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Abstract

Questions: Heinz Ellenberg classically defined “indicator” scores for species representing their typical positions along gradients of key environmental variables, and these have proven very useful for designating ecological distributions. We tested a key tenet of trait-based ecology, i.e. the ability to predict ecological preferences from species’ traits. More specifically, can we predict Ellenberg indicator scores for soil nutrients, soil moisture and irradiance from four well-studied traits: leaf area, leaf dry matter content, specific leaf area (SLA) and seed mass? Can we use such relationships to estimate Ellenberg scores for species never classified by Ellenberg?

Location: Global.

Methods: Cumulative link models were developed to predict Ellenberg nutrients, irradiance and moisture values from Ln-transformed trait values using 922, 981 and 988 species, respectively. We then independently tested these prediction equations using the trait values of 423 and 421 new species that occurred elsewhere in Europe, North America and Morocco, and whose habitat affinities we could classify from independent sources as three-level ordinal ranks related to soil moisture and irradiance. The traits were SLA, leaf dry matter content, leaf area and seed mass.

Results: The four functional traits predicted the Ellenberg indicator scores of site fertility, light and moisture with average error rates of <2 Ellenberg ranks out of nine. We then used the trait values of 423 and 421 species, respectively, that occurred (mostly) outside of Germany but whose habitat affinities we could classify as three-level ordinal ranks related to soil moisture and irradiance. The predicted positions of the new species, given the equations derived from the Ellenberg indices, agreed well with their independent habitat classifications, although our equation for Ellenberg irradiance levels performed poorly on the lower ranks.

Conclusions: These prediction equations, and their eventual extensions, could be used to provide approximate descriptions of habitat affinities of large numbers of species worldwide.

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Introduction

Plant ecology, emerging from plant geography, has existed as an academic discipline for more than a century (Warming & Vahl 1909). A major recurring theme in this discipline is that plant species are differentially distributed along important abiotic gradients with respect to the most common environmental variables that control plant growth and survival. Given this history, one might think that basic information concerning the range and modal values of most plant species along such abiotic gradients (i.e. their habitat “affinities”) would be generally available. In fact, such basic ecological information is often missing, with the exception of species like aquatics, desert species or understorey herbs that are restricted to clearly differentiated habitats.

One exception is the German flora. Heinz Ellenberg (1978, 1988, 1992), working with this flora, defined a series of ordinal scales for seven major environmental variables (irradiance level; soil moisture, pH, N availability, soil salinity; average yearly temperature and continentality). He then assigned a single “indicator” score for each species with respect to each environmental value, identifying the position along the environmental gradient at which the species was most common. These indicator scores can be viewed collectively as very approximate descriptions of the mode of the realized Hutchinsonian niche (Hutchinson 1957) of each species. The scales are ordered and go from one (lowest level) to nine (highest level), except for moisture which goes to 12. We use three Ellenberg indicator scores that are directly linked to resource capture: “nitrogen” (better interpreted as a description of site productivity or soil nutrient levels),

“irradiance” and “moisture”. Ellenberg values have proven very popular since Ellenberg (1978, 1988, 1992) and have been cited over 7000 times in the ecological literature.

These ordinal scales, and the indicator value assigned to a species for a given scale, were not based on direct physical measurements of the environment but rather on Ellenberg’s own field observations, with input from his collaborators. Ellenberg indicator scores, being based on expert opinion rather than direct physical measurement of the abiotic variables, require the sort of extensive and exhaustive knowledge of a local flora that takes a lifetime to obtain, and that few people possess. Their subjective nature also makes them very difficult to generalize to new geographic locations in a way that is comparable (Valdadares & Niinemets 2008). Strictly speaking, since these are expert *opinions* rather than objective *measurements*, the only people who could truly extend such indicator scores to new locations would be Heinz Ellenberg (who died in 1997), or someone who trained with him. Similar, but not identical, schemes have been produced for other European countries such as Austria (Karrer 1992), Switzerland (Landolt 1977), and Italy (Pignatti 2005; Guarino et al. 2012).

