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Title: Disturbance indicator values for European plants

Keywords: bioindicator; ecological niche; Ellenberg value; expert judgement; functional trait; plant life form

Manuscript category: DATA ARTICLE

Abstract

Motivation Indicator values are numerical values used to characterize ecological niches of species and estimate their occurrence along gradients. While indicator values on climatic and edaphic niches of plant species hare received considerable attention in ecological research, data on species optimal positioning along disturbance gradients are less developed. Here, we present a new data set of disturbance indicator values identifying optima along gradients of natural and anthropogenic disturbance for 6,382 vascular plant species based on the analysis of 736,366 European vegetation plots and using expert-based characterization of disturbance regimes in 236 habitat types. The indicator values presented here are crucial for integrating disturbance niche optima into large-scale vegetation analyses and macroecological studies.

Main types of variables contained We set up five main continuous indicator values for European plants: disturbance severity, disturbance frequency, mowing frequency, grazing pressure and soil disturbance. The first two indicators are provided separately for the whole community and the herb layer. We calculated the values as the average of expert-based estimates of disturbance values in all habitat types where a species occurs, weighted by the number of plots in which the species occurs within a given habitat type.

Spatial location and grain Europe. Vegetation plots ranging in size from 1 m^2 to 1,000 m^2.

Time period and grain Vegetation plots mostly sampled between 1956 and 2013 (= 5th and 95th quantiles of the sampling year, respectively).

Major taxa and level of measurement Species-level indicator values for vascular plants.

Software format .csv file.

1 Introduction

Disturbance is a major driver of vegetation dynamics, influencing plant growth and species interactions (Huston 1979; Pickett & White 1985; McIntyre, Lavorel, Landsberg, & Forbes 1999), with consequences for the realized niche and distribution of species (Sheil, 2016). For practical purposes, disturbance has been defined by plant ecologists as mechanisms that limit plant biomass through its partial loss or complete destruction (Grime, 1979; van der Maarel, 1993; White & Jentsch, 2001). Thus, disturbance is thought to play a strong role in the functional differentiation of plant communities (Grime, 1979; Westoby, 1998).

In contrast to the major climatic and soil niches of species described by, for instance, Ellenberg indicator values (EIVs) (Ellenberg et al., 1992), the estimation of species disturbance optima has received less attention in the literature (but see Frank & Klotz 1990; Landolt et al. 2010; Grime, Hodgson, & Hunt 2014). Thus, to deepen our understanding of plant community responses to global environmental changes, as well as to improve disturbance–dependent ecosystem management strategies, we need to integrate analyses of the disturbance niche (namely, the species optimal positioning within disturbance gradients) into ecological studies.

A common approach in ecology is to link species response to disturbance with morpho-physiological functional traits (Laliberté, Shipley, Norton, & Scott 2012; Vandewalle et al. 2013; Jäschke, Heberling, & Wesche 2020). For example, the 'competitor, stress-tolerator, ruderal' (CSR) theory has been proposed to identify main plant strategy classes based on functional traits (Grime, 1979; Pierce et al., 2017).

Nonetheless, approaches based on functional traits are problematic for many reasons. First, we cannot expect traits and trait combinations to describe disturbance with sufficient accuracy because plants may respond to the same disturbance event with alternative strategies (Marks & Lechowicz, 2006). Second, disturbance consists of at least two separate dimensions, the severity of an event and its frequency (Turner, 2010), which are not easily separated by the use of plant traits. In addition, the large variety of physical processes characterizing disturbance (such as fire, wind, grazing, cutting and soil disturbance) further complicates trait-based characterization of disturbance regimes in vegetation. Finally, circular reasoning may occur in studies examining the response of plant traits to disturbance gradients when plant traits are used as proxies for disturbance, which precludes testing trait-disturbance relationships (Götzenberger, Kühn, & Klotz 2008).

For these reasons, Herben, Chytrý, & Klimešová (2016) proposed an alternative approach to estimate species-level disturbance indicator values independently of plant traits. Such indicator values were based on the number of species' occurrences in vegetation plots classified by severity and frequency of disturbance regimes estimated by experts for different habitat types. The indicator values reported by Herben et al. (2016) have been proved to meet theoretical expectations for functional differentiation in plants, particularly with respect to life history categories and clonality (Herben, Klimešová, & Chytrý 2018a). However, such indicator values have been calculated only for 1,248 vascular plant species occurring in the Czech Republic and did not include specific indicator values for mowing frequency and grazing pressure – two key disturbance types affecting European vegetation of managed herbaceous ecosystems. Other expert-based indicator values have been proposed for mowing and grazing in Europe. However, they are limited in terms of the species pool and region, such as Central Russia (Ramenskii, Tsatsenkin, Chizhikov, & Antipin 1956), Germany (Briemle, Nitsche, & Nitsche 2002) and the Alps (Jouglet, 1999; Landolt et al., 2010). In addition, disturbance indicators related to the concept of hemeroby (i.e. unnaturalness of vegetation due to human impacts) have been proposed for some European plants (see e.g. Hill et al. 2002), but they do not distinguish between frequency and severity and combine other human-affected processes with disturbance, namely nutrient availability and dispersal.

Here we present a data set of species-level disturbance indicator values for 6,382 vascular plants commonly found in Europe. The large number of species and geographic extent covered by our data set can stimulate the integration of plant-disturbance relationships in the field of macroecology, functional biogeography and large-scale European vegetation monitoring and assessment.

2 Materials and Methods

We followed three main methodological steps to calculate disturbance indicator values (Figure 1): *a*) we selected vegetation plots and classified these to habitat types; *b*) we assigned expert-based disturbance values to the different habitat types; and *c*) we calculated species indicator values by averaging the disturbance values of the habitat types where the species occurred. Finally, we examined how indicator values were distributed across different main plant life forms and how they responded to functional traits and CSR values (Grime, 1979; Pierce et al., 2017). All analyses were performed using R version 4.1.0 (R Core Team, 2021).

2.1 Vegetation data and habitat classification

We based the calculation of indicator values on 1,263,388 georeferenced vegetation plots from the European Vegetation Archive (EVA; project 123; Chytrý et al. 2016; data retrieved on 5 May 2021). The plots were mostly located mostly in Europe, including a few sites in Greenland. Plots ranged from 53.5°W to 62.2°E longitude and 34.8°N to 80.1°N latitude.

We used the revised version of the EUNIS (European Nature Information System) Habitat Classification described by Chytrý et al. (2020) to classify vegetation plots to EUNIS habitat types (hereafter, 'habitats'). The classification was performed using the classification expert system EUNIS-ESy (Chytrý et al. (2020); version 2021-06-01, DOI: 10.5281/zenodo.4812736). This system identifies habitats based on species composition and cover-abundances of particular species or species groups, accounting for the abiotic environment and geographic location as classification criteria (Chytrý et al., 2020). The system evaluates each vegetation plot in terms of species composition and cover and checks whether it meets the formal pre-defined assignment criteria of different habitats. Some plots cannot be classified to a specific habitat, either because transitional species compositions are simultaneously assigned to multiple habitats or the unusual species composition prevents the classification of the plot to an existing habitat.

We classified 842,218 plots into 236 EUNIS habitats. The remaining plots could not be classified. We further removed plots with coordinate uncertainty greater than 5 km and plots with an area smaller than 1 m^2 and greater than 1,000 m^2, leaving 736,662 vegetation plots available for indicator value calculations. In the final selection, we retained plots with unknown coordinate uncertainty (18.5%) and plot size (26.0%), otherwise an important part of the geographical coverage (e.g. France) would have been lost. The selected plots were mostly sampled between 1956 and 2013 (= 5^{th} and 95^{th} quantiles of the sampling year, respectively).

The vegetation plots from EVA cover a substantial part of the geographical range of most native European plants, but the native range of alien species is obviously not well represented by these data. We assume that species-disturbance relationships are constant within species geographic range. However, we acknowledge the importance of future investigation of species-disturbance relationships depending on species ranges, particularly for non-native species.

2.2 Estimation of habitat-level disturbance values

To calculate species-level indicator values, we assigned expert-based disturbance values to each of the 236 habitats, assuming that habitats are sufficiently homogeneous in this respect and that the same disturbance values can be reasonably assigned to different plots classified within each habitat. The values of disturbance variables were estimated based on the personal field experience of members of our author team and information from the literature.

To evaluate disturbance regimes in habitats, we used the absolute definition of disturbance (White & Jentsch, 2001), which relates disturbance to measurable changes (losses) in plant community biomass (Grime, 1979). In addition, we only considered disturbance of the whole community (or its whole vegetation layers) and not disturbance affecting just small patches or single individuals within the community (van der Maarel, 1993). For example, in forests, the destruction of the tree layer by stand-replacing windstorm was considered a disturbance event, but not the fall of individual dead trees. We considered both regular disturbances (e.g. annual mowing or burning of grassland, agricultural management of arable land or planned logging of a mature managed forest) and irregular disturbances (e.g. wildfires or extreme drought events).

The estimated variables included disturbance severity, disturbance frequency, mowing frequency, grazing pressure, and soil disturbance. Disturbance severity and frequency refer to all possible types of disturbance that may occur in a given habitat, including anthropogenic and natural disturbance as well as grazing and mowing. Conversely, mowing frequency, grazing pressure and soil disturbance were estimated separately for such factors. Soil disturbance specifically refers to any factor causing plant biomass death from soil turning and furrowing.

Because one habitat can be affected by more than one disturbance, we estimated values for the disturbance severity and disturbance frequency of the disturbance type we considered most important for a given habitat. If we considered two or more disturbance types with comparable importance in the same habitat (for example, soil erosion and grazing in rocky grasslands), we estimated their combined effects. We considered the following disturbance types (from most to least frequent): grazing, fire, logging, substrate movement, vegetation removal by humans, wave and current action, erosion, flooding, trampling, pathogen outbreaks, mowing, windthrow, arable land management, drought, inundation, frost, volcanic activity and snow movement. All disturbance types are described in Table S1.1 (Appendix S1 Supporting Information).

Estimates of disturbance severity, grazing pressure and soil disturbance reflect the mean fraction of above-ground vegetation biomass destroyed by a single disturbance event typical of that habitat. We estimated one value for each variable and habitat type, ranging from 0 (no change in biomass) to 1 (complete loss of plant cover). Disturbance frequency and mowing frequency correspond to the estimated mean interval (in years) between two consecutive disturbance or mowing events.

We further considered separate values of disturbance frequency and severity estimated for the whole plant community (including all vegetation layers) and values considering only the herb layer (Herben et al., 2016). This separation was necessary to account for the fact that disturbance regimes in the tree and shrub layers differ in severity and frequency from the disturbance regimes in the herb layer of the same community. For habitats with herbaceous vegetation only, the whole-community values were equal to the herb-layer values.

In Appendix S1 (Supporting Information), we report additional details on the criteria used to assign disturbance values to habitats. Table S1.1 also includes the description and range of periodicity of disturbance types that were used to assign mean disturbance frequency on the habitats. The list of habitats, their disturbance values and the most important type of disturbance evaluated for each of them are reported in the Zenodo public data repository (link).

2.3 Indicator value calculation

Before calculating species indicator values, we stratified vegetation plots by geographical location and habitat to reduce local oversampling of certain vegetation types. We randomly selected one plot for each habitat that fell within each cell of a grid with a resolution of 0.00225°, corresponding approximately to a 250 m grid. We repeated this process 999 times. Each repetition resulted in a selection of 439,213 plots. Across all draws, 736,366 different vegetation plots were used (see Figure S2.1; Appendix S2 Supporting Information).

We followed an approach similar to Herben et al. (2016) to calculate disturbance indicator values. For each repetition of vegetation plot selection, we calculated disturbance indicator values for each species occurring in at least 20 plots as the average of the expert-based disturbance values, weighted by the number of plots where the species occurs in each habitat. We then calculated the final indicator value for each species by taking the median of the weighted mean of the disturbance values over the whole set of repetitions. Finally, we excluded those species that were retained for the indicator values calculation fewer than 10 times across the whole set of repetitions, resulting in 6,382 species. We did not include cultivated plant species because indicator values for these species were increased by disturbance in cultivated land affecting all other species. Nevertheless, we included fruit tree species (e.g. *Prunus domestica*) or occasionally cultivated species (e.g. *Fragaria vesca*) because they may occur spontaneously in the vegetation.

For habitats that are never mown (207 of 236), we assigned a default value of 100 years of mowing return time to calculate mowing frequency values for species occurring in both mown and unmown habitats. To calculate disturbance and mowing frequency of species, we used the inverse of return time, which is the mean interval between successive disturbance events. We $\log_{10}$-transformed disturbance and mowing frequency to account for their positively skewed distribution. To avoid negative values in the scale after the log-transformation, we expressed return times in centuries (i.e. years/100).

To provide a measure of uncertainty due to the 999 draws following a stratified resampling design of vegetation data from EVA, we also calculated and reported the standard deviation of the weighted mean of disturbance values. Furthermore, we explored whether plot size had an effect on indicator values and if the minimum threshold of 20 plots retained for each species is sufficient to perform the calculation. We report methodological details and results of these analyses in Appendix S3 (Supporting Information).

