the characteristic of the scale that it offers an estimation of the reliability of predictions and thus has the potential to serve as detailed indicators based on the comparison of predictions and observations. This way, we aim to employ the information in mismatches rather than attributing them to errors from start. While the procedure has only been applied in the MPNV framework yet, it is readily applicable to any potential vegetation models (Franklin, 1995, PVMs), where vegetation types are predicted separately and thus offers the opportunity to calculate the proposed indicators for predictions produced by other types of models as well. Furthermore, other ecological models relying on observed absences also can benefit from the approach, including a non-negligible portion of SDMs utilising observed absences also (Pasanisi et al., 2024). Application of the approach to presence-only model outcomes, however, will need adaptation yet as their pseudo-absences need to be screened appropriately.

In a very general sense rank0 and 1 have been interpreted as unsuitable locations so far (Konrád et al., 2022), rank2 as uncertain, rank3 and 4 as suitable with increasing strength (Török et al., 2018; Konrád et al., 2022; Somodi et al., 2024; Vörös et al., 2025).

Cross-tabulating these categories with observations yields a 10-cell contingency table (Table 1).

Cells of the contingency table were considered for usefulness as indicator in this paper both as absolute counts per spatial units ("absolute indicator") as well as a ratio compared to bottom marginals ("relative indicator"). Technically, this was realised by dividing the absolute counts by the sum of all absences or presences depending on the column, i.e., whether indicators connected to presence or absence observations were considered. The utility and potential information content of each match and mismatch was individually examined.

2.2. Case study

To test the usefulness and indicator value for conservation, we applied the indicators for the Hungarian vegetation as a case study (Fig. 2). For Hungary, MPNV predictions are already at hand as produced by gradient boosting models in a previous study (Somodi et al., 2017, updated with emerging data for Somodi et al., 2024), for further detail see Supplementary material S1 and Supplementary material S3.

We demonstrate the behaviour and applicability of the proposed indicators with the help of a case study. Although, it is based on one coherent dataset, this dataset encompasses a wide range of model behaviours as it is the set of habitat distribution predictions underlying the

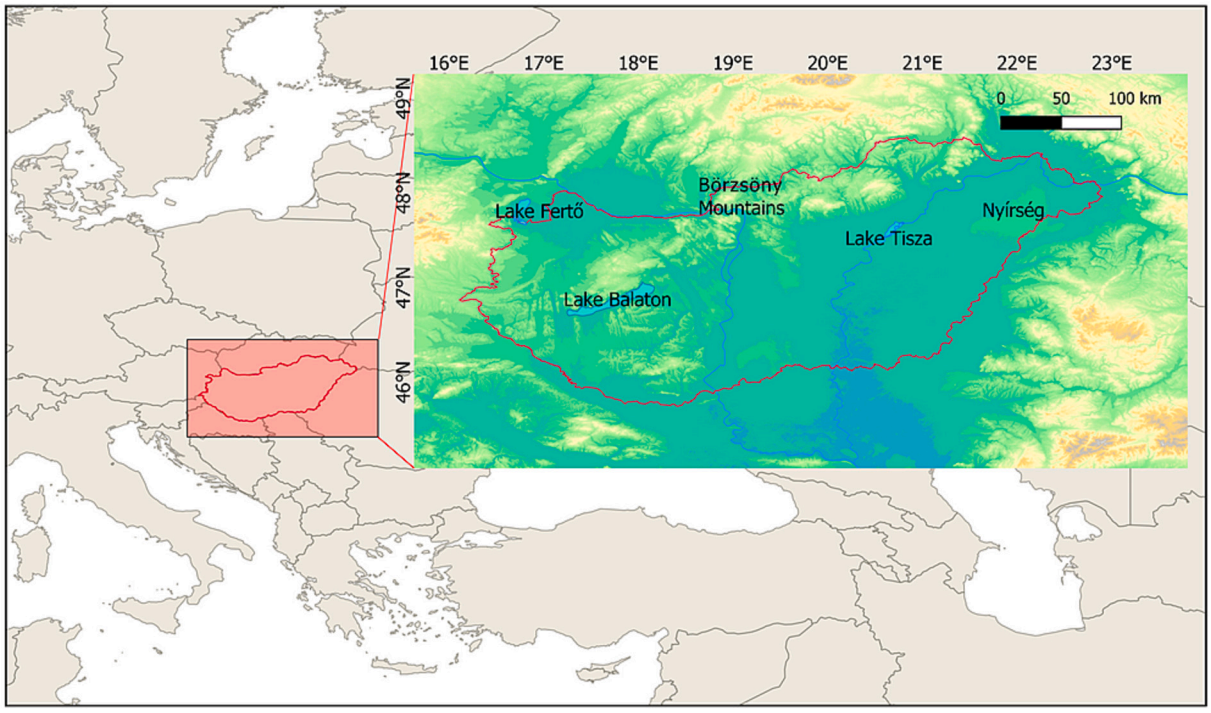

Fig. 2. Location of Hungary within Europe and relief map. Geographic coordinate system: WGS-84 (EPSG: 4326). Major geographic names mentioned in the text are also given.

complete multiple potential natural vegetation (MPNV) estimation in Hungary (39 vegetation types) complemented with habitat distribution predictions for 8 further vegetation types that can be considered as potential replacement vegetation (PRV, Chytrý, 1998, Supplementary material S2). To reflect the inclusion of PRV habitats, we refer to the estimations as multiple potential vegetation (MPV = MPNV + MPRV) further on as in Konrád et al., 2022.

The estimation process, including introduction to data underlying the model has been described in Somodi et al. (2017). However, during the years we aimed to perfect the model and thus a few changes occurred:

- grasslands classifying as potential replacement vegetation (PRV) were added to the range of types modelled
- we experimented with additional explanatory variables and as a results some were replaced or added

