



**HAL**  
open science

## Calibrating ecological indicator values and niche width for a Mediterranean flora

Arne Saatkamp, Nicolas Falzon, Olivier Argagnon, Virgile Noble, Thierry Dutoit, Eric Meineri

► **To cite this version:**

Arne Saatkamp, Nicolas Falzon, Olivier Argagnon, Virgile Noble, Thierry Dutoit, et al.. Calibrating ecological indicator values and niche width for a Mediterranean flora. *Plant Biosystems*, 2022, 157 (2), pp.301-311. 10.1080/11263504.2022.2104399 . hal-03782767

**HAL Id: hal-03782767**

**<https://hal.science/hal-03782767v1>**

Submitted on 21 Sep 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0  
International License

# Calibrating ecological indicator values and niche width for a Mediterranean flora

Arne Saatkamp<sup>a</sup>, Nicolas Falzon<sup>a</sup>, Olivier Argagnon<sup>b</sup>, Virgile Noble<sup>b</sup>, Thierry Dutoit<sup>a</sup> and Eric Meineri<sup>a</sup>

<sup>a</sup>Aix Marseille Université, Université Avignon, CNRS, IRD, UMR IMBE, Marseille, France; <sup>b</sup>Conservatoire botanique national méditerranéen, Hyères, France

## ABSTRACT

Bioindication of ecological variables such as humidity, temperature or pH by ecological indicator values of plants is a powerful tool for research in plant ecology, e.g. to detect early vegetation changes. Here, we provide a data set of ecological indicator values including niche width for an entire regional flora. We used an extensive data-base with floristic relevés from Southern France to recalibrate indicator values for light (L), temperature (T), continentality (K), air humidity (A), soil moisture (F), pH (R), productivity (N), soil texture (G), soil organic matter content (O) and salinity (S). Values were recalibrated using average values from co-occurring plants, enabling to develop indicator values for species not yet evaluated previously. Recalibrated values are on a continuous scale and we add standard deviation, median, first and third quartile for each indicator value. Linear regression of average indicator values against measured factors showed higher correlation with recalibrated values compared to original indicator values for temperature, pH and nitrogen, and comparable  $R^2$  for moisture. Individual indicator systems performed better than a combination and applying different weighting procedures demonstrated the usefulness of inverse variance. We further illustrate graphically how recalibrated values and niche width increase ecological knowledge on plants.

## KEYWORDS

Bioindication; Ellenberg; ecological gradients; ecological indicator values; niche width

## Introduction

Ongoing man-made global changes in terrestrial ecosystems affect a large number of physical and chemical environmental properties, including temperature and soil moisture (Peñuelas et al. 2004; King and Karoly 2017) but also soil acidity and soil nutrient status (Ochoa-Hueso et al. 2014; Meesenburg et al. 2016). These changes have cascading effects on ecosystems and plant community composition. Effects of changes in primary climatic factors such as temperature and rainfall are now becoming intensively studied thanks to experimental rain-exclusion and heating (Bloor et al. 2010; Ogaya et al. 2011; Wolkovich et al. 2012; Martin-StPaul et al. 2013; Liu et al. 2018) and thanks to species distribution modelling (Thuiller et al. 2005; Engler et al. 2011) using spatially continuous data-sets on climatic factors (Fick and Hijmans 2017; Meineri and Hylander 2017). Changes in important soil and ecosystem properties such as pH, light or nutrient status are less well studied (Martinez-Almoyna et al. 2020). Soil characteristics are highly heterogeneous in time and space, such as soil acidity, nutrient status or salinity that may vary on short time scales or distances due to organic matter accumulation, decomposition, weathering or lateral transport of sediments. Measuring these variables in a relevant way is particularly costly and time consuming and few directly

measured data exist, despite the high explanative power of these variables for community composition and plant distribution (Diekmann 2003; Lenoir et al. 2013). Ecological indicator values (EIVs) for plants (Ellenberg et al. 1992; Julve 1998; Pignatti et al. 2005; Landolt et al. 2010) bridge this gap by providing a standardised characterization of realized niche optima in many abiotic variables for most species. While EIVs were initially based on expert opinion, biogeographic and phytosociological data, numerous studies demonstrated the relation of EIVs to measured ecological factors (Ellenberg et al. 1992; Oomes et al. 1996; Wamelink et al. 1998; Dzwonko 2001). In return, floristic inventories can be used to infer relevant meso- and microclimate variables as well as some soil factors (Diekmann 2003). For example, recent studies have used weighed means of EIVs based on inventories to infer high-resolution climatic conditions (Lenoir et al. 2013; Descombes et al. 2020). Similarly, studies on environmental changes through time using EIVs enable the detection of subtle early changes (Kapfer et al. 2011; Matteodo et al. 2013; Kapfer et al. 2016; Carroll et al. 2018) and the identification of underlying changes in ecosystem properties (Diekmann 2003; Fernández-Pascual et al. 2015). Nevertheless, quality of EIV systems progressed little in recent years and EIVs are still lacking for many regions.

Ecological indicator values (EIVs) characterise the realized niche optima in terms of local conditions of light (L), temperature (T), continentality (K), soil moisture (F), soil reaction (R), soil nutrient status (N) and salinity (S) (Ellenberg et al. 1992). Later EIV systems added information on air humidity (A), soil organic matter (M) and soil texture (G) (Julve 1998; Landolt et al. 2010). After the initial proposal of EIVs for the central European flora by Ellenberg (1974) recent and historical floristic inventories available from large floristic data-bases (Gégout et al. 2005; Dengler et al. 2011) have allowed the development of EIVs for Switzerland (Landolt et al. 2010), Italy (Pignatti et al. 2005) and France (Julve 1998). Indicator value systems have then also been adapted for other biogeographic regions (Loopstra and van der Maarel 1984; Hill et al. 2000; Lawesson et al. 2003), often by averaging known values of co-occurring species in field inventories to estimate new indicator values for species lacking EIVs. However, in biodiversity hotspots, such as the Mediterranean region (Médail and Quézel 1999), many local endemic species still lack EIVs and species with large distributional areas might have evolved regional ecotypes differing in realized niche (Ågren and Schemske 2012). In such a highly impacted region by global changes as the Mediterranean (Doxa et al. 2017; Marignani et al. 2017), understanding limitations of plants for multiple ecological gradients and local conditions becomes increasingly important (Böhling et al. 2002).

EIVs contain information on relative position in ecological gradients with no formalized information on niche width (Ellenberg 1974; Ellenberg et al. 1992; but see Landolt et al. 2010), on discontinuous scales, which reduces the possibilities of representing ecological differences between species. This is at odds with the finely differentiated habitat requirements between species along environmental gradients (Bátori et al. 2017). Differences in niche width are fundamental in plant ecology and small ecological ranges correspond to the concept of ecological rarity (Rabinowitz et al. 1981). Reduced niche widths and limited tolerances are often invoked but rarely quantified when evaluating conservation status and when conceiving action plans (Noble et al. 2015). Including a measurement of ecological niche width around an optimal ecological indicator value for a large set of species, represents hence a considerable advance for understanding and evaluating threats to declining plants.

Not all plants are equally useful while finding the ecological conditions indicated by a local plant community. Ellenberg and co-workers (1992) underline that many plants have so large niche widths that they are not helpful to indicate a specific ecological condition. In order to take into account the specificity of plants for a niche position, Landolt et al. (2010) proposed two classes of narrow and wide niche widths. A weighting based on the niche width of a species could use a continuous measure, such as the inverse of variance when comparing values indicated by a local community with measured factors. This approach is a promising alternative to the rarely effective weighing by a plant's abundance for conditions indicated by a plant community (Ter Braak and Barendregt 1986; Schaffers and Sýkora 2000; Diekmann 2003).

In this paper we develop a comprehensive set of EIVs for the entire vascular flora of Southern France, covering the

continental Mediterranean area and surrounding mountain ranges. Specifically, our work aims to (i) develop continuous indicator values for a species-rich Mediterranean flora and quantify niche width of plants; (ii) evaluate the predictive power of indicator values using field measurements of soil moisture, pH, mean annual air temperature and soil nitrogen content; (iii) evaluate the usefulness of abundance and inverse-variance weighting when linking environmental factors to plant requirements.