2.4 Indicator value relationship with plant characteristics

We further assessed how the indicator values were distributed across the main plant life forms described by Raunkiær (1905) (i.e. therophyte, hydrophyte, geophyte, hemicryptophyte, chamaephyte and phanerophyte) and how they were related to the plant traits of the leaf-height-seed (LHS) scheme (Westoby, 1998), namely, specific leaf area (SLA), plant vegetative height and seed mass. These functional traits represent fundamental trade-offs of plants controlling their growth rate, competitive ability and dispersal ability. Therefore, all of these traits have been hypothesized to be involved in the response to disturbance (Laliberté et al., 2012; Vandewalle et al., 2013).

Plant life forms were compiled for a subset of 6,116 species. We discarded those species for which we were not able to determine their plant life form. Functional trait data were compiled for a subset of 5,057 species in total (2,369 for SLA; 4,717 for plant height; 3,391 for seed mass) using the

LEDA trait database (Kleyer et al., 2008). Missing values that could not be retrieved from LEDA were taken from TRY (Kattge et al., 2020) and other databases to obtain as much trait information as possible. Additional databases consulted for functional traits were Flora d'Italia (Pignatti, Guarino, & La Rosa 2017-2019) and the Pladias Database of the Czech Flora and Vegetation (Chytrý et al. 2021, www.pladias.cz) for plant height; D^3 (Hintze et al., 2013), the Seed Information Database (Royal Botanic Gardens Kew, 2021) and PICOS (García-Gutiérrez et al., 2018) for seed mass; trait data reported by Ladouceur et al. (2019) for SLA; and BROT2.0 (Tavşanoğlu & Pausas, 2018) for both seed mass and SLA. See Table S4.1 and Table S4.2 (Appendix S4, Supporting Information) for additional details on the number of species for each plant life form and the number of trait data observations retrieved from each database, respectively.

We visually inspected box plots to explore how indicator values were distributed across different plant life forms. Based on the rationale that the positioning along the disturbance gradient affects plant functional traits of individual species, we fitted linear mixed-effect models using functional traits as dependent variables and the disturbance indicator values as predictors allowing for inclusion of a quadratic term when significantly improving the goodness of fit (i.e., the Akaike Information Criterion). We modeled potential phylogenetic dependencies by using family and genus of the species as a nested random intercept term ($\sim 1 \mid \textit{family} \;/\; \textit{genus}$). We applied such analyses on the five main indices reported here, namely disturbance severity and frequency (both measured at the whole-community disturbance level), mowing frequency, grazing pressure and soil disturbance.

Finally, we also compared the 'competitor, stress-tolerator, ruderal' (CSR) scores defined by Pierce et al. (2017) to the disturbance indicator values and reported the results of these analyses in Appendix S4 (Supporting Information). We fitted linear mixed effect models to test how the C, S and R scores explain variation in disturbance indicator values (Figure S4.2) and we compared indicator values grouped by main categorical strategy classes (Figure S4.3). To calculate CSR values, we used a subset of 1,683 species present in our data set for which SLA, leaf dry matter content (LDMC) and leaf area (LA) were available from the Pladias Databasee (Chytrý et al. 2021) and TRY (Kattge et al., 2020).

3 Data structure and patterns

3.1 General description

The data set contains five main independent indicator values encompassing different dimensions of disturbance for 6,382 species of the European vascular flora: disturbance severity, disturbance frequency, grazing pressure, mowing frequency and soil disturbance. In addition, the data set includes species indicator values for disturbance severity and frequency for the herb layer (Table 1). The data set includes the most frequent species of the European flora based on the frequency of their records in the EVA database, including both native European and alien plant species belonging to 166 plant families. We report figures on how the species are distributed into habitat groups and most frequent families in Appendix S5. In addition, for each species we report both the number of times the species was present in at least 20 plots of the 999 repetitions used to calculate the indicator values and the number of habitats (median) in which the species occurred in the repetitions. We also include the uncertainty (standard deviation) of each indicator value obtained across the 999 repetitions (see Figure S6.1,

Appendix S6, Supporting Information). Uncertainty is higher in species occurring in a low number of habitats with contrasting disturbance regimes. The nomenclature of species and families found in the data set is based on Euro+Med PlantBase (2021).

In general, disturbance indicator values estimate the realized disturbance niche optimum of a species because they are based on species occurrences in sampled vegetation. These indicator values provide information about the ecology of the species in terms of the main characteristics of the disturbance events that occur in the vegetation types where the species most frequently occurs. For example, the highest values of disturbance severity are found in weed flora of arable land (e.g. *Cyanus segetum*, *Ranunculus arvensis*). In contrast, the lowest values of disturbance severity are found in many species occurring in marshes (e.g. *Carex limosa*), high-mountain cliffs (e.g. *Campanula morettiana*, *Androsace* spp.) and some aquatic plants (e.g. *Potamogeton* spp.). Similarly, the lowest values of mowing frequency are found in all the species associated with various never-mown habitats, while the highest values are found in species commonly occurring in fertile hay meadows (e.g. *Crepis biennis*, *Schedonorus pratensis*, *Trisetum flavescens*), which are the most frequently mown habitats.

The indicator values presented here showed low correlation among each other (Figure 2). This result supports the multidimensional nature of disturbance as a factor and highlights the importance of using different facets of indicator values when assessing disturbance in vegetation. However, disturbance severity and frequency in the herb layer showed higher correlations with other indicator values (Figure S6.2, see Appendix S6 Supporting Information). For this reason, in this manuscript we focused on disturbance severity and frequency at the whole-community level in this manuscript, rather than focusing on disturbance values in the herb layer.

3.2 Potential for ecological research

The indicator values proposed here are a tool for evaluating plant community composition and function in relation to disturbance. For example, by calculating community-level means of disturbance values, our indicator values could be used to explore plant taxonomic and functional diversity along disturbance gradients. Furthermore, we believe that characterizing species disturbance niche optima could be used to improve the effectiveness of restoration and conservation strategies based on modifying disturbance regimes in vegetation.

Importantly, the disturbance indicator values were determined based on species occurrence in habitats. Our approach makes them independent of species traits and allows us to avoid circular reasoning when focusing on the response of plant functional traits to disturbance gradients. When analyzed in relation to plant characteristics, we encountered clear differences in all types of indicator values between plant life forms (Figure 3). For example, annual plants (therophytes) had higher values of disturbance severity, disturbance frequency and soil disturbance, consistent with the theoretical expectation by Grime (1979) that disturbance favour more annual plants in vegetation. Similarly, lower disturbance frequency for phanerophytes and, to a lesser extent, geophytes, reflects that less intensive disturbance regimes favour the establishment of slow-growing woody plants and those with underground storage organs (McIntyre et al., 1995). These results are consistent with the analyses of Herben et al. (2018a), but with a larger number of species and a wider geographical extent. Nevertheless, both mowing frequency and grazing pressure showed little difference among plant life forms, except for hydrophytes and phanerophytes, which usually grow at other sites than those managed by mowing or grazing.

Although the linear models showed very low R^2 values, we detected some significant relationships between plant functional traits (plant height, seed mass and SLA) and disturbance indicator values (Figure S2.2, Appendix S2 Supporting Information). Overall, most of the models analyzed indicated significant quadratic relationships, reflecting previous results obtained for Czech flora (Herben et al., 2018a). For example, the functional traits initially decreased and then increased with increasing disturbance frequency. Furthermore, SLA and height generally decreased with increasing grazing pressure. Overall, these results suggest that the disturbance indicator values presented here can be used as explanatory variables to explore the underlying mechanisms of trait variation along disturbance gradients. However, the mechanisms explaining why the relationships are mostly quadratic (rather than linear) are still poorly understood, and previous analyses have shown that productivity, rather than disturbance, is a better predictor of the plant functional traits of the LHS scheme (Herben et al., 2018a). Finally, we highlight that the low association of the CSR scores with disturbance indicator values (see Appendix S4) likely depend on the differences between the theory of (Grime, 1979) and our approach. The CSR scores represent the trade-off in terms of both disturbance and productivity along three main axes (= plant strategies) so that the adaptation to disturbance is not the same under different levels of productivity (Herben et al., 2018b). Conversely, although distinguishing between frequency and severity, our indicator values focus on disturbance only, independently of the functional adaptation of plants to other components.

4 Conclusions

Quantifying disturbance niche and disturbance optimum of individual plant species is a relevant goal for ecological research, as disturbance is an important driver of plant biodiversity and function. Here we presented disturbance indicator values based on expert quantification of disturbance in different habitats. This data set extends previous work conducted for the Central European flora (Herben et al. 2016; Herben et al. 2018a) by including a larger pool of species for the whole European continent and introducing new indicator types – specifically, grazing pressure and mowing frequency.

While our data set focused specifically on disturbance for the European flora, we believe that our approach can be used to develop indicator values in any other system where sufficient species occurrence data and expert knowledge on habitats is available. We nevertheless emphasize that using expert estimates of habitat types to quantify species' ecological optima is based on some assumptions that must be considered when using the indicator values. In particular, we assume that disturbance regimes within the same habitat type are the same in time and space, and that species occurrence in such habitats corresponds to their optimal ecological positioning. Nevertheless, the approach presented here allows us to assess disturbance across a large number of species and, more importantly, to disentangle disturbance from other – often confounded – ecological components, such as stress, competition and productivity.

For these reasons, we anticipate that the data set presented here may facilitate and stimulate the inclusion of disturbance into macroecological research. Such indicator values can be used, for instance, to test how plant morpho-physiology and functional composition of plant communities respond along disturbance gradients (Herben et al. 2018a), and can help improve the characterization of plant functional groups for dynamic models of vegetation and plant biodiversity (Boulangeat et al., 2012).

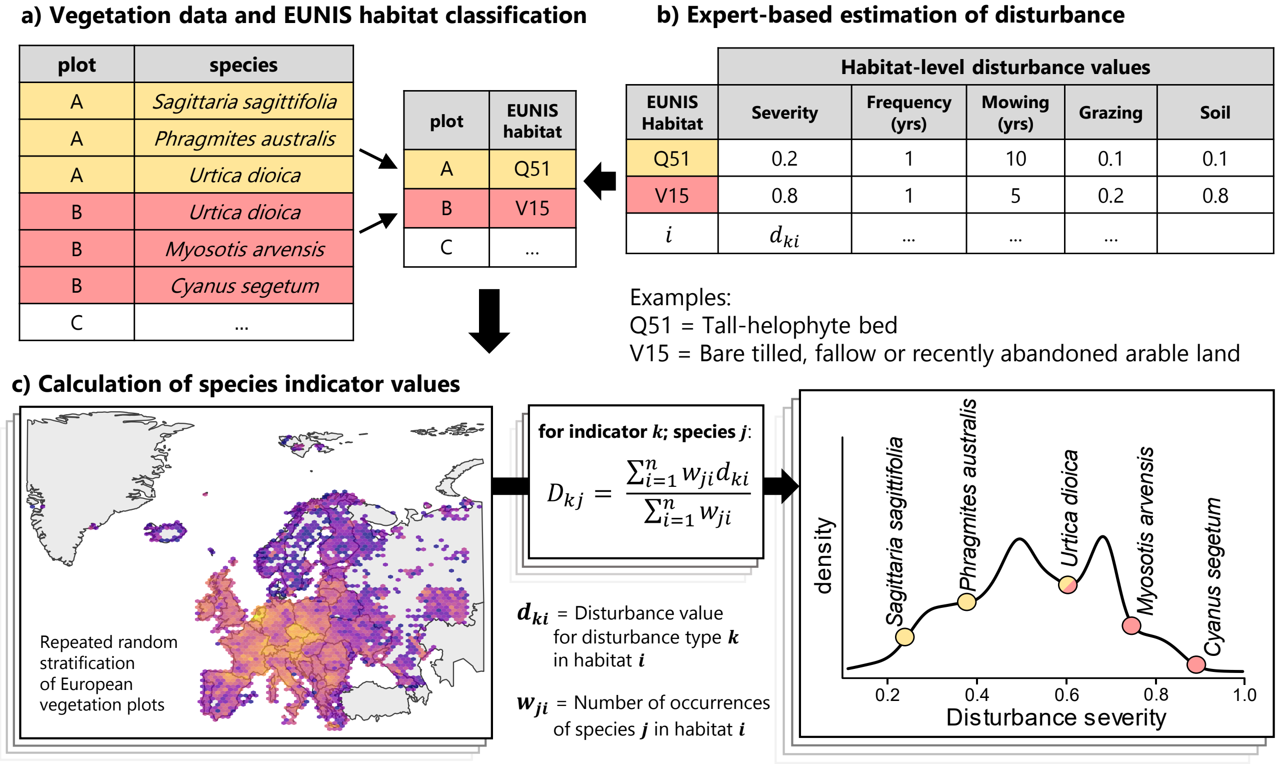
DATA AVAILABILITY STATEMENT

The data set is freely available in the Zenodo public data repository (https://zenodo.org/). *N.B: the data will be made freely available at the time this manuscript is accepted for publication.* **Since Zenodo does not support the upload of data for double-blind revision, the data can be currently downloaded at the following link: https://figshare.com/s/63ea83c4d650c5fdddea**)

Table 1: Summary of the disturbance indicator values reported in the data set.

