Ecological Indicators 136 (2022) 108707

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Original Articles

Species-based indicators to assess habitat degradation: Comparing the conceptual, methodological, and ecological relationships between hemeroby and naturalness values

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A R T I C L E I N F O

Keywords:
Bioindication
Ecological indicator values
Habitat degradation
Hemerobiotic state
Naturalness continuum

A B S T R A C T

Naturalness and hemeroby indicator values are specialized species-based indicators used in Continental Europe that reflect plant species' affinity to degraded habitats. Despite their potential utility for basic and applied science, their similarities have gone unnoticed, and they have yet to be studied together. Here, we combine literature review and novel data analyses to ask 1) How are the naturalness and hemeroby indicator systems related, and 2) Do naturalness and hemeroby indicator values reflect similar functional patterns? To address these questions, we first reviewed the conceptual and methodological differences underlying naturalness and hemeroby values. We then directly compared the indicator values, including splitting species by origin. Next, to determine if the values capture similar ecological patterns, we related the indicator values to leaf traits, specifically leaf area, dry matter content, and specific leaf area. The main conceptual difference we identified was the differing reference states of the systems: naturalness values are value-laden and emphasize a lack of human influence, whereas hemeroby values are evaluative and apply the potential natural vegetation concept. Naturalness and hemeroby indicators have contrasting resolutions on opposite ends of the naturalness/degradation continuum, with naturalness placing greater emphasis on lightly impacted areas, whereas hemeroby divides degraded contexts more finely. Overall, naturalness and hemeroby values were inversely related. Naturalness and hemeroby values were strongly (rho $<$ -0.6) correlated in direct comparisons. These correlations were curvilinear due to the scoring differences for non-native species: the systems had contrasting score variances (i.e., resolution) between non-native and native species. Leaf traits were generally "mirror images" between the systems; hemeroby was negatively associated with dry matter content and positively associated with specific leaf area, and vice versa for naturalness.. However, these relationships were weak ($R^2 < 0.05$). The weakness of these patterns implies that species' degradation tolerance may not be generalizable by simple leaf traits. Our work showed that hemeroby and naturalness are inverse, bilaterally consistent indicator systems. These indicator values, or improved versions of them, could be better utilized in the future for applied management and conservation.

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https://doi.org/10.1016/j.ecolind.2022.108707
Received 9 January 2022; Received in revised form 17 February 2022; Accepted 19 February 2022
Available online 24 February 2022

1. Introduction

Bioindication is the ability of biological entities to indicate the condition of their environment; its use has a long history in plant ecology (Ellenberg, 1974; Zonneveld, 1983; Zinnen et al., 2021). Some of the best tools of bioindication are ecological indicator values, expert-assigned ordinal categories that express species' realized niche optima for specified environmental gradients. Examples of this include species' temperature, soil moisture, and light requirements (Ellenberg et al., 1992). For example, in the Ellenberg indicator system, a plant species with a nutrient value of 1 is most frequent on extremely nutrient-poor soils, whereas a species with a value of 9 thrives in nutrient-rich soils. Unweighted or cover-weighted indicator value means are routinely used to estimate ambient environmental factors (Diekmann, 2003).

Plant species' ecological indicator values are widely used to assess a site's environmental conditions (Diekmann, 2003). Ecological indicator values of vascular plants were originally defined for Central Europe (Ellenberg, 1974) but have since been adapted to other areas such as Great Britain (Hill et al., 1999; Hill et al., 2000) and Greece (Böhling et al., 2002). Ecological indicators have several benefits because they can (1) provide a reliable estimate of environmental conditions, (2) integrate environmental parameters over long periods, (3) bypass time-consuming costly instrumental measurements, and (4) be applied to old relevés to provide information on past environmental conditions (Zonneveld, 1983; Diekmann, 2003; Erdős et al., 2017). As a result, ecological indicators have had consistent popularity among vegetation ecologists (e.g., Tölgyesi et al., 2014; Breg Valjavec et al., 2018; Scherrer and Guisan, 2019; Descombes et al., 2020).

Indicator values have also been developed to reflect human impacts. Similar to abiotic environmental factors, naturalness and degradation can be understood as a continuum ranging from artificial (i.e., degraded) to "natural" conditions (Anderson, 1991; Winter et al., 2010). Species react differently to anthropogenic degradation: while some plants are frequent under mostly natural or near-natural conditions, others can tolerate, benefit from, or even require anthropogenic impacts (Hill et al., 2002; Fanelli and Lillis, 2004; Pinke et al., 2011). In other words, species' realized optima differ along the naturalness/degradation continuum (Erdős et al., 2017). This fact provides an opportunity to assess the naturalness or degradation of a site based on its species composition. For this purpose, two types of indicator value systems have been developed in Europe: Hemeroby indicator values were originally defined for Germany, hemeroby meaning the degree of human influence on the plant community (Kowarik, 1988; Frank and Klotz, 1990), and naturalness indicator values for the Hungarian flora (Borhidi, 1995). Naturalness values are expert-assigned values; lower values are assigned to species that indicate human impacted areas, whereas higher values are species restricted to natural areas. Hemeroby values are also expert-assigned; however, low hemeroby values indicate species that inhabit less impacted areas, and vice versa. Although the two systems were developed independently, their underlying concepts are strongly related (Zinnen et al., 2021).