## Materials and methods

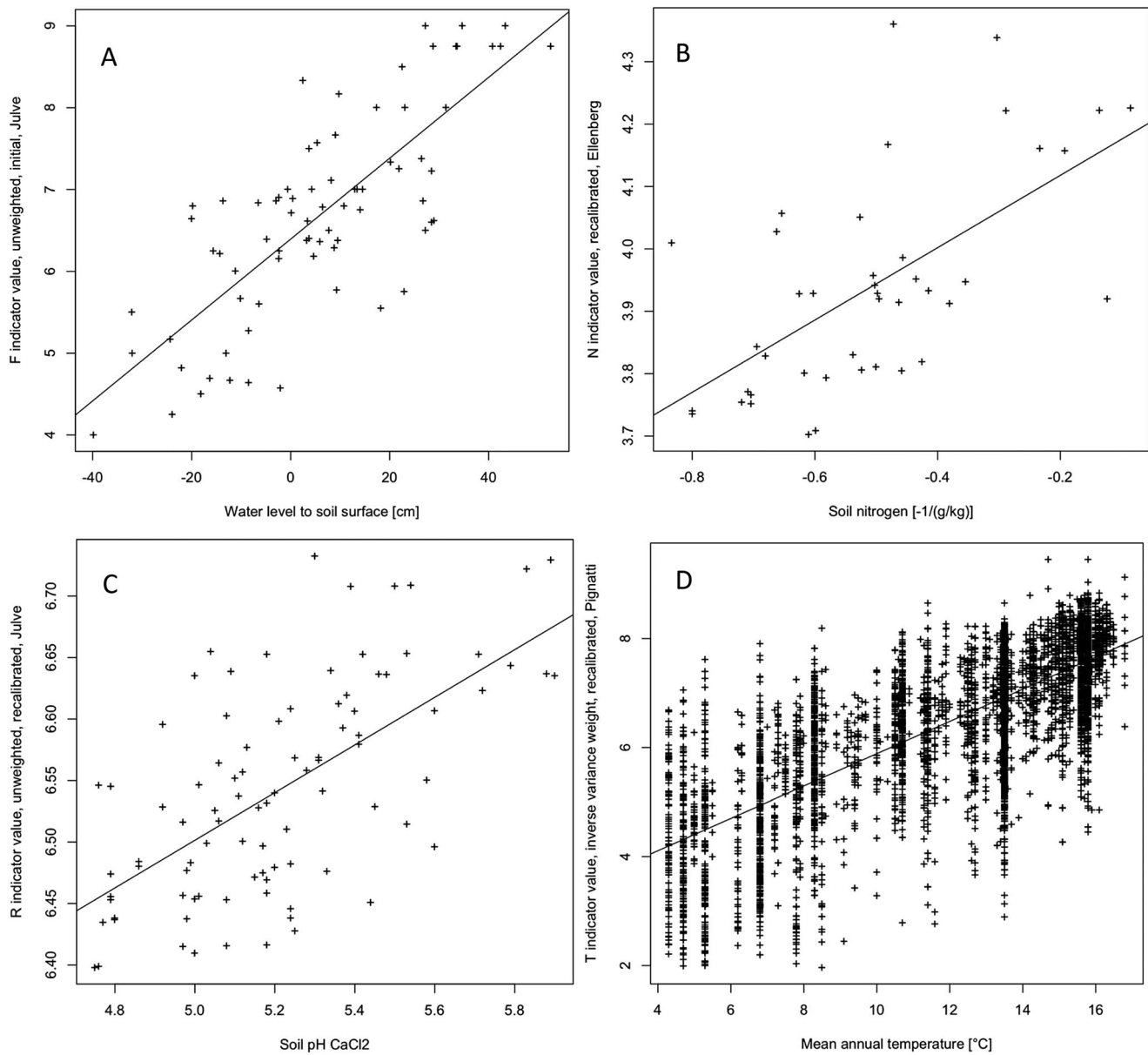
### Ecological indicator systems

We use four different ecological indicator systems for Germany (Ellenberg 1974; Ellenberg et al. 1992) Switzerland (Landolt et al. 2010), Italy (Pignatti et al. 2005) and France (Julve 1998). All four systems contain positions of taxa on gradients of six common environmental parameters: light (L), temperature (T), continentality (K), soil moisture (F), reaction (R), productivity/soil nitrogen (N). The Ellenberg, Pignatti and Julve system also contained a salinity value (S), but only a restricted set of species have salinity values indicating saline soils. The Julve and Landolt systems additionally include air relative humidity (H) and soil organic matter content (O) and Julve as well as parameter for soil texture (G) (Julve 1998) and Landolt a parameter for soil aeration (A) (Landolt et al. 2010). Only the Landolt system included two classes of niche width (narrow or wide). We summarized the indicator values in Appendix S1.

### Floristic data

Floristic co-occurrence data were extracted from the SILENE database (<http://flore.silene.eu>, version 22/11/2021). This database contains over 6 million plant observations for more than 6300 species and subspecies from Southern France, extending 320 km in Latitude from 42°20' to 45°6' North, and 480 km in Longitude from 1°41' to 7°43' East, from sea level to an altitude of 4102 m at *Barre des Ecrins*, including observations from all plants known from the area to date. We extracted species lists containing at least 3 and at most 50 species or subspecies, based on their co-occurrence, obtaining 236,131 lists of co-occurring species, hereafter called "relevés." These were mostly phytosociological relevés of varying surface, but also included some systematic samplings and non-exhaustive floristic lists. We used 3 plant taxa as a minimum to enable estimation of indicator values, and we chose 50 taxa as a maximum in order to exclude putatively heterogeneous records. While most observations come from Mediterranean climate areas, the data also cover the adjacent alpine, atlantic and continental bioclimatic regions. Hence, the data contain extended gradients for mean annual temperature (MAT) and precipitation (P), including dry and warm Mediterranean sites (MAT > 16°C, P < 470 mm), moist atlantic sites (P > 1900 mm) and cold areas at high altitudes (MAT < 5°C, Figure 1).

We standardized plant taxonomy and nomenclature between our floristic data and names used in the ecological indicator systems using TAXREF12, the nomenclatural



**Figure 1.** (A) Community average of humidity indicator values based on the Julve-system (1998) and water levels measured for 75 relevés from temporal pools ( $R^2 = 0.59$ ,  $p < 0.001$ ). (B) Average of nitrogen indicator values, weighted by abundance, recalibrated based on Ellenberg et al. (1992) and soil total nitrogen content (g/kg transformed to  $-1/x$ ) for 42 relevés from dry grasslands ( $R^2 = 0.37$ ,  $p < 0.001$ , transformed to  $-1/x$ ). (C) average of reaction indicator values, unweighted, recalibrated based on Julve (1998) and soil pH (CaCl<sub>2</sub>) from 91 relevés in dry grasslands ( $R^2 = 0.39$ ,  $p < 0.001$ ). (D) average of temperature indicator values, weighted by inverse of variance based on Pignatti et al. (2005) and mean annual temperature for 7065 relevés ( $R^2 = 0.58$ ,  $p < 0.001$ ).

reference list for vascular plants in France (Gargominy et al. 2014). We tried to find relevant synonyms for taxa that do not correspond literally to accepted names in TAXREF12 by using the TNRS algorithm (<http://tnrs.iplantcollaborative.org/>). Remaining taxa with no nomenclatural correspondence in TAXREF12 were solved using two regional floras (Tison et al. 2014; Tison and de Foucault 2014). We omitted taxa occurring only in Italy, Switzerland or Germany but not in France. Since data contained various levels of taxonomic resolution, and sometimes higher, sometimes lower taxonomic levels are of interest in terms of conservation strategies (Noble et al. 2015), we run our analysis separately at the level of species and subspecies/varieties, this means that we calculated EIVs for the species combining all data from subordinated taxa, and then calculated EIVs for subordinate taxa on the same

data set but separating subspecies level, enabling us to represent both levels as present in our data-set.