Indicator (species-level)	**Description (habitat-level)**	**Values**	
		Scale	**Range**
Disturbance severity at the whole-community level	Mean magnitude of disturbance events (proportion of aboveground biomass killed by disturbance)	Proportional (0–1)	0.10 – 0.96
Disturbance severity in the herb layer			0.10 – 0.96
Disturbance frequency at the whole-community level	Mean frequency of disturbance events	$\log_{10}(100/\text{years})$	0 – 2.63
Disturbance frequency in the herb layer			0.40 – 2.63
Mowing frequency	Mean frequency of mowing (i.e. cutting of plant biomass)	$\log_{10}(100/\text{years})$	0 – 2.12*
Grazing pressure	Severity of grazing (proportion of aboveground biomass killed by grazing)	Proportional (0–1)	0 – 0.78
Soil disturbance	Proportional increase in cover of bare ground by furrowing or soil turning	Proportional (0–1)	0 – 0.94

∗ Values equal to zero correspond to 100-year return mowing time assigned by default to never-mown habitats (see Materials and Methods)



plot	species
A	*Sagittaria sagittifolia*
A	*Phragmites australis*
A	*Urtica dioica*
B	*Urtica dioica*
B	*Myosotis arvensis*
B	*Cyanus segetum*
C	...

plot	EUNIS habitat
A	Q51
B	V15
C	...

	Habitat-level disturbance values				
EUNIS Habitat	Severity	Frequency (yrs)	Mowing (yrs)	Grazing	Soil
Q51	0.2	1	10	0.1	0.1
V15	0.8	1	5	0.2	0.8
i	d_{ki}	...	...	...	

Examples:
Q51 = Tall-helophyte bed
V15 = Bare tilled, fallow or recently abandoned arable land

$$D_{kj} = \frac{\sum_{i=1}^{n} w_{ji} d_{ki}}{\sum_{i=1}^{n} w_{ji}}$$

$\boldsymbol{d_{ki}}$ = Disturbance value for disturbance type $\boldsymbol{k}$ in habitat $\boldsymbol{i}$

$\boldsymbol{w_{ji}}$ = Number of occurrences of species $\boldsymbol{j}$ in habitat $\boldsymbol{i}$

Figure 1: Methodological workflow to calculate disturbance indicator values including some examples for contrasting species and habitats. *a)* Based on vegetation-plot data from the European Vegetation Archive (EVA), we classified plots to habitat types of the European Nature Information System (EUNIS). *b)* We assigned disturbance values to each EUNIS habitat based on expert judgement. *c)* We stratified vegetation plots by geographical location and for each disturbance indicator and species, we calculated disturbance indicator values as the average of expert-based disturbance values, weighted by the number of plots where the species occurs in each habitats.

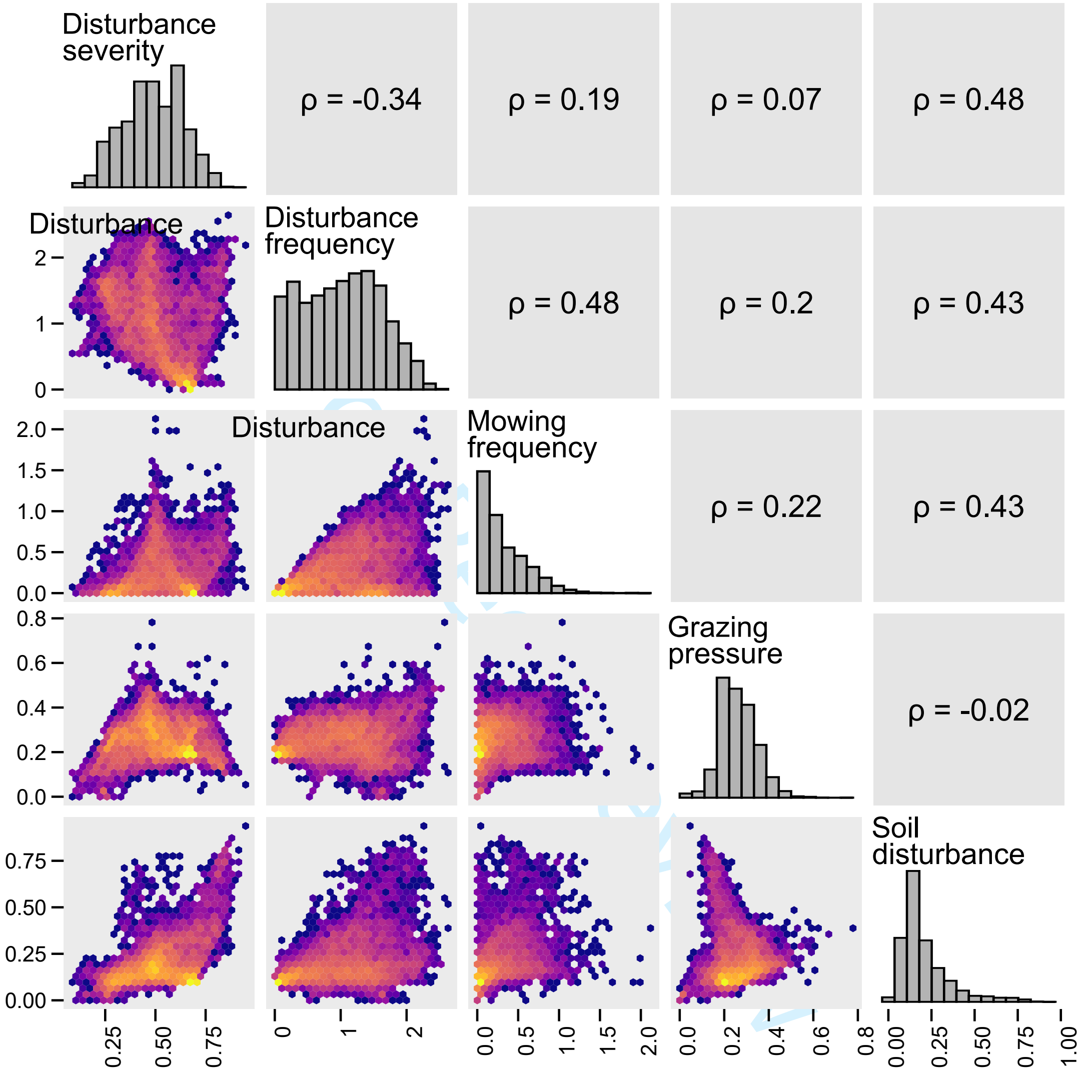


Figure 2: Distributions and pairwise correlations between the main disturbance indicator values in the data set. The diagonal represents the distribution of indicator values. The top-right panels show Pearson's correlation coefficient. The bottom-left panels show density scatter plots, with lighter colors corresponding to a higher density of data points. Disturbance severity and frequency correspond to indicator values estimated at the whole-community level. See Figure S6.2 (Appendix S6 Supporting Information) for a complete correlation matrix including values for disturbance severity and frequency in the herb layer.

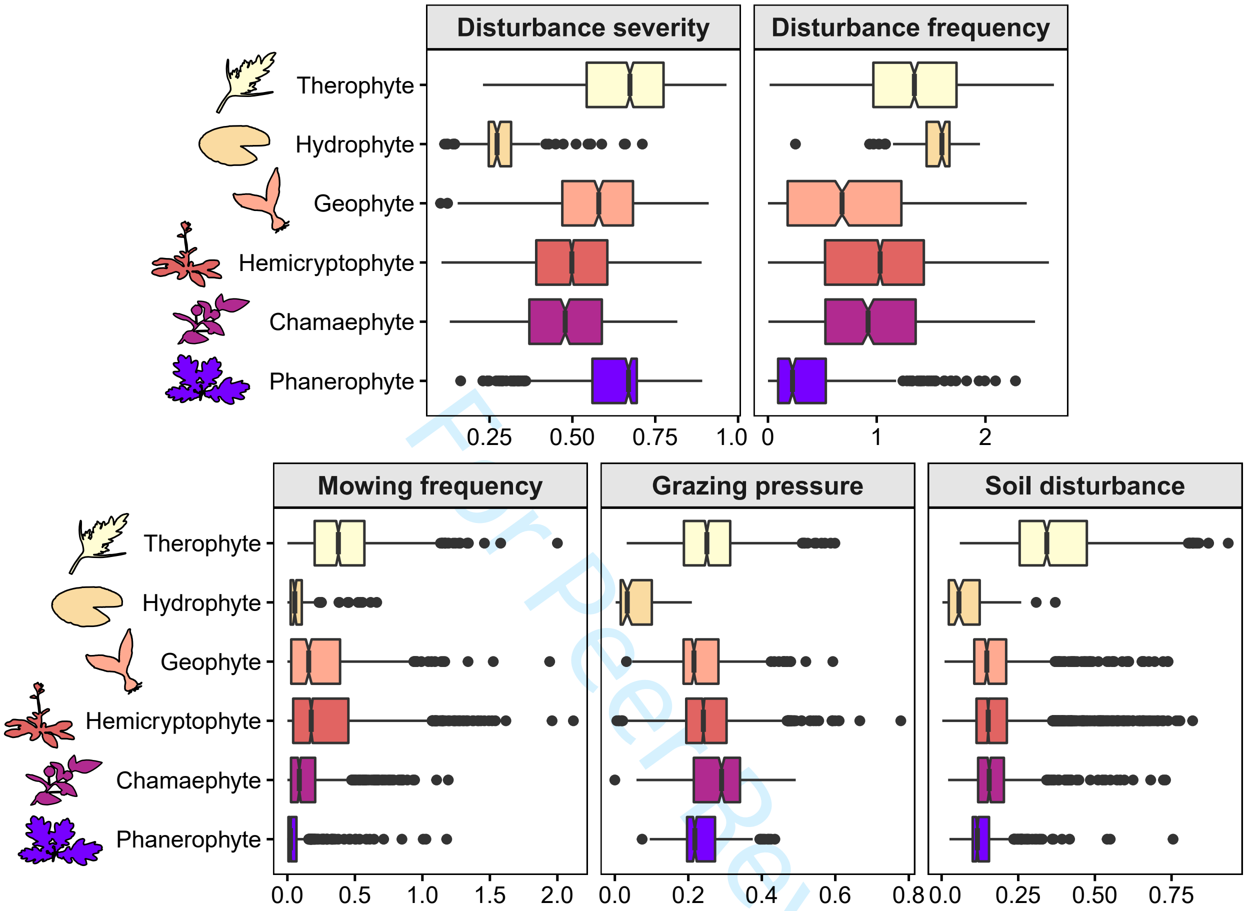


Figure 3: Distribution of the main disturbance indicator values across major plant life forms. Box-plots were generated for a subset of 6,116 species for which data on plant life form were available. The box represents the 50% of the central data, with the line inside corresponding to the median and the notches to the confidence interval of the median. The whiskers represent the observations within 1.5 * interquartile range values. Disturbance severity and frequency correspond to indicator values estimated at the whole-community level.

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SUPPORTING INFORMATION

Appendix S1: Summary of expert-based assessment of disturbance in habitats

In this appendix, we provide additional information on the criteria applied to estimate disturbance values for different habitats of the European Nature Information System (EUNIS) habitat classification. The disturbance indicators were assigned by our author team based on our field experience and literature information.

Disturbance definition. We use the absolute definition of disturbance (White and Jentsch 2001, p. 405), relating disturbance to loss of plant community biomass (Grime 1979).

Community disturbance vs patch disturbance. We focused on disturbance of the whole communities or their highest vegetation layers rather than disturbance of small patches within the community (van der Maarel 1993). For example, we consider the destruction of the forest tree layer by stand-replacing windstorm, but we do not consider the fall of individual old trees in a forest.

Regular and irregular disturbances. We consider both the regular disturbances (e.g. annual mowing or burning of grassland, agricultural management of arable land or planned logging of a mature managed forest) and irregular disturbances (e.g. wildfires or extreme drought events in grasslands), and estimated the inverse of disturbance frequency as the mean return time.

Habitat-transforming vs non-transforming disturbances. We consider only those disturbances that do not transform a particular habitat type to another habitat type. For example, grazing in a pasture is considered.

Forest fire or logging is also considered when a forest regenerates in a disturbed area. In contrast, ploughing of a meadow that changes it to arable land is not considered. Mire draining and peat extraction are also not considered because they change the mire to a grassland, shrubland or successional forest.

Defining the most important disturbance type for each habitat. To assess disturbance in vegetation we considered the disturbance types reported in Table S1.1. Most habitats are affected by varying disturbance types characterized by different frequency and severity. For each habitat, we estimated disturbance frequency and severity for those disturbance types that cumulatively remove the most biomass over a long period (longer than the return time of the least frequent disturbance). For example, a temperate semi-dry grassland can be disturbed by both grazing that occurs in intervals of several weeks in particular spots and extreme drought events that occur irregularly once in 5 to 15 years. In this system, grazing cumulatively removes more biomass over a long period (e.g. 20 years); therefore, we consider grazing as the main disturbance type and estimate the disturbance frequency and severity for grazing, not drought events. In contrast, Mediterranean annual grasslands are occasionally grazed, but most of their biomass is killed annually by the advent of the dry period in the late spring. In this system, drought cumulatively removes more biomass than grazing; therefore, we consider drought as the main disturbance type.

