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Disturbance indicator values for European plants

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1 **Title:** Disturbance indicator values for European plants

2 **Keywords:** bioindicator; ecological niche; Ellenberg value; expert judge-  
3 ment; functional trait; plant life form

4 **Manuscript category:** DATA ARTICLE

## 5 **Abstract**

6 **Motivation** Indicator values are numerical values used to characterize eco-  
7 logical niches of species and estimate their occurrence along gradients. While  
8 indicator values on climatic and edaphic niches of plant species have received  
9 considerable attention in ecological research, data on species optimal posi-  
10 tioning along disturbance gradients are less developed. Here, we present a  
11 new data set of disturbance indicator values identifying optima along gra-  
12 dients of natural and anthropogenic disturbance for 6,382 vascular plant  
13 species based on the analysis of 736,366 European vegetation plots and  
14 using expert-based characterization of disturbance regimes in 236 habitat  
15 types. The indicator values presented here are crucial for integrating distur-  
16 bance niche optima into large-scale vegetation analyses and macroecological  
17 studies.

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

25 **Spatial location and grain** Europe. Vegetation plots ranging in size  
26 from 1 m<sup>2</sup> to 1,000 m<sup>2</sup>.

27 **Time period and grain** Vegetation plots mostly sampled between 1956  
28 and 2013 (= 5<sup>th</sup> and 95<sup>th</sup> quantiles of the sampling year, respectively).

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

31 **Software format** .csv file.

## 32 1 Introduction

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

42 In contrast to the major climatic and soil niches of species described by,  
43 for instance, Ellenberg indicator values (EIVs) (Ellenberg et al., 1992), the  
44 estimation of species disturbance optima has received less attention in the  
45 literature (but see Frank & Klotz 1990; Landolt et al. 2010; Grime, Hodgson,  
46 & Hunt 2014). Thus, to deepen our understanding of plant community re-  
47 sponses to global environmental changes, as well as to improve disturbance-  
48 dependent ecosystem management strategies, we need to integrate analyses

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8 of the disturbance niche (namely, the species optimal positioning within  
9 disturbance gradients) into ecological studies.

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11 A common approach in ecology is to link species response to disturbance  
12 with morpho-physiological functional traits (Laliberté, Shipley, Norton, &  
13 Scott 2012; Vandewalle et al. 2013; Jäschke, Heberling, & Wesche 2020). For  
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17 example, the ‘competitor, stress-tolerator, ruderal’ (CSR) theory has been  
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19  
20 proposed to identify main plant strategy classes based on functional traits  
21 (Grime, 1979; Pierce et al., 2017).

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23 Nonetheless, approaches based on functional traits are problematic for  
24  
25 many reasons. First, we cannot expect traits and trait combinations to de-  
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27 scribe disturbance with sufficient accuracy because plants may respond to  
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29 the same disturbance event with alternative strategies (Marks & Lechowicz,  
30  
31 2006). Second, disturbance consists of at least two separate dimensions, the  
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33 severity of an event and its frequency (Turner, 2010), which are not eas-  
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35 ily separated by the use of plant traits. In addition, the large variety of  
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37 physical processes characterizing disturbance (such as fire, wind, grazing,  
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39 cutting and soil disturbance) further complicates trait-based characteriza-  
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41 tion of disturbance regimes in vegetation. Finally, circular reasoning may  
42  
43 occur in studies examining the response of plant traits to disturbance gradi-  
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45 ents when plant traits are used as proxies for disturbance, which precludes  
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47 testing trait-disturbance relationships (Götzenberger, Kühn, & Klotz 2008).

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49 For these reasons, Herben, Chytrý, & Klimešová (2016) proposed an al-  
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51 ternative approach to estimate species-level disturbance indicator values in-  
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53 dependently of plant traits. Such indicator values were based on the number  
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55 of species’ occurrences in vegetation plots classified by severity and frequency  
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57 of disturbance regimes estimated by experts for different habitat types. The  
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59 indicator values reported by Herben et al. (2016) have been proved to meet  
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8 theoretical expectations for functional differentiation in plants, particularly  
9 with respect to life history categories and clonality (Herben, Klimešová, &  
10 Chytrý 2018a). However, such indicator values have been calculated only  
11 for 1,248 vascular plant species occurring in the Czech Republic and did not  
12 include specific indicator values for mowing frequency and grazing pressure –  
13 two key disturbance types affecting European vegetation of managed herba-  
14 ceous ecosystems. Other expert-based indicator values have been proposed  
15 for mowing and grazing in Europe. However, they are limited in terms of  
16 the species pool and region, such as Central Russia (Ramenskii, Tsatsenkin,  
17 Chizhikov, & Antipin 1956), Germany (Briemle, Nitsche, & Nitsche 2002)  
18 and the Alps (Jouglet, 1999; Landolt et al., 2010). In addition, disturbance  
19 indicators related to the concept of hemeroby (i.e. unnaturalness of vegeta-  
20 tion due to human impacts) have been proposed for some European plants  
21 (see e.g. Hill et al. 2002), but they do not distinguish between frequency  
22 and severity and combine other human-affected processes with disturbance,  
23 namely nutrient availability and dispersal.  
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37 Here we present a data set of species-level disturbance indicator values  
38 for 6,382 vascular plants commonly found in Europe. The large number of  
39 species and geographic extent covered by our data set can stimulate the inte-  
40 gration of plant-disturbance relationships in the field of macroecology, func-  
41 tional biogeography and large-scale European vegetation monitoring and  
42 assessment.  
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## 50 2 Materials and Methods

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

## 108 2.1 Vegetation data and habitat classification

109 We based the calculation of indicator values on 1,263,388 georeferenced veg-  
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111 etation plots from the European Vegetation Archive (EVA; project 123;  
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113 Chytrý et al., 2016; data retrieved on 5 May 2021). The plots were mostly  
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115 located mostly in Europe, including a few sites in Greenland. Plots ranged  
116  
117 from 53.5°W to 62.2°E longitude and 34.8°N to 80.1°N latitude.

118 We used the revised version of the EUNIS (European Nature Information  
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120 System) Habitat Classification described by Chytrý et al. (2020) to classify  
121  
122 vegetation plots to EUNIS habitat types (hereafter, 'habitats'). The clas-  
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124 sification was performed using the classification expert system EUNIS-ESy  
125  
126 (Chytrý et al. (2020); version 2021-06-01, DOI: 10.5281/zenodo.4812736).  
127  
128 This system identifies habitats based on species composition and cover-  
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130 abundances of particular species or species groups, accounting for the abi-  
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132 otic environment and geographic location as classification criteria (Chytrý  
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134 et al., 2020). The system evaluates each vegetation plot in terms of species  
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136 composition and cover and checks whether it meets the formal pre-defined  
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138 assignment criteria of different habitats. Some plots cannot be classified to a  
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140 specific habitat, either because transitional species compositions are simul-  
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142 taneously assigned to multiple habitats or the unusual species composition  
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144 prevents the classification of the plot to an existing habitat.



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8 128 We classified 842,218 plots into 236 EUNIS habitats. The remaining  
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10 129 plots could not be classified. We further removed plots with coordinate  
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12 130 uncertainty greater than 5 km and plots with an area smaller than 1 m<sup>2</sup>  
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14 131 and greater than 1,000 m<sup>2</sup>, leaving 736,662 vegetation plots available for  
15  
16 132 indicator value calculations. In the final selection, we retained plots with  
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18 133 unknown coordinate uncertainty (18.5%) and plot size (26.0%), otherwise  
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20 134 an important part of the geographical coverage (e.g. France) would have  
21  
22 135 been lost. The selected plots were mostly sampled between 1956 and 2013  
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24 136 (= 5<sup>th</sup> and 95<sup>th</sup> quantiles of the sampling year, respectively).

25  
26 137 The vegetation plots from EVA cover a substantial part of the geo-  
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28 138 graphical range of most native European plants, but the native range of  
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30 139 alien species is obviously not well represented by these data. We assume  
31  
32 140 that species-disturbance relationships are constant within species geographic  
33  
34 141 range. However, we acknowledge the importance of future investigation of  
35  
36 142 species-disturbance relationships depending on species ranges, particularly  
37  
38 143 for non-native species.

## 39 144 **2.2 Estimation of habitat-level disturbance values**

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41 145 To calculate species-level indicator values, we assigned expert-based distur-  
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43 146 bance values to each of the 236 habitats, assuming that habitats are suffi-  
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45 147 ciently homogeneous in this respect and that the same disturbance values  
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47 148 can be reasonably assigned to different plots classified within each habitat.  
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49 149 The values of disturbance variables were estimated based on the personal  
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51 150 field experience of members of our author team and information from the  
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53 151 literature.

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55 152 To evaluate disturbance regimes in habitats, we used the absolute def-  
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57 153 inition of disturbance (White & Jentsch, 2001), which relates disturbance

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8 154 to measurable changes (losses) in plant community biomass (Grime, 1979).  
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10 155 In addition, we only considered disturbance of the whole community (or its  
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12 156 whole vegetation layers) and not disturbance affecting just small patches or  
13  
14 157 single individuals within the community (van der Maarel, 1993). For exam-  
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16 158 ple, in forests, the destruction of the tree layer by stand-replacing windstorm  
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18 159 was considered a disturbance event, but not the fall of individual dead trees.  
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20 160 We considered both regular disturbances (e.g. annual mowing or burning of  
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22 161 grassland, agricultural management of arable land or planned logging of a  
23  
24 162 mature managed forest) and irregular disturbances (e.g. wildfires or extreme  
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26 163 drought events).

26 164 The estimated variables included disturbance severity, disturbance fre-  
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28 165 quency, mowing frequency, grazing pressure, and soil disturbance. Distur-  
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30 166 bance severity and frequency refer to all possible types of disturbance that  
31  
32 167 may occur in a given habitat, including anthropogenic and natural distur-  
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34 168 bance as well as grazing and mowing. Conversely, mowing frequency, graz-  
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36 169 ing pressure and soil disturbance were estimated separately for such factors.  
37  
38 170 [Soil disturbance specifically refers to any factor causing plant biomass death](#)  
39  
40 171 [from soil turning and furrowing.](#)

41 172 Because one habitat can be affected by more than one disturbance, we  
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43 173 estimated values for the disturbance severity and disturbance frequency of  
44  
45 174 the disturbance type we considered most important for a given habitat. If  
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47 175 we considered two or more disturbance types with comparable importance in  
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49 176 the same habitat (for example, soil erosion and grazing in rocky grasslands),  
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51 177 we estimated their combined effects. We considered the following distur-  
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53 178 bance types (from most to least frequent): grazing, fire, logging, substrate  
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55 179 movement, vegetation removal by humans, wave and current action, ero-  
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57 180 sion, flooding, trampling, pathogen outbreaks, mowing, windthrow, arable

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8 181 land management, drought, inundation, frost, volcanic activity and snow  
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10 182 movement. All disturbance types are described in Table S1.1 (Appendix S1  
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12 183 Supporting Information).