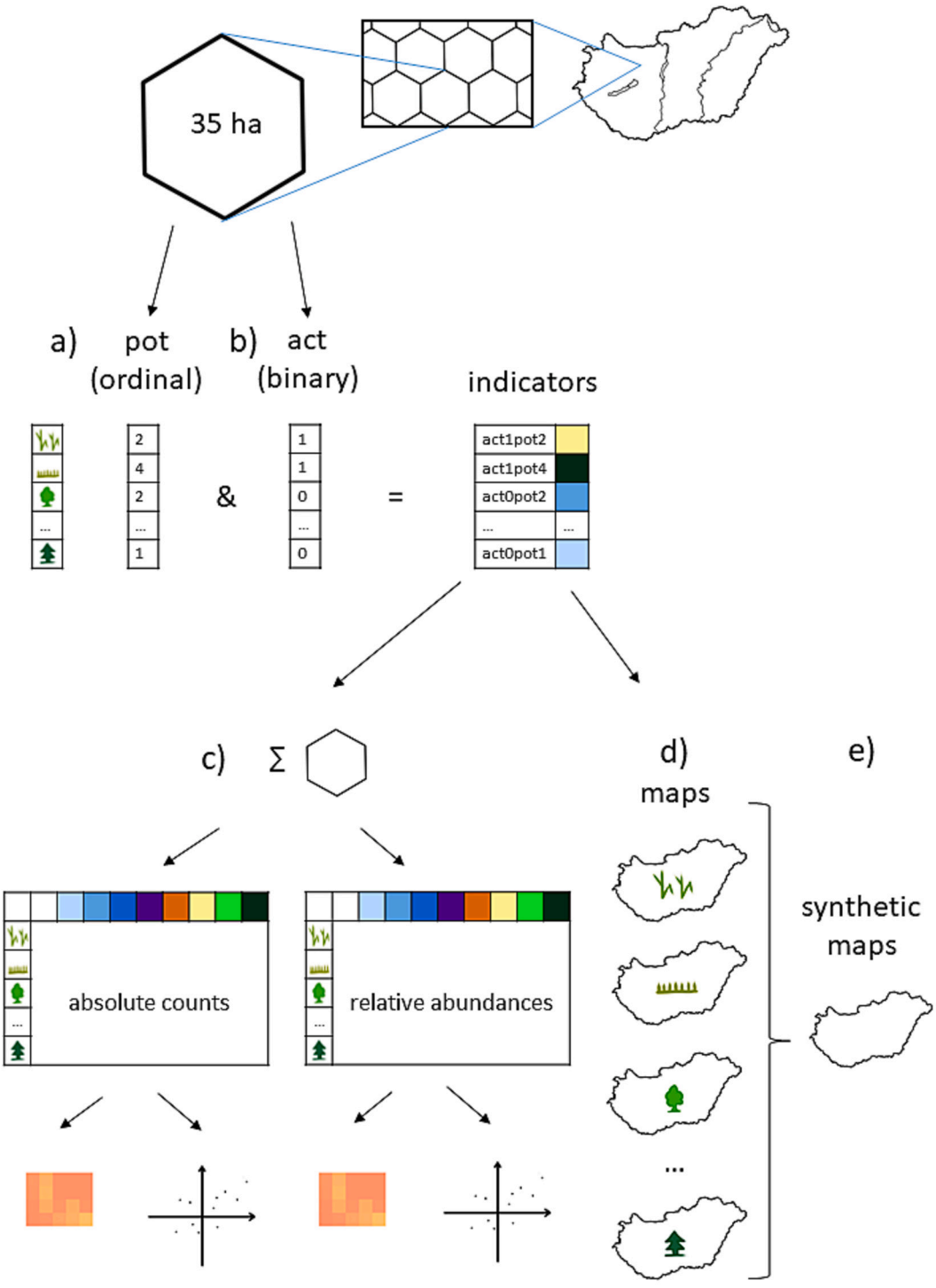

Fig. 3. Overview of the workflow of the study. a) predicted MPV ranks, b) binary observations, c) analysis of frequencies, d) individual indicator maps, e) synthetic indicator maps.

– statistical criteria of multicollinearity (VIF) for inclusion of an explanatory variable into the starting set was tightened for enhanced reliability.

The model details corresponding to the current study coincide with those used in Somodi et al. (2024). A brief description of the modelling process and model structure optimised for readers of this study is also available in the Supplementary material S1.

Thus, effectively the data used now, are the predicted distribution maps of the 39 PNV vegetation types plus 8 PRV types (total = 47 types) (Fig. 3a, Supplementary material S3). Predictions are handled at the 5-level rank scale according to Somodi et al., 2017 to ensure comparability of the local suitability for different habitats (Fig. 3a). Although uncertainty associated with individual model predictions is not explicitly propagated into the indicator values, the use of a relative, rank-based framework partially mitigates calibration uncertainty by focusing on comparative rather than absolute suitability estimates, consistent with current PDM best-practice guidelines (Araújo et al., 2019; Feng et al., 2019).

Observations were extracted from the Hungarian Actual Habitat Database (MÉTA, Molnár et al., 2007, Fig. 3b, Supplementary material S4). MÉTA is a database built by field observations of (semi-)natural vegetation types between 2003 and 2006 and covers the entire territory of Hungary. The country is gridded with hexagonal cells of 35 ha size (~ 700 m diameter), embedded in a grid of 5.5*6.5 km quadrats. However, since 199 MÉTA quadrats have no observations and thus the status of actual vegetation is unknown, we excluded the hexagons within those quadrats from the study. These quadrats are masked out with grey in the maps.

Matches and mismatches between predictions and observations were identified per spatial units (hexagons in the case study).

We examined the usefulness of all possible combination of potentiality and observations as indicators (Table 1). We both exploited the number of hexagons and their number divided by the respective marginal (the sum of all absences or presences) in the contingency table as indicators and term them absolute and relative indicators respectively (Table 2).

Indicator values were also subjected to analysis of spatial correlation. First, Moran's I (Moran, 1950) values were calculated for each combination of vegetation type and indicator to identify the presence of spatial autocorrelation. For combinations, where Moran's I indicated the presence of spatial autocorrelation, semivariograms were also produced using the spherical model (Oliver and Webster, 2014). Maximum cutoff was set at 130 km reflecting the general advice to maximise cutoffs in half of the complete study area (Jin and Kelly, 2017). Inspection of empirical semivariograms supported this distance as suitably reaching the plateau for each vegetation type. Based on the semivariograms, the range parameter, i.e. the distance in which spatial autocorrelation is detectable was calculated. Pearson correlation between autocorrelation characteristics (Moran's I values and range parameters) and our indicators was also calculated.

To understand the indicator values, we produced frequency representations per vegetation type (Fig. 3c) and Principal Component Analysis (PCA) was carried out as an exploratory analysis to examine the interrelationships of indicator values both with regards to counts and relative abundance variants. PCA was used as an exploratory tool to identify dominant gradients and redundancies among indicators, rather than to infer causal relationships. Furthermore, we produced maps of indicator values per vegetation type (Fig. 3d) and synthetic maps (Fig. 3e) adding up indicator values across vegetation types to represent conservation and restoration hotspots in the country. Maps were projected in WGS-84 (EPSG: 4326).

In order to assess how the information uncovered by our indicator relates to existing assessment of ecosystem conditions, we also carried out a comparison with the national ecosystem condition indicators (Tanács et al., 2022). The national ecosystem indicators were developed in particular detail for forested habitats. There were habitat types that were completely corresponding to one of our vegetation types thus we carried out a comparison between our indicators and the national ecosystem condition indication for these five types. The forest condition indicators (FCI) by Tanács et al. (2022) range between 1 and 5 increasing with habitat quality. To explore the data we calculated median FCIs across our indicators in general and for indicator-vegetation type combinations. As the FCI dataset only applies for existing stands, only indicators associated with presences were used. To formally test the differences, we calculated a cumulative link model (CLM; McCullagh, 1980) appropriate for the ordinal response FCI presents. Our indicators and vegetation type identity served as categorical explanatory variables. Interaction of the two explanatory variable was also added to model formula. To avoid nestedness and ensure convergence, one spatial unit of the FCI dataset (20 m wide cells) was randomly selected from each of our spatial units (700 m wide hexagons) as data record.

All data processing and analysis were performed in R language for statistical computing (R Core Team, 2025). We used the sf package (Pebesma and Bivand, 2023) for operations with spatial vector data, the raster package (Hijmans, 2025) for operations with rasters, the moranfast package (Cooper, 2020) for Moran's I calculations, the gstat package (Pebesma, 2004) for the semivariogram and range parameter calculations and the ordinal package (Christensen, 2025) for cumulative link model calculations.

Table 2
Indicator names, descriptions and logical interpretations. Indicators are both introduced as absolute vs relative numbers. Due to the close relatedness of the two variants, these are shown in one row each.