In addition to the quantification of general disturbances, we estimated separately three specific types of disturbances: grazing pressure, mowing frequency and soil disturbance. These disturbance types were assessed for all the habitats, including those in which they are not the most important habitat types.

Table S1.1: Disturbance types considered for habitat-level estimation of disturbance values and their range of periodicity. The table reports number of times each disturbance type was considered as a main disturbance type in the 236 habitats.

Disturbance type	**Periodicity**	**Notes**	**Number of habitats**
Wave and current action	weeks to years	Mainly extreme events in water bodies during storms.	18
Flooding	years to decades	Biomass removals in terrestrial or semi-aquatic environments by the kinetic energy of sudden water flow, not due to inundation.	14
Inundation	years to decades	Longer inundations that kill the whole plant communities by submerging vegetation (not the kinetic energy of water), e.g. filling a drained pond; excludes, for example, daily inundation in saltmarshes in coastal tidal zones.	4
Frost	months to decades	Frost events that kill the whole plant communities, such as in the aquatic environment; excludes regular seasonal losses of foliage or shoots in perennial herbs.	2
Frost-related mechanical disturbance	weeks to years	Movement due to freeze-and-thaw cycles.	1
Drought	years to decades	Drought period coming suddenly after a period with abundant moisture; drought kills the whole plant communities and most or all plant individuals.	5
Windthrow	decades to centuries	Stand-replacing events in forest vegetation. It does not includes single tree falls.	8
Fire	years to decades		44
Volcanic activity	months to centuries		3
Substrate movement	weeks to years	Includes both gravitation-driven movements (such as on screes) and wind-driven movements (such as in sand dunes)	19
Erosion	days to millenia	Erosion of substrate (e.g. on cliffs and steep slopes)	17
Snow movement	years to decades	Avalanches and creeping snow movement on slopes	2
Logging	decades		40
Mowing	months to years	Including cutting of dwarf-shrub vegetation	9
Grazing	weeks to years	Including trampling by grazing animals	118
Trampling (humans)	days to weeks	Trampling by humans. Includes the movement of vehicles.	14

Vegetation removal by humans in settlements, around buildings and infrastructures	weeks to months	Including cuttings and herbicide application	18
Arable land management	months	Including tillage, herbicide application, weeding, hoeing	5
Pathogen outbreaks	decades	Outbreaks of pathogenic organisms (e.g. insect herbivores, fungi and bacteria)	11

- **Grazing pressure** included grazing by large herbivores, both domestic and wild, mainly mammals, but in saltmarshes, aquatic habitats and wetlands also by birds. Grazing by invertebrates and small vertebrate herbivores was not considered. Grazing pressure was estimated on a scale from 0 to 1, where 0 means that the habitat is not grazed and 1 means that all the vegetation is removed by grazing at least once a year.
- **Mowing return time (frequency)** is the time between two consecutive mowings *
- **Soil disturbance includes** mechanical disturbance of the soil surface or the upper soil layer by furrowing or soil turning. It is estimated on a scale from 0 to 1, where 0 means no soil disturbance and 1 means soil turning across the whole area of the habitat, such as ploughing on arable land.

* = For the habitats that are never mown, a value of 100 years was used for the calculation of species indicator values. See Materials and Methods of the main article.

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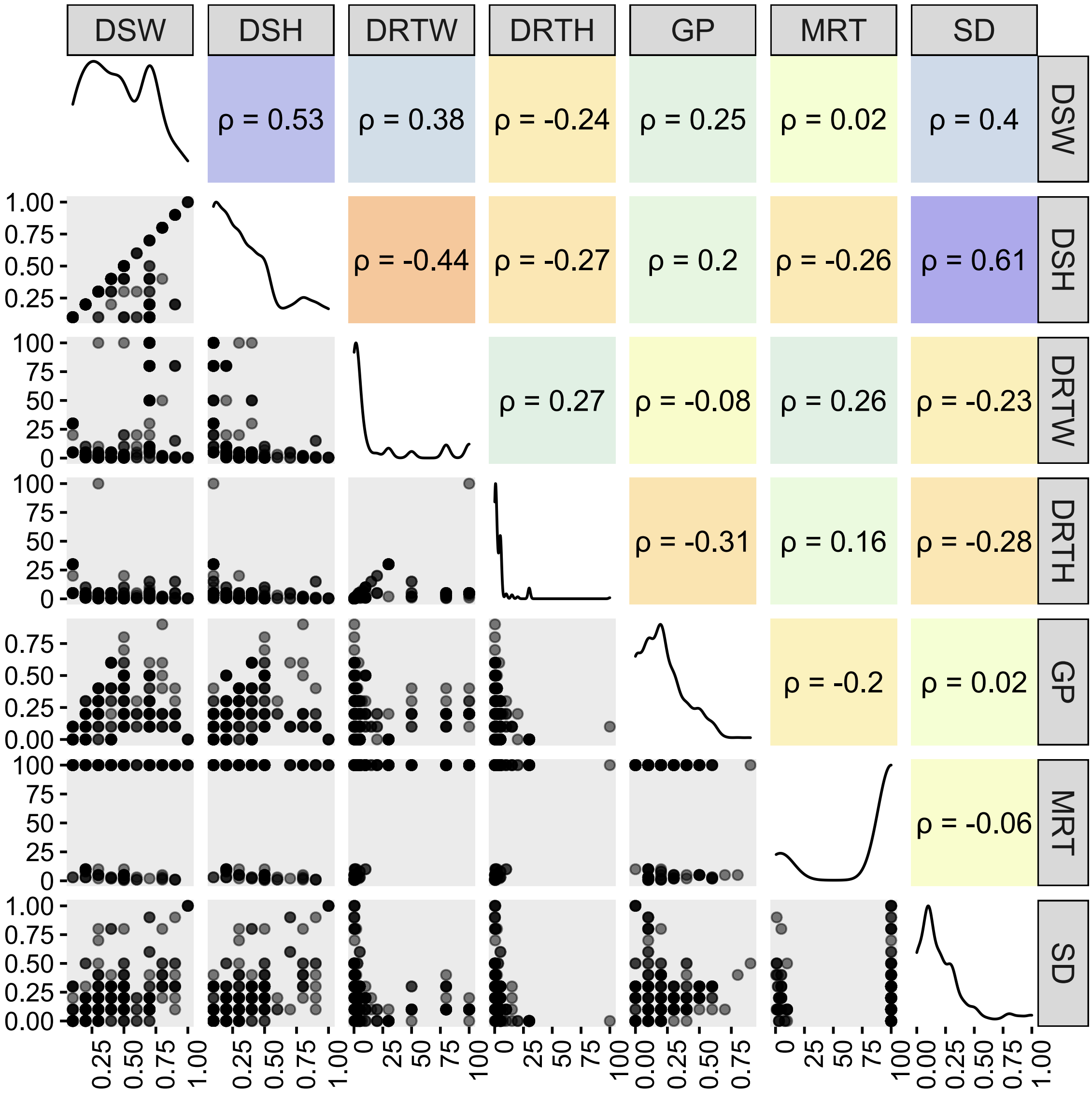

Figure S1.1: Density plots (diagonal), pairwise correlations (top-right) and scatter plots (bottom-left) for the disturbance values assigned to the 236 habitats. DSW = disturbance severity (at the whole community level); DSH = disturbance severity in the herb layer; DRTW = disturbance return time (at the whole community level); DRTH = disturbance return time in the herb layer; MRT = mowing return time; GP = grazing pressure; SD = soil disturbance. Return time for disturbance and mowing is expressed in years. A 100-year value was assigned by default to MRT for never mown habitats.

Appendix S2: Geographic distribution of vegetation data

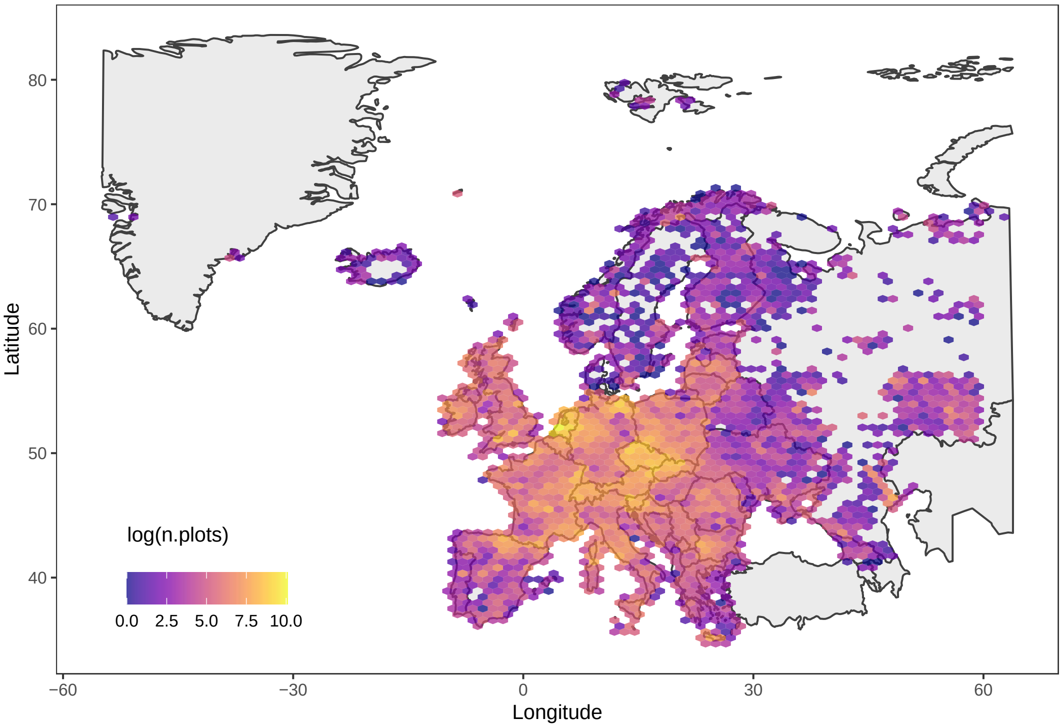

Figure S2.1: Geographic distribution of the density (on a natural logarithm scale) of vegetation plots from the European Vegetation Archive (EVA) used to calculate disturbance indicator values (736,366 in total, after 999 random stratification rounds).

Appendix S3: Sensitivity analyses

In this appendix we describe the methods and results of sensitivity analyses exploring the role of plot size in affecting indicator values and test the minimum plot number to calculate the indicator values.

First, to test the role of plot size on the indicator values, we subset our vegetation plot data by excluding plots with missing information on plot size and stratified the data set into three categories based on plot sizes ranges (i.e., ‘small’, ‘medium’, ‘large’), resulting in a total of 544,433 plots. The assignment to the three categories depended upon the vegetation type (see Table S3.1). Then, we recalculated the indicator values for each plot size range category and compared the results to our original values.

Table S3.1: Ranges of plot size for each category (= ’Small’, ’Medium’ and ’Large’). Range values were assigned differently to forest or non-forest vegetation. The table report the total percentage for each category over 544,433 plots.

Plot size category	**Plot size range (m^2)**		**% of plots**
	Forest	**Non-forest**	
‘Small‘	1 - 50	1 - 4	29.9
‘Medium‘	51 - 100	5 - 81	50.2
‘Large‘	101 - 1000	82 - 1000	19.9

We argue that plot size cannot affect directly disturbance indicators because expert-based disturbance values of habitat types were assigned independently from vegetation plot characteristics. Indeed, we show that patterns are consistent to our original indicator values (Pearson’s $r \geq 0.84$) (see Figure S3.1 and Figure S3.2). However, the values of disturbance indicators can slightly vary depending on plot size because the latter depend upon habitat types, from which disturbance values are derived.