13  
14 184 Estimates of disturbance severity, grazing pressure and soil disturbance  
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16 185 reflect the mean fraction of above-ground vegetation biomass destroyed by  
17  
18 186 a single disturbance event typical of that habitat. We estimated one value  
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20 187 for each variable and habitat type, ranging from 0 (no change in biomass)  
21  
22 188 to 1 (complete loss of plant cover). Disturbance frequency and mowing  
23  
24 189 frequency correspond to the estimated mean interval (in years) between two  
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26 190 consecutive disturbance or mowing events.

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28 191 We further considered separate values of disturbance frequency and sever-  
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30 192 ity estimated for the whole plant community (including all vegetation layers)  
31  
32 193 and values considering only the herb layer (Herben et al., 2016). This sep-  
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34 194 aration was necessary to account for the fact that disturbance regimes in  
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36 195 the tree and shrub layers differ in severity and frequency from the distur-  
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38 196 bance regimes in the herb layer of the same community. For habitats with  
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40 197 herbaceous vegetation only, the whole-community values were equal to the  
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42 198 herb-layer values.

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44 199 In Appendix S1 (Supporting Information), we report additional details  
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46 200 on the criteria used to assign disturbance values to habitats. Table S1.1  
47  
48 201 also includes the description and range of periodicity of disturbance types  
49  
50 202 that were used to assign mean disturbance frequency on the habitats. The  
51  
52 203 list of habitats, their disturbance values and the most important type of  
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54 204 disturbance evaluated for each of them are reported in the Zenodo public  
55  
56 205 data repository ([link](#)).

### 206 **2.3 Indicator value calculation**

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

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

229 For habitats that are never mown (207 of 236), we assigned a default value  
230 of 100 years of mowing return time to calculate mowing frequency values  
231 for species occurring in both mown and unmown habitats. To calculate  
232 disturbance and mowing frequency of species, we used the inverse of return

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8 233 time, which is the mean interval between successive disturbance events. We  
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10 234  $\log_{10}$ -transformed disturbance and mowing frequency to account for their  
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12 235 positively skewed distribution. To avoid negative values in the scale after the  
13  
14 236 log-transformation, we expressed return times in centuries (i.e. years/100).

15 237 To provide a measure of uncertainty due to the 999 draws following a  
16  
17 238 stratified resampling design of vegetation data from EVA, we also calculated  
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19 239 and reported the standard deviation of the weighted mean of disturbance  
20  
21 240 values. Furthermore, we explored whether plot size had an effect on indicator  
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23 241 values and if the minimum threshold of 20 plots retained for each species is  
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25 242 sufficient to perform the calculation. We report methodological details and  
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27 243 results of these analyses in Appendix S3 (Supporting Information).

#### 244 **2.4 Indicator value relationship with plant characteristics**

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

255 Plant life forms were compiled for a subset of 6,116 species. We dis-  
256 carded those species for which we were not able to determine their plant life  
257 form. Functional trait data were compiled for a subset of 5,057 species in  
258 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<sup>3</sup> (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 ( $\sim 1 \mid \text{family} / \text{genus}$ ). 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

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8 286 reported the results of these analyses in Appendix S4 (Supporting Informa-  
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10 287 tion). We fitted linear mixed effect models to test how the C, S and R scores  
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12 288 explain variation in disturbance indicator values (Figure S4.2) and we com-  
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14 289 pared indicator values grouped by main categorical strategy classes (Figure  
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16 290 S4.3). To calculate CSR values, we used a subset of 1,683 species present in  
17  
18 291 our data set for which SLA, leaf dry matter content (LDMC) and leaf area  
19  
20 292 (LA) were available from the Pladias Database (Chytrý et al. 2021) and  
21  
22 293 TRY (Kattge et al. 2020).

## 294 **3 Data structure and patterns**

### 295 **3.1 General description**

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

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8 311 Appendix S6, Supporting Information). Uncertainty is higher in species oc-  
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10 312 ccurring in a low number of habitats with contrasting disturbance regimes.  
11  
12 313 The nomenclature of species and families found in the data set is based on  
13 314 Euro+Med PlantBase (2021).

15 315 In general, disturbance indicator values estimate the realized disturbance  
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17 316 niche optimum of a species because they are based on species occurrences  
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19 317 in sampled vegetation. These indicator values provide information about  
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21 318 the ecology of the species in terms of the main characteristics of the dis-  
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23 319 turbance events that occur in the vegetation types where the species most  
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25 320 frequently occurs. For example, the highest values of disturbance severity  
26  
27 321 are found in weed flora of arable land (e.g. *Cyanus segetum*, *Ranunculus*  
28  
29 322 *arvensis*). In contrast, the lowest values of disturbance severity are found in  
30  
31 323 many species occurring in marshes (e.g. *Carex limosa*), high-mountain cliffs  
32  
33 324 (e.g. *Campanula morettiana*, *Androsace* spp.) and some aquatic plants (e.g.  
34  
35 325 *Potamogeton* spp.). Similarly, the lowest values of mowing frequency are  
36  
37 326 found in all the species associated with various never-mown habitats, while  
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39 327 the highest values are found in species commonly occurring in fertile hay  
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41 328 meadows (e.g. *Crepis biennis*, *Schedonorus pratensis*, *Trisetum flavescens*),  
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43 329 which are the most frequently mown habitats.

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45 330 The indicator values presented here showed low correlation among each  
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47 331 other (Figure 2). This result supports the multidimensional nature of dis-  
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49 332 turbance as a factor and highlights the importance of using different facets  
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51 333 of indicator values when assessing disturbance in vegetation. However, dis-  
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53 334 turbance severity and frequency in the herb layer showed higher correlations  
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55 335 with other indicator values (Figure S6.2, see Appendix S6 Supporting In-  
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57 336 formation). For this reason, in this manuscript we focused on disturbance  
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59 337 severity and frequency at the whole-community level in this manuscript,  
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8 338 rather than focusing on disturbance values in the herb layer.  
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### 10 339 **3.2 Potential for ecological research**

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13 340 The indicator values proposed here are a tool for evaluating plant com-  
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15 341 munity composition and function in relation to disturbance. For example,  
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17 342 by calculating community-level means of disturbance values, our indicator  
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19 343 values could be used to explore plant taxonomic and functional diversity  
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21 344 along disturbance gradients. Furthermore, we believe that characterizing  
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23 345 species disturbance niche optima could be used to improve the effectiveness  
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25 346 of restoration and conservation strategies based on modifying disturbance  
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27 347 regimes in vegetation.

28 348 Importantly, the disturbance indicator values were determined based on  
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30 349 species occurrence in habitats. Our approach makes them independent of  
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32 350 species traits and allows us to avoid circular reasoning when focusing on the  
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34 351 response of plant functional traits to disturbance gradients. When analyzed  
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36 352 in relation to plant characteristics, we encountered clear differences in all  
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38 353 types of indicator values between plant life forms (Figure 3). For exam-  
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40 354 ple, annual plants (therophytes) had higher values of disturbance severity,  
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42 355 disturbance frequency and soil disturbance, consistent with the theoretical  
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44 356 expectation by Grime (1979) that disturbance favour more annual plants in  
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46 357 vegetation. Similarly, lower disturbance frequency for phanerophytes and,  
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48 358 to a lesser extent, geophytes, reflects that less intensive disturbance regimes  
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50 359 favour the establishment of slow-growing woody plants and those with un-  
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52 360 derground storage organs (McIntyre et al., 1995). These results are consis-  
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54 361 tent with the analyses of Herben et al. (2018a), but with a larger number  
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56 362 of species and a wider geographical extent. Nevertheless, both mowing fre-  
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58 363 quency and grazing pressure showed little difference among plant life forms,  
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8 364 except for hydrophytes and phanerophytes, which usually grow at other sites  
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10 365 than those managed by mowing or grazing.

11 366 Although the linear models showed very low  $R^2$  values, we detected some  
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13 367 significant relationships between plant functional traits (plant height, seed  
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15 368 mass and SLA) and disturbance indicator values (Figure S2.2, Appendix S2  
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17 369 Supporting Information). Overall, most of the models analyzed indicated  
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19 370 significant quadratic relationships, reflecting previous results obtained for  
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21 371 Czech flora (Herben et al., 2018a). For example, the functional traits ini-  
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23 372 tially decreased and then increased with increasing disturbance frequency.  
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25 373 Furthermore, SLA and height generally decreased with increasing grazing  
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27 374 pressure. Overall, these results suggest that the disturbance indicator values  
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29 375 presented here can be used as explanatory variables to explore the underly-  
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31 376 ing mechanisms of trait variation along disturbance gradients. However, the  
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33 377 mechanisms explaining why the relationships are mostly quadratic (rather  
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35 378 than linear) are still poorly understood, and previous analyses have shown  
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37 379 that productivity, rather than disturbance, is a better predictor of the plant  
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39 380 functional traits of the LHS scheme (Herben et al., 2018a). Finally, we high-  
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41 381 light that the low association of the CSR scores with disturbance indicator  
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43 382 values (see Appendix S4) likely depend on the differences between the theory  
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45 383 of (Grime, 1979) and our approach. The CSR scores represent the trade-  
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47 384 off in terms of both disturbance and productivity along three main axes (=   
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49 385 plant strategies) so that the adaptation to disturbance is not the same under  
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51 386 different levels of productivity (Herben et al., 2018b). Conversely, although  
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53 387 distinguishing between frequency and severity, our indicator values focus on  
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55 388 disturbance only, independently of the functional adaptation of plants to  
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57 389 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

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8 417 improve the characterization of plant functional groups for dynamic models  
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10 418 of vegetation and plant biodiversity (Boulangeat et al., 2012).