### Initial ecological indicator values and recalibration

We used EIVs from the four systems to calculate average values for every relevé in our floristic data set, hereafter “relevé EIVs.” We then derived new indicator values for each taxon by using mean of all relevé EIVs including occurrence of the given taxon in the floristic dataset, similar to Hill et al. (2000). We then used all relevé EIVs to calculate standard deviation as well as median, first and third quartile. Using averages reduced range and standard deviation of recalibrated EIVs compared to the initial scale. In order to keep range and standard deviation comparable after recalibration,

we multiplied the initial standard deviation by the ratio of initial on recalibrated standard deviation, this resulted in recalibrated values equalling the standard deviation of initial values. However, this yielded sometimes single values outside the range of the initial values, we chose to keep this information and not to restrict recalibrated values to the initial range. Further on, we chose not to combine values from different indicator systems during recalibration, since they were developed on different scales and with a different scientific background, and also to enable a comparison of indicator values with field measurements in this and future studies. However, in the comparison with measured variables detailed below we also used means values across all four systems in order to be able to study the effects of a combined system.

### **Testing EIVs with field measurements**

We used floristic relevés for which measurements of pH, total soil nitrogen, water levels and mean annual temperatures have been done within or close to the sampled plot to evaluate the relevance of our recalibrated ecological indicator values. These were (i) a set of 91 pH measurements and associated relevés in the La Crau area with 178 taxa (Saatkamp et al. 2010) that we compared to mean R indicator values, (ii) measurements of maximum water level in ephemeral ponds in Southern France (Metzner et al. 2017) that we compared with mean F indicator values for 75 relevés, (iii) a dataset with 41 total soil nitrogen measurements containing 131 taxa in the La Crau area (Saatkamp et al. 2018) that we compared with mean N indicator values and (iv) mean annual temperature from 269 standard meteorological stations of the Météo-France network together with 7094 relevés with less than 500m of horizontal and less than 50m of altitudinal distance that we compared to mean T indicator values. We chose these data sets because they reflect ecological gradients in the study region and are particularly species rich. While calculating the mean indicator values for each relevé in the testing data-sets, we applied three different methods (i) simple mean based on presence-absence of species (ii) means weighted by the abundance of species in each relevé and (iii) mean values weighting each species by its niche width giving more weight to species with specialized niches, in order to achieve this we used the inverse of variance. We multiplied individual indicator values of species with the associated  $1/\text{variance}$ , summed it up for the relevé and divided this by the sum of  $1/\text{variance}$  for the relevé. Variance is based on squared standard deviation as calculated during the recalibration method detailed above. We compared the three different weighting methods, different EIV systems and tested the relationship between mean indicator values and field measurements using linear regression. Since simple community averages can overestimate significance in environment-species descriptor relationships (Zelený and Schaffers 2012; Peres-Neto et al. 2017; Zelený 2018), we also implemented the maximum  $p$ -value method as suggested by ter Braak and co-workers (ter Braak 2019). This approach retains the maximum of  $p$ -values from regressions using

permutations of plots and species, as a conservative estimate in order to minimise extreme influences of single species or plots. All data-handling, calculations and statistical analyses were performed in the R statistical environment (R-Core-Team 2014).

## **Results**

### **Newly calibrated indicator values**

We present the main outcome of newly calibrated indicator values in appendix S4 for 4955 plant taxa. Compared to the previously most complete indicator system developed by Julve (1998), we propose new EIVs for over 1700 taxa that have never been evaluated for light, humidity, soil acidity, temperature, continentality air humidity, soil particle size and salinity values. We refined niche positions of plants for these factors using mean and median values for the flora of Southern France according to the Julve system (e.g. light). We were also able to calculate standard deviations and the 1st and 3rd quartiles for the same plant taxa.

Linear regressions of recalibrated on initial EIVs show that all recalibrated values are positively related to the initial values with  $R^2$  above 0.57 except for continentality (Appendix S2 Table A). Plots of recalibrated on initial values show that values are linearly related, that the extremes of recalibrated values tend to be closer to the middle of the gradient compared to the initial values (Appendix S2 Figures B), a few single recalibrated values differ substantially from original ones. However, density distribution of the residuals show that most recalibrated values differ less than one unit from original values (Appendix S2 Figures C). EIVs for the same ecological factor but from different systems were strongly correlated in most cases (Appendix S3). Landolt's class of narrow niche width had significantly smaller standard deviations compared to the class of wide niches, as calculated using our data-set (t-test, all factors  $p < 0.001$  except continentality with  $p = 0.006$ ). When we compared the niche widths (standard deviations) calculated in this work with niche width classes in Landolt et al. (2010) with a t-test, all factors show significantly higher standard deviations for the large niche width class compared to the narrow niche width class (Figure in Appendix S5), except for continentality and soil aeration.

### **Correlations between measured and indicated variables**

Linear regressions of indicator values for moisture, reaction, productivity as a function of measured water level, soil pH, soil nitrogen and mean annual temperatures revealed strong, significantly positive relationships in all cases (Figure 1, Table 1). However, best correlations between measured variables and indicator values were obtained with different EIV systems for the different variables. We found the highest correlations between indicator values and measured values for soil moisture based on the Julve and Landolt systems ( $R^2 = 0.59$ ,  $p < 0.001$ , Figure 1A) when species values were

**Table 1.** Regressions of mean indicator values as a function of measured factors for (F) moisture levels in ephemeral ponds, (N) soil total nitrogen content in dry grasslands (transformed to  $-1/x$ ), (R) pH in dry grasslands and (T) mean annual temperature at Météo-France stations; weights are (pa) presence-absence, (vw)—inverse variance, (ab)—abundance, o: original estimates from (j) Julve (1998), (l) Landolt et al. (2010), (p) Pignatti et al. (2005) and (e) Ellenberg et al. (1992) or (c) combined by average of relevé mean EIV for each system; i—initial non recalculated values, N—number of relevés used, R<sup>2</sup>—adjusted r squared from linear regression and p-values, p-max, R<sup>2</sup> max—p- and R<sup>2</sup> values according to permutation test by ter Braak (2019); bold for the three highest ranking R2.