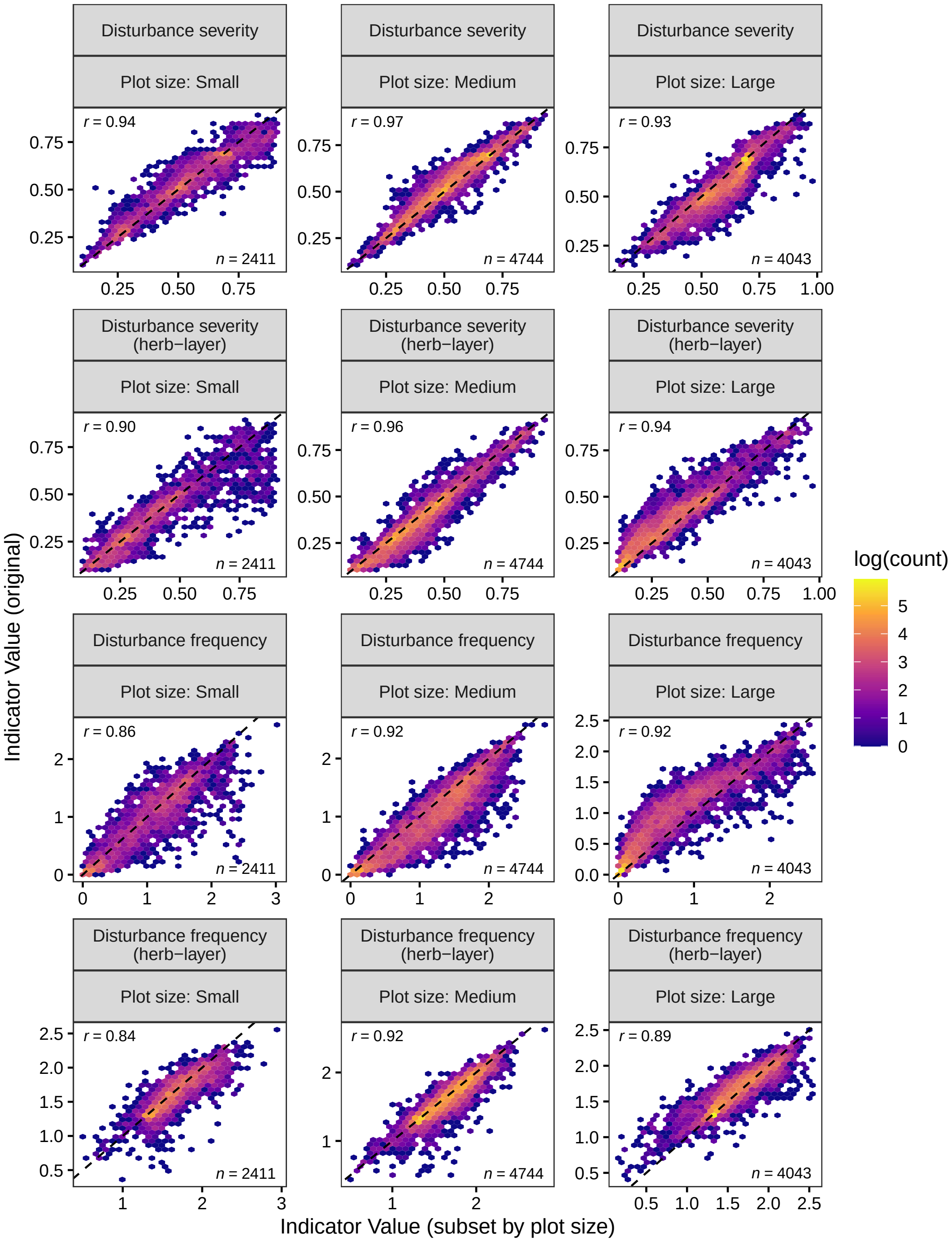

Figure S3.1: Relationship between our original indicator values (y-axis) and indicator values re-calculated for each subset of plot size category (= 'Small', 'Medium', 'Large') (x-axis) for disturbance severity and frequency (at the whole community level) and disturbance severity and frequency in the herb layer. The panels include the Pearson's correlation (r) and number of observations.

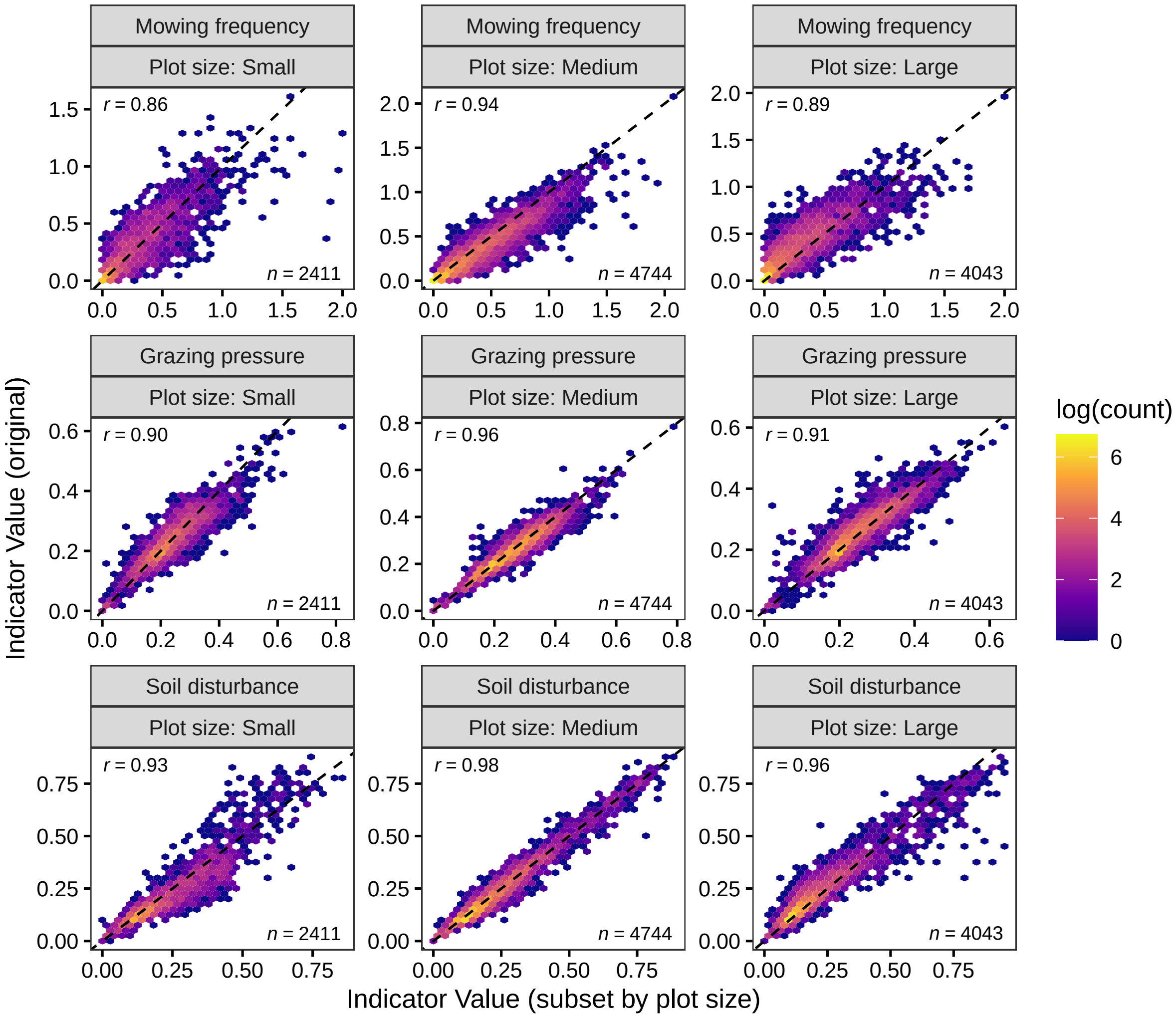

Figure S3.2: Relationship between our original indicator values (y-axis) and indicator values re-calculated for each subset of plot size category (= 'Small', 'Medium', 'Large') (x-axis) for Mowing frequency, Grazing pressure and Soil disturbance. The panels include the Pearson's correlation (r) and number of observations.

Second, to test that a minimum of 20 plots per species is sufficient for estimating disturbance indicator values, we report the results of a sensitivity analysis in which we recalculated the indicator values by randomly selecting, where possible, 20 plots only for each species in each of the 999 repetitions in which we calculated the disturbance indicator values. We show that the values obtained this way are nearly the same to disturbance indicator values reported in our main manuscript (Pearson's $r \geq 0.99$) (Figure S3.3), demonstrating that a minimum of 20 plots per species represent a robust threshold for calculating disturbance indicator values.

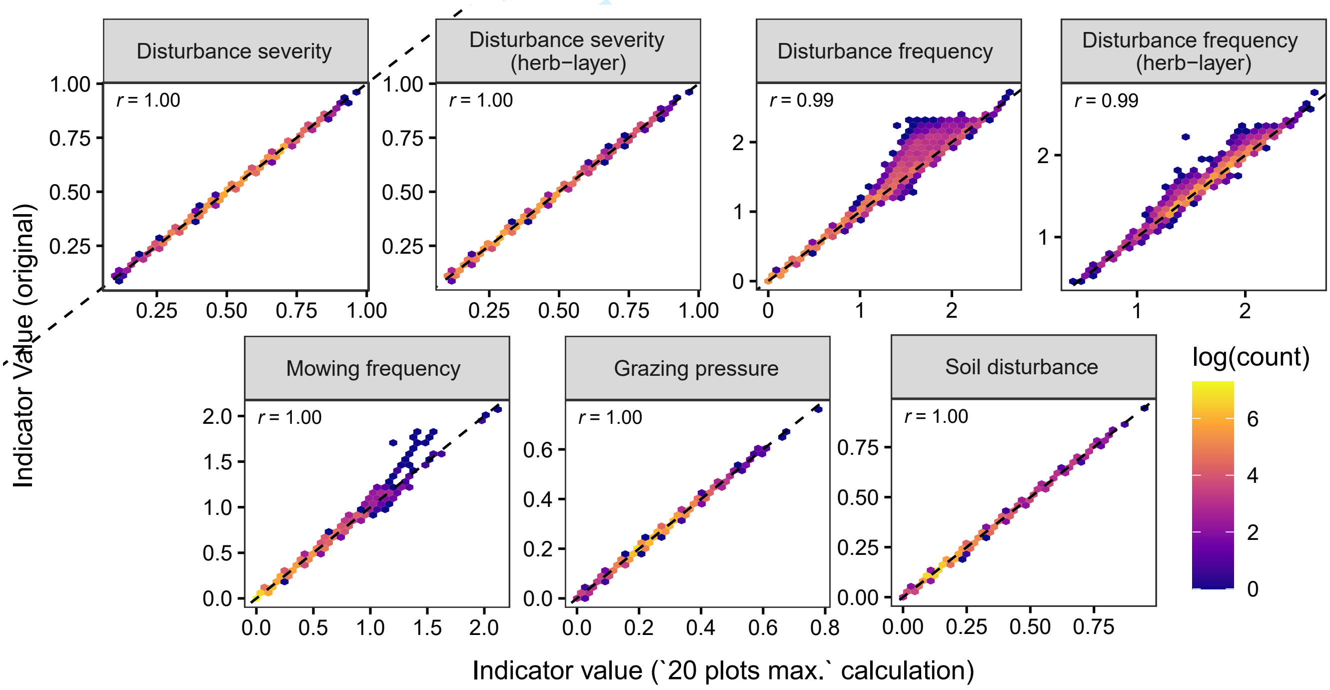

Figure S3.3: Relationship between our original indicator values (y-axis) and indicator values re-calculated by randomly selecting 20 plots for each species in each round (x-axis) across the 6,382 species. Pearson's correlation (r) was higher than 0.99 across all the pairwise comparisons.

Appendix S4: Plant functional traits and C-S-R data relationships with disturbance indicator values

Table S4.1: Number of species (observations) available for each plant life form. The table report both counts including those species that falls into more plant life form categories (data used for Figure 3 in the main manuscript), as well as the number of species for each category excluding the species falling into more than one plant life form category.

	Species number (observations)	
Plant life form	Multiple plant life form	Unique plant life form
Phanerophyte	546	508
Chamaephyte	656	437
Hemicryptophyte	3584	2902
Geophyte	700	364
Hydrophyte	120	89
Therophyte	1272	1059

Table S4.2: Number of species-level observations (trait data) retrieved from each database for each plant functional trait.

Database name	Plant height	Seed mass	SLA	Source
BROT2.0	-	361	305	Tavşanoğlu & Pausas (2018)
D^3	-	169	-	Hintze et al. (2013)
Flora d'Italia	2304	-	-	Pignatti et al. (2017-2019)
SID-KEW	-	89	-	Royal Botanic Gardens Kew (2021)
Ladouceur	-	-	48	Ladouceur et al. (2019)
LEDA	2149	244	1803	Kleyer et al. (2008)
PICOS	-	50	-	García-Gutiérrez et al. (2018)
PLADIAS	122	-	-	Chytrý et al. (2021)
TRY	142	678	213	Kattge et al. (2020)

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Ladouceur, E., Bonomi, C., Bruelheide, H., Klimešová, J., Burrascano, S., Poschlod, P., ... & Jiménez-Alfaro, B. (2019). The functional trait spectrum of European temperate grasslands. *Journal of Vegetation Science*, *30*(5), 777-788.