## 419 DATA AVAILABILITY STATEMENT

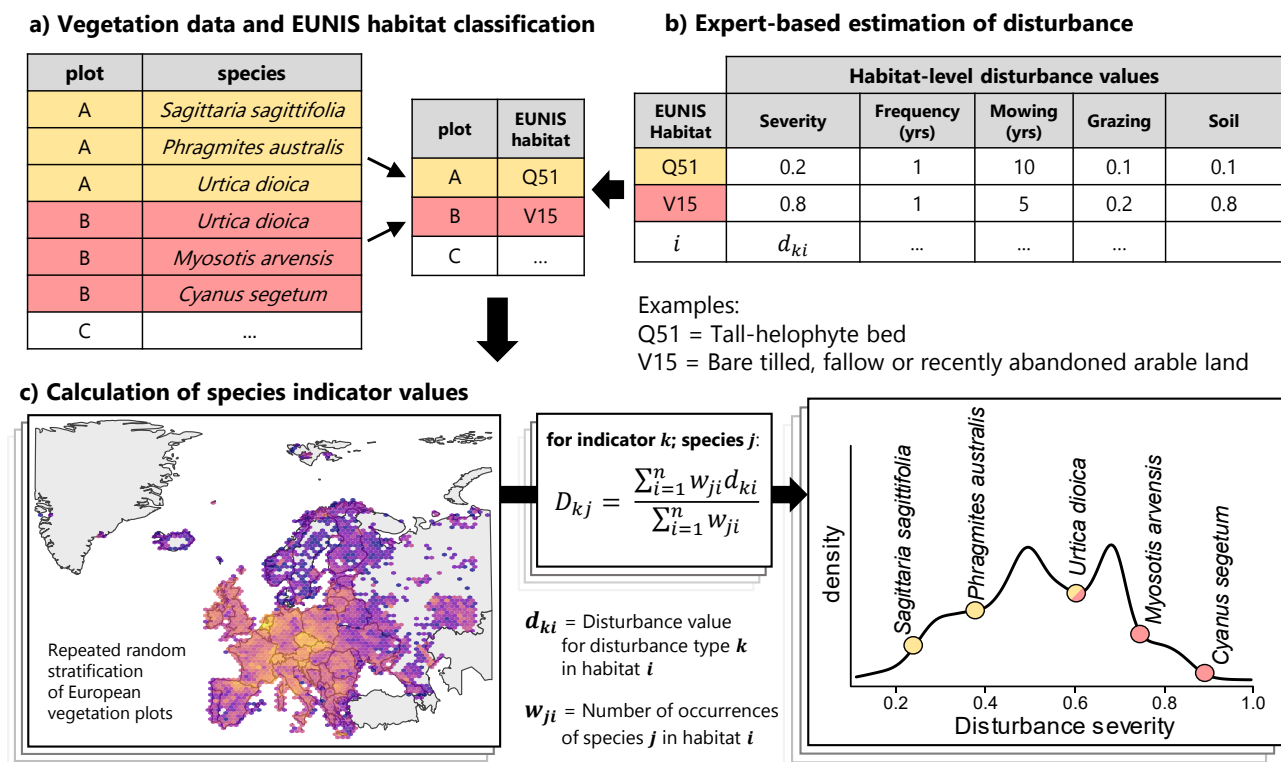
420 The data set is freely available in the Zenodo public data repository (<https://zenodo.org/>).  
421 *N.B: the data will be made freely available at the time this manuscript is ac-*  
422 *cepted for publication. Since Zenodo does not support the upload*  
423 *of data for double-blind revision, the data can be currently down-*  
424 *loaded at the following link: <https://figshare.com/s/63ea83c4d650c5fdddea>*

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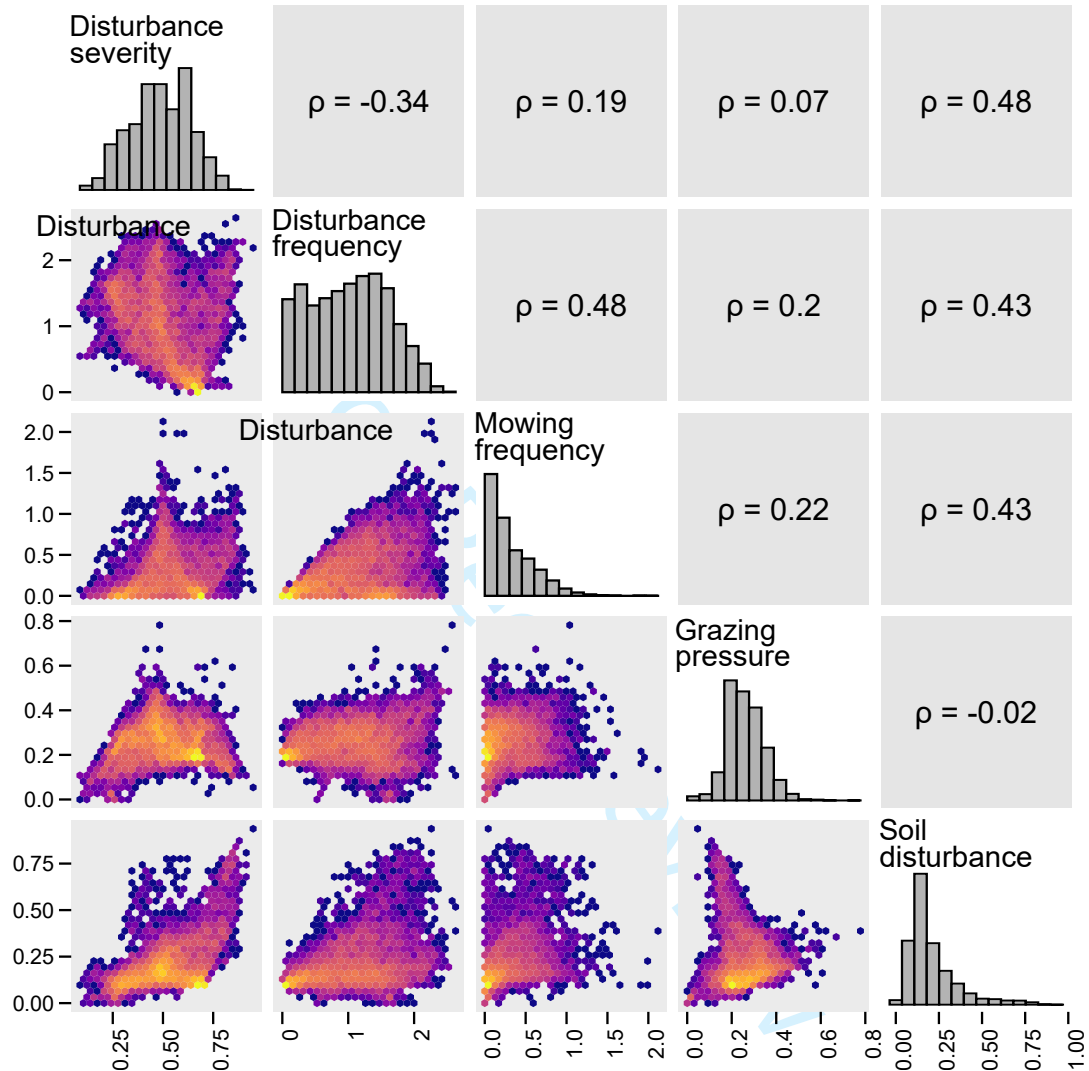
**Table 1:** Summary of the disturbance indicator values reported in the data set.

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
	Proportional increase in cover of bare ground by furrowing or soil turning		
Soil disturbance	Proportional increase in cover of bare ground by furrowing or soil turning	Proportional (0–1)	0 – 0.94

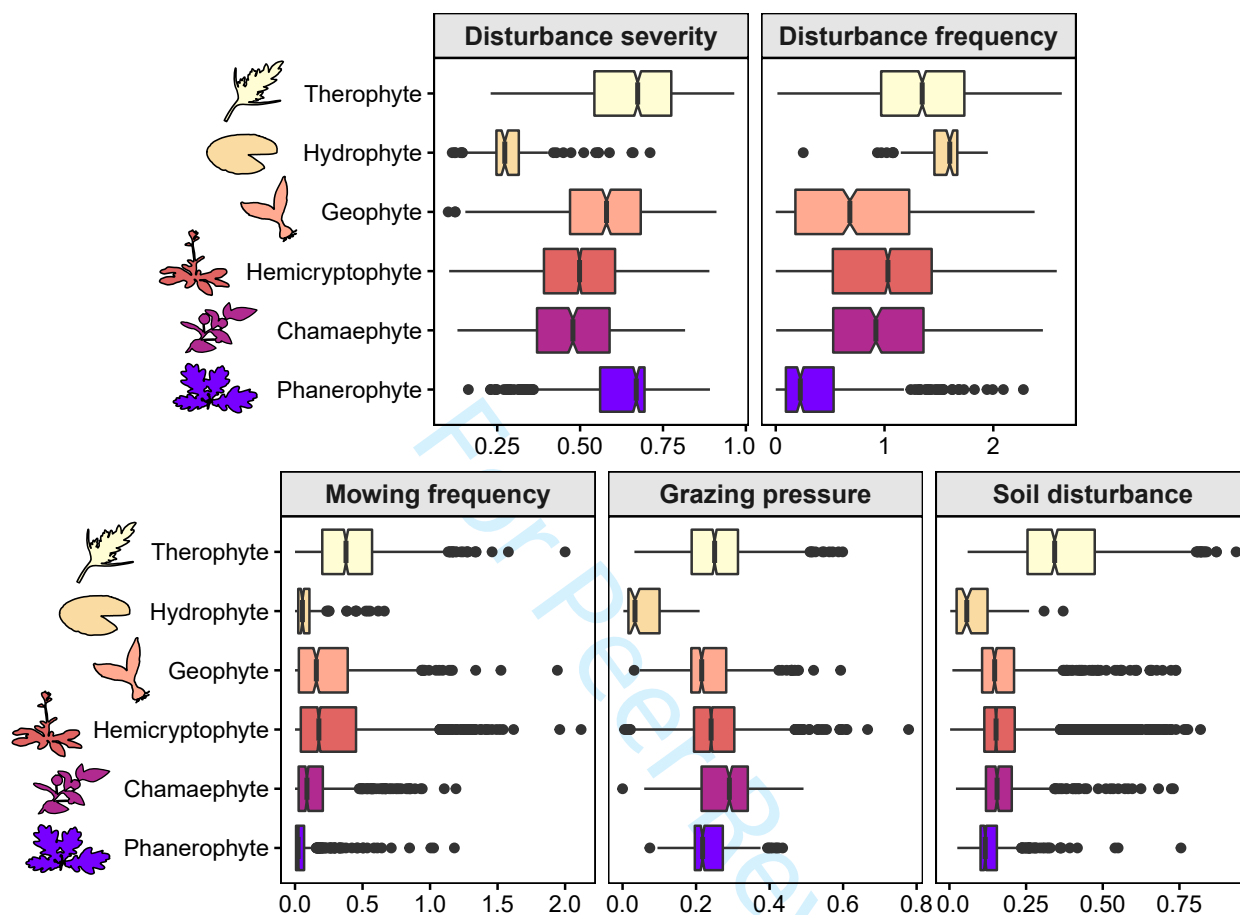
\* Values equal to zero correspond to 100-year return mowing time assigned by default to never-mown habitats (see Materials and Methods)

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**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  $1.5 \times$  interquartile range values. Disturbance severity and frequency correspond to indicator values estimated at the whole-community level.



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## 1 SUPPORTING INFORMATION

### 2 **Appendix S1: Summary of expert-based assessment of distur-** 3 **bance in habitats**

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

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

12 **Community disturbance vs patch disturbance.** We focused on dis-  
13 turbance of the whole communities or their highest vegetation layers rather  
14 than disturbance of small patches within the community (van der Maarel  
15 1993). For example, we consider the destruction of the forest tree layer by  
16 stand-replacing windstorm, but we do not consider the fall of individual old  
17 trees in a forest.