Naturalness and hemeroby indicator values are potentially useful tools in conservation biology. Both naturalness and hemeroby indicator values are integrated measures that combine all human impacts into a single value (Jalas, 1955; Sukopp, 1969, 1976; Borhidi, 1995; Winter, 2012). While individual degradation components can be directly measured, degradation as a complex process cannot (Kowarik, 1990; Erdős et al., 2017). Thus, naturalness or hemeroby indicator values offer a simple and powerful method to systematically estimate the naturalness/degradation status of sites and habitats (e.g., Kim et al., 2002; Erdős et al., 2017; Sengl et al., 2017).

Although the concepts of naturalness and degradation are prominent topics, the species-based indicator values of the two systems have infrequently been used. Although it has been suggested that naturalness and hemeroby indicator values can be applied similarly to Ellenberg indicator values to reveal trends in habitat degradation (Kowarik, 1990; Borhidi, 1995), the use of these indicator values have been uncommon (Zinnen et al., 2021). Because habitat degradation is one of the most pressing issues for conservationists and habitat managers, these indicator values could become increasingly important metrics for future research and site management.

Despite their past but limited use, and future potential as tools, the connection between naturalness and hemeroby values has received surprisingly little attention (Zinnen et al., 2021). Two broad questions emerge from this lack of knowledge:

(i) Are the naturalness and hemeroby indicator systems related?
(ii) Can these systems reflect similar ecological patterns?

To address these questions, we combined a review of existing literature with novel data analyses to clarify the knowledge about these underutilized indicator values. Our specific objectives were to 1) identify the conceptual differences between the naturalness and hemeroby approaches, 2) provide an overview of the methodological dissimilarities among existing species-based naturalness and hemeroby value systems, and 3) assess how consistent the systems are by 3A) directly comparing naturalness and hemeroby indicator values and 3B) comparing leaf functional traits associated with the values.

2. Differences between the concepts of naturalness and hemeroby

Kowarik (2014) and Walz and Stein (2014) argue that a basic distinction should be made between the concepts of naturalness and hemeroby since their reference states differ substantially. In their understanding, naturalness compares the current vegetation to historical natural vegetation that was present at the site before major human impacts. In contrast, hemeroby compares the present vegetation to "potential natural vegetation"—the vegetation that could survive under current conditions if every human influence disappeared immediately (Tüxen, 1956; Somodi et al., 2021). The difference may have important implications for sites with severely modified environmental conditions, where an "original" pre-human state would not be able to successfully maintain itself in the long term without active human management (Kowarik, 1990; Somodi et al., 2017; Zinnen et al., 2021). For example, a spontaneous stand of invasive trees has low naturalness but also has low hemeroby, provided that its development has not been controlled by humans (Kim et al., 2002; Kowarik, 2014). However, it has not been evaluated if this conceptual difference is reflected in species-based naturalness and hemeroby indicator values.

A second contrast is the evaluative versus descriptive nature of the two concepts (Zinnen et al., 2021). Naturalness is a value-laden concept because it signifies more natural habitats as more desirable and worthy of protection than impacted habitats. Similarly, species-based naturalness indicator values describe the quality or favorability of species. In contrast, hemeroby is neutral, meaning that it is used for vegetation description rather than appraisal. It should be emphasized, however, that the evaluative component of naturalness should not be interpreted as a disadvantage; on the contrary, it reflects the science of conservation biology, which is inherently value-laden (e.g., Meine et al., 2006; Noss, 2007).

Most authors assume that naturalness and hemeroby scales cover the same range of the naturalness/degradation continuum and are thus of the same length (e.g., van der Maarel, 1975; Colak et al., 2003; Winter et al., 2010; Yorkina et al., 2020). In contrast, Coté et al. (2019) argued that the hemeroby scale is longer, extending beyond the scale of naturalness at the degraded end of the continuum (meaning that the naturalness concept has low resolution below a certain level of naturalness). Though this view is not generally accepted, it connects to a related topic: the resolution of naturalness and hemeroby scales in the degradation continuum.

Winter (2012) stated that the resolution of the naturalness and hemeroby scales differs fundamentally: hemeroby uses finer resolution where the vegetation is degraded (i.e., hemeroby classes get narrower towards the degraded end of the naturalness/degradation continuum) whereas naturalness uses finer resolution where the vegetation is more natural. Thus, naturalness and hemeroby classes do not correspond to one another (i.e., they cannot be matched along the continuum, particularly near the end points of the continuum) according to Winter (2012). However, they can be matched according to van der Maarel (1975), Steinhardt et al. (1999), Colak et al. (2003) and Reif and Walentowski (2008).

3. Methodological differences between different species-based indicator value systems of naturalness and hemeroby

In addition to the conceptual differences between hemeroby and naturalness, there are more subtle practical differences between species' indicator values. For example, the number of classes (i.e., naturalness and hemeroby values or scores) differs. For naturalness values, Borhidi (1995) used a 9-grade scale, ranging from −3 to + 6 (Borhidi omitted scores of 0 from the axis). The number of hemeroby classes varies by user, usually between 5 and 10 classes (Kowarik, 2014). For example, Kowarik (1990) and Fanelli et al. (2006) use a 10-grade scale, while Kim et al. (2002) apply a 5-grade scale. Frank and Klotz (1990), Klotz and Kühn (2002) and the BiolFlor Database (Kühn et al., 2004) use a 7-grade scale. Note that some systems do not use numerical hemeroby values but use terms such as "oligohemerob" or "mesohemerob" that are arranged along an ordinal scale.