Factor	Weights	o	i	R2	N	F-value	p-value	p-max	R2 max
F	pa	c	i	0.43	75	57.7	<0.001	<0.001	0.44
F	pa	c		0.52	75	82.7	<0.001	<0.001	0.53
F	pa	e	i	0.02	75	2.9	0.094	0.842	0.00
F	ab	e		0.28	75	29.3	<0.001	<0.001	0.29
F	pa	e		0.22	75	21.8	<0.001	<0.001	0.23
F	vw	e		0.33	75	37.1	<0.001	<0.001	0.34
F	pa	j	i	0.59	75	109.3	<0.001	<0.001	0.47
F	ab	j		0.52	75	82.0	<0.001	<0.001	0.53
F	pa	j		<b>0.58</b>	75	101.5	<0.001	<0.001	<b>0.58</b>
F	vw	j		<b>0.58</b>	75	101.8	<0.001	<0.001	<b>0.58</b>
F	pa	l	i	<b>0.59</b>	75	106.2	<0.001	<0.001	<b>0.60</b>
F	ab	l		0.52	75	81.9	<0.001	<0.001	0.53
F	pa	l		0.56	75	95.5	<0.001	<0.001	0.57
F	vw	l		0.52	75	82.6	<0.001	<0.001	0.53
F	pa	p	i	0.48	75	70.3	<0.001	<0.001	0.38
F	ab	p		0.49	75	72.7	<0.001	<0.001	0.50
F	pa	p		0.54	75	86.6	<0.001	<0.001	0.54
F	vw	p		0.51	75	76.8	<0.001	<0.001	0.51
N	pa	c	i	0.24	42	13.9	<0.001	<0.001	0.24
N	pa	c		0.26	42	15.6	<0.001	<0.001	0.28
N	pa	e	i	0.19	42	10.8	0.002	0.002	0.28
N	ab	e		<b>0.37</b>	42	25.0	<0.001	<0.001	<b>0.35</b>
N	pa	e		0.27	42	16.0	<0.001	<0.001	0.29
N	vw	e		0.22	42	12.8	<0.001	0.004	0.22
N	pa	j	i	0.25	42	14.5	<0.001	<0.001	0.23
N	ab	j		0.31	42	19.3	<0.001	<0.001	<b>0.36</b>
N	pa	j		0.24	42	13.7	<0.001	0.002	0.25
N	vw	j		<b>0.32</b>	42	20.5	<0.001	0.004	0.24
N	pa	l	i	0.23	42	13.4	<0.001	<0.001	0.26
N	ab	l		<b>0.33</b>	42	20.9	<0.001	<0.001	<b>0.38</b>
N	pa	l		0.26	42	15.7	<0.001	<0.001	0.28
N	vw	l		0.30	42	18.5	<0.001	0.002	0.22
N	pa	p	i	0.25	42	14.4	<0.001	<0.001	0.27
N	ab	p		0.31	42	19.2	<0.001	<0.001	0.33
N	pa	p		0.26	42	15.7	<0.001	<0.001	0.28
N	vw	p		0.32	42	19.9	<0.001	0.002	0.26
R	pa	c	i	0.20	91	23.9	<0.001	0.887	0.04
R	pa	c		0.22	91	26.0	<0.001	0.051	0.23
R	pa	e	i	0.00	91	0.3	0.615	0.422	0.11
R	ab	e		0.21	91	25.3	<0.001	0.408	0.20
R	pa	e		0.14	91	15.7	<0.001	0.172	0.15
R	vw	e		0.28	91	36.2	<0.001	0.160	0.15
R	pa	j	i	0.31	91	40.9	<0.001	0.159	0.05
R	ab	j		<b>0.32</b>	91	43.7	<0.001	<0.001	<b>0.39</b>
R	pa	j		<b>0.39</b>	91	58.4	<0.001	<0.001	<b>0.40</b>
R	vw	j		<b>0.35</b>	91	50.1	<0.001	<0.001	<b>0.38</b>
R	pa	l	i	0.30	91	40.2	<0.001	0.564	0.00
R	ab	l		0.26	91	31.8	<0.001	0.337	0.24
R	pa	l		0.16	91	18.4	<0.001	0.132	0.17
R	vw	l		0.22	91	26.8	<0.001	0.141	0.13
R	pa	p	i	0.00	91	0.9	0.347	0.439	0.01
R	ab	p		0.22	91	27.0	<0.001	0.897	0.07
R	pa	p		0.01	91	1.9	0.176	0.645	0.02
R	vw	p		0.22	91	25.8	<0.001	0.648	0.00
T	pa	c	i	0.40	2671	1780.6	<0.001	<0.001	0.18
T	pa	c		0.55	7092	8837.6	<0.001	<0.001	<b>0.54</b>
T	pa	e	i	0.28	3230	1253.5	<0.001	0.011	0.01
T	pa	e		0.48	7092	6577.3	<0.001	<0.001	0.46
T	vw	e		0.47	7063	6369.6	<0.001	<0.001	0.46
T	pa	j	i	0.40	5308	3482.5	<0.001	<0.001	0.06
T	pa	j		0.55	7094	8802.9	<0.001	<0.001	<b>0.54</b>
T	vw	j		<b>0.56</b>	7065	8839.8	<0.001	<0.001	<b>0.54</b>
T	pa	l	i	0.42	5411	3959.3	<0.001	0.002	0.01
T	pa	l		0.55	7094	8736.3	<0.001	<0.001	<b>0.54</b>
T	vw	l		0.55	7065	8712.7	<0.001	<0.001	<b>0.54</b>
T	pa	p	i	0.34	5750	2906.7	<0.001	<0.001	0.09
T	pa	p		<b>0.57</b>	7094	9484.4	<0.001	<0.001	<b>0.56</b>
T	vw	p		<b>0.58</b>	7065	9561.0	<0.001	<0.001	<b>0.56</b>

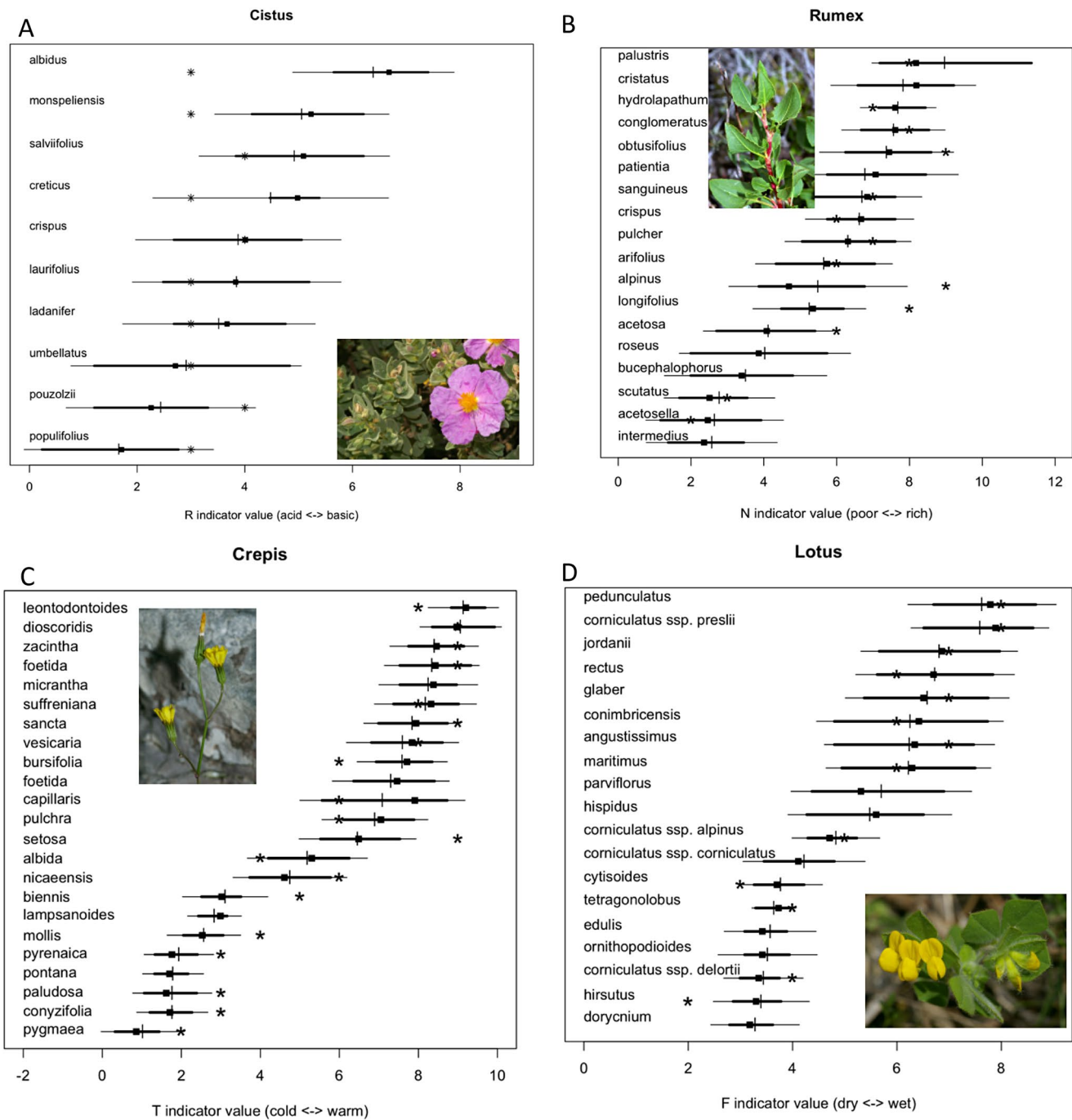
weighted by the inverse of variance to calculate the plant community mean. Comparatively high relations ( $R^2 = 0.58$ ,  $p < 0.001$ , Figure 1D) were also found when mean annual temperature was related to recalibrated temperature indicator values based on the Pignatti system using inverse variance weighting. Reaction and productivity indicator values also showed significantly positive relations to respectively, soil pH and soil total nitrogen content (Table 1). Overall, no single indicator system performed better than others, while the Julve system worked well for soil reaction and together with Landolt for soil moisture, Ellenberg values performed better for productivity values and the Pignatti system better for temperature. Combining the different systems decreased correlations with field measured data in every case (Table 1). Except for moisture where initial not recalibrated values performed slightly better, the recalibrated indicator values showed higher correlations to field measurements compared to the initial indicator values, this effect was most pronounced for temperature and productivity. Considering different weighting procedures, abundance weighting increased  $R^2$  for productivity values in the Ellenberg and Landolt system; inverse variance weighting was able to increase correlations with measured variables for temperature, but there was no clear best weighting procedure when all factors were considered.