Despite the subjective nature of Ellenberg indicator scores, a number of independent publications have shown that average Ellenberg numbers, based on weighted or unweighted vegetation relevés, do correlate well with more explicit environmental measurements (Ertzen et al. 1998; Franzaring et al. 2007; Douma et al. 2012; Bartelheimer & Poschlod 2014; Carpenter & Goodenough 2014). Mean Ellenberg indicator scores of plots in a large vegetation data set representing all terrestrial

habitats across the Netherlands were also highly correlated to the position of plots across the main gradients in species composition as revealed by ordination models (Ozinga et al. 2005). Although Ellenberg indicator scores are only approximate and non-metric descriptions of the mode of a species' distribution along such environmental gradients, they might better integrate the effect of temporal and spatial variation of such environmental conditions on plant performance in ways in which more explicit but short-term environmental measurements cannot. Some of the environmental properties referenced by Ellenberg indicator scores can be measured using well-established methods and are sufficiently stable in time and well-defined (soil pH or salt content) that they can be directly measured using samples taken at a single point in time. Habitat affinities based on such direct measurements are rare in practice because one must take them over large spatial extents in order to properly quantify the distribution of a species along such gradients and to identify the values at which a species reaches maximum abundance. Other variables, such as soil moisture, irradiance level or temperature, can be measured using well-established methods. However, they are so temporally and spatially variable that one would require both spatially extensive sampling and long-term monitoring in order to quantify them in a way that is meaningful to plant performance; such studies are even rarer. Finally, even if the above practical problems can be overcome, there does not even exist a generally accepted method of quantifying an important soil property like soil nutrient availability (or "fertility"), which is determined by a complicated interaction of both a number of soil properties (Fujita et al. 2013) and plant and fungal properties that enable uptake of different limiting nutrients. Such difficulties explain, in large part, why we do not yet possess even basic information concerning the habitat affinities of most plant species and why we are unlikely to fill this knowledge gap in the near future. If this is true, then can we generalize this expert knowledge to new geographic areas?

One method, developed by Hill et al. (1999) for the British flora, uses co-occurrence data of vegetation, in conjunction with the Ellenberg indicator scores of the subset of species for which this information is available, to generalize to new species and to adjust the values of other species as needed. Although this method worked well for the British flora, which contains many species in common with the German flora, it would not work when extrapolating to geographic areas with few or no species for which Ellenberg numbers are available. Another method (Klaus et al. 2012) of generalizing Ellenberg numbers to new locations was based on calibration curves linking Near

Infrared Spectrometric signatures (NIRS) of vegetation samples in Germany with averaged Ellenberg values of these samples. In this paper we evaluate a trait-based method for predicting Ellenberg indicator scores and evaluate its potential to predict habitat affinities of new species around the world for which Ellenberg indicator scores do not exist.

A functional trait is any phenotypic attribute, measurable on an individual plant, that affects its growth, survival or reproductive success and thus its fitness in a given environmental context (Violle et al. 2007). Extrapolating to all individuals of a given species in a local area, such functional traits affect the demographic performance of the species and so a basic postulate of trait-based ecology is that a species' demographic performance along major environmental gradients is partly determined by the values of at least some of its functional traits at some stage in its ontogeny (Grime 1979). Ideally, when estimating a species' habitat from its traits, one would choose traits that are simultaneously the most important mechanistic determinants of plant fitness along the chosen environmental gradients, are widely measured for many plant species, and are easily measurable for new species. In practice these criteria are often strongly conflicting. For instance, the ability to survive and grow in drying soils is partly determined by physiological properties related to leaf gas exchange, turgor maintenance and the hydraulic conductivity of water through its roots, stem and leaves (Bartlett et al. 2012). However, such traits are not currently available for most species, necessitating approaches from more widely measured traits for large-scale prediction, such that additional traits can be utilized as they become available.

In this study we evaluate four widely measured traits (leaf area, leaf dry matter content [LDMC], specific leaf area [SLA] and seed mass [SM]) as predictors of Ellenberg indicator scores for light, soil moisture and soil nutrient availability. Average values of each of these traits are already available for large numbers of plant species worldwide, each can be quickly and easily measured with minimal cost, and each has been shown to vary along these environmental gradients for at least some sites and combinations of species, as reviewed in Garnier & Navas (2013). For instance, small leaf size has often been associated with dry (Greive 1956; Monk 1966; Scoffoni et al. 2011) and/or nutrient-poor soils (McDonald et al. 2003). Species having large leaves or large SLA are often associated with low light conditions (Hodgson et al. 2011). Increasing SLA and decreasing LDMC have been associated with higher soil fertility (Hodgson et al. 2011). Larger seeds have been associated with dry, poorer soils and more shaded habitats (Tautenhahn et al. 2008).