Most species-based naturalness and hemeroby value systems use discrete categories along the naturalness/degradation continuum, i.e., they assign each species an integer (or a class corresponding to an integer) (e.g., Kowarik, 1988; Borhidi, 1995). Fanelli and Lillis (2004), however, argue that the underlying gradient is continuous, and accordingly, any rational number can be assigned to the species.

Methods used to assign values for species vary between the systems. Borhidi (1995) based his scoring of naturalness values on Grime's (1979) competitor-ruderal-stress tolerator (CSR) framework. Grime (1979) posited that plants exhibit three life history strategies that relate to growth and survival limitations imposed by the interactions of three factors: competitiveness, disturbance adaptation, or stress tolerance. Thus, species which thrive when these factors are high are considered competitors (C), ruderals (R), and stress tolerators (S). Borhidi (1995) increased the number of the classes by further subdividing the categories "stress tolerant" and "ruderal." Borhidi's (1995) process was based on expert judgment. In contrast, Kowarik (1988, 1990), Fanelli and Lillis (2004) and Fanelli et al. (2006) used a large number of relevés, which they ordinated according to how much they were influenced by human impact. Then they analyzed the hemeroby spectra for each species and identified their greatest concentrations of occurrence. A similar approach was followed by Kim et al. (2002). In contrast, the hemeroby values of Frank and Klotz (1990) and the BiolFlor Database (Kühn et al., 2004) are mainly based on expert judgment, thus they are more like Borhidi's (1995) values in this respect.

Species that have strong responses to human impacts are optimal for indicating naturalness or degradation. However, naturalness and hemeroby systems can differ by how they treat species with wide tolerances. Borhidi (1995) assigned each species a single naturalness value irrespective of the tolerance width of the species. Kowarik (1988) and the PHANART Database (Lindacher, 1995) also assigned one value for each species, but species with wide tolerances received the value 0 and were treated as indifferent. Kim et al. (2002) did not assign any value to indifferent species and excluded these from further analyses. In contrast, Frank and Klotz (1990) and the BiolFlor Database (Kühn et al., 2004) use multiple values for species with wide tolerances, which then can be averaged if single values are needed for additional analyses (e.g., Berg et al., 2016).

Finally, the species-based indicator values can vary with geographical area. Indicator values are usually valid for a given region only because the ecological tolerance of a particular species may change across its range (Diekmann, 2003). Naturalness and hemeroby values are no exception (Kowarik, 2014); therefore, these values must be applied with caution outside their original region. The naturalness values of Borhidi (1995) were defined for Hungary, while those of Goncharenko (2017) were intended for Ukraine. Hemeroby values have been assigned for plant species in Germany (Kowarik, 1988; Frank and Klotz, 1990; Kühn et al., 2004), Italy (Fanelli et al., 2006), and South Korea (Kim et al., 2002).

4. The connection and consistency of naturalness and hemeroby indicator values

To assess the consistency of these indicator values and to clarify their meaning, we first directly compared (i.e., correlated) the indicator values. Then, we supplemented these findings by testing if the values coincided with functional trait data.

4.1. Direct comparisons and indicator value data

To compare naturalness and hemeroby indicator values, we first obtained naturalness indicator values from Borhidi (1995) and hemeroby values from the BiolFlor Database (Kühn et al., 2004). Second, we prepared a list of species that were present in both databases. We used the Catalogue of Life (www.catalogueoflife.org) to identify synonyms. We found 1744 species that had both naturalness and hemeroby values. Data from the BiolFlor Database (Kühn et al., 2004) were transformed into numeric values along an ordinal scale (the resulting numerical values ranged between 1 for "ahemerobic" or natural to 6 for "polyhemerobic" or degraded). Because the BiolFlor Database defines a hemeroby range (multiple values rather than a single one, up to 6 values) for species with broad degradation tolerances, there were multiple hemeroby values for many species. For each species, minimum, median and maximum of the hemeroby range were calculated as an 11-grade ordinal scale, which ranged from 1 to 6.

Next, we collated the origin status of the species, differentiating native species (historically present in the study area), archaeophytes (introduced to the study area before 1492), and neophytes (introduced to the study area after 1492, often from other continents). For origin status, we primarily relied on Borhidi (1995) and Balogh et al. (2004) for Hungary and the BiolFlor database for Germany; we also consulted the Euro + Med database (www.europlusmed.org) in some instances. Species with unknown status or inconsistent status between Hungary and Germany (n = 167) were excluded from analyses dealing with origin status.

4.2. Direct comparisons between indicator values

To achieve a non-directional comparison of the two indicator values, naturalness and hemeroby, we used Spearman's rank correlation (Spearman, 1904) using midranks in case of ties (Hollander and Wolfe, 1973). Correlation coefficients and significance were calculated after dividing the dataset following four different methods described below. Division by intervals (i.e., methods no 3 and 4) was done to study whether the relationship between the indicator values changes along the naturalness and hemeroby continuum. Indicator values may be nebulously different between individual values, but may provide additional information when aggregated into coarser classes.