### Detailed niches for congeneric species

In Figure 2 we illustrate the detailed niche data we generated using the recalibration procedure and the difference between initial and recalibrated ecological indicator values for moisture, productivity, reaction and temperature for congeneric species in the genera *Lotus*, *Rumex*, *Cistus* and *Crepis*, for which contrasting niches for these factors are well known. Compared to the initial EIV systems, the use of a continuous scale in our recalibrated EIV systems shows a finer differentiation among species. The use of a standard deviation adds considerable information about all species, as well as medians and 1st and 3rd quartile do by indicating eventual skew. We could find indicator values with large standard deviations for reaction values in *C. laurifolius* and *C. monspeliensis* (Figure 2A). For productivity values in the genus *Rumex*, two contrasting ecological groups can be observed, a group around *Rumex scutatus* and *R. acetosella* on poor soils and a group with *R. palustris*, *R. obtusifolius*, and *R. patientia* on highly productive soils (Figure 2B). *R. hydrolapathum* appears to have a limited ecological preference since its standard deviation is comparatively low. Figure 2(C) shows *Crepis* species in Southern France to show differentiated niches across all temperature conditions, while highlighting two more speciose groups with perennial high-altitude plants (*C. pygmaea*, *C. conyzaefolia*, *C. paludosa*, *C. pontana*, *C. pyrenaica*) and annual Mediterranean plants (*C. doiscoridis* to *C. foetida*). Figure 2(D) shows that dry-land *Lotus* species have reduced niche-width compared to wetland *Lotus spp.* having wider moisture niches. In all gradients, as expected, species at the gradient-end tend to show a median shifted compared to the mean in direction of the gradient end.

## Discussion

Our results provide a detailed assessment of realized niches of plants along the main ecological factors spanning Mediterranean to alpine vegetation types, including both position as well as information on niche width. Our data include taxa from two major European centres of endemism, Eastern Pyrenees and South-Western Alps and we cover a larger number of taxa and with a higher taxonomic detail than any previous indicator value system in Europe. Increasing taxonomic cover and detail is an important first step towards a pan-European bioindication system for plants (Hájek et al. 2020), complements similar recent assessments in other European biogeographical regions (Chytrý et al. 2018; Tyler et al. 2021) and different plant groups e.g. for bryophytes (Simmel et al. 2021). We make here use of a continuous scale which further increases precision on relative positions of niches and based on earlier work using a continuous scale derived from Ellenberg (Hill et al. 2000) or increasing the number of units (Dengler et al. 2016; Tyler et al. 2021). We use standard deviations as main information on the niche width—the range of ecological conditions occupied by plants in ecosystems. Previous authors of EIV systems, (Ellenberg et al. 1992; Pignatti et al. 2005) frequently decided not to assign EIVs to taxa with comparatively large niches, confounding large niche width with the possibility of missing information. However, this precludes analysing niche width per se and omits position of these species in gradients and it is a large barrier to perform analyses on entire plant communities. The system by Landolt et al. (2010) was the first to provide niche width in a two class system. Standard deviations we calculated for our data-set are consistently related to Landolt's classes of niche width (Appendix S5), an important new finding since it indicates that niche width also remains stable in different parts of the distributional area. Ellenberg et al. (1992) already reviewed that his indicator values were related to measured ecological factors far beyond the areas for which they have been developed originally, a finding that has since been confirmed, notably by a detailed study in Scandinavia (Hedwall et al. 2019). This study suggests that relative niche positions remain stable even under different biogeographical settings, highlighting the need of information on niche width. This is also underlined by our observation during data accuracy checks, which showed a strong pair-wise relation in linear regression (Appendix S3) between different original EIV systems for the same environmental factor (e.g. between Ellenberg's L and Julve's L values,  $R^2 = 0.54$ ,  $p < 0.001$ ). This is in contrast to the more limited comparability found earlier (Godefroid and Dana 2006) when comparing data from Italy (Pignatti et al. 2005) with Greece (Böhling et al. 2002). Altogether, evidence presented here and in earlier works on niche width and relative positions suggests that ecological indicator values are a consistent description of the realized niche of plants with high degree of generality. For temperature indicator values, the factor for which we had the largest amount of experimentally measured data, we could demonstrate that using the niche width (inverse of variance) as a weight while calculating the community mean of an indicator value increased the correlation compared to no weighting (Table 1). This underlines that niche width contains



**Figure 2.** Niche differences among congeneric species according to ecological factors as evaluated by indicator values; (A) reaction indicator values for the genus *Cistus* (Cistaceae) recalibrated based on Julve (1998) (B) nitrogen indicator values for the genus *Rumex* (Polygonaceae) recalibrated based on Ellenberg et al. (1992) (C) temperature indicator values for the genus *Crepis* (Asteraceae) recalibrated based on Pignatti et al. (2005), (D) humidity indicator values for the genus *Lotus* (Fabaceae) recalibrated based on Julve (1998), vertical bars are mean values, squares are median values, bold line are interquartile range and thin lines are one standard deviation on both sides of the mean, stars denote the original indicator values, pictures: *Cistus albidus*, *Rumex roseus*, *Crepis leontodontoides*, *Lotus ornithopodioides* (by Daniel Pavon).

valuable information useful for understanding plant community composition in ecological gradients. By providing data on many ecological factors and a high number of taxa spanning strong environmental gradients, our work provides an important basis to explore in more details the relations between niche width, plant community composition and ecological factors.

Following recommendations by Ellenberg et al. (1992) and together with later works (Wamelink et al. 1998; Szymura

et al. 2014; Pinto et al. 2016; Hájek et al. 2020) we tested recalibrated EIVs with field measurements of relevant factors in our study area. For all factors, for which we were able to find relevant field data from within our study region our recalibrated values performed well, with R2 in the upper range of typical relations between mean indicator values and measured ecological factors (Ellenberg et al. 1992; Diekmann 2003). This underlines the high quality of EIVs provided here and demonstrates usefulness in our study region and beyond.



Inspection of regression plots indicated that all relationships were linear, contrasting with other works that have shown non-linear relationship between R indicator and measured pH (Schaffers and Sýkora 2000; Chytrý et al. 2018). Moreover, N indicator value is considered to better represent annual productivity or nutrient status than simple total nitrogen (Diekmann and Falkengren-Grerup 1998), contrasting to our analyses, where N values correlated best to total nitrogen and much less to other nutrients. This result might stem from differences in limiting factors in the ecosystems considered, the dry mediterranean grasslands in our system might be more nitrogen limited compared to humid central European ecosystems in the cited works. EIVs are correlated among each other, e.g. light values are lower on intermediate compared to very dry or very moist F values, F and N values are related (Schaffers and Sýkora 2000; Seidling and Fischer 2008). We think that this is not an artifact, but rather reflects the reality of situations in the field and the underlying structure of species pools, since at intermediate moisture values, productivity is highest and most ecosystems reach their closest canopy cover, leaving little space for light-demanding plants. Since the EIVs provided here encapsulate information that is not readily available in forms of continuous maps of ecological factors, they have repeatedly proven an important source of information for plant distribution modelling (Dupré and Diekmann 1998; Descombes et al. 2020) or even modelling the distributions of other organisms than plants (Horsák et al. 2007). Therefore, calibrated EIVs, such as those we present here, tested with field measurements are of high value to ecological research. Since our data show that some systems seem to perform much better than others when compared to measured data we think that it is premature to combine them since this would mean that we degrade the information contained in the initial EIV systems. Future EIV systems should make strong use of measured variables and if possible express EIVs on a meaningful scale of the measured environmental variable (see e.g. Coudun and Gégout 2006), since this would deepen our understanding of the link between plant distribution and environmental gradients.