Name	Abbreviation	Description	Interpretation
unsuitability1	act0pot0	vegetation type absent and predicted with lowest probability	unsuitable site – matrix
unsuitability2	act0pot1	vegetation type absent and predicted with low probability	unsuitable site closer to suitability - less hostile matrix
uncertain potential	act0pot2	vegetation type absent and predicted with medium probability	uncertain environment, may be possible to establish
potential site	act0pot3	vegetation type absent and predicted with high probability	confirmed suitability
exceptional potentiality	act0pot4	vegetation type absent and predicted with near-certain probability	confirmed above-average suitability
extreme inertia	act1pot0	vegetation type present and predicted with lower probability than any presence location within the evaluation data	extremely unsuitable presence (no example in the case study)
vegetation inertia	act1pot1	vegetation type present and predicted with low probability	instability / low quality, strong indication of vegetation inertia
uncertain fate	act1pot2	vegetation type present and predicted with medium probability	questionable suitability, possible vegetation inertia
sustainable presence	act1pot3	vegetation type present and predicted with high probability	high suitability, high conservation values
exceptionally strong presence	act1pot4	vegetation type present and predicted with near-certain probability	outstanding suitability, indication for high conservation value at spot

3. Results

3.1. Indicators

Logically, there are 10 combinations of the matches and mismatches that emerge as candidate indicators, which we linked to logical interpretations (Table 2).

However, the combination of extreme inertia (act1pot0) in our case study is a theoretical possibility only. Pot0 is defined as predictions lower than the minimum of predictions within observations. We propose to identify indicators based on the evaluation dataset and then apply it to the full dataset. Therefore theoretically, there could be predictions of act1pot0 in the complete dataset, but no such case was recorded in the case study. While theoretically act1pot0 could occur, apparently none of the known vegetation stands exhibited this strong level of vegetation inertia in Hungary. Such cases might however occur in other datasets.

Moran's I values showed significant spatial autocorrelation for most of the vegetation type-indicator combinations. Spatial autocorrelation is high for indicators based on observed absence (act0), in particular for unsuitability and uncertainty indicators, but were also significant for the rest of the absence and for most of presence-based indicators (act1; Supplementary material S5), too. Among presence-based indicators a few vegetation types showed patterns without spatial autocorrelation among indicators reflecting presence observations in the lowest or highest potentiality, i.e. rank 1 and 4 respectively (H1 – act1pot1, J1a – act1pot4, M5 – act1pot4, M6 – act1pot4, N13 – act1pot1).

Range parameters clearly responded to the abundance of the specific indicator, particularly in the higher rank ranges as also shown by correlation coefficients between indicators and spatial autocorrelation measures: Moran's I and the range parameter (Supplementary material S5). In most cases the range parameter is relatively low, so the pattern is clearly aggregated. Large range values occur in particular within the unsuitability1 indicator and for potential presence of forest steppe forest types.

Comparison of indicator values with the national ecosystem condition dataset did show certain similarities, though highly dependent on the vegetation type studied. Median FCI corresponded to FCI = 3 for each indicator, i.e., medium condition, for all indicators with which comparison was meaningful, i.e. presence-based ones. Thus overall, there was no general association discernible between FCI and our indicators. When studied across vegetation types, oak-hornbeam and mixed coniferous forests had higher median FCI (4) across all indicator levels except for the vegetation inertia indicator. These two types had lower median FCI coinciding with act1pot1 than medians FCI for the rest of indictors. On the other hand, lowland edaphic types (gallery forests) showed intermediate median FCI (3) irrespective of the indicator.

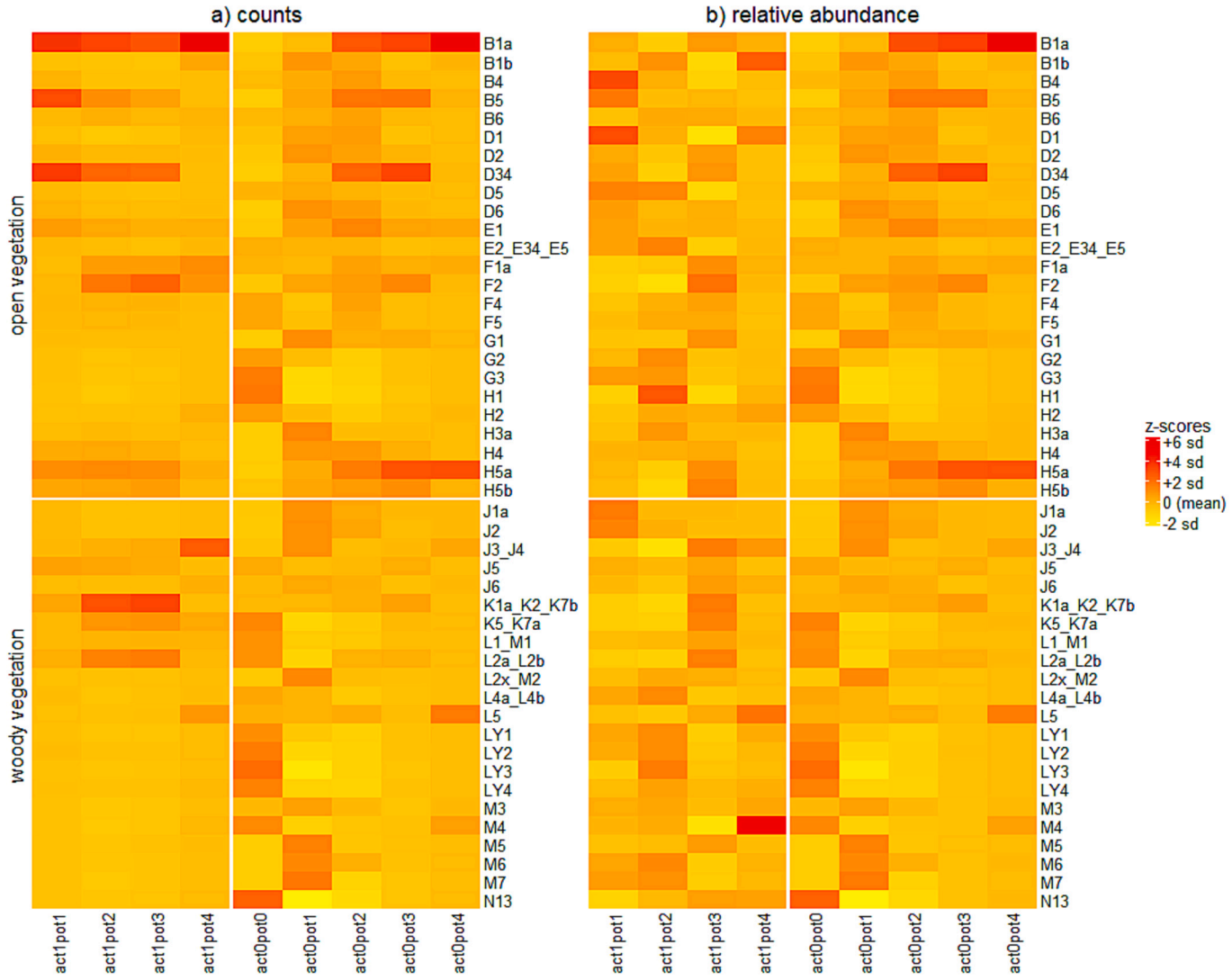

Fig. 4. Comparison of basic indicator values: a) counts b) relative abundances. Values were scaled relative to other values columnwise: centred on the means then divided by the standard deviation.

Correspondingly, whether indicators had an association with FCI according to the CLM, appeared to be highly vegetation-type specific. Interactions were significant in 4 combinations of indicators and vegetation types and these interactions were mirrored in the significance of main effects (Supplementary material S6).