1) full dataset (n = 1744);
2) native species (n = 1219), archaeophytes (n = 175) and neophytes (n = 183);
3) dataset was split to three parts along the naturalness continuum using 33.33th and 66.67th percentiles as limits of the middle closed

interval, resulting in the following subsets: −3–1 (n = 446), 2–4 (n = 845), and 5–6 (n = 453);

4) dataset was split to 3 × 3 parts along the naturalness and hemeroby continua using 33.33th and 66.67th percentiles as limits of the middle closed intervals.

In each analysis, hemeroby was described in three different ways: by the minimum, the median and the maximum of the hemeroby range of the species.

4.3. Functional traitcomparisons

In addition to direct comparisons of the indicator values, we hypothesized that these indicator values reflect similar functional patterns. In other words, if the indicator values were associated with degradation tolerance, it could be expected that there would be predictable relationships with functional and ecological traits.

One way to test this hypothesis was by using leaf traits. Leaf traits are of special relevance to species' degradation tolerance. High specific leaf area (SLA) is associated with resource capture and fast growth, whereas high leaf dry matter content (LDMC) is associated with slow growth and greater resource sequestration (Pérez-Harguindeguy et al. 2013). Hence, low LDMC and high SLA could generally be advantageous for species inhabiting disturbed environments (Pérez-Harguindeguy et al., 2013; Ficken and Rooney, 2020).

We compiled leaf trait data for the full dataset (n = 1744) of species. Leaf trait data included leaf area (LA; mm^2), LDMC (g dry mass/g fresh mass), and SLA (mm^2/mg). We obtained these data from the TRY database (Kattge et al., 2020) and a leaf trait database of Pannonian flora from E-Vojtkó et al. (2020). In total, 1,240 species had at least one of the three leaf functional traits available.

We used linear models to assess if naturalness values and median hemeroby values were associated with LA, LDMC, SLA. Although these indicator values are ordinal, using linear models to connect indicator values to measurements is reliable and useful for interpreting ecological patterns (see Bartelheimer and Poschlod, 2016). Because some of the relationships between traits and indicator values appeared quadratic, we created three candidate models to determine the best supported model: a null model, or the mean of the response variable where the coefficients of independent variables are 0, a first order linear relationship, and a second order relationship. We used Akaike Information Criterion corrected for small sample size (AICc) to select the best of the three models. Akaike weights were calculated and the best model, assuming one correct model exists in the candidate set, was selected as the model with the greatest Akaike weight value. AICc and weights were calculated by using the package MuMIn (Barton, 2020). To improve the normality of model residuals, we log-transformed leaf area, logit-transformed LDMC, and square-root transformed SLA. We expected that SLA would increase and LDMC would decrease with hemeroby, and vice versa for naturalness indicator values. We expected a weak, negative relationship between leaf area and hemeroby values, and vice versa for naturalness indicator values.

We conducted all analyses in R (R Core Team, 2020) using the packages "corrplot" (Wei and Simko, 2021), "ggplot2" (Wickham, 2016) "MuMIn" (Barton, 2020), and "Hmisc" (Harrell, 2020).

4.4. Results

Across the full dataset, most species were situated in the 2–6 interval along the naturalness gradient (with a peak at 4 of the left-skewed distribution) (leftmost column of Fig. 1). The distribution along the hemeroby gradient was right-skewed with a peak at 2, 2.5 and 3 if minimum, median and maximum of the hemeroby range were studied, respectively. Naturalness showed a strong negative correlation (rho = -0.69) to