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Tavşanoğlu, Ç., & Pausas, J. G. (2018). A functional trait database for Mediterranean Basin plants. *Scientific Data*, *5*(1), 1-18

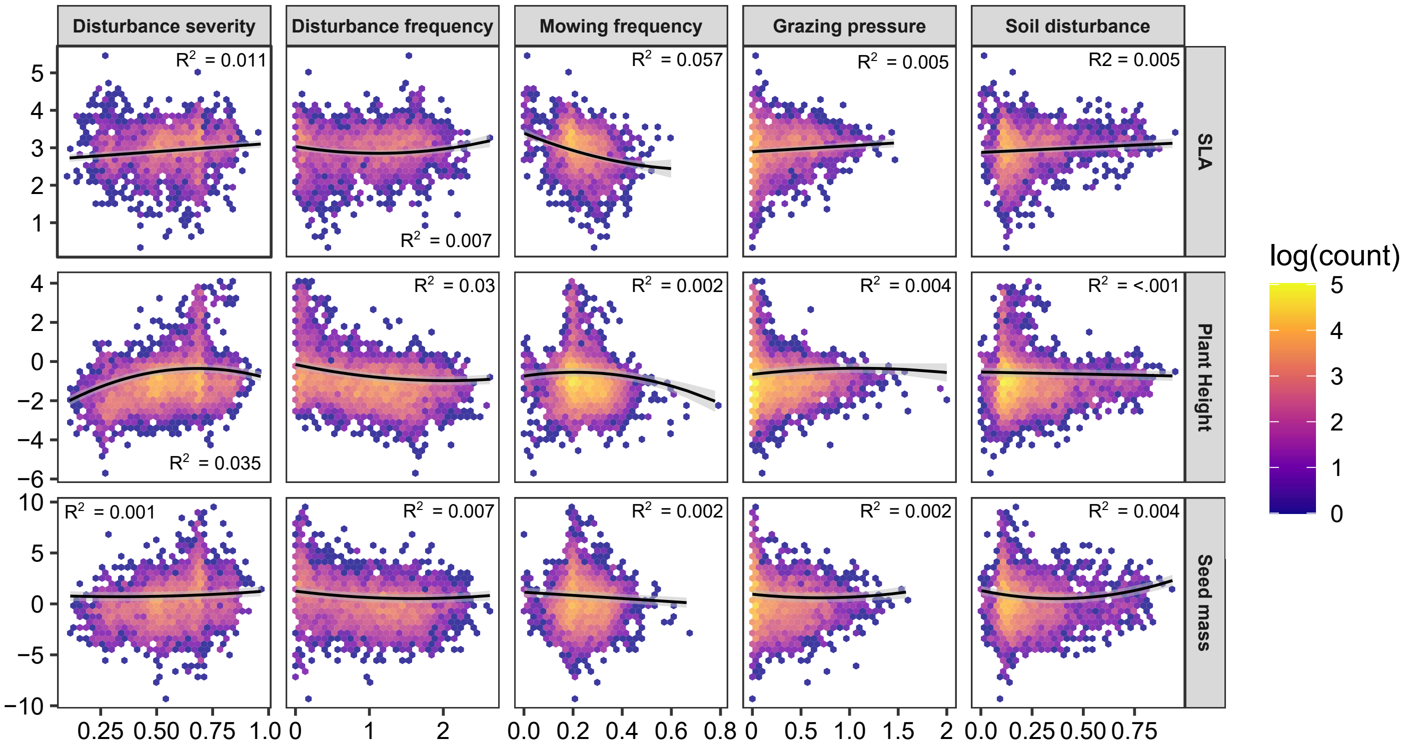


Figure S4.1: Relationship between plant functional traits (y-axes) and main disturbance indicator values (x-axes) across individual species. Lighter colors of the bins correspond to a higher density of data points. The panels include the predicted line of the linear mixed-effect model and related marginal R^2. The line is fitted from a quadratic relationship if this significantly improved the goodness of fit (= Akaike Information Criterion, AIC). Plant functional trait values are on a log scale.

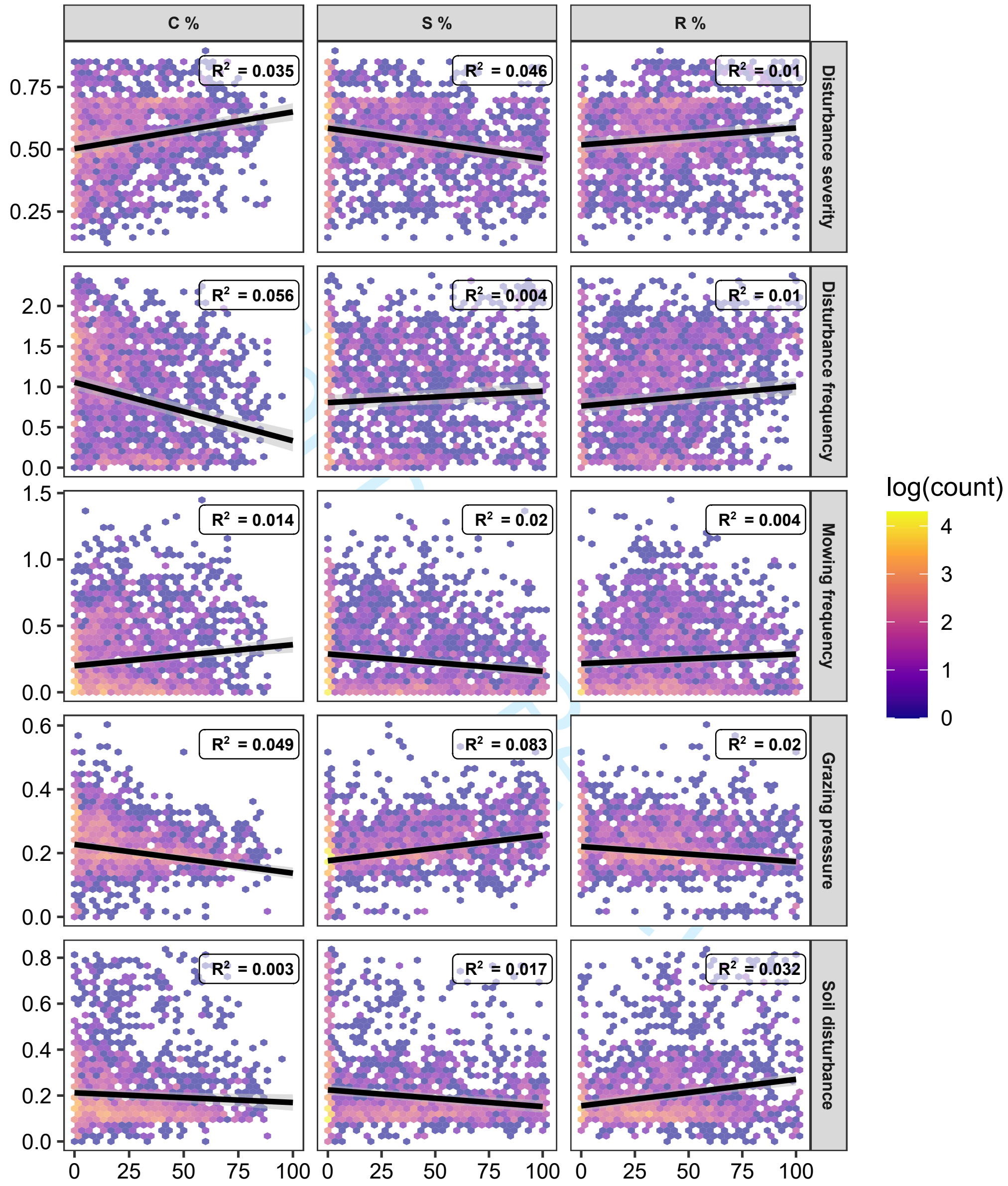


Figure S4.2: Relationship between competitor (C), stress-tolerator (S) and ruderal (R) Grime's scores (x-axes) and main disturbance indicator values (y-axes) across individual species for a subset of 1,683 species. Lighter colors of the bins correspond to a higher density of data points. The panels include the predicted line of the linear mixed-effect model and related marginal R^2.

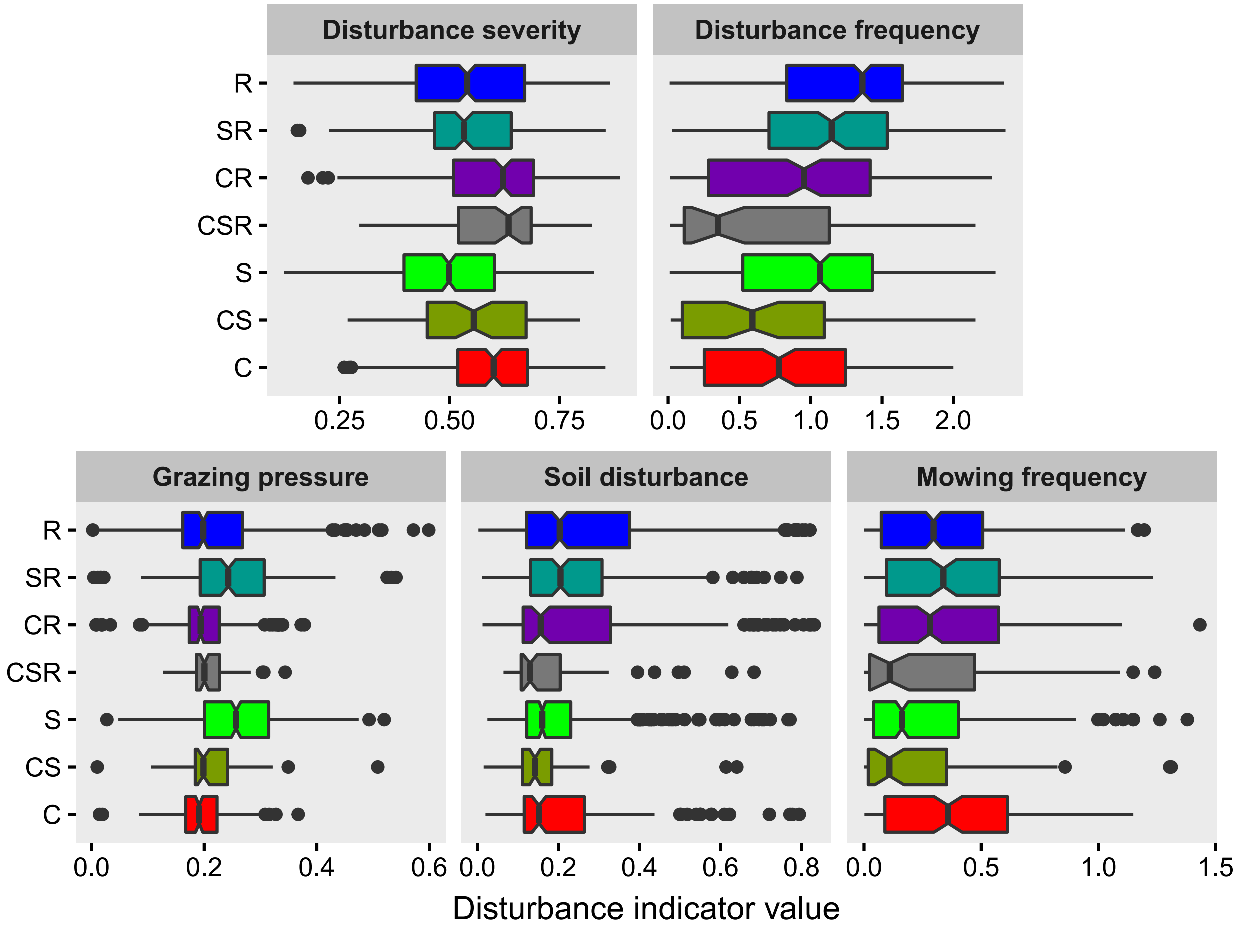


Figure S4.3: Distribution of the main disturbance indicator values across the main Grimes' plant strategy categories (C = competitor; S = stress-tolerator; R = ruderal). The box plots are obtained on a subset of 1,683 species for which data on C-S-R scores where available. The colors of the box represent the positioning of each category in the color wheel of the CSR triangle by Pierce et al. (2017). The box represents the 50% of the central data, with the line inside corresponding to the median and the notches to the confidence interval of the median. The whiskers represent the observations within 1.5 * interquartile range values.

Appendix S5: Number of species per plant family and habitat groups

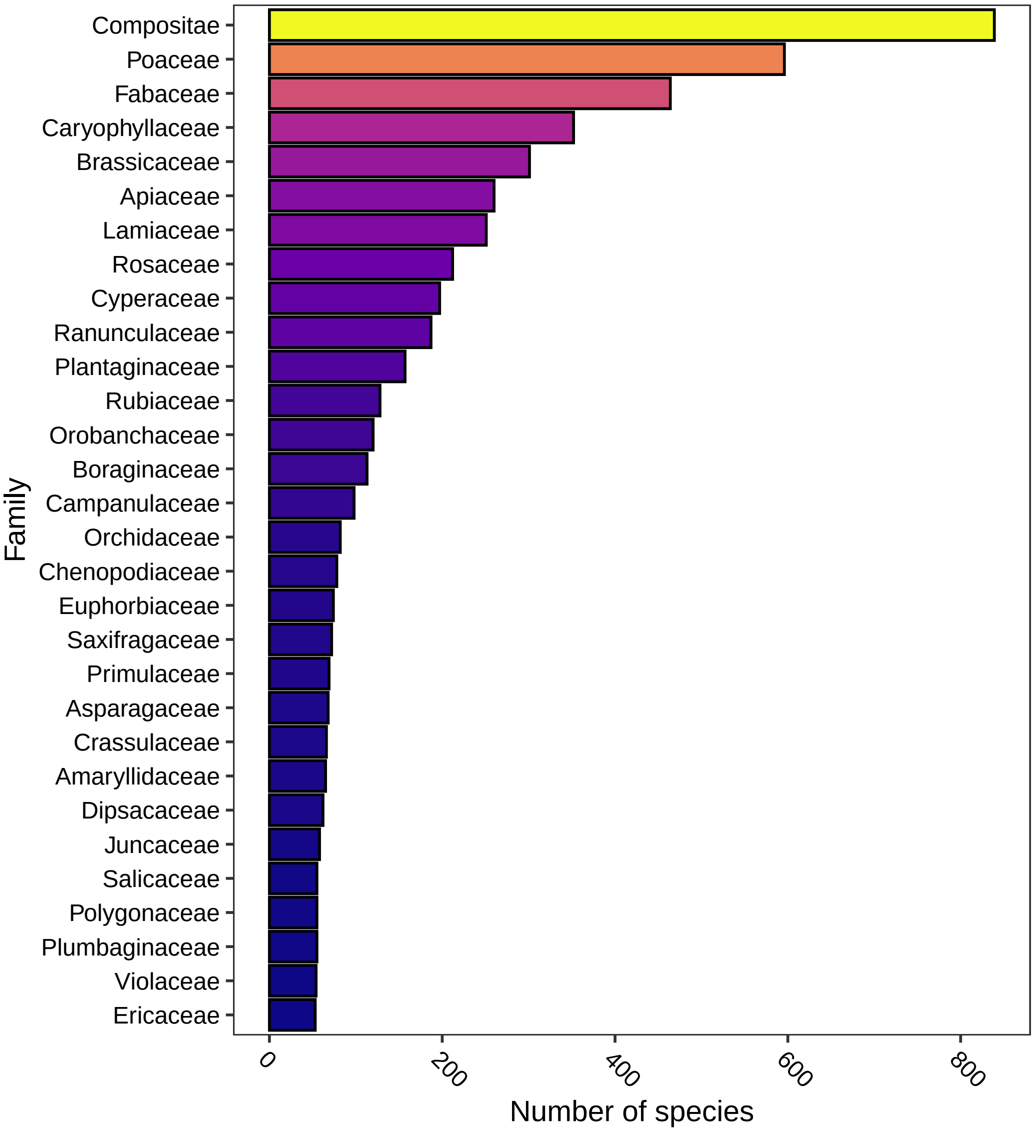


Figure S5.1: Number of species included in the data set for each plant family. Only the 30 most frequent families are shown.