3.2. Capacity of indicators to characterise vegetation types

As a first assessment we compared absolute and relative values of the indices for our case study and visualised them on heatmaps (Fig. 4). Absolute (number of cells in a category represented by the index) and relative values (amount divided by the relative marginal, i.e. all observed presences/absences) show different relationships between indicators, i.e. assessing index values in the two settings can be complementary.

As for counts (Fig. 4a), B1a scores one of the highest absolute values in exceptional potentiality (act0pot4), i.e. for sites highly suitable, but not occupied. Here loess steppes (H5a) and wet meadows (D34) also show high values, i.e. a high number of further suitable sites. H5a shows outstanding numbers in the exceptional potentiality and the potential site (act0pot3) also, while for D34, only the potential site is high, though this still corresponds to reliable suitability. Potentiality estimates in known presences are also very heterogeneous. It was expectable that the vegetation types with the highest known presences, such as reeds (B1a) and oak-hornbeam forests (K1a_K2_K7b) receive high absolute scores in index values referring their potentials at known presence locations. However, even in this comparison it is striking that while reeds occurrences mostly fall within exceptionally strong presence (act1pot4), occurrences of oak-hornbeam woodlands more typically fall into the uncertain fate (act1pot2) and sustainable presence (act1pot3) category. Sustainable presence still indicates highly suitable sites, but the comparable number of sites with uncertain fate indicates that for a high number of locations suitability is uncertain.

Relative index values (Fig. 4b) highlight partly matching, partly different patterns in suitability. Here again, one of the highest values can be seen for B1a and in exceptional potentiality (act0pot4) again. H5a and D34 still scores high for suitability for further occurrences, however, this is less outstanding compared to all unoccupied sites respective to these types. It is also worth noting, that there are a range of types with sharp environmental preferences and corresponding distribution that is indicated by the high values of unsuitability1 (act0pot0), such as mixed coniferous woodlands (N13) and forests of steep terrain (LY1-LY4). The high values of exceptionally strong presence (act1pot4) for M4 indicates a high suitability at a high portion of known occurrences. It is also interesting, for which types the suitability is most lacking. Inspecting oak-hornbeam woodlands (K1a_K2_K7b) regarding relative values, we can see that even though uncertain fate (act1pot2) cases are high in numbers, they are not numerous compared to all occurrences of this vegetation type. To the contrary, wetlands of emergent macrophytes (B4, B5 and D1) occur on certainly unsuitable sites (indicated by high relative abundance of vegetation inertia (act1pot1)) even if the number of such sites are not strikingly high.

3.3. Interrelationship of indicators

The two PCAs run separately for the absolute counts and the relative abundances of indicators showed clear differences. PCA of absolute counts showed some redundancy in indices (Fig. 5ace), while PCA of relative counts hardly any (Fig. 5bdf).

Even in the presence of a level of redundancy, PCA of absolute values was also informative. The first, the second and the third component explained 57%, 22% and 11% of the variation in the data, respectively (Supplementary material S7). Except for unsuitability1 (act0pot0) and unsuitability2 (act0pot1), indicators showed in the same direction along the first axis (Fig. 5ac). This axis stretched from widespread types to rare types, all indicators aligning with this axis increasing towards the more widespread types. The second axis was determined by the unsuitability indices (Fig. 5ae). Interestingly, unsuitability1 (act0pot0) and unsuitability2 (act0pot1), both indicating unsuitable and unoccupied sites, pointed towards opposite directions (Fig. 5ace). Thus these indicators corresponded to clearly different situations. In the case of unsuitability1, suitability estimates are the lowest possible, while unsuitability2 indicates slightly higher suitability values. These latter still correspond to unsuitability, the difference in the raw probabilities rather reflect model uncertainty. Unsuitability2 corresponds to more uncertainty in the assignment of the location as unsuitable. Inspecting the types that receive unsuitability2, we could identify that it was high for those types which are rare (i.e. have much actually absent sites).

The third axis differentiated among habitats with high exceptional potentiality (act0pot4) and exceptionally strong presence (act1pot4) together, i.e. for which the models found numerous suitable locations within presences and absences also (Fig. 5ce). Such were reeds (B1a), Salix-Populus gallery forests (J3_J4) and lowland oak forests (L5). The opposite direction was highlighted by uncertain fate (act1pot2) and sustainable presence (act1pot3), i.e., this direction identified types with numerous presences both in the suitable and in the uncertain range at the same time. Such were oak-hornbeam forests (K1a_K2_K7b) and Turkey oak forests (L2a_L2b).

The PCA of relative abundances showed more scattering (Fig. 5bdf). The first, the second and the third component explained 41%, 23% and 16% of the variation in the data, respectively (Supplementary material S7). The first axis had a high negative correlation with medium to high suitability in absence locations (act0pot2, act0pot3, act0pot4) (Fig. 5bd). Similarly to heatmap interpretation reeds (B1a), wet meadows (D34) and lowland steppes (H5a and H5b) were in this domain of the PCA biplot. The second axis was dominated by the very strong negative correlation with vegetation inertia (act1pot1), while unsuitability2 (act0pot1) also pointed in this direction mainly (Fig. 5bf). Thus, axis 2 can be interpreted as indication of a suitability gradient within current occurrences. Closed forests (K1a_K2_K7b, K5_K7a, L2a_L2b, N13) scored high on this axis while wetland vegetation types (B4, D1, D5) scored low. The third axis was associated with exceptionally strong presence (act1pot4) and exceptional potentiality (act0pot4) (Fig. 5df), similarly to the case of count-based PCAs (Fig. 5ce). Here, largely the same habitats scored high as in the case of counts: lowland oak forests (M4, L5), reeds (B1a) and lowland loess steppes (H5a). However, the position of M4 was more extreme for the relative value-based PCA, indicating that M4 has few actual occurrences and suitable sites, where it could potentially occur compared to all presences. At the same time, there appeared a high share of exceptionally strong presence and exceptional potentiality occurrences. Which means, that even though indicators showed only a low ratio of potential occurrences, the share of exceptionally suitable potential sites was high within them.

3.4. Spatial distribution of indicators

While overall statistics of the basic indicators can help to assess the condition and the potential of specific types, map representations convey important spatial information to support planning. Location of potential sites (act0pot3) and exceptional potentiality (act0pot4) help to assess the most suitable, yet unoccupied sites. At the same time, sustainable presence (act1pot3) and exceptionally strong presence (act1pot4) can identify existing stands with high stability. For example, the high potentiality areas of loess steppes concentrated in southeastern Hungary, regarding both the existing stands and potential sites (Fig. 6a). Indicators reflecting vegetation inertia (act1pot1) and uncertain fate (act1pot2) support recognition of vulnerable stands. In our case study, the vegetation inertia and uncertain fate stands were mostly at the fringes of the high potential distribution. This pattern applied to the loess steppes (Fig. 6a) and to the oak-hornbeam forests (Fig. 6b) as well. The oak-hornbeam forests had spatially continuous stable stands in the suitable zones of mountain and hilly regions, with few unfilled high