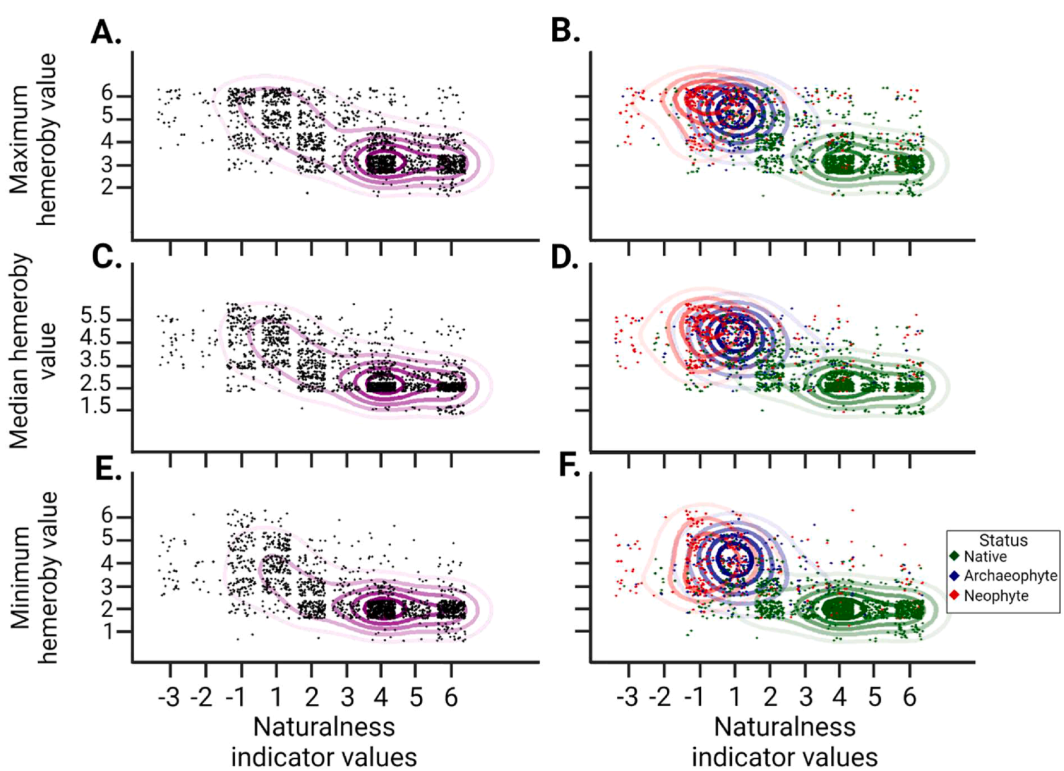

Fig. 1. Distribution of the studied species (dots) along the naturalness (horizontal axes) and different hemeroby (vertical axes) gradients. The leftmost column shows the distribution of all species' minimum (A), median (C), and maximum (E) hemeroby values. The rightmost column organizes the species by origin; shown are native (green), archaeophyte (blue), or neophyte (red) species' minimum (B), median (D), and maximum (F) hemeroby values. We added random noise to data points to improve visualization and prevent overplotting. Density contour lines highlight the concentration of the points overall (purple, left) or by origin (red, blue, and green on the right).

median hemeroby values, and slightly weaker correlations with the minimum and maximum hemeroby values (rho = -0.67 and rho = -0.66, respectively). All three were highly significant ($p < 0.001$).

The source of the overall non-linearity of the naturalness-hemeroby relationship for the full database (left column of Fig. 1) was revealed by splitting the dataset according to the origin status of the species (right column of Fig. 1). Native species showed more variance along the naturalness gradient and a right-skewed distribution along the hemeroby gradient with the same peaks (i.e., 2, 2.5 and 3) as in the case of the full dataset analysis. In contrast, distribution of non-natives was more extended along the hemeroby gradient and showed little variation along the naturalness gradient. While naturalness separated archaeophytes (peak at 1) from neophytes (peak at −1), hemeroby values poorly distinguished these two groups from each other. Compared to the full dataset, when we split the dataset according to the origin status, correlations weakened consistently. Native species showed the strongest correlations, followed by archaeophytes and neophytes. In the case of natives, correlation of naturalness was found to be the strongest with median hemeroby (rho = -0.52), and slightly weaker with the maximum (rho = -0.50) and minimum hemeroby values (rho = -0.46). In the case of archaeophytes, correlation with the median hemeroby was the strongest (rho = -0.28) followed by the minimum (rho = -0.27) and maximum (rho = -0.26) hemeroby. All six of these correlation coefficients were significant ($p < 0.001$). Results for the neophytes differ substantially. All the correlations were weak, and only naturalness and the maximum hemeroby showed significant correlation (rho = -0.16, $p < 0.05$). The correlation between naturalness and median hemeroby was weaker and marginally significant (rho = -0.14, p = 0.051), whereas the correlation with minimum hemeroby was not significant (rho = -0.12, p = 0.120).

When we split the dataset along the naturalness gradient, the naturalness-hemeroby relationship was the most pronounced in the middle interval (2–4): rho = -0.50, −0.48 and −0.39 with $p < 0.001$ for median, maximum and minimum hemeroby values, respectively. The correlations in the lower (-3–1) and upper (5–6) quantiles were much weaker, with no significant correlation in the case of the lower quantile. Considering the upper quantile, we found a significant ($p < 0.001$) correlation with the maximum hemeroby (rho = -0.18) and the median hemeroby (rho = -0.17), while naturalness showed no correlation (rho = -0.07, p = 0.15) with the minimum hemeroby.

The analysis of the dataset split along both the naturalness and hemeroby gradients revealed additional nuances in the data (Fig. S1). Available comparisons indicated that negative correlation was the strongest in the middle quantile (rho = -0.42, −0.39 and −0.35 with p <