18 **Regular and irregular disturbances.** We consider both the regu-  
19 lar disturbances (e.g. annual mowing or burning of grassland, agricultural  
20 management of arable land or planned logging of a mature managed for-  
21 est) and irregular disturbances (e.g. wildfires or extreme drought events in  
22 grasslands), and estimated the inverse of disturbance frequency as the mean  
23 return time.

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

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8 27 Forest fire or logging is also considered when a forest regenerates in a dis-  
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10 28 turbed area. In contrast, ploughing of a meadow that changes it to arable  
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12 29 land is not considered. Mire draining and peat extraction are also not consid-  
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14 30 ered because they change the mire to a grassland, shrubland or successional  
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16 31 forest.

17 32 **Defining the most important disturbance type for each habitat.**

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19 33 To assess disturbance in vegetation we considered the disturbance types re-  
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21 34 ported in Table S1.1. Most habitats are affected by varying disturbance  
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23 35 types characterized by different frequency and severity. For each habitat,  
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25 36 we estimated disturbance frequency and severity for those disturbance types  
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27 37 that cumulatively remove the most biomass over a long period (longer than  
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29 38 the return time of the least frequent disturbance). For example, a tem-  
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31 39 perate semi-dry grassland can be disturbed by both grazing that occurs in  
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33 40 intervals of several weeks in particular spots and extreme drought events  
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35 41 that occur irregularly once in 5 to 15 years. In this system, grazing cumu-  
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37 42 latively removes more biomass over a long period (e.g. 20 years); therefore,  
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39 43 we consider grazing as the main disturbance type and estimate the distur-  
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41 44 bance frequency and severity for grazing, not drought events. In contrast,  
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43 45 Mediterranean annual grasslands are occasionally grazed, but most of their  
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45 46 biomass is killed annually by the advent of the dry period in the late spring.  
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47 47 In this system, drought cumulatively removes more biomass than grazing;  
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49 48 therefore, we consider drought as the main disturbance type.

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50 49 In addition to the quantification of general disturbances, we estimated  
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52 50 separately three specific types of disturbances: grazing pressure, mowing  
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54 51 frequency and soil disturbance. These disturbance types were assessed for  
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56 52 all the habitats, including those in which they are not the most important  
57  
58 53 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 include 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

54 • **Grazing pressure** included grazing by large herbivores, both domes-  
 55 tic and wild, mainly mammals, but in saltmarshes, aquatic habitats  
 56 and wetlands also by birds. Grazing by invertebrates and small verte-  
 57 brate herbivores was not considered. Grazing pressure was estimated  
 58 on a scale from 0 to 1, where 0 means that the habitat is not grazed  
 59 and 1 means that all the vegetation is removed by grazing at least once  
 60 a year.

61 • **Mowing return time (frequency)** is the time between two consec-  
 62 utive mowings \*

63 • **Soil disturbance includes** mechanical disturbance of the soil surface  
 64 or the upper soil layer by furrowing or soil turning. It is estimated on  
 65 a scale from 0 to 1, where 0 means no soil disturbance and 1 means  
 66 soil turning across the whole area of the habitat, such as ploughing on  
 67 arable land.

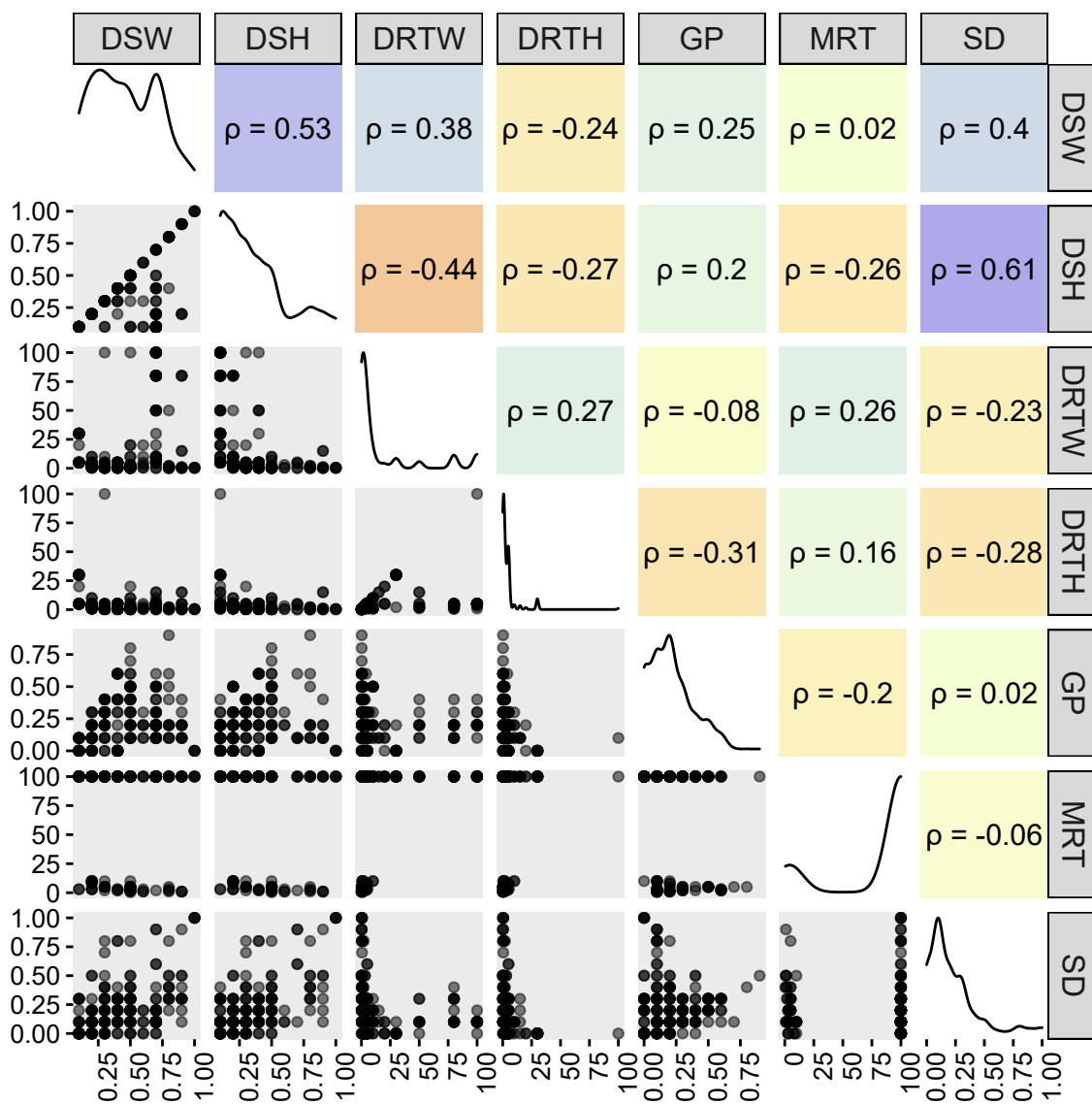
68 \* = For the habitats that are never mown, a value of 100 years was used  
 69 for the calculation of species indicator values. See Materials and Methods  
 70 of the main article.

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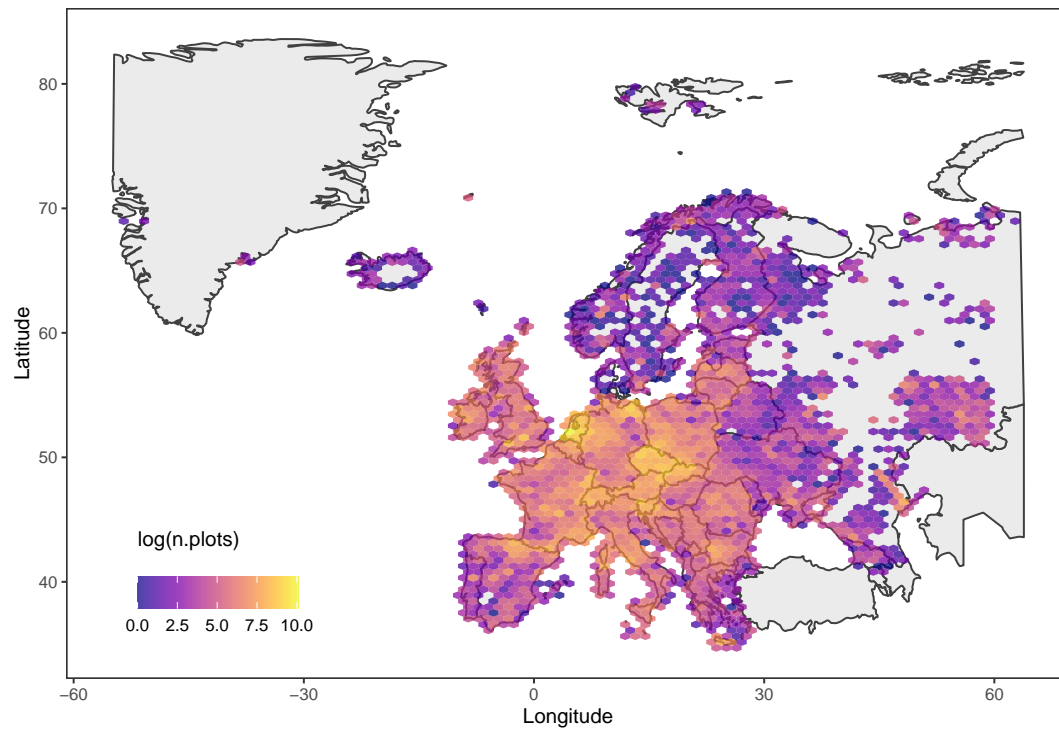
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**Figure S1.1:** Density plots (diagonal), pairwise correlations (top-right) and scatter plots (bottom-left) for the disturbance values assigned to the 236 habitats. DSW = disturbance severity (at the whole community level); DSH = disturbance severity 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.