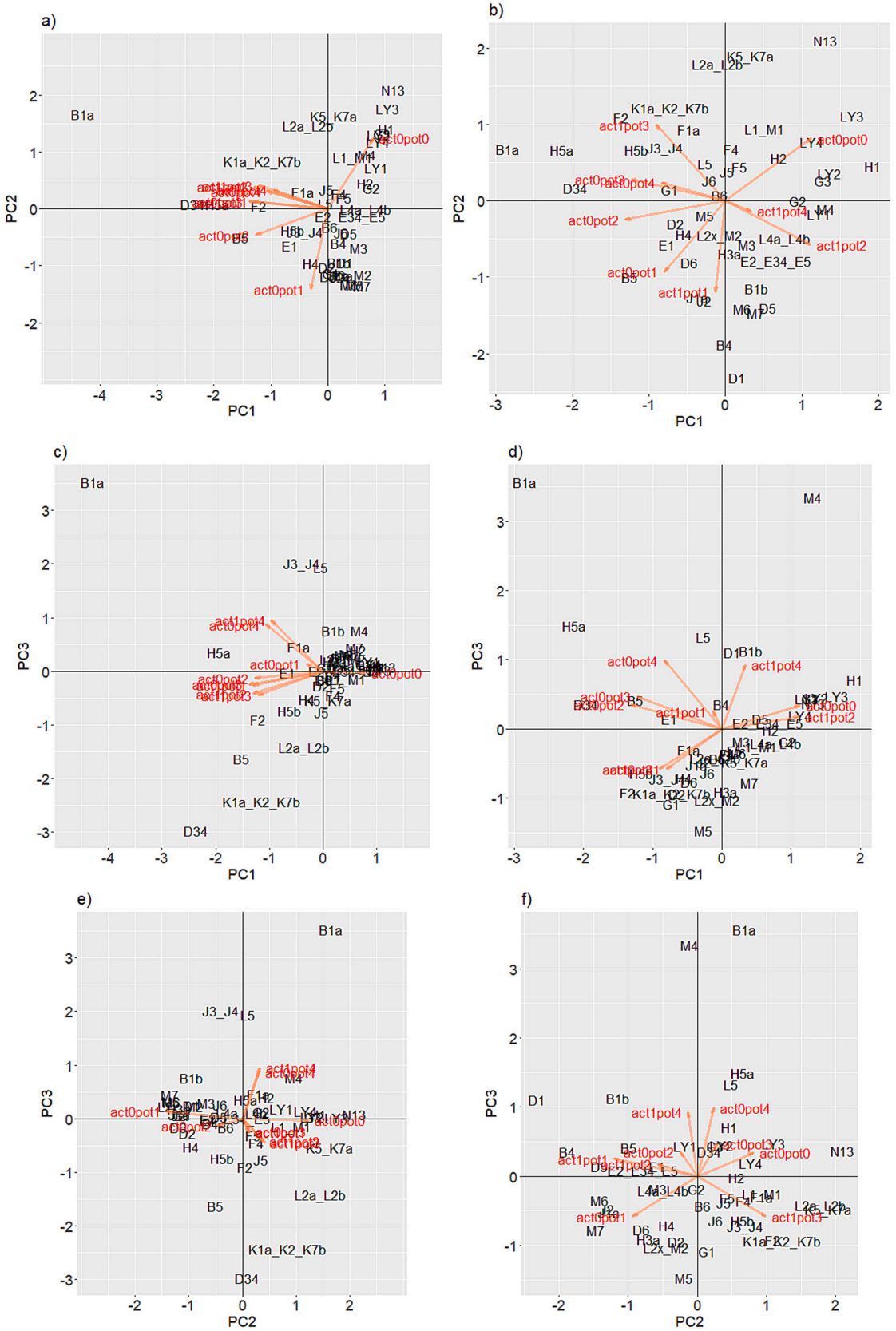

Fig. 5. PCA biplots of indicators: a) counts, first and second axes b) relative abundances, first and second axes c) counts, first and third axes d) relative abundances, first and third axes e) counts, second and third axes f) relative abundances, second and third axes.

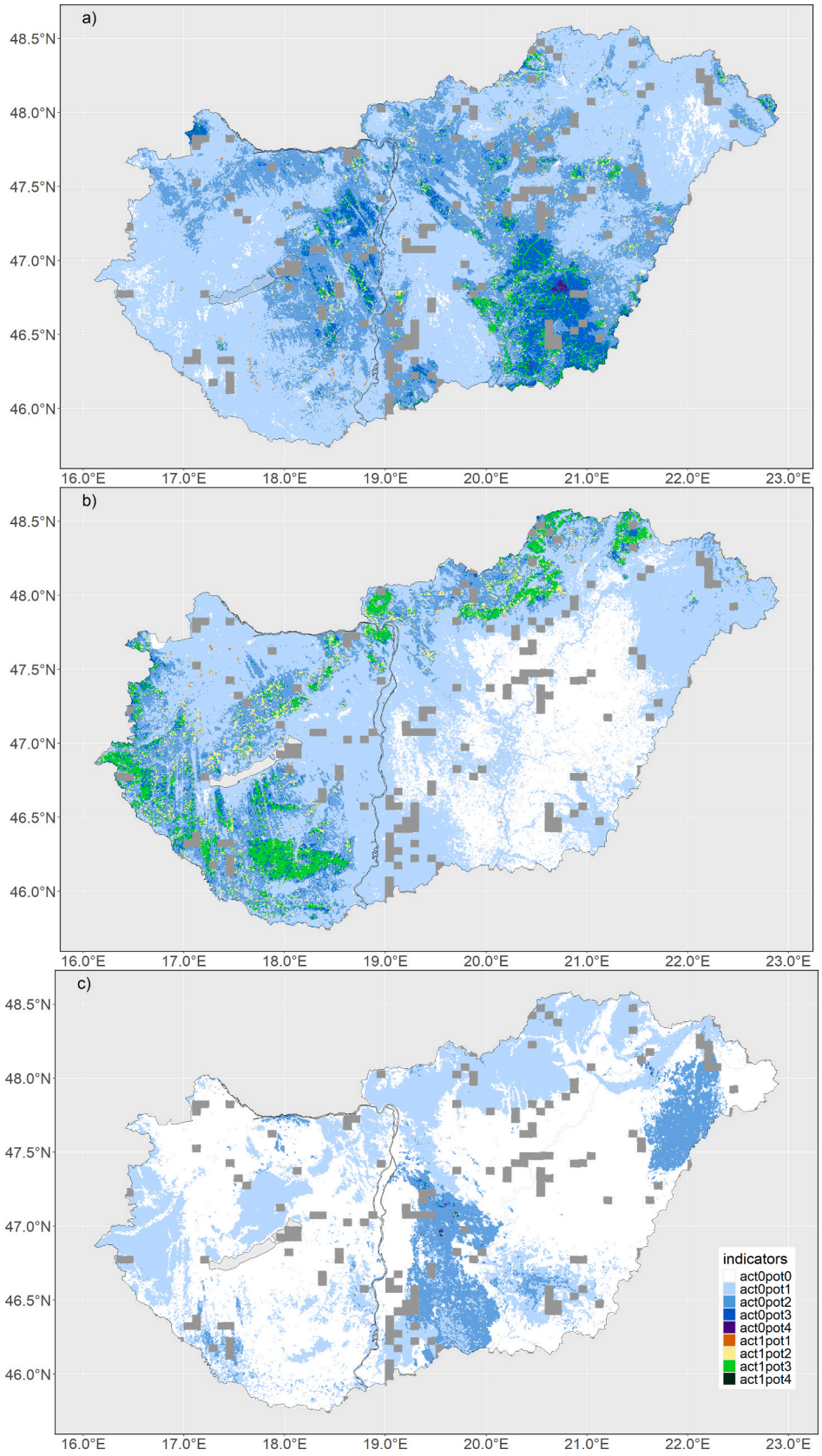

Fig. 6. Spatial distribution of basic indicators within selected vegetation types: a) loess steppes (H5a) b) oak-hornbeam forests (K1a-K2-K7b) c) lowland forest steppe forests on sand (M4). Dark grey corresponds to lack of observed data.

potentiality sites in the adjacent areas. The lowland oak steppe forests (Fig. 6c) exhibited a different pattern. Exiting stands are rare, but further potential sites showed different patterns in different regions. Interestingly, the potential site (act0pot3) and exceptional potentiality (act0pot4) locations were close to the existing stands in central Hungary, but more separate in the eastern region. Maps of other vegetation types are available in Supplementary material S8.