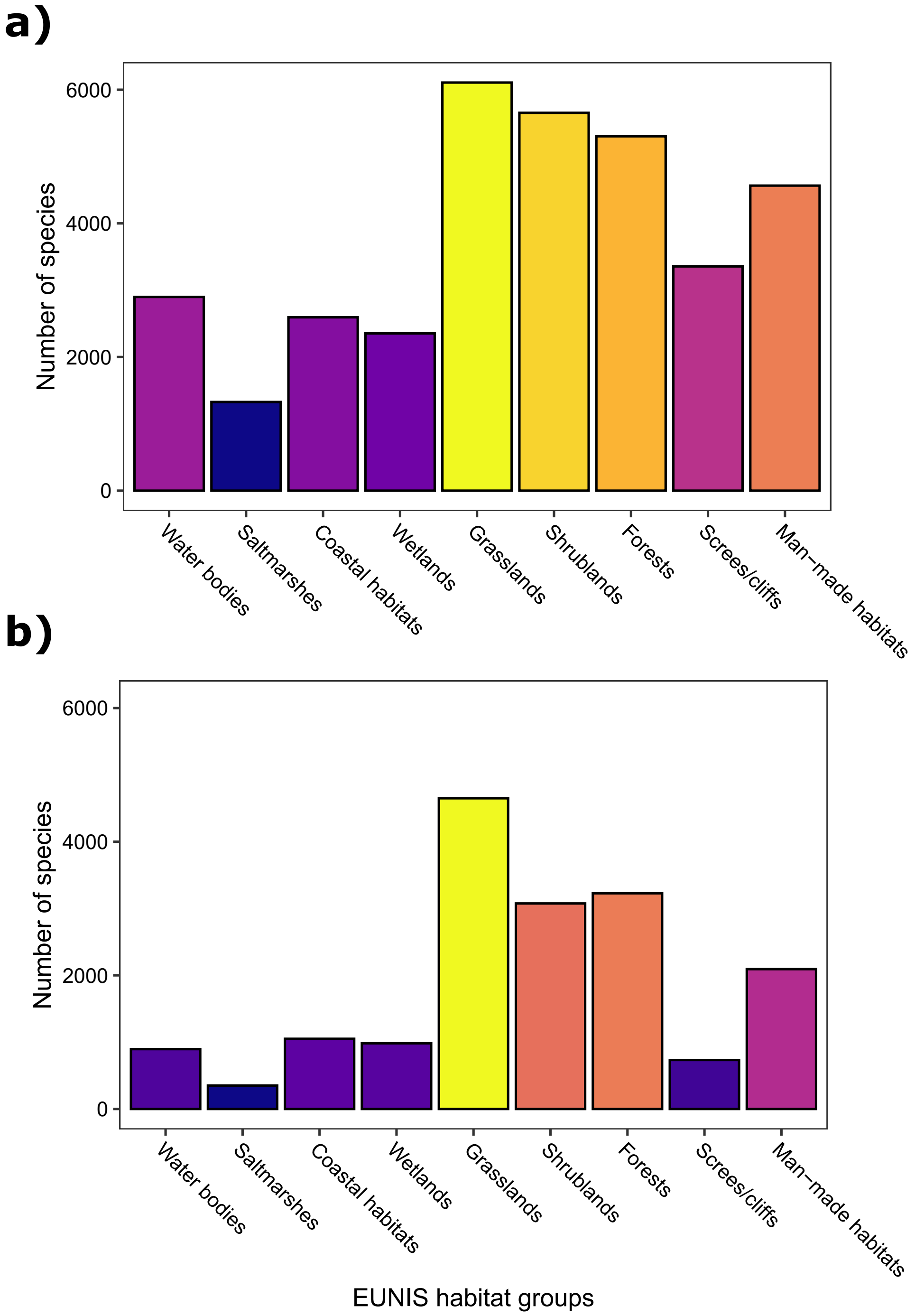


Figure S5.2: Number of species included in the data set found in different EUNIS habitat groups (see Chytrý et al., 2020) based on 736,366 EVA plots. Panel a) displays species found in at least one plot belonging to a given habitat group. Panel b) displays species found in at least 20 plots belonging to a given habitat group.

Appendix S6: Distribution of uncertainty and pairwise correlation matrix of indicator values

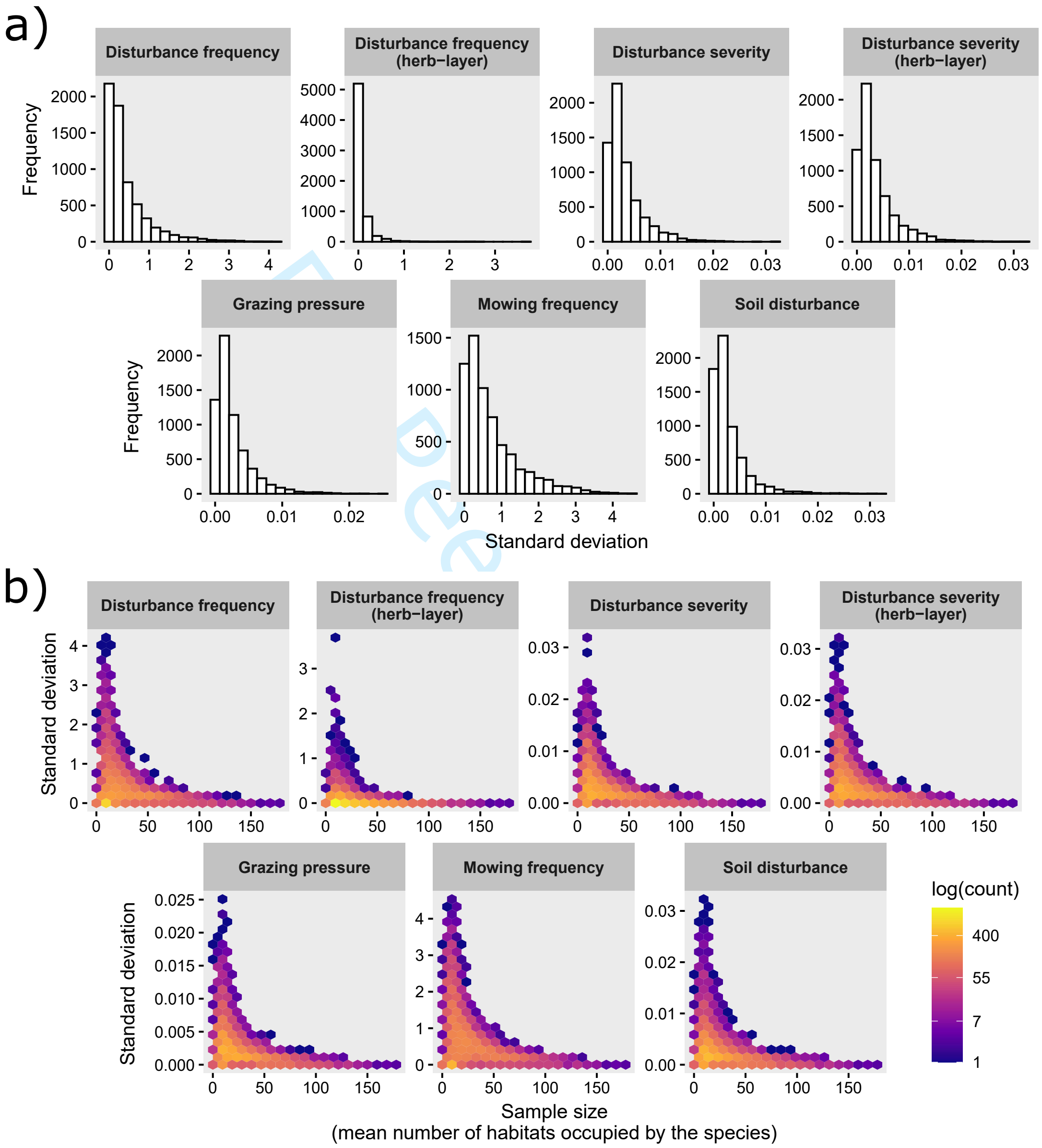


Figure S6.1: *a)* Distribution of uncertainty for the whole set of indicator values available in the data. Uncertainty is calculated as the standard deviation of mean indicator values across the 999 draws of randomly sampled vegetation data. *b)* Relationship between the standard deviation values and sample size, namely, the mean number of habitats where the species is found across the 999 draws. Higher values of standard deviation are found in those species occurring in low number of habitats with contrasting disturbance regimes.

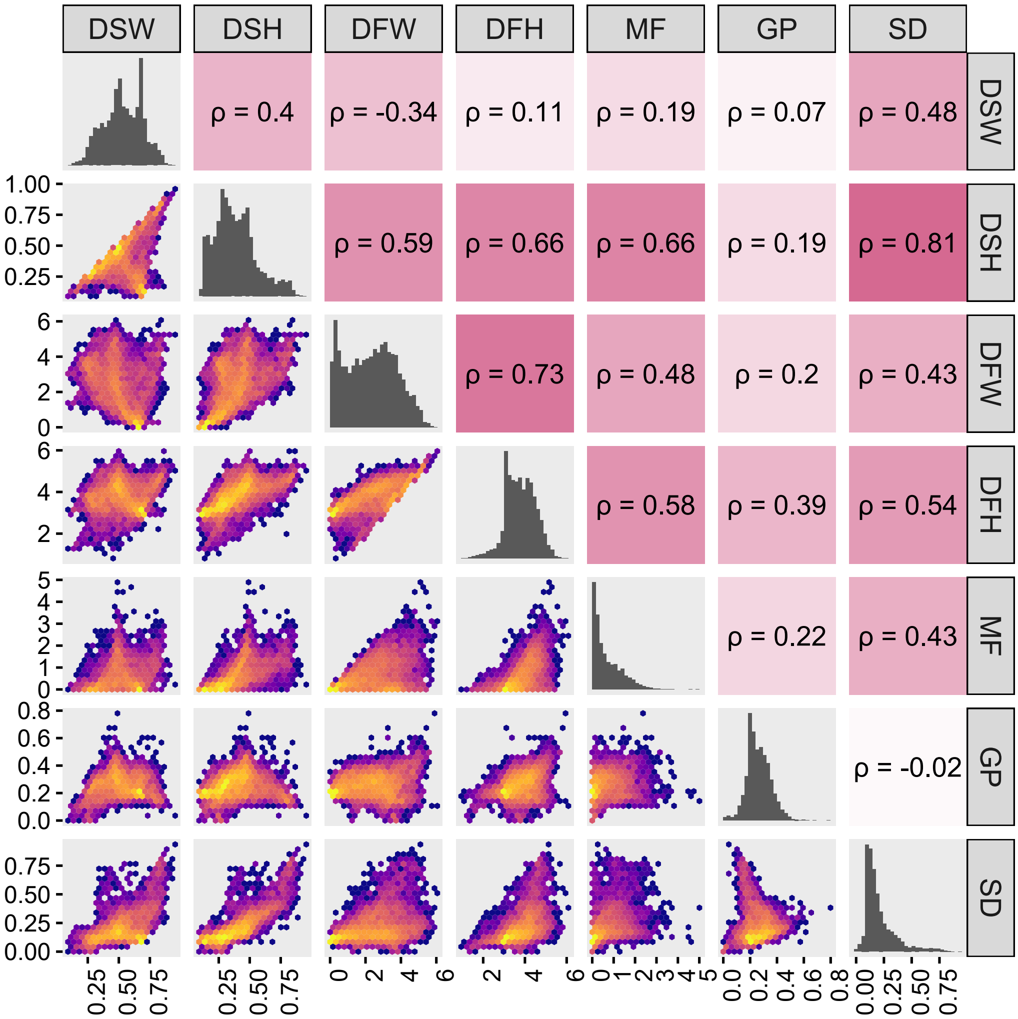
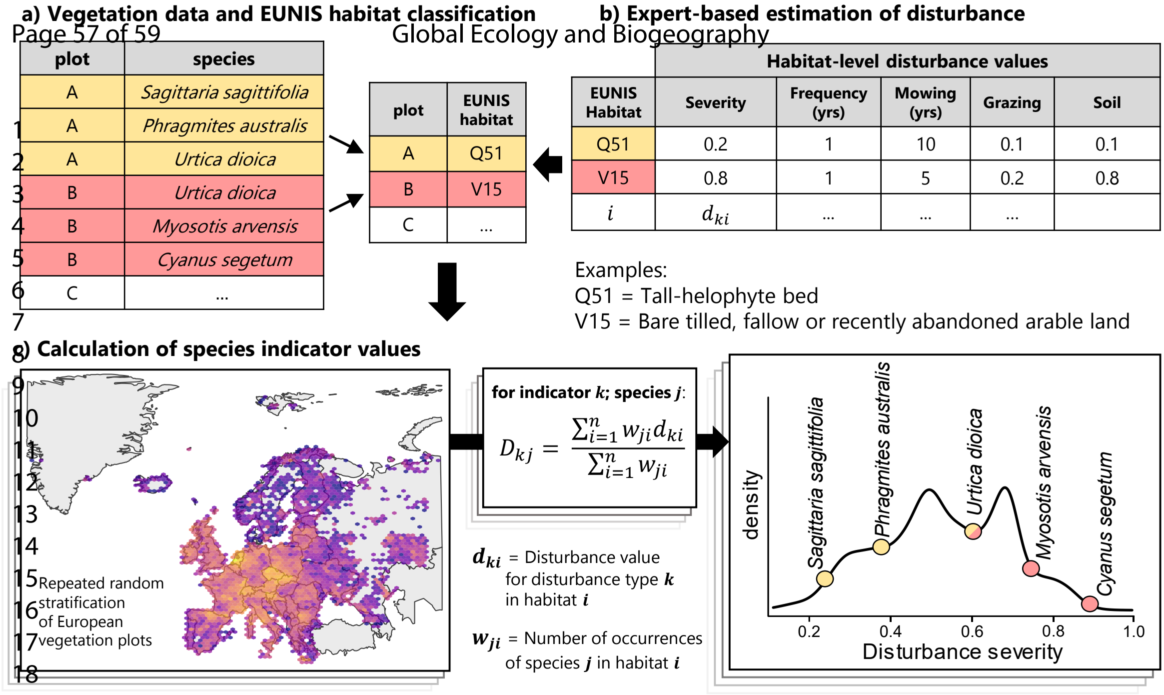