## 79 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).

### 80 Appendix S3: Sensitivity analyses

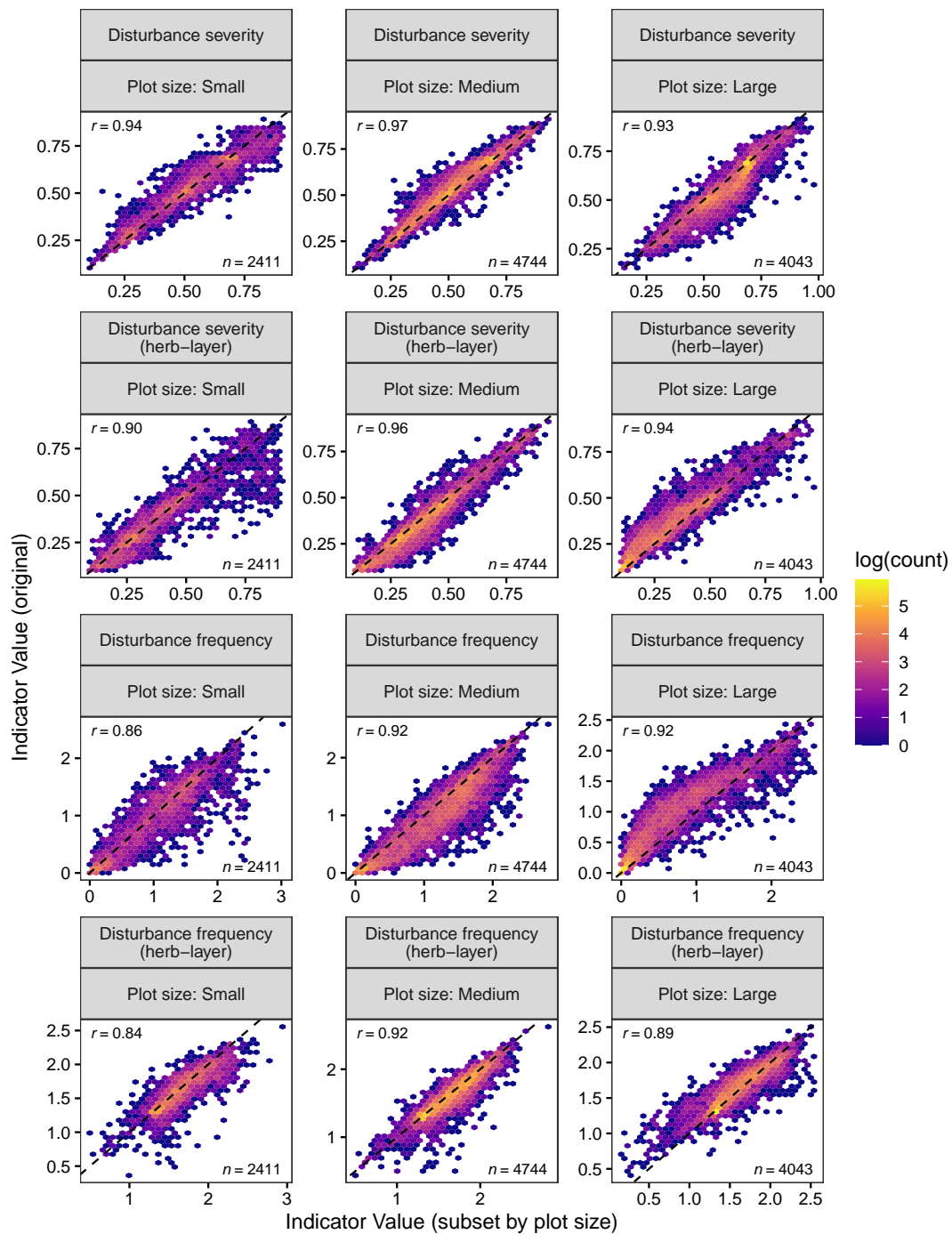
81 In this appendix we describe the methods and results of sensitivity analy-  
82 ses exploring the role of plot size in affecting indicator values and test the  
83 minimum plot number to calculate the indicator values.

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

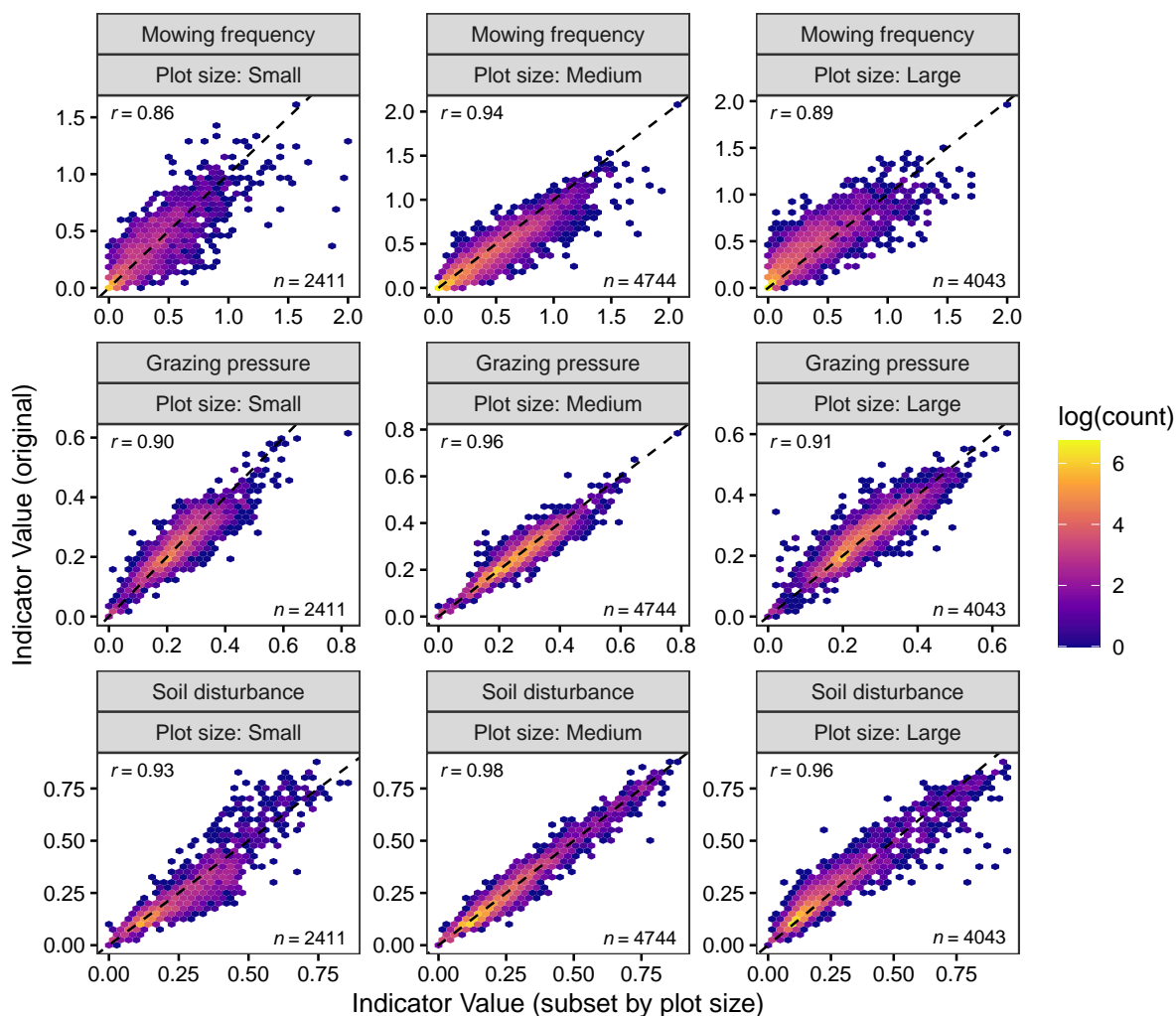
**Table S3.1:** Ranges of plot size for each category (= 'Small', 'Medium' and 'Large'). Range values were assigned differently to forest or non-forest vegetation. The table report the total percentage for each category over 544,433 plots.

Plot size category	Plot size range (m <sup>2</sup> )		% 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

91 We argue that plot size cannot affect directly disturbance indicators be-  
92 cause expert-based disturbance values of habitat types were assigned inde-  
93 pendently from vegetation plot characteristics. Indeed, we show that pat-  
94 terns are consistent to our original indicator values (Pearson's  $r \geq 0.84$ ) (see  
95 Figure S3.1 and Figure S3.2). However, the values of disturbance indicators  
96 can slightly vary depending on plot size because the latter depend upon  
97 habitat types, from which disturbance values are derived.



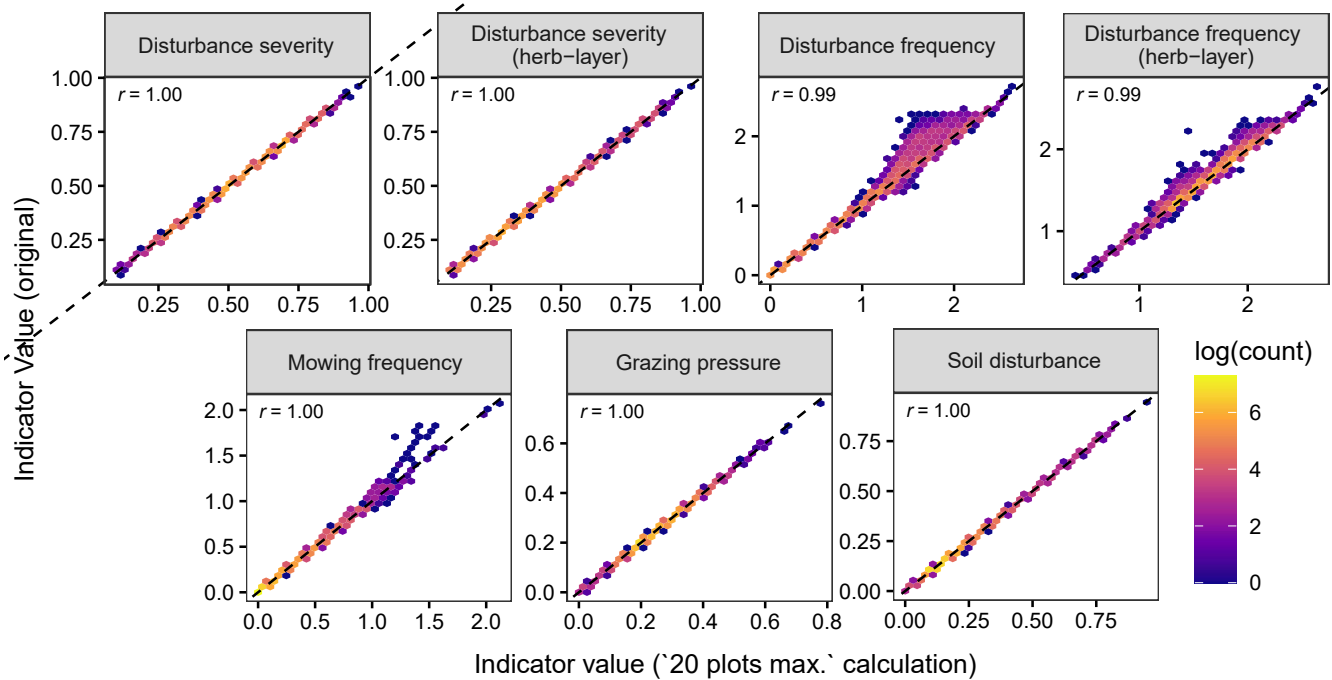
**Figure S3.1:** Relationship between our original indicator values (y-axis) and indicator values re-calculated for each subset of plot size category (= 'Small', 'Medium', 'Large') (x-axis) for disturbance severity and frequency (at the whole community level) and disturbance severity and frequency in 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.