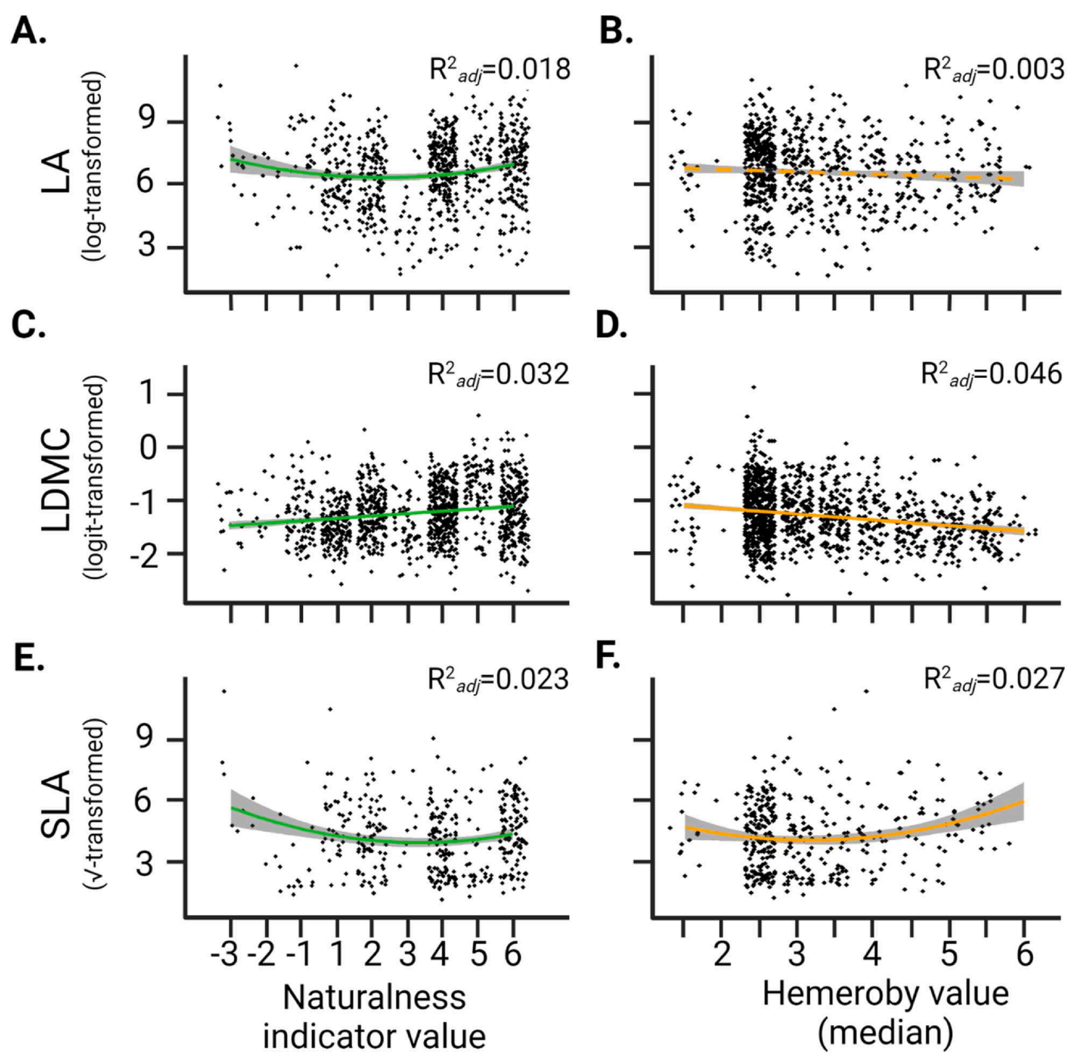

Fig. 2. The relationship between leaf traits and naturalness and median hemeroby indicator values. Each column represents the listed degradation indicator value, while each row represents one of the three leaf functional traits. We added random noise to data points to improve visualization and prevent overplotting. Sample sizes: LA n = 774, LDMC n = 1228, and SLA n = 407. Model trendlines for second or first order linear models are shown; the dashed lines indicate a model had ambiguous model support (i.e. marginal significance, $p < 0.1$). Gray 95% confidence intervals are shown for trendlines.

0.001 for median, maximum and minimum hemeroby values, respectively). However, an unexpected, strong positive correlation was found between naturalness and maximum hemeroby (rho = 0.46, $p < 0.05$, n = 26) and median hemeroby (rho = 0.44, $p < 0.05$, n = 20) in the upper quantile of naturalness and the upper quantile of hemeroby. However, this pattern did not arise with minimum hemeroby.

Leaf traits were significantly related to naturalness and hemeroby indicator values; these relationships generally varied between weak second- and first-order linear relationships (Fig. 2). Apart from the model explaining leaf area using median hemeroby values (weight = 0.28, Table S1), the null models had little support (weight < 0.07; Tables S1–S3). Leaf trait patterns were generally reciprocal between naturalness and hemeroby values. A second order model was the best supported when relating naturalness values to leaf area (weight = 0.991, Fig. 2A, Table S1). A decreasing first-order model was best supported for median hemeroby, though it had ambiguous support (weight = 0.503, Fig. 2B, Table S1). LDMC had a first order increase for naturalness values (weight = 0.696, Table S2) and a first order decrease for median hemeroby values (weight = 0.561, Fig. 2C-D, Table S2); second-order models also had some support relating the values to LDMC (weight > 0.3, Table S2). The first-order model predicted that LDMC would decline by 45% from the lowest median hemeroby to the highest; the first-order naturalness model predicted a LDMC increase by nearly 25% from the lowest to the highest naturalness indicator value. There was strong evidence (weight = 0.961) that SLA declined quadratically with naturalness indicator values (Fig. 2E, Table S3). Conversely, there was a moderately supported (weight = 0.649) quadratic increase of SLA for median hemeroby value (Fig. 2F). Leaf traits were weakly associated with either naturalness ($R^2_{adj} < 0.04$) or median hemeroby indicator ($R^2_{adj} < 0.05$) values.

5. Discussion

5.1. Overview

Hemeroby and naturalness values are similar but not identical bioindicators. The core conceptual differences between hemeroby and naturalness values include their differing reference vegetation states, their descriptive versus evaluative nature, the section of the continuum covered by the values, and the resolutions towards the endpoints of the continuum. Also, notable methodological differences have been identified among different species-based indicator value systems, including the number of classes (scores) along the naturalness/degradation continuum, the treatment of species with wide tolerances, and the divergent scoring practices used for non-natives. We found consistent reciprocal relationships when directly comparing the indicator values, and some evidence that they capture similar functional characteristics. Naturalness and hemeroby indicator values may be better suited (i.e., have superior resolution) in degraded contexts: hemeroby is less variable in natural and near-natural conditions, whereas the variability of naturalness indicator values decreases in impacted conditions.