Niche positions for congeneric plants (Figure 2) highlight that a continuous scale for indicator values together with data on niche width provide a more detailed view on differences in realized niches between species. Positions corroborate earlier non-quantified data from floras and geological maps for the genus *Cistus* (Tison et al. 2014): *Cistus populifolius*, *C. pouzolzii* known to be restricted to siliceous bedrock showed low R indicator values and *Cistus albidus*, *C. salviaefolius* and *C. monspeliensis*, known to also occur on calcareous bedrock with the latter two preferring superficially decalcified soils with higher R indicator values. Results also highlighted differences in the genus *Rumex* for soil nutrient status: *Rumex scutatus* and *R. acetosella* preferring nutrient-poor soils were opposed to *R. obtusifolius* and *R. palustris* preferring nutrient-rich soil, both groups are also well distinguished from a morphological and systematic point of view (Tison et al. 2014) indicating a phylogenetic signal in our data (Prinzinger et al. 2001; Blomberg and Garland 2002). The recalibrated temperature indicator values in *Crepis* illustrate several cases with initially identical values, while inter-quartile

ranges in our data do not overlap. Skew is indicated by the differences between mean and median in our data, and in both illustrations of *Rumex* and *Lotus* it appears well that niches are systematically skewed towards gradient ends. Skew in distributions is an argument against use of mean values, however overall departures are limited and only few cases reverse rank-order of species along gradients in Figure 2.

We chose, similar to Hill et al. (2000), to use mean indicator values of relevés to recalibrate values for species without adjusting the scale afterwards. A consequence of this method is that recalibrated values moved towards the average of all taxa for a given ecological factor, decreasing extreme values. This effect is non-linear since it is necessarily stronger at gradient ends compared to the centre (Hill et al. 2000). Any further averaging would increase this effect and potentially move away from the original information content in indicator values, so we chose not to iterate averaging. The characteristics of indicator values in terms of number of classes and extent are arbitrary (Ellenberg et al. 1992) and even though an algorithm, as suggested by Hill et al. (2000), might be used to adjust mean values, it is not clear how the remaining information on niche width might be conserved in a meaningful fashion. Also, as for the initial scales, an arbitrary scale does not impede its use, and delivering standard deviations together with original and recalculated values gives future users a good amount of information to adapt if necessary. Moreover, a continuous scale as presented in our work based on thousands of relevés, seems less arbitrary to us than an ordered class system, since we found no clear argumentation in favour of using classes for continuously varying ecological factors. We think however that our results are only a gradual advance, and that in ideal future indicator value system, continuous scales might be used that are on the scale of the relevant, measurable ecological variable, and which are already a feature of plant distribution modelling (Coudun and Gégout 2006) and have been developed for some limited set of plants and ecosystems (Wamelink et al. 1998; Pinto et al. 2016).

Contrasting indicator values with the reality of experimentally measured variables gives a deeper understanding on major niche axes in plants. Even the most intuitive indicated factors e.g. the reaction values (R), are conceptual, since along the gradient either pH in pure water or pH measured in solutions of KCl or CaCl<sub>2</sub> or even directly measuring exchangeable cations give the highest correlations to R indicator values (Szymura et al. 2014). For other ecological gradients, such as temperature, moisture and light, the experimentally measurable variables are highly temporally variable, and e.g. Ellenberg et al. (1992) already pointed out that depending on the ecosystem the measuring ecological factors might be in a very specific situation, e.g. the lowest soil water content throughout the year for relation to moisture values, or light during days with a homogenous continuous cloud cover during full expansion of canopy leaves, which both are related to the difficulties to follow with sufficient temporal and spatial resolution the relevant environmental factor. We think that modern high-resolution measurements together with indicator values can contribute a great deal to better understand how temporally varying factors translate into differences of realized

niches of plants. Still other ecological gradients are related to different factors depending on the context of the ecosystem and might be dependent on other ecological factors, e.g. for nutrient values, for which there is a higher relevance of  $\text{NH}_4^+$  in acid, and  $\text{NO}_3^-$  in basic environments (Bartelheimer and Poschlod 2014) or for phosphorus in ancient oligotrophic ecosystems (Löfgren et al. 2020), underlining the integrative nature of the reaction values. Finally, a continuous scale enables to compare the complex constraints between niche components such as between components of humidity and temperature, or light and humidity (see Appendix S6 for examples) which are of fundamental significance for plant community assembly.

Indicator values as presented here might be of high use for conservation purposes, since they enable to evaluate the position of a plants niche towards actual realized conditions and in this way evaluate both the ecological factors contributing to the decline of plants at larger spatial scales as well as evaluating drift away from their optimal realized niche in local situations (e.g. Ellenberg et al. 1992), both enabling to take conservation actions before plants of interest disappear. They also enable the detection of impacts of human activities on ecosystems in terms of relevant ecological factors and contribute in this way to the restoration of ecosystems (Oomes et al. 1996; Bauer and Albrecht 2020). From a more theoretical perspective, detailed recalibrated indicator values bring a wealth of opportunities to understand relations between plant niches and plant communities, e.g. by analysing vegetation data using different weightings of abundance and niche width in order to identify factors acting on species pools (Pärtel 2002; Zobel et al. 2011) compared to factors acting on abundance (Ellenberg et al. 1992) or diversity (Seidling and Fischer 2008); and to re-analyse phylogenetic correlation of niches in order to understand evolutionary history of plant niches (Prinzing et al. 2001; Vandeloos et al. 2018).

We illustrate niches described by our data for examples of closely related taxa and give prospects for future improvements of ecological indicator value systems. We hope that providing an analysis of different systems, with large floristic data and measured environmental data-sets will help future works to re-evaluate the usefulness of different bioindication system and pave the way to a unified, detailed system of niche descriptors and bioindication in plants. We think that major challenges for future systems describing plant's realized niches are (i) to increase the geographical coverage to include the complete distribution areas of most species, e.g. by using all available data for a larger biogeographical region, e.g. western palearctic, (ii) to identify meaningful measurable factors corresponding to the major compositional gradients reflected by EIVs, such as pH for reaction values and (iii) to express plant's niche preferences on the scale of this environmental factor, (iv) to include further meaningful environmental factors encapsulating compositional variation in plant assemblages not yet included, ideally not correlated to existing factors. Finally, we think that EIVs as descriptors for realized niches are an important viewpoint to deepen our understanding of underlying adaptations (traits), niche construction and assembly processes.

## Acknowledgements

We thank the *Conservatoire Botanique National Méditerranéen de Porquerolles* and regional environmental agencies of the regions *SUD-PACA* and *Occitanie* for providing the database we used in this study. We thank Frederic Henry for sharing data on soil chemistry and vegetation relevés and Daniel Pavon for help in nomenclatural problems.

## Authors' contributions

AS conceived research idea; AS, NF and VN curated data; AS, NF and EM performed statistical analyses; AS, EM, VN, OA, VN and TD, wrote the paper; all authors discussed the results and commented on the manuscript. We thank Daniel Pavon for help with fieldwork, taxonomy and providing pictures in Figure 2.

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Data availability statement

Floristic occurrence data are available through the SILENE database (<http://flore.silene.eu>, version 9/12/2021).