98 Second, to test that a minimum of 20 plots per species is sufficient for  
 99 estimating disturbance indicator values, we report the results of a sensitivity  
 100 analysis in which we recalculated the indicator values by randomly selecting,  
 101 where possible, 20 plots only for each species in each of the 999 repetitions  
 102 in which we calculated the disturbance indicator values. We show that  
 103 the values obtained this way are nearly the same to disturbance indicator  
 104 values reported in our main manuscript (Pearson's  $r \geq 0.99$ ) (Figure S3.3),  
 105 demonstrating that a minimum of 20 plots per species represent a robust  
 106 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.

107 **Appendix S4: Plant functional traits and C-S-R data rela-**  
 108 **tionships 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.

Plant life form	Species number (observations)	
	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 <sup>3</sup>	-	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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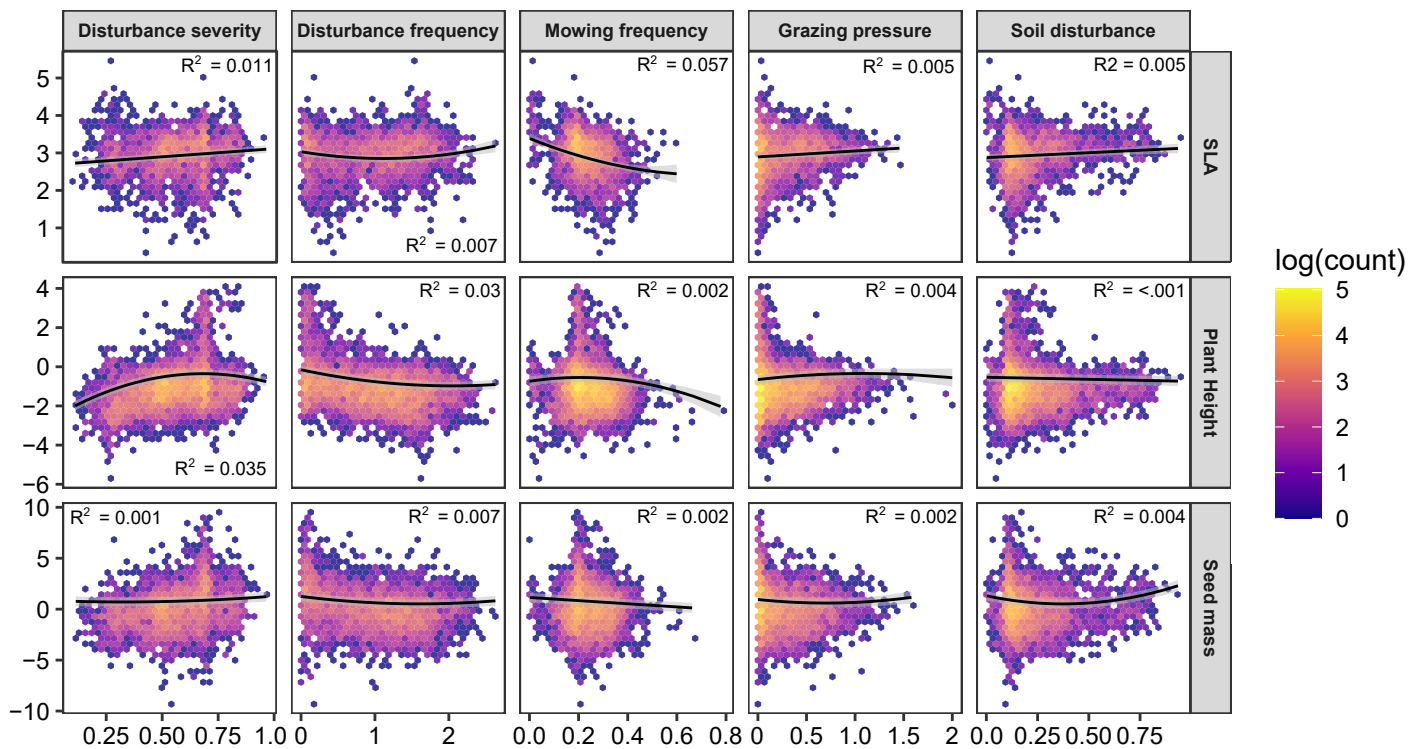
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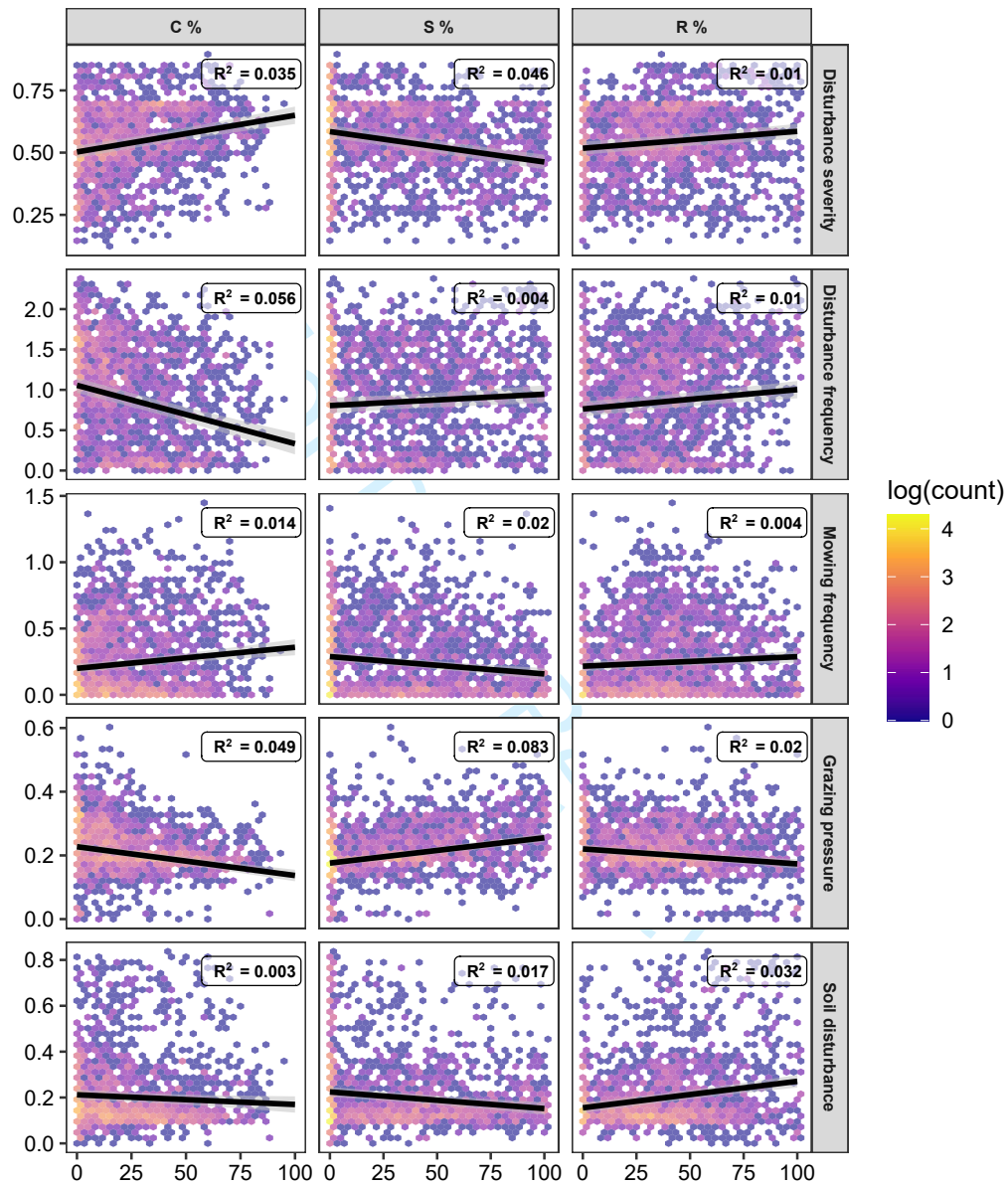
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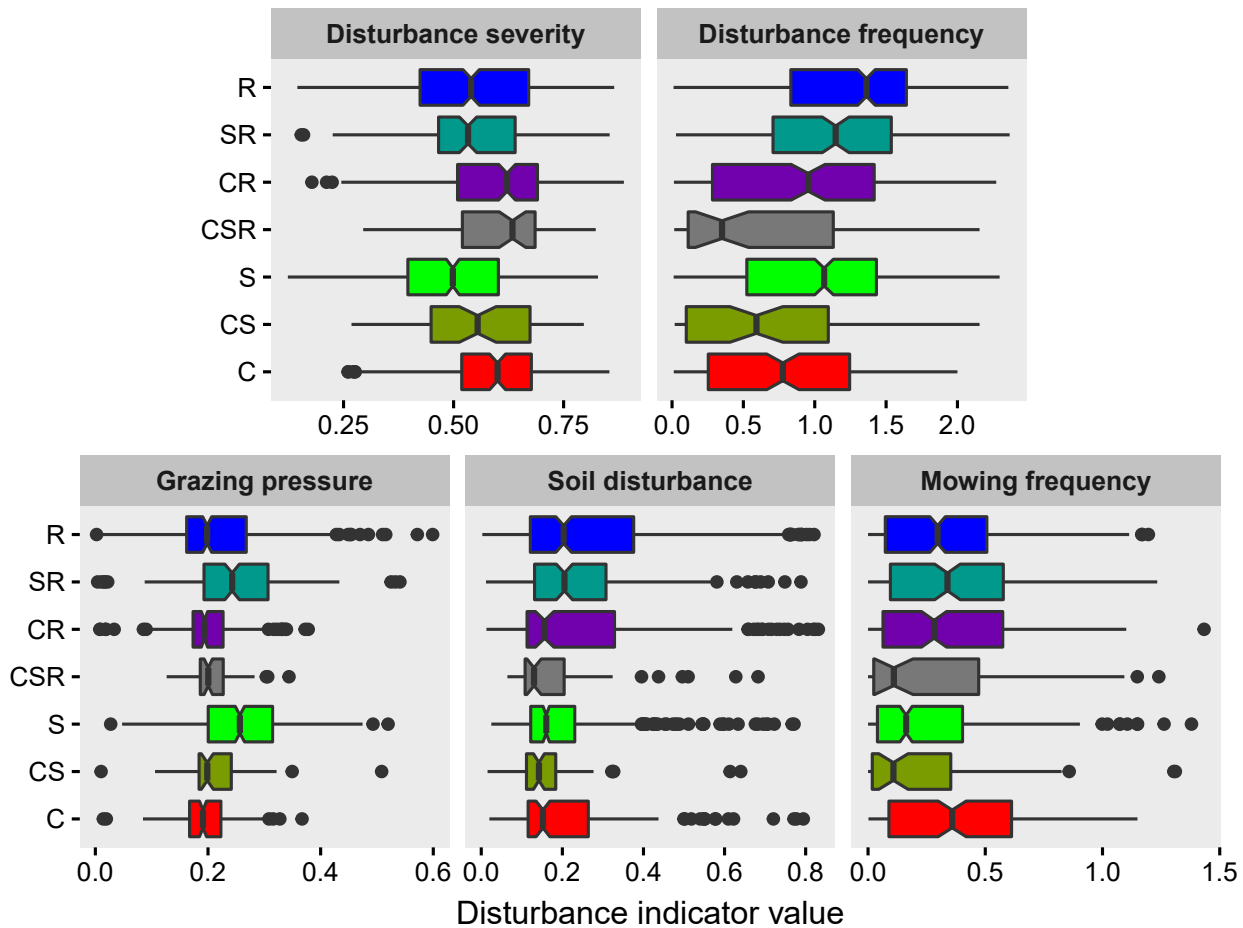
For Peer Review