5.2. Direct relationships of the values

Although there are some conceptual differences between hemeroby and naturalness, particularly regarding their reference states (historical vs. current perspective, Kowarik, 2014; Walz and Stein, 2014), we found strong negative correlations between naturalness indicator values and minimum, median, and maximum hemeroby values (Fig. 1). These correlations were nonlinear and indicated a reciprocal relationship. Thus, our results support the view of Winter (2012), who stated that hemeroby has a finer resolution where vegetation is degraded, while naturalness has finer resolution where vegetation is less impacted.

We note that the species-based indicator values we used in this analysis were defined for different regions. Nonetheless, the strong negative relationships we showed here suggest that the two systems are robust and that the values are loosely interchangeable. Similarly, species' hemeroby values independently calculated for Berlin and Rome were also similar in other studies (Fanelli and Lillis, 2004; Fanelli and Testi, 2008). Thus, a species' tolerance to degradation may be consistent throughout its range.

When treating species with different origin status separately, we found that there was a strong negative correlation between hemeroby and naturalness values for native species, while the correlation was weaker for archaeophytes and even weaker or non-significant for neophytes (right column of Fig. 1). This is ostensibly due to how experts who defined the values judged non-native species. Borhidi (1995) made sharp distinctions between natives and non-natives in scoring: non-natives always received negative scores. This means that non-natives always received naturalness scores in a very narrow range (-3 to −1), whereas their hemeroby scores vary in a much wider range (3 to 6). Moreover, Borhidi's naturalness values varied between archaeophytes and neophytes. In contrast, for hemeroby values, origin status is not necessarily reflective of a species' tolerance to anthropogenic impacts (Kühn et al., 2004). This may reflect the conceptual differences between the ideas underlying naturalness and hemeroby (Kim et al., 2002; Kowarik, 2014): naturalness refers to an "original" (pre-human) state of nature, which means that non-natives are regarded by Borhidi (1995) as "unnatural" and thus inherently reflect degradation. In contrast, non-natives could inhabit the potential natural vegetation, the reference state of the hemeroby concept. In such cases, non-natives may be associated with low human impacts and thus may have low hemeroby values. There are several differences between archeophytes and neophytes besides their date of arrival, including the cause of their arrival (e.g., accidental vs. intentional introduction), their impacts on the ecosystem, and the attitude of the botanists when they scored the species. This complex nature of the archeophyte-neophyte classification suggests that further research is needed to better understand their hemeroby and naturalness values.

We found that hemeroby and naturalness classes may be regarded as corresponding to one another near the centre but not towards the endpoints of the naturalness/degradation continuum. This reinforces the view of Winter (2012), who stated that the widths of hemeroby and naturalness classes differ near the extremes of the continuum. When the dataset was split along the naturalness gradient only or along both the naturalness and the hemeroby gradients, negative correlations were the strongest in the middle quantiles. In the upper quantile of naturalness and the upper quantile of hemeroby, strong positive correlations were revealed between naturalness on the one hand and maximum or median hemeroby on the other. In contrast, the same correlation did not exist for minimum hemeroby values (Fig. S1). This suggests that the minimum hemeroby value should be preferred if hemeroby is interpreted as the inverse of naturalness.

The distributions of both values were skewed with peaks at the natural end of the continuum. In addition to the right skewness of hemeroby, our results suggested that hemeroby values are less variable at the natural and near-natural end of the continuum. This implies that the hemeroby concept loses resolution above a certain naturalness (Coté et al., 2019). Because naturalness was left skewed, it had more variability at the degraded end of the continuum than hemeroby values at the natural end. This could suggest that naturalness indicator values are more capable of reflecting a wider range of the naturalness/degradation continuum and are more appropriate than hemeroby if this wide range should be described by a sole index.

5.3. Functional trait relationships

Naturalness and hemeroby values were associated with leaf functional traits reciprocally, which led to "mirror image-like" relationships that generally matched our expectations. This reinforces that both indicator systems highlight similar groups of species that tolerate or shun human impacts. However, since the relationships were overall weak, the reasons underlying degradation tolerance may be eclectic and poorly explained by a small number of traits (see also Ficken and Rooney, 2020). Leaf traits are influenced by other factors besides human impacts. For example, studies of indicator values have associated high SLA with shade tolerance (Bartelheimer and Poschlod, 2016). Thus, studying trait relationships to indicator values alone may be pooling species with vastly different ecologies. However, these indicator values were not assigned with specific functional traits in mind.