3.5. Landscape-level synthesis

Synthesizing indicators across types, e.g. counting how many habitats exhibit certain indication, can serve the identification of hotspots. The map of the sum of exceptional potentiality and exceptionally strong presence (Fig. 7a) revealed that a few of Hungary's major wetland areas (Lake Fertő, Lake Balaton, Lake Tisza) present landscapes with current

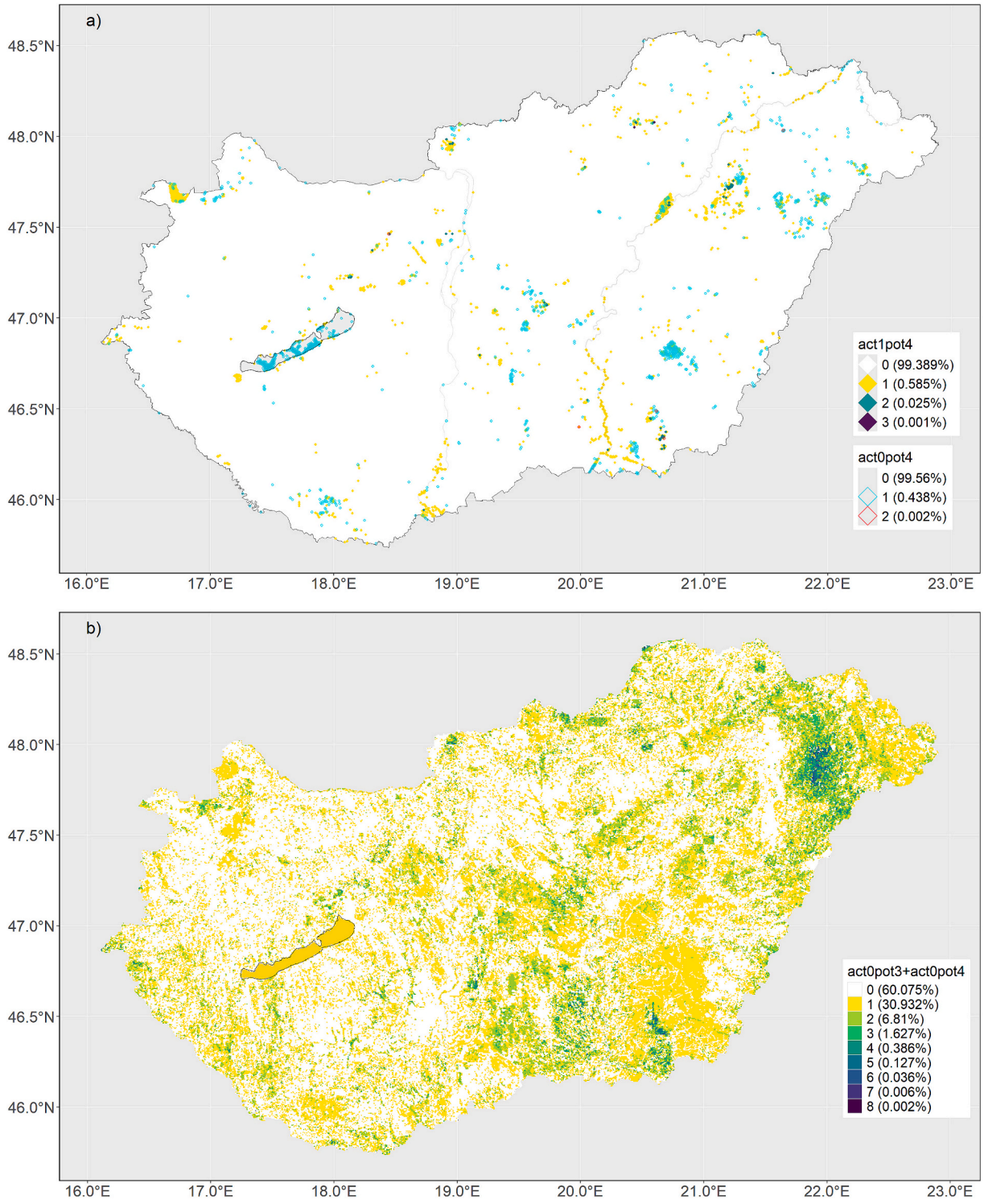

Fig. 7. Maps of hotspots based on sum of high potentiality indicators across all vegetation types. a) Number of vegetation types having received exceptional potentiality (act0pot4) or exceptionally strong presence (act1pot4) at the specific locality. b) Number of vegetation types having received act0pot3 or act0pot4. Dark grey corresponds to lack of observed data. Territorial share of each number of indicator values per hexagon are provided in the legend.

vegetation representing exceptional suitability plus embedded patches of exceptionally suitable, but unoccupied sites. Besides wetlands, such areas were also apparent both in the Great Hungarian Plain and in the Börzsöny Mountains. The map of potential site and exceptional potentiality locations (Fig. 7b) indicates there that there are vast areas in Hungary where at least one vegetation type is highly self-sustaining even though not present. Notably, high potentiality sites concentrated in a wide stripe in northeastern Hungary (largely corresponding to the Nyírség region, near 22°E).

4. Discussion

We proposed 10 indicators based on prediction/observation matches and mismatches in the footsteps of Barbosa et al. (2013) to support prediction of survival chance of vegetation stands and types, and thus contribute to better restoration planning. We identified interpretation to all combinations relying on an extended understanding of the predicted values thus allowing for finer assessment of self-sustainability status. The use of PNV and specifically MPNV has already shown promises in ecological restoration planning (Török et al., 2018; Peng et al., 2023) as well as green infrastructure design (Szitár et al., 2024). However, MPNV applications were case-specific and restricted to Hungary so far, likely because no generalised indicator framework was available.

Our analysis has shown that each rank of the five-rank scale introduced in the MPNV framework has an indicator function in combination with known presences and absences. While no differentiated interpretation was assigned to rank 0 vs 1 and rank 3 vs 4 earlier (Konrád et al., 2022; Somodi et al., 2024) they proved to carry valuable information in combination with presence and absence observations. Thus using the five-rank scale added further opportunities of characterisation of self-sustainability to initiatives relying on binarised predictions (Barbosa et al., 2013). Furthermore, while the introduction of the indicator framework in this paper relies on specific rescaling of predicted probabilities published by Somodi et al. (2017), the thresholds used in the rescaling can be adapted to the nature of predictions if necessary. Any rescaling thresholds can be suitable as long as the five category maintain the same message as also argued in Somodi et al. (2024) in detail, for example modifying the criterion that divides highly probable or probable presence.

While we focused on predictive vegetation models, the set of indices are also readily applicable for any potential distribution model that rely on known absences, including a subset of species distribution models also (Pasanisi et al., 2024). As with other PDM applications, the transferability of the proposed indicators depends on data quality, sampling completeness and the availability of reliable absence or background information (Araújo et al., 2019, Sillero and Barbosa, 2021).