**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.



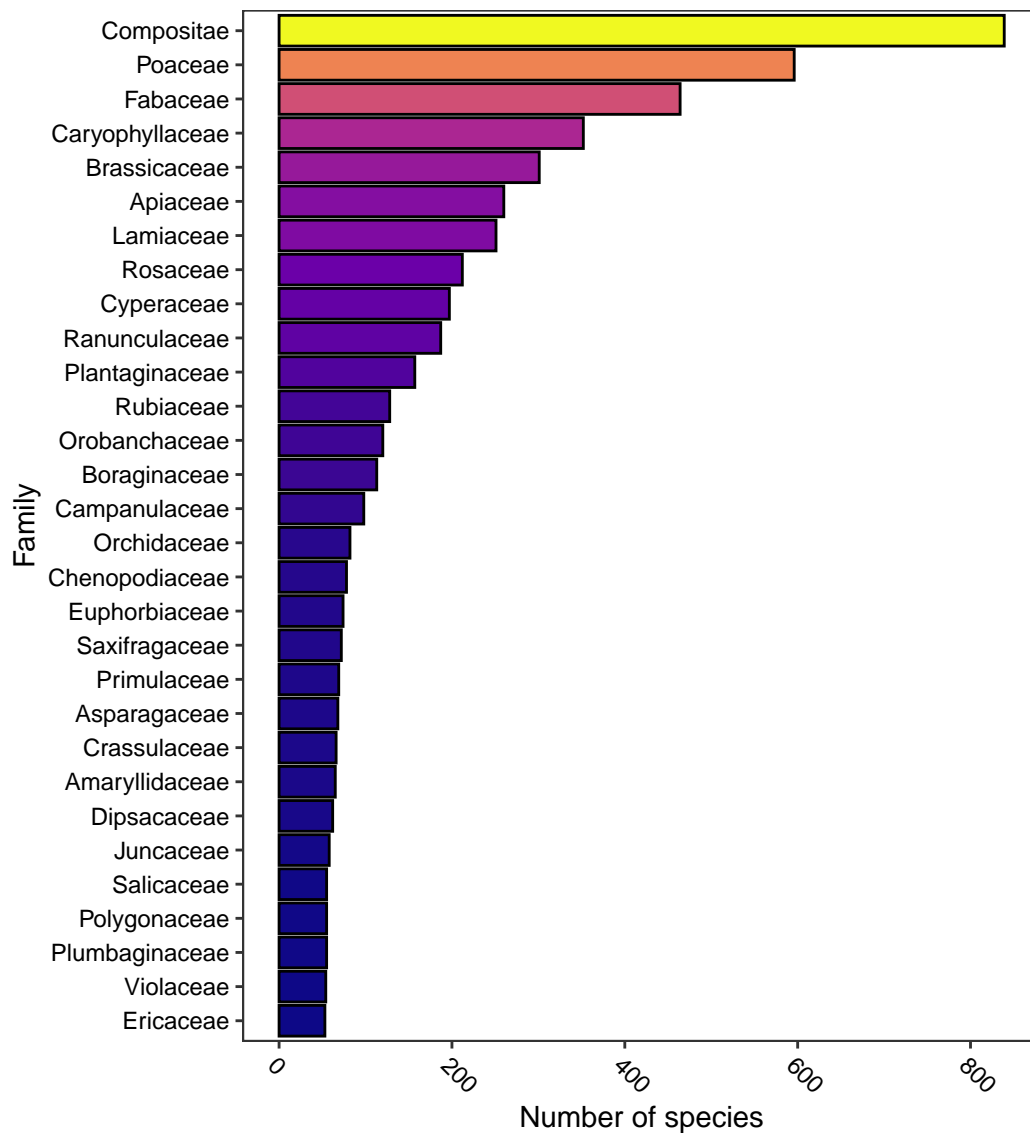
**Figure S4.2:** Relationship between competitor (C), stress-tolerator (S) and ruderal (R) Grime's scores (x-axes) and main disturbance indicator values (y-axes) across individual species for a subset of 1,683 species. Lighter colors of the bins correspond to a higher density of data points. The panels 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 were 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  $1.5 \times$  interquartile range values.

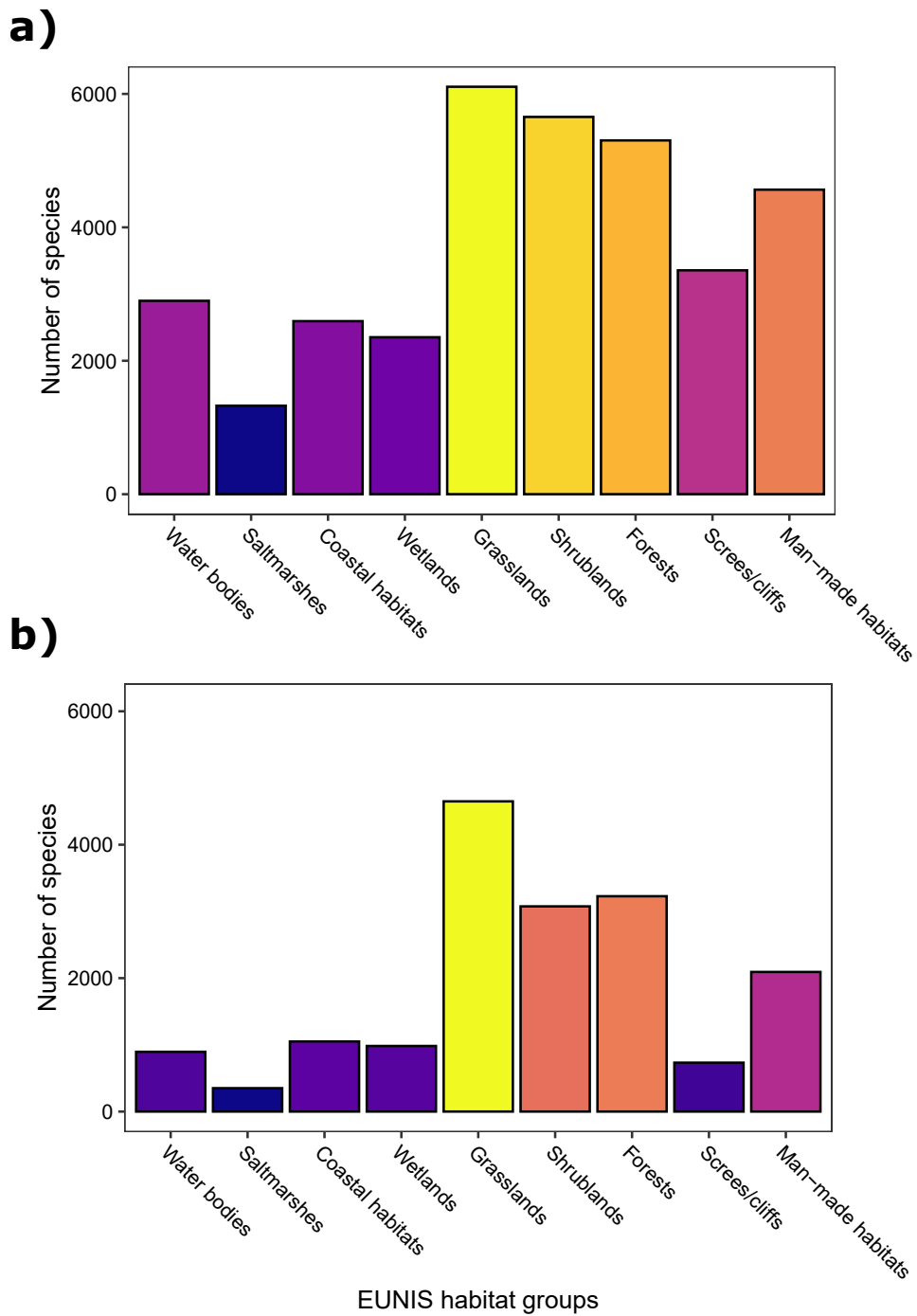
138 **Appendix S5: Number of species per plant family and habitat**