Our findings comparing the indicator values to leaf traits matched the patterns found by other researchers. Specifically, we found that indicator values associated with degradation tolerance were associated with higher SLA and lower LDMC. In highly modified environments, SLA may confer an advantage to resource capture and growth. For example, Fanelli and Lillis (2004) found that relative growth rate and SLA were associated with greater hemeroby values for some plant species in Rome. In contrast, others have shown that greater leaf tissue density is ill-suited in disturbed environments, which includes physical destruction or eutrophication (e.g., Craine et al., 2001). Low SLA and high LMDC have also been weakly associated with greater coefficients of conservatism (Ficken and Rooney, 2020), expert-assigned bioindicators similar to naturalness values that reflect intolerance to degradation (Zinnen et al., 2021). Indeed, although Ficken and Rooney (2020) showed significant relationships between LDMC and SLA to coefficients of conservatism, the explained variation was also weak ($R^2 < 0.05$ for both leaf traits).

5.4. The application of hemeroby and naturalness indicator values

Applying the naturalness concept in nature conservation and restoration is a useful practice (Angermeier, 2000). Hemeroby and naturalness indicator values are simple, consistent tools to measure the degradation or quality of a plant community. However, they have been applied only in a handful of cases (Zinnen et al., 2021). Hemeroby values have been used in temporal biological monitoring (Rockinger, 2013; Berg et al., 2016), including monitoring biological invasions (Berg et al., 2017). Naturalness values have been used in basic ecology to estimate site degradation (Sengl et al., 2016; Erdős et al., 2017; Yorkina et al., 2020), and for assessing ecological restoration (Sengl et al., 2017). However, these examples are eclipsed by the widespread use of more typical ecological indicator values (Zinnen et al., 2021).

The applications of hemeroby and naturalness are more limited compared to a similar species-based indicator system, coefficients of conservatism (C-values). Developed for the Chicago region, C-values range from 0 to 10 and indicate plant species' tolerance to anthropogenic degradation (Swink and Wilhelm, 1979). C-values are widely used throughout the USA and Canada (Spyreas, 2019). The widespread and effective use of C-values implies that naturalness and hemeroby values have greater potential for applications in the field of conservation biology and restoration ecology. For example, hemeroby and naturalness indicators could be used in tandem with other methods to identify areas of high naturalness for conservation prioritization. Furthermore, these indicators can be used to track succession, which could be particularly useful when monitoring restoration projects. Herben et al. (2016), who defined species-level indicator values of disturbance for the Czech flora, also predicted that similar indicators would gain popularity in plant and landscape ecology.

As a potential future direction, the development of a unified scale may be desirable, using both naturalness and hemeroby systems as initial references for new expert-based scoring. This scale could improve the systems by being equally sensitive at both ends of the naturalness/degradation continuum. Alternatively, the performance of these indicator values can be compared to those derived from objective methods (e.g., Herben et al., 2016).

6. Conclusions

Despite their conceptual and methodological differences, our results showed that hemeroby and naturalness values are reciprocally related. We have elucidated how non-native species are scored differently between the systems, which results from the value-laden component of the naturalness concept. This causes distinctive clustering of the indicator values based on origin. An important practical consideration we found is that hemeroby and naturalness values have different resolutions near the end points of the degradation scale. We suggest that the use of hemeroby indicators is more useful in degraded sites, whereas naturalness is better-suited for near-natural and natural habitats. Hemeroby and naturalness values capture similar but reciprocal ecological characteristics among species. However, the relationships between the traits and indicator values were weak, so more research is needed to contextualize the ecology underlying human impact tolerance. Because plant community degradation is an important consideration of current and future plant conservation, these indicator values could be advantageous tools for basic and applied ecology. Nevertheless, the lack of resolution at some ends of the naturalness/degradation continuum suggests improved indicator values could be developed in the future.

Funding

The funding source had no involvement in study design, in the collection, analysis and interpretation of data, in the writing of the report, and in the decision to submit the article for publication.

CRediT authorship contribution statement

László Erdős: Conceptualization, Investigation, Data curation, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Ákos Bede-Fazekas:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – review & editing, Visualization. **Zoltán Bátori:** Investigation, Writing – original draft, Writing – review & editing. **Christian Berg:** Investigation, Writing – original draft, Writing – review & editing. **György Kröel-Dulay:** Investigation, Writing – original draft, Writing – review & editing. **Martin Magnes:** Investigation, Writing – original draft, Writing – review & editing, Project administration, Funding acquisition. **Philipp Sengl:** Investigation, Writing – original draft, Writing – review & editing, Visualization. **Csaba Tölgyesi:** Investigation, Writing – original draft, Writing – review & editing. **Péter Török:** Investigation, Writing – original draft, Writing – review & editing, Funding acquisition. **Jack Zinnen:** Conceptualization, Methodology, Software, Formal analysis, Writing – original draft, Visualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Laszlo Erdos reports financial support was provided by Tempus Public Foundation. Zoltan Batori reports financial support was provided by National Research Development and Innovation Office. Peter Torok reports financial support was provided by National Research, Development and Innovation Office. Csaba Tolgyesi reports financial support was provided by National Research Development and Innovation Office.

Acknowledgements

The authors are thankful to Dolly Tolnay for her work with the databases during this research. The work of L. Erdős was supported by the Hungarian Eötvös Scholarship (grant number 156951). Z.Bátori was supported by the NKFIH K 124796, while P. Török by the NKFIH K 119225 and K 137573 grants. C. Tölgyesi was supported by the Hungarian National Research, Development and Innovation Office (Grant No. PD132131). Special thanks to J.W. Matthews and C. Peterson for feedback on writing and content during the later phases of the manuscript. Feedback from an anonymous reviewer improved the earlier

version of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.108707.

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