As indices compare predictions and observations, map representations will only provide indicators for locations with data. This might mean for study areas not fully covered by observations that indicator maps will have blank parts. Nonetheless, as long as there is enough training data to train the models, and places of interest for the conservation decisions have data reflecting the current state, the indicators will provide insight into self-sustainability of the stands there. Similarly, once absence of a vegetation type is confirmed at a location, indices can be calculated even well after modelling and provide insight into the restoration potential at locations void of vegetation.

In general, spatial autocorrelation of indicator values were high, which is expectable considering that vegetation type stability is in connection with background factors that are also autocorrelated. This effect is typically mentioned, when explanatory models retain spatial autocorrelation in residuals pointing to the possible omission of an explanatory variable (Pace and LeSage, 2009, Kim, 2021). As our efforts were not connected to explanation of variance in indicator values, but identification of indications, presence of spatial autocorrelation is part of the information content. It has also been noted that high abundance of a phenomenon in the landscape makes spatial autocorrelation more likely (Brown et al., 1995) and corresponds to higher range parameter. Actually, spatially autocorrelated indicator occurrences signal to nature conservation for a potential to act more effectively as the phenomena in question (potentiality or inertia for example) are located close. There is ample evidence that spatially clustered species or habitats are often easier to conserve because conservation measures can protect many nearby individuals or patches at once (Carroll, 2006; Nagkoulis et al., 2025). Similarly, larger restoration sites have been shown to require less ongoing treatments after the initial restoration effort (Eppinga et al., 2023; Vörös et al., 2025). It is also noteworthy that if any, the highest (and rarest) rank often lacks spatial autocorrelation and thus needs to be considered together with other indicators in spatial planning of conservation efforts, which validates the use of synthetic maps of indicators we also propose.

4.1. Indicators characterising known presences

Effective prioritisation and cost-effective conservation planning is a key challenge today, when conservation actions are highly needed beyond available budgets (Wilson et al., 2006, Pienkowski et al., 2021,). However, in conservation a typical assumption is that if a stand is long present at a location, that location is also suitable for it. A sign of this approach is that any absence prediction by predictive distribution models is typically regarded as model error (Lawson et al., 2014; Somodi et al., 2024). However, modern ecology has identified that this cannot be taken for granted both due to alternative stable states and frequent lack of equilibrium (Svenning and Sandel, 2013; Birks, 2019). As opposed to automatically interpreting known presences as being at suitable locations, our indicators help to differentiate between occurrences at suitable and less suitable or unsuitable sites.

From the range of the proposed indicators, the indicator exceptionally strong presence (act1pot4) pointed out the stands in best conditions. These stands are the most valuable for conservation as they are in good conditions and can be expected to remain such further on. While rank 3 moved together with rank 2 in the ordination in our case, rank 4 clearly differentiated stands in the ordination of both the absolute and relative values. Thus, differentiating between rank 3 and 4 has proved to be informative.

Regarding the case study, it was particularly informative that the highest share of exceptionally strong presences (act1pot4) was found for the lowland oak forest steppe forests on sand (M4). This habitat has become very rare due to human land use and few locations have been preserved (Molnár et al., 2012). According to our results most of these locations have the potential to survive in Hungary and thus conservative protection is sufficient. At the same time, even stands characterised with uncertain fate (act1pot2) can be identified from the maps of the indicators for this type. Maps showed that stands with uncertain potential are in the vicinity of high potential occupied and unoccupied sites supporting effective conservation. Such stands on lower potential sites, if possible to conserve or site conditions can be improved, can serve as corridors.

In the face of global changes, the identification of stands that dwell at locations that have become unsuitable for them has particular significance. Vegetation inertia as a notion has been described by Erikkson in 1996 in the footsteps of Westman (1978), who introduced the concept of ecosystem inertia. Vegetation inertia refers to the phenomenon, when a vegetation stand survives with intact species composition corresponding past environmental conditions, while the contemporary conditions are not suitable for that type any more (Eriksson, 1996; Lloret et al., 2012). No indicators of vegetation inertia have been introduced yet, thus our two indices reflecting on this ecological phenomenon are new additions to the arsenal of tools of vegetation ecology.

Global and climate change makes the measurement of ecosystem and thus also vegetation inertia particularly important (Lloret et al., 2012). Climate change is not only a future expectation, but it is already in action (IPCC, 2021). While it has been shown to have modified the abiotic

environment relevant to species already, ecological reactions are less obvious yet. Most of the recorded reactions relate to species phenology (Auffret, 2021; Inouye, 2022), distribution of marine species (Lenoir et al., 2020; Le Luherne et al., 2024) and species with high mobility (e.g. mosquitos and butterflies; Pecl et al., 2017, Rödder et al., 2021). Vegetation changes in response to climate change clearly separable from human land use has been less often reported yet (though for a few examples see Pecl et al., 2017), showing that vegetation inertia is likely a widespread phenomenon. Our indices offer a mean to disentangle cases, when a background change has made the environment already unsuitable before a catastrophic event occurs from stable stands. Thus by identifying vegetation inertia, they point out where stands susceptible to change after an extreme event are located even before any visible change occurred. Higher vegetation inertia (act1pot1) or uncertain fate (act1pot2) sites often occurred at the fringes of the potential distribution of vegetation types in our case study. This pattern reflects populations being more vulnerable at the edges (Pearson et al., 2009; Anderegg et al., 2019), notwithstanding that edge effect can depend on the substrate and the vegetation type (Chytrý et al., 2022).

Table 3 summarises the implications of the results for conservation and restoration.

Our indicators show coherence with existing national ecosystem condition assessment for certain vegetation type-indicator combinations. However, differences also emerged. There was a striking homogeneity of median FCI across our indicators for all vegetation types, signalling that information content in the proposed indicators not captured by FCI. Correspondance of conditions values applied only for two of the four tested types. The national ecosystem condition assessment employed an expert-based rating of types and stands (Tanács et al., 2022), which reflect canopy composition and structure. However, being based on forest inventory data, naturally, FCI cannot reflect species composition in the undergrowth or suitability of local environmental. Our results showed that ecosystem condition if understood as degree of human transformation does not necessarily fully reflect habitat suitability. Human transformation is more dependent on accessibility of stands and economic value (Yackulic et al., 2011; Perlik, 2019), thus leaving difficult-to access, remote and edaphic fragments untouched or less affected (Mikoláš et al., 2019; Perlik, 2019). We also found uniform medians across different indicators for edaphic types mainly. Such a pattern might create an impression that these vegetation types are not in danger of disappearance, while the change of environmental factors depending in a more distal nature of human activites, such as climate change or depletion of groundwater might threaten these stand also. In forests, however as long as the dominant species is in place and human transformation is lacking such change is suitability can stay masked harboring the danger of nature conservation remaining uninformed of the threat to the specific stands. This can be particularly true for forests, where the microclimate-creating potential of the dominant species is strong (von Arx et al., 2012; Kovács et al., 2017).