## References

- Ågren J, Schemske DW. 2012. Reciprocal transplants demonstrate strong adaptive differentiation of the model organism *Arabidopsis thaliana* in its native range. *New Phytol.* 194(4):1112–1122.
- Bartelheimer M, Poschlod P. 2014. The response of grassland species to nitrate versus ammonium coincides with their pH optima. *J Veg Sci.* 25(3):760–770.
- Bátori Z, Vojtkó A, Farkas T, Szabó A, Havadtői K, Vojtkó AE, Tölgyesi C, Cseh V, Erdős L, Maák IE, et al. 2017. Large- and small-scale environmental factors drive distributions of cool-adapted plants in karstic microrefugia. *Ann Bot.* 119(2):301–309.
- Bauer M, Albrecht H. 2020. Vegetation monitoring in a 100-year-old calcareous grassland reserve in Germany. *Basic Appl Ecol.* 42:15–26.
- Blomberg SP, Garland T. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *J Evol Biol.* 15(6):899–910.
- Bloor JMG, Pichon P, Falcimagne R, Leadley P, Soussana J-F. 2010. Effects of warming, summer drought, and CO<sub>2</sub> enrichment on aboveground biomass production, flowering phenology, and community structure in an upland grassland ecosystem. *Ecosystems.* 13(6):888–900.
- Böhling N, Greuter W, Raus T. 2002. Indicator values for vascular plants in the Southern Aegean (Greece). *Braun-Blanquetia.* 32:1–109.
- Carroll T, Gillingham PK, Stafford R, Bullock JM, Diaz A. 2018. Improving estimates of environmental change using multilevel regression models of Ellenberg indicator values. *Ecol Evol.* 8(19):9739–9750.
- Chytrý M, Tichý L, Dřevojan P, Sádlo J, Zelený D. 2018. Ellenbergtype indicator values for the Czech flora. *Preslia.* 90(2):83–103.
- Coudun C, Gégout J-C. 2006. The derivation of species response curves with Gaussian logistic regression is sensitive to sampling intensity and curve characteristics. *Ecol Model.* 199(2):164–175.
- Dengler J, Hüllbusch E, Bita-Nicolae C, Chytrý M, Didukh YP, Diekmann M. 2016. Ecological Indicator Values of Europe (EIVE) 1.0: a powerful open-access tool for vegetation scientists. 25th European Vegetation Survey Meeting, Rome, 6–9 April 2016.
- Dengler J, Jansen F, Glöckler F, Peet RK, De Cáceres M, Chytrý M, Ewald J, Oldeland J, Lopez-Gonzalez G, Finckh M, et al. 2011. The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. *J Veg Sci.* 22(4):582–597.

- Descombes P, Walthert L, Baltensweiler A, Meuli RG, Karger DN, Ginzler C, Zurell D, Zimmermann NE. 2020. Spatial modelling of ecological indicator values improves predictions of plant distributions in complex landscapes. *Ecography*. 43(10):1448–1463.
- Diekmann M. 2003. Species indicator values as an important tool in applied plant ecology – a review. *Basic Appl Ecol*. 4(6):493–506.
- Diekmann M, Falkengren-Grerup U. 1998. A new species index for forest vascular plants: development of functional indices based on mineralization rates of various forms of soil nitrogen. *J Ecol*. 86(2):269–283.
- Doxa A, Albert CH, Leriche A, Saatkamp A. 2017. Prioritizing conservation areas for coastal plant diversity under increasing urbanization. *J Environ Manage*. 201:425–434.
- Dupré C, Diekmann M. 1998. Prediction of occurrence of vascular plants in deciduous forests of South Sweden by means of Ellenberg indicator values. *Appl Veg Sci*. 1(1):139–150.
- Dzwonko Z. 2001. Assessment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values. *J Appl Ecol*. 38(5):942–951.
- Ellenberg H. 1974. Zeigerwerte der Gefäßpflanzen Mitteleuropas. *Scripta Geobotanica* 9:1–97.
- Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulissen D. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scr Geobot*. 18:1–258.
- Engler R, Randin CF, Thuiller W, Dullinger S, Zimmermann NE, Araújo MB, Pearman PB, Le Lay G, Piedallu C, Albert CH, et al. 2011. 21st century climate change threatens mountain flora unequally across Europe. *Glob Change Biol*. 17(7):2330–2341.
- Fernández-Pascual E, Jiménez-Alfaro B, Hájek M, Díaz TE, Pritchard HW. 2015. Soil thermal buffer and regeneration niche may favour calcareous fen resilience to climate change. *Folia Geobot*. 50(4):293–301.
- Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol*. 37(12):4302–4315.
- Gargominy O, Terceira S, Régnier C, Ramage T, Schoelinc C, Dupont P, et al. 2014. TAXREF v8. 0, référentiel taxonomique pour la France: Méthodologie, mise en oeuvre et diffusion. Rapport SPN 2014–42.
- Gégout J-C, Coudun C, Bailly G, Jabiol B. 2005. EcoPlant: a forest site database linking floristic data with soil and climate variables. *J Veg Sci*. 16(2):257–260.
- Godefroid S, Dana ED. 2006. Can Ellenberg's indicator values for Mediterranean plants be used outside their region of definition? *J Biogeogr*. 34(1):62–68. ED.
- Hájek M, Dítě D, Horsáková V, Mikulášková E, Peterka T, Navrátilová J, Jiménez-Alfaro B, Hájková P, Tichý L, Horsák M. 2020. Towards the pan-European bioindication system: assessing and testing updated hydrological indicator values for vascular plants and bryophytes in mires. *Ecol Indic*. 116:106527.
- Hedwall P-O, Brunet J, Diekmann M. 2019. With Ellenberg indicator values towards the north: does the indicative power decrease with distance from Central Europe? *J Biogeogr*. 46(5):1041–1053.
- Hill MO, Roy DB, Mountford JO, Bunce RG. 2000. Extending Ellenberg's indicator values to a new area: an algorithmic approach. *J Appl Ecol*. 37(1):3–15.
- Horsák M, Hájek M, Tichý L, Juříčková L. 2007. Plant indicator values as a tool for land mollusc autecology assessment. *Acta Oecol*. 32(2):161–171.
- Julve PH. 1998. Baseflor. Index botanique, écologique et chorologique de la flore de France. Lille: Institut Catholique de Lille.
- Kapfer J, Grytnes J-A, Gunnarsson U, Birks HJB. 2011. Fine-scale changes in vegetation composition in a boreal mire over 50 years. *J Ecol*. 99(5):1179–1189.
- Kapfer J, Hédél R, Jurasinski G, Kopecký M, Schei FH, Grytnes J-A. 2016. Resurveying historical vegetation data—opportunities and challenges. *Appl Veg Sci*. 20(2):164–171.
- King AD, Karoly DJ. 2017. Climate extremes in Europe at 1.5 and 2 degrees of global warming. *Environ Res Lett*. 12(11):114031.
- Landolt E, Bäumler B, Erhardt A, Hegg O, Klötzli F, Lämmler W. 2010. Flora indicativa=Ecological indicator values and biological attributes of the flora of Switzerland and the Alps: ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen. Haupt Verlag.
- Lawesson JE, Fosaa AM, Olsen E. 2003. Calibration of Ellenberg indicator values for the Faroe Islands. *Appl Veg Sci*. 6(1):53–62.
- Lenoir J, Graae BJ, Aarrestad PA, Alsos IG, Armbruster WS, Austrheim G, Bergendorff C, Birks HJB, Bråthen KA, Brunet J, et al. 2013. Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Glob Change Biol*. 19(5):1470–1481.
- Liu D, Peñuelas J, Ogaya R, Estiarte M, Tielbörger K, Slowik F, Yang X, Bilton MC. 2018. Species selection under long-term experimental warming and drought explained by climatic distributions. *New Phytol*. 217(4):1494–1506.
- Löfgren O, Hall K, Schmid BC, Prentice HC. 2020. Grasslands ancient and modern: soil nutrients, habitat age and their relation to Ellenberg N. *J Veg Sci*. 31(3):367–379.
- Loopstra IL, van der Maarel E. 1984. Toetsing van ecologische soortengroepen voor de Nederlandse flora aan het systeem van indicatiewaarden volgens Ellenberg. Rijksinstituut voor Onderzoek in de Bos-en Landschapsbouw "De Dorschkamp."
- Marignani M, Bruschi D, Astiaso Garcia D, Frondoni R, Carli E, Pinna MS, Cumo F, Gugliermetti F, Saatkamp A, Doxa A, et al. 2017. Identification and prioritization of areas with high environmental risk in Mediterranean coastal areas: a flexible approach. *Sci Total Environ*. 590–591:566–578.
- Martin-StPaul NK, Limousin J-M, Vogt-Schilb H, Rodríguez-Calcerrada J, Rambal S, Longepierre D, Misson L. 2013. The temporal response to drought in a Mediterranean evergreen tree: comparing a regional precipitation gradient and a throughfall exclusion experiment. *Glob Change Biol*. 19(8):2413–2426.
- Martinez-Almoyna C, Piton G, Abdulhak S, Boulangeat L, Choler P, Delahaye T, Dentant C, Foulquier A, Poulenard J, Noble V, The ORCHAMP Consortium, et al. 2020. Climate, soil resources and microbial activity shape the distributions of mountain plants based on their functional traits. *Ecography*. 43(10):1550–1559.
- Matteodo M, Wipf S, Stöckli V, Rixen C, Vittoz P. 2013. Elevation gradient of successful plant traits for colonizing alpine summits under climate change. *Environ Res Lett*. 8(2):024043.
- Médail F, Quézel P. 1999. Biodiversity hotspots in the Mediterranean basin: setting global conservation priorities. *Conserv Biol*. 13:1510–1513.
- Meesenburg H, Ahrends B, Fleck S, Wagner M, Fortmann H, Scheler B, Klinck U, Dammann I, Eichhorn J, Mindrup M, et al. 2016. Long-term changes of ecosystem services at Solling, Germany: recovery from acidification, but increasing nitrogen saturation? *Ecol Indic*. 65:103–112.
- Meineri E, Hylander K. 2017. Fine-grain, large-domain climate models based on climate station and comprehensive topographic information improve microrefugia detection. *Ecography*. 40:1003–1013.
- Metzner K, Gachet S, Rocarpin P, Saatkamp A. 2017. Seed bank, seed size and dispersal in moisture gradients of temporary pools in Southern France. *Basic Appl Ecol*. 21:13–22.
- Noble V, Van Es J, Michaud H, Garraud L. 2015. Liste Rouge de la flore vasculaire de Provence-Alpes-Côte d'Azur. Aix-en-Provence, France: DREAL Provence-Alpes-Côte d'Azur.
- Ochoa-Hueso R, Bell MD, Manrique E. 2014. Impacts of increased nitrogen deposition and altered precipitation regimes on soil fertility and functioning in semiarid Mediterranean shrublands. *J Arid Environ*. 104:106–115.
- Ogaya R, Peñuelas J, Asensio D, Llusià J. 2011. Chlorophyll fluorescence responses to temperature and water availability in two co-dominant Mediterranean shrub and tree species in a long-term field experiment simulating climate change. *Environ Exp Bot*. 71(2):123–127.
- Oomes MJM, Olf H, Altena HJ. 1996. Effects of vegetation management and raising the water table on nutrient dynamics and vegetation change in a wet grassland. *J Appl Ecol*. 33(3):576–588.
- Pärtel M. 2002. Local plant diversity patterns and evolutionary history at the regional scale. *Ecology*. 83:2361–2366.
- Peñuelas J, Filella I, Zhang X, Llorens L, Ogaya R, Lloret F, Comas P, Estiarte M, Terradas J. 2004. Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytol*. 161(3):837–846.