Methods

Database for developing prediction equations

The trait data for specific leaf area (SLA, $\text{mm}^2\cdot\text{mg}^{-1}$), leaf dry matter content (LDMC, $\text{g}\cdot\text{g}^{-1}$), leaf area (LA, mm^2) and seed mass (SM, mg) were previously published values obtained from the TRY database (Kattge et al. 2011), www.try-db.org, accessed 10/07/2013. We calculated the mean value for each species across all observations of the species in TRY. We used Ellenberg indicator scores that can be directly related to resource availability: irradiance (light) level, soil nutrients and moisture, which take integer values from 1 to 9. Although the full range of Ellenberg indicator scores for moisture go to 12, we excluded aquatics, thus limiting this indicator range to 9. Note that Ellenberg (1978) originally described one of his indices as an index of soil N, but this index is more properly interpreted as a more general description of soil fertility, soil nutrient availability or site productivity (Hill et al. 1999; Schaffers & Sykora 2000) and is here called a “nutrient” index. These Ellenberg indicator scores are ordinal scores and their English descriptions are given in Appendix S1. The TRY database contains Ellenberg numbers for 1835 species.

We chose four traits that previous authors have associated with one or more of these resources and that were sufficiently documented in the TRY database along with the Ellenberg values: SLA ($\text{mm}^2\cdot\text{mg}^{-1}$), LDMC ($\text{g}\cdot\text{g}^{-1}$), LA (mm^2) and SM (mg). We then calculated the mean value of each trait. Other plant traits from the TRY database that can reasonably be linked to these resource gradients, such as leaf N concentration, leaf thickness, net photosynthetic rate or leaf lifespan, did not have sufficient coverage with respect to the Ellenberg indicator scores and so were not included in this analysis. For instance, the total number of species with complete data with respect to Ellenberg nutrients goes from 922 using our chosen four traits to 399 if we include leaf N content, and to only 55 if we also include leaf lifespan. Finally, since the relationships between traits and habitat affinities might differ between different basic plant types, we included the “graminoid/herb/shrub/tree” classification in TRY as a categorical factor. A few species, classified as “ferns” were excluded since they do not have a seed size. A few species, ambiguously classified as “herb/shrub” or “shrub/tree”, were classified as “herbs” and “trees”, respectively. The number of species having complete coverage for all four traits and each Ellenberg score, as well as the distribution of species among the different Ellenberg scores, are given in Table 1. Of the three Ellenberg scores, the distribution of species for Ellenberg irradiance was the most problematic, since 86% of the 981 species had Ellenberg scores of 6 or more.

Table 1. The number of species (% of total) having complete information on the four traits and for which the Ellenberg scores for nutrients, moisture and light are known.

Ellenberg Score	Soil Nutrients	Habitat Moisture	Irradiance Level
1	48 (5.2%)	2 (0.2%)	1 (0.1%)
2	141 (15.3%)	36 (3.6%)	6 (0.6%)
3	127 (13.8%)	130 (13.2%)	19 (1.9%)
4	128 (13.9%)	214 (21.7%)	60 (6.1%)
5	141 (15.3%)	228 (23.1%)	51 (5.2%)
6	111 (12.0%)	107 (10.8%)	141 (14.4%)
7	118 (12.8%)	88 (8.9%)	317 (32.3%)
8	85 (9.2%)	92 (9.3%)	276 (28.1%)
9	23 (2.5%)	91 (9.2%)	110 (11.2%)
Total	922	988	981

Statistical analysis and development of the prediction equations

Since the Ellenberg values are only ordered ranks, we used cumulative link models to predict these Ellenberg scores from the four traits. This was done using the `clm` function of the ordinal library of R (R Foundation for Statistical Computing, Vienna, AT). Cumulative link models are generalizations of maximum likelihood logistic regression to more than two ordered states (Agresti 2002). Given an Ellenberg scale with 9 ordered states ($j = 1, 9$), the probability that species i will be found in a state less than, or equal to level j , given its trait values is given in Eq. 1. Here we present only the simplest version in Eq. 1 but this can be generalized to include the “plant form” factor and any combination of interaction terms, just as in any other GLM. LS_i is the latent score for species i , α_i is the intercept, or “threshold value”, i.e. the value of the latent score for which a species has a higher probability of being classified in state j than in a lower state, and β ’s are partial slopes. The latent score can be interpreted as the predicted position of a species along the unmeasured latent environmental gradient, measured on a continuous scale as defined by the traits, and which is then divided into ordinal classes as represented by the Ellenberg indicator scores. The probability of a species i being associated with each state j of an Ellenberg scale is given in Eq. 2.