139 **groups**



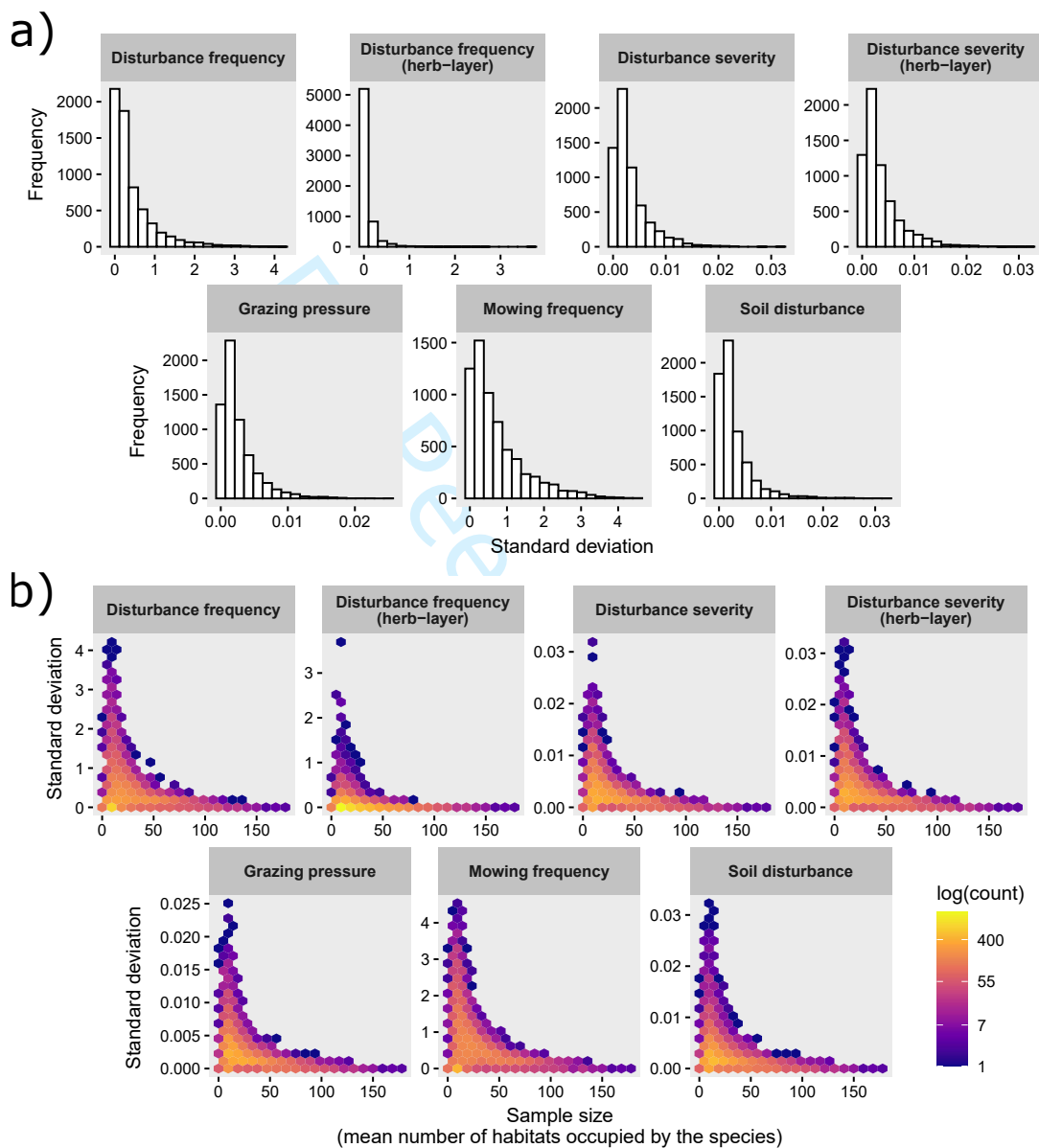
48 **Figure S5.1:** Number of species included in the data set for each plant  
 49 family. Only the 30 most frequent families are shown.



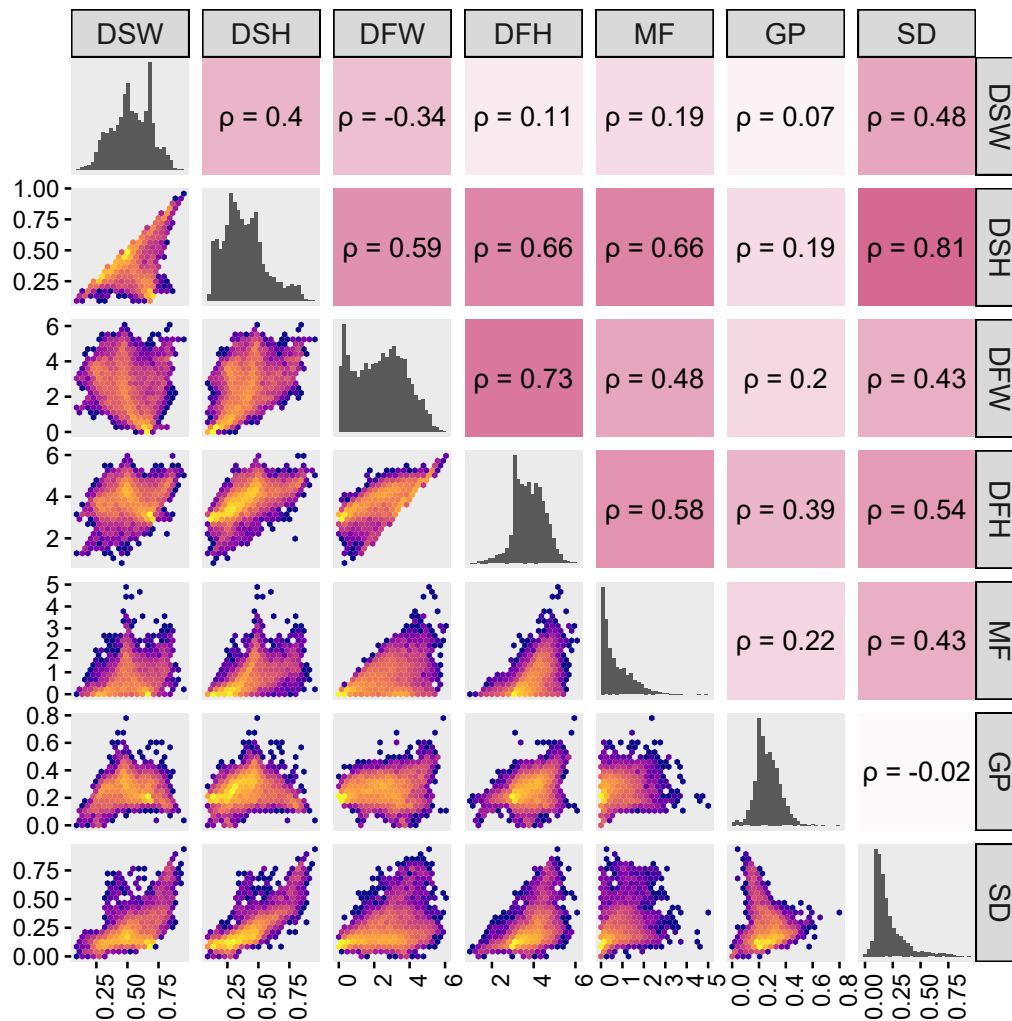


**Figure S5.2:** Number of species included in the data set found in different EUNIS habitat groups (see Chytrý et al., 2020) based on 736,366 EVA plots. Panel a) displays species found in at least one plot belonging to a given habitat group. Panel b) displays species found in at least 20 plots belonging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

140 **Appendix S6: Distribution of uncertainty and pairwise corre-**  
 141 **lation 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

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plot	species
A	<i>Sagittaria sagittifolia</i>
A	<i>Phragmites australis</i>
A	<i>Urtica dioica</i>
B	<i>Urtica dioica</i>
B	<i>Myosotis arvensis</i>
B	<i>Cyanus segetum</i>
C	...

## b) Expert-based estimation of disturbance

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plot	EUNIS habitat
A	Q51
B	V15
C	...

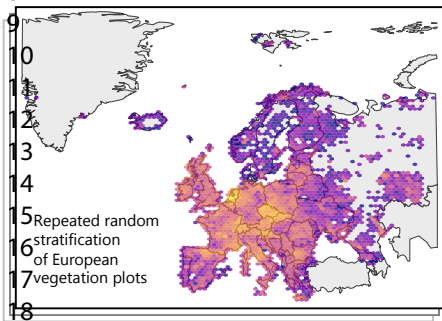
EUNIS Habitat	Habitat-level disturbance values				
	Severity	Frequency (yrs)	Mowing (yrs)	Grazing	Soil
Q51	0.2	1	10	0.1	0.1
V15	0.8	1	5	0.2	0.8
<i>i</i>	<i>d<sub>ki</sub></i>	...	...	...	...

Examples:

Q51 = Tall-helophyte bed

V15 = Bare tilled, fallow or recently abandoned arable land

## c) Calculation of species indicator values

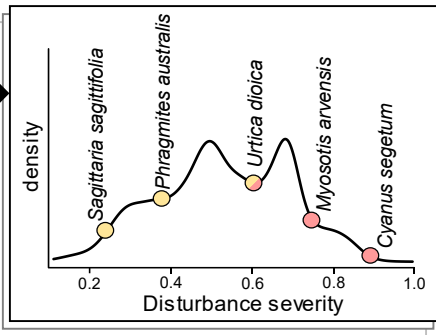


for indicator *k*; species *j*:

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

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

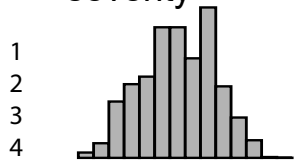
$w_{ji}$  = Number of occurrences of species *j* in habitat *i*



Disturbance severity

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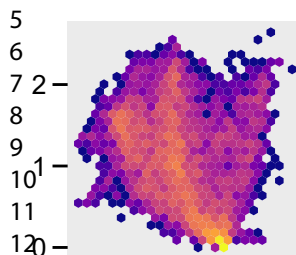


$\rho = -0.34$

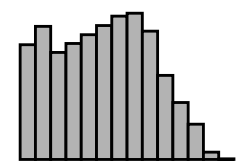
$\rho = 0.19$

$\rho = 0.07$

$\rho = 0.48$



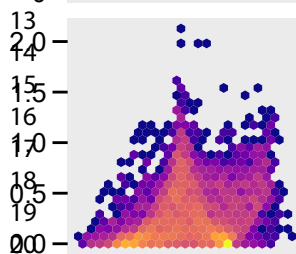
Disturbance frequency



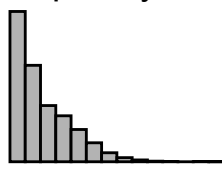
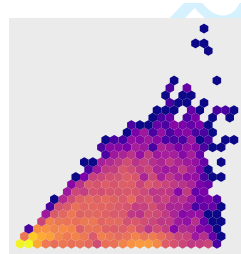
$\rho = 0.48$

$\rho = 0.2$

$\rho = 0.43$

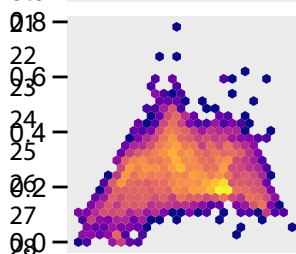


Mowing frequency

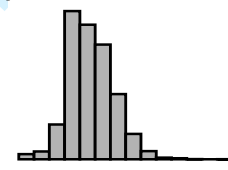
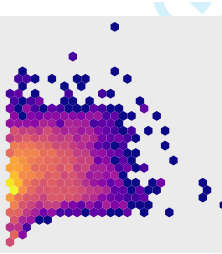
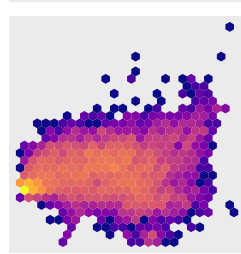


$\rho = 0.22$

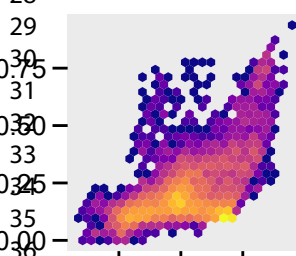
$\rho = 0.43$



Grazing pressure



$\rho = -0.02$



Soil disturbance