Figure S6.2: Pairwise correlations (top-right) and density scatter plots (bottom-left) for the whole set of indicator values available in the data. Lighter colors in the bottom-left panels correspond to a higher density of data points. The first five indicators starting from top left (DSW, DFW, MF, GP and SD), correspond to the main indicators presented in the main manuscript. DSW = disturbance severity (at the whole community level); DSH = disturbance severity in the herb layer; DFW = disturbance frequency (at the whole community level); DFH = disturbance frequency in the herb layer; MF = mowing frequency; GP = grazing pressure; SD = soil disturbance.



a) Vegetation data and EUNIS habitat classification

plot	species
A	*Sagittaria sagittifolia*
A	*Phragmites australis*
A	*Urtica dioica*
B	*Urtica dioica*
B	*Myosotis arvensis*
B	*Cyanus segetum*
C	...

plot	EUNIS habitat
A	Q51
B	V15
C	...

b) Expert-based estimation of disturbance

EUNIS Habitat	Habitat-level disturbance values				
	Severity	Frequency (yrs)	Mowing (yrs)	Grazing	Soil
Q51	0.2	1	10	0.1	0.1
V15	0.8	1	5	0.2	0.8
i	d_{ki}	...	...	...	

Examples:
Q51 = Tall-helophyte bed
V15 = Bare tilled, fallow or recently abandoned arable land

c) Calculation of species indicator values

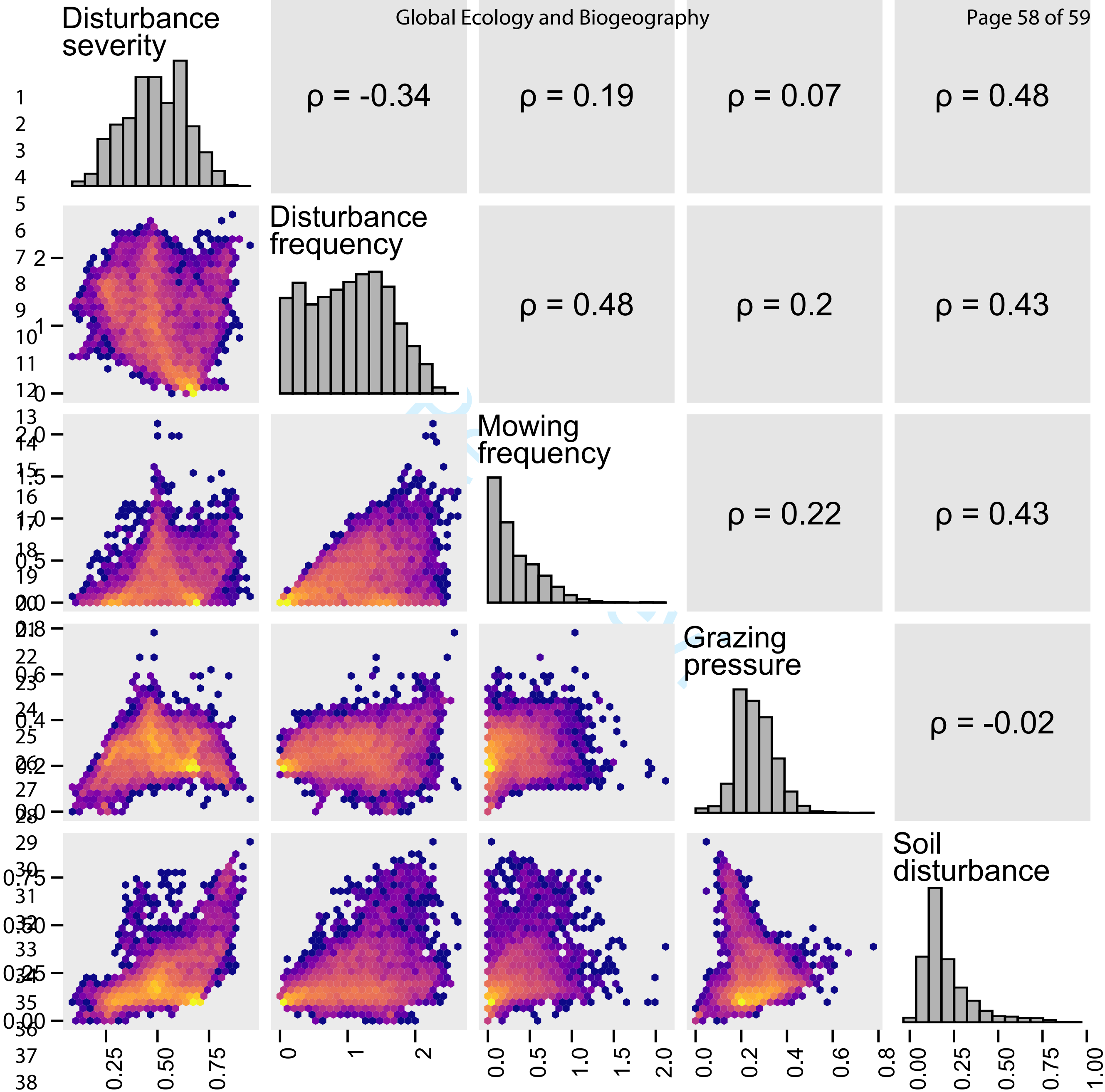
Repeated random stratification of European vegetation plots

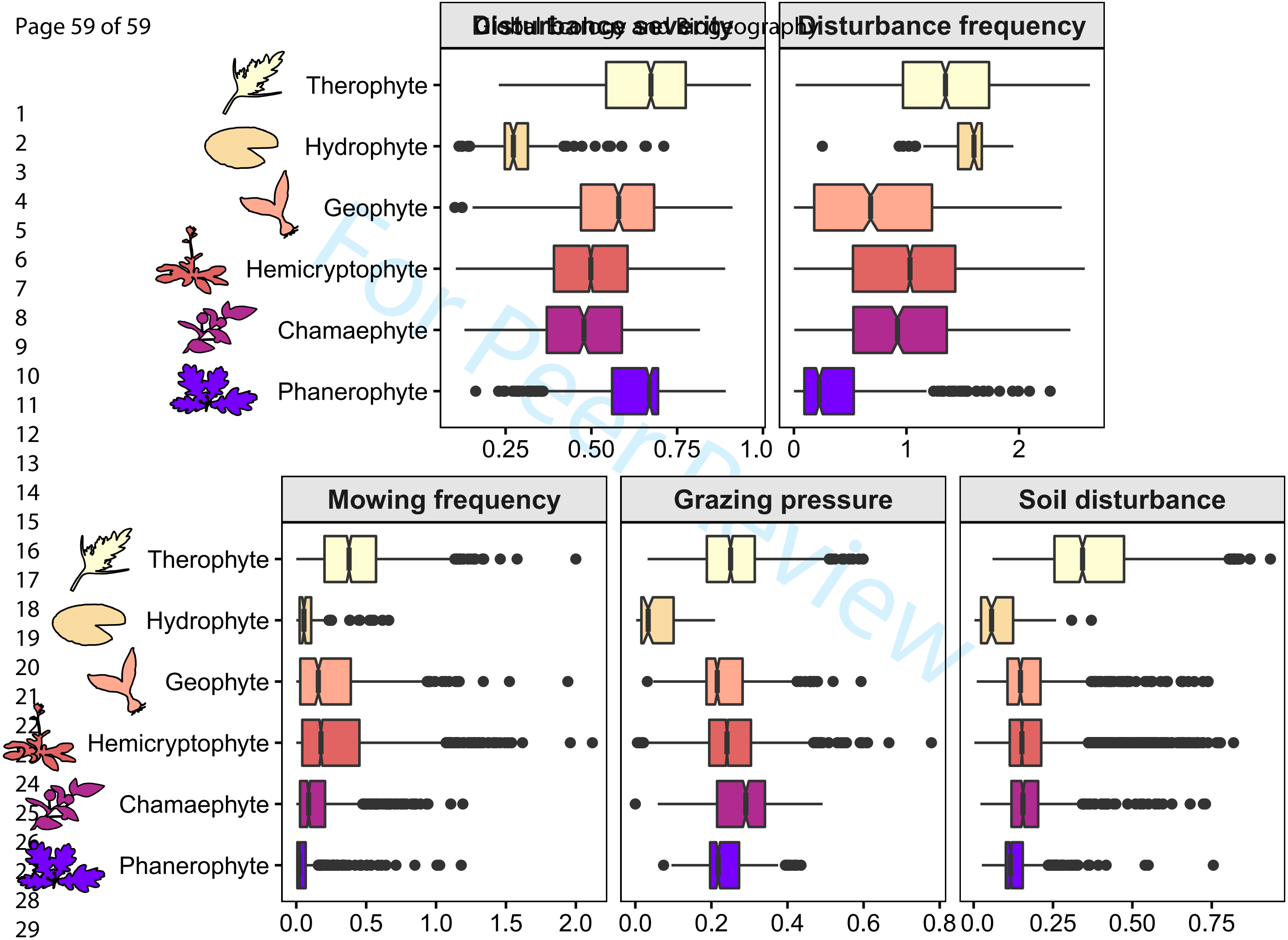
for indicator k; species j:

$$D_{kj} = \frac{\sum_{i=1}^{n} w_{ji} d_{ki}}{\sum_{i=1}^{n} w_{ji}}$$

d_{ki} = Disturbance value for disturbance type k in habitat i

w_{ji} = Number of occurrences of species j in habitat i


Disturbance severity
ρ = -0.34
ρ = 0.19
ρ = 0.07
ρ = 0.48
Disturbance frequency
ρ = 0.48
ρ = 0.2
ρ = 0.43
Mowing frequency
ρ = 0.22
ρ = 0.43
Grazing pressure
ρ = -0.02
Soil disturbance
0
1
2
0.0
0.5
1.0
1.5
2.0
0.0
0.2
0.4
0.6
0.8
0.00
0.25
0.50
0.75
0.25
0.50
0.75
0
1
2
0.0
0.5
1.0
1.5
2.0
0.0
0.2
0.4
0.6
0.8
0.00
0.25
0.50
0.75
1.00


Disturbance severity
Disturbance frequency
Therophyte
Hydrophyte
Geophyte
Hemicryptophyte
Chamaephyte
Phanerophyte
0.25
0.50
0.75
1.0
0
1
2
Mowing frequency
Grazing pressure
Soil disturbance
Therophyte
Hydrophyte
Geophyte
Hemicryptophyte
Chamaephyte
Phanerophyte
0.0
0.5
1.0
1.5
2.0
0.0
0.2
0.4
0.6
0.8
0.0
0.25
0.50
0.75