- Peres-Neto PR, Dray S, ter Braak CJF. 2017. Linking trait variation to the environment: critical issues with community-weighted mean correlation resolved by the fourth-corner approach. *Ecography*. 40(7):806–816.
- Pignatti S, Menegoni P, Pietrosanti S. 2005. Bioindicator values of vascular plants of the flora of Italy. *Braun-Blanquetia*. 39:3–95.
- Pinto PE, Dupouey J-L, Hervé J-C, Legay M, Wurpillot S, Montpied P, Gégout J-C. 2016. Optimizing the bioindication of forest soil acidity, nitrogen and mineral nutrition using plant species. *Ecol Indic*. 71:359–367.
- Prinzing A, Durka W, Klotz S, Brandl R. 2001. The niche of higher plants: evidence for phylogenetic conservatism. *Proc R Soc B: Biol Sci*. 268:2383–2389.
- R-Core-Team. 2014. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Rabinowitz D, Cairns S, Dillon T. 1981. Seven forms of rarity. In *The biological aspects of rare plants conservation*. New York: Wiley. p. 205–218.
- Saatkamp A, Henry F, Dutoit T. 2018. Vegetation and soil seed bank in a 23-year grazing exclusion chronosequence in a Mediterranean dry grassland. *Plant Biosyst*. 152(5):1020–1030.
- Saatkamp A, Römermann C, Dutoit T. 2010. Plant functional traits show non-linear response to grazing. *Folia Geobot*. 45(3):239–252.
- Schaffers AP, Sýkora KV. 2000. Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *J Veg Sci*. 11(2):225–244.
- Seidling W, Fischer R. 2008. Deviances from expected Ellenberg indicator values for nitrogen are related to N throughfall deposition in forests. *Ecol Indic*. 8(5):639–646.
- Simmel J, Ahrens M, Poschlod P. 2021. Ellenberg N values of bryophytes in Central Europe. *J Veg Sci*. 32:e12957.
- Szymura TH, Szymura M, Macioł A. 2014. Bioindication with Ellenberg's indicator values: a comparison with measured parameters in Central European oak forests. *Ecol Indic*. 46:495–503.
- ter Braak CJ. 2019. New robust weighted averaging-and model-based methods for assessing trait–environment relationships. *Methods Ecol Evol*. 10(11):1962–1971.
- Ter Braak CJ, Barendregt LG. 1986. Weighted averaging of species indicator values: its efficiency in environmental calibration. *Math Biosci*. 78(1):57–72.
- Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC. 2005. Climate change threats to plant diversity in Europe. *Proc Natl Acad Sci U S A*. 102: p. 8245–8250.
- Tison JM, de Foucault B. 2014. *Flora Gallica–Flore de France: Biotope Éditions. Mèze: Société botanique de France.*
- Tison JM, Jauzein P, Michaud H. 2014. *Flore de la France méditerranéenne continentale. Vol. 1. Turriers: Naturalia Publications.*
- Tyler T, Herbertsson L, Olofsson J, Olsson PA. 2021. Ecological indicator and traits values for Swedish vascular plants. *Ecol Indic*. 120:106923.
- Vandelook F, Janssens SB, Matthies D. 2018. Ecological niche and phylogeny explain distribution of seed mass in the central European flora. *Oikos*. 127(10):1410–1421.
- Wamelink GWW, Van Dobben HF, Van der Eerden LJM. 1998. Experimental calibration of Ellenberg's indicator value for nitrogen. *Environ Pollut*. 102(1):371–375.
- Wolkovich EM, Cook BI, Allen JM, Crimmins TM, Betancourt JL, Travers SE, Pau S, Regetz J, Davies TJ, Kraft NJB, et al. 2012. Warming experiments underpredict plant phenological responses to climate change. *Nature*. 485(7399):494–497.
- Zelený D. 2018. Which results of the standard test for community-weighted mean approach are too optimistic? *J Veg Sci*. 29(6):953–966.
- Zelený D, Schaffers AP. 2012. Too good to be true: pitfalls of using mean Ellenberg indicator values in vegetation analyses. *J Veg Sci*. 23:419–431.
- Zobel M, Otto R, Laanisto L, Naranjo-Cigala A, Pärtel M, Fernández-Palacios JM. 2011. The formation of species pools: historical habitat abundance affects current local diversity. *Global Ecol Biogeogr*. 20(2):251–259.