Table 3
Application potential of the proposed indicators for nature conservation, ecological restoration and management.

name	abbreviation	relevance for management/conservation
unsuitability1	act0pot0	location outside of interest
unsuitability2	act0pot1	location outside of interest
uncertain potential	act0pot2	In the absence of higher-rank potentiality, these locations can serve as a second-row candidate for conservation or restoration. High share of uncertain predictions for a type indicates low model confidence and thus cautions stakeholders.
potential site	act0pot3	Cost-effective target sites for ecological restoration or forest management
exceptional potentiality	act0pot4	Particularly cost-effective target sites for ecological restoration or forest management
extreme inertia	act1pot0	Very low chance of the survival of the stand at the given location, indication for the need to restore the abiotic environment before attempting restoration.
vegetation inertia	act1pot1	Low chance of the survival of the stand at the given location, indication for the need to restore the abiotic environment before attempting restoration.
uncertain fate	act1pot2	Stands at location with questionable suitability, indicates the need to local data collection and examination of the situation of conservation is targeted.
sustainable presence	act1pot3	Stands with high chance of survival without interference, offering cost-effective conservation.
exceptionally strong presence	act1pot4	Stands with particularly high chance of survival without interference, offering cost-effective conservation. Prime target for conservation efforts.

4.2. *Indicators characterising unoccupied sites*

Barbosa et al. (2013) found a variant of the ratio of potential presences to actual presences useful as a possible indicator of species distribution status. Our indicators of potential site (act0pot3) and exceptional potentiality (act0pot4) further elaborate on this aspect. We found that separating the two levels of potential suitability is most relevant in characterising habitats. The exceptional potentiality indicator (act0pot4) identifies the most promising places for restoration. This indicator of exceptional suitability had its own indicator value besides the potential site indicator (act0pot3). Therefore this indicator has the potential to support restoration prioritisation. As restoration funds are often limited (Reynolds and Hessburg, 2005; Hoffmann, 2022), this exceptional potentiality indicator can direct efforts to those sites, where restoration would result in the most self-sustaining habitat, requiring the least further human input.

While the exceptional potentiality indicator exhibited a unique pattern, interestingly the amount of sites with potential site (act0pot3) and uncertain potential (act0pot2) moved together in our case study. This draws the attention that if types have considerable amount of potentially suitable but unoccupied sites (i.e. ground for large-scale restoration) also appear to have a high amount of further sites, where the model is uncertain.

Not only indicators supporting identification of further suitable locations proved to be informative for known absences. Unsuitability1 and 2, relying on the two ranks (0 and 1) usually identified as pointing out unsuitable places both (Konrád et al., 2022; Somodi et al., 2024), diverged into completely opposite direction in the ordination of absolute values. The unsuitability1 indicator (act0pot0) identified vegetation types with sharp and thus well-modellable environmental requirements (such as N13 – mixed coniferous forests), while vegetation types with less sharp tolerance boundaries received less unsuitability1, but rather unsuitability2 (act0pot1) in places unsuitable for them (such as B5 – non-tussock tall sedge beds). Thus, these two indicators do not differ in the message they carry regarding the location in space (i.e. unsuitable places), but indicate characteristics of the vegetation type. Alignment with unsuitability1 appear to indicate a more concise response to environment, while if unsuitability2 is more typical for the vegetation type, its tolerance boundaries are less sharp. The difference between the two indicators has relevance for forestry and landscape planning, particularly in the face of climate change mitigation efforts. A chief form of nature-based climate change mitigation is forest planting (Kirschbaum et al., 2024), so that the tree growth sequesters carbon-dioxide. However, forest planting at places with no forest potential cannot be sustainable and thus serving this goal and may even be ecologically harmful (Tölgyesi et al., 2022; Kirschbaum et al., 2024). In our case study, for example economically important forest vegetation types (K5_K7a – beech woodlands, L2a_L2b – sessile or pedunculate oak forests with Turkey oak) showed a high unsuitability1 amounts compared to other absence indicators. This indicates well-identified

environmental preferences and low potential for further expansion of their territory even by plantation. These examples underline that interpretation of low potentiality indicators can also be meaningful.

4.3. Support for spatial planning

Broad scale restoration planning has been identified as a key factor, relatively neglected so far (Gilby et al., 2018). Restoration hotspots have been understood in various ways (Brancalion et al., 2019; Gilby et al., 2020; Lewis et al., 2023). Our indicators specifically reflect on vegetation type composition; however, vegetation provides habitats for species in general. Thus, we can assume that our approach provides a proxy for restoration hotspots regarding species as well. The proposed indicators showed high potential to support not only the selection of individual suitable sites but consideration of spatial proximity and networks. Furthermore, we demonstrated that the combination of our maps can also identify restoration hotspots (sensu Gilby et al., 2020). We could demonstrate distribution of restoration hotspots with the example of Hungary, where several habitats have a good chance of self-sustainability. For example, we identified a possible restoration hotspot in northeastern Hungary, where exceptional potentiality and potential sites for multiple vegetation types aggregate and thus present restoration opportunity for multiple vegetation types.

Knowledge of the location and configuration of these hotspots is a prerequisite of landscape scale restoration also – a highly endorsed approach (Menz et al., 2013; von Holle et al., 2020) – as well as habitat complex restoration (Moreno-Mateos et al., 2020; Holl et al., 2022), such as restoring a forest steppe mosaic, a highly neglected habitat complex in the temperate biome (Erdős et al., 2018; Erdős et al., 2022).

Furthermore, it has been noted that maximising biodiversity protection is enhanced when directing actions to areas that are both conservation and restoration hotspots (Brancalion et al., 2019). The co-occurrence of exceptionally strong presence and exceptional potentiality indicators (act1pot4 and act0pot4, respectively) exactly allows for such considerations, for which no indicators have been available yet. Mapping of these indicators in our case study identified large water bodies (Lake Fertő, Lake Balaton and Lake Tisza) as good candidates for large-scale conservation schemes, but also pointed out combined conservation and restoration hotspots for grasslands and steppic oak woodlands in the Great Hungarian Plain and forests in the Börzsöny Mountains. Individual indicator maps for habitats reveal that the hotspots on the Great Hungarian Plain would exactly serve the joint conservation of steppe habitats that has become rare with human activities, such as loess and sand steppes (H5a, H5b) as well as forest steppe forests (e.g. M4).

5. Conclusion

Considering all combination of a refined assessment of predicted suitability and observation we arrived at the introduction of ten indicators of self-sustainability potential that offer both ecological insight and practical guidance in biological conservation and ecological restoration. With the help of these indicators, it is possible to characterise habitat types, the self-sustainability of existing occurrences as well as availability of further suitable sites. The indices were developed for vegetation types, but are readily applicable to any potential distribution models relying on known absences, including a subset of species distribution models.

Indices rating known absences are helpful to identify further suitable places, to direct restoration efforts in space and regarding target, as well as identify the location and nature of further stepping stones or corridors for the green infrastructure. At the same time, indices relying on mismatches of occurrences and suitability provide basic ecological insight, e.g. through indicating vegetation inertia as well as warnings for conservation planning. We suggest the following triage steps to translate our indicator framework into practice:

(1) Conserve: exceptionally strong presence (act1pot4) and sustainable presence (act1pot3);
(2) Restore: exceptional potentiality (act0pot4) and potential site (act0pot3);
(3) Monitor / assist: vegetation inertia (act1pot1) and uncertain fate (act1pot2).

Spatial representation of the indicators for vegetation supports the identification of most promising target sites for restoration of preselected vegetation types, as well as most self-sustaining target vegetation in the restoration of a specific location. Furthermore, by combination of indicators we could point out restoration and conservation hotspots that could underpin the transition from stand restoration to landscape scale and habitat complex restoration.

CRediT authorship contribution statement

Adrienn Gyalus: Writing – original draft, Visualization, Formal analysis. **Ákos Bede-Fazekas:** Writing – review & editing, Visualization, Formal analysis. **Zsolt Molnár:** Writing – review & editing, Conceptualization. **Imelda Somodi:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2026.115409.

Data availability

Data will be made available on request.

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