$$LS_i = \beta_1 \ln(LA_i) + \beta_2 \ln(LDMC_i) + \beta_3 \ln(SLA_i) + \beta_4 \ln(SM_i) \quad (1a, b)$$

$$p_i(\leq j) = \frac{e^{\alpha_j - LS_i}}{1 + e^{\alpha_j - LS_i}}$$

$$\begin{aligned} p_i(j = 1) &= p_i(\leq 1) \\ p_i(j) &= p_i(\leq j) - p_i(\leq j - 1); \quad 1 < j < 9 \\ p_i(j = 9) &= 1 - p_i(\leq 8) \end{aligned} \quad (2a, b, c)$$

To use these prediction equations for a new species, once parameterized, one would first enter its trait values in Eq. 1a to obtain the latent score (LS_i), then enter this latent score into Eq. 1b to obtain the probability that this species has an Ellenberg indicator value of j or less. To obtain the probability that the species has an Ellenberg indicator value of exactly j , one would apply Eqs. 2a,b,c. A worked example is provided in Appendix S1. These calculations are automated using the “predict” function associated with the *clm* function in R. Although a very large number of possible models can be generated given four traits plus the categorical “plant type” including all possible interactions, we present two for each Ellenberg indicator variable: (1) a simplified model involving only the four traits as main effects for each of the four plant types, and (2) the best model, based on AIC values and obtained using the “stepAIC” function in the MASS library of R (Venables & Ripley 1994). Given the large sample sizes and resulting statistical power, this second model was invariably more complicated and involved several higher-order interaction terms.

Evaluating predictive error

The above equations only predict the probability that any species will be classified into each level of a given Ellenberg scale. By multiplying each level ($j = 1$ to 9) to the predicted probability (p_{ij}) of a species i being classified into each level, i.e. ($\hat{s}_i = \sum_j j \cdot p_{ij}$) we obtain the mean predicted Ellenberg score for each species, which varies continuously between 1 and 9. To determine how well the average predicted score of the species agrees with the actual scores (s_i), we estimated the distribution of errors as the percentage of species having a given difference between the observed (s_i) and predicted scores and the mean predictive error (MPE, Eq. 3) of cross-validated models (see below), which measures the average error (number of Ellenberg levels) between the observed (s) and predicted scores.

$$\text{MPE} = \sqrt{\frac{\sum_{i=1}^n (s_i - \bar{s}_i)^2}{n}} \quad (3)$$

Independent validation of the prediction equations

We evaluated the predictive ability of our equations with respect to independent observations in two ways. First, we used cross-validation, i.e. we randomly chose 80% of our data to fit the equation and then used these parameterized equations to predict the mean Ellenberg scores of the remaining 20%, after which we calculated the mean predictive error. We did this 100 times, each time randomly subdividing the data into the calibration and evaluation

subsets. This determines the likely error rate when extending the equations to new species whose Ellenberg values are known.

However, the main objective of the study was to extend our predictive ability to species that were never classified by Ellenberg, including species that are found outside of Central Europe. We therefore identified species for which we had trait data but for which Ellenberg values did not exist, and for which we could obtain habitat descriptions. Such habitat descriptions are very approximate (“under-story species”, “typically found in wetlands”, etc.) and not as detailed as those of Ellenberg. We therefore concentrated on species with clearly different habitat affinities. First, we identified 1134 species in the TRY database for which there was information on all four traits but for which Ellenberg scores were missing. Of these 1134 new species, we then identified 55 species, mostly in North America, for which available habitat descriptions (local floras, field guides, online sites such as that managed by the United States Department of Agriculture) clearly indicate that they are most commonly found in wet, but not permanently inundated, soils (approximate Ellenberg moisture values of >6), and 43 species that are most commonly found in shaded or partially shaded habitats (approximate Ellenberg irradiance values of <5). Next, using the same 1134 species from the TRY database, we combined this with the BioFlor database (Klotz et al. 2002; www.ufz.de/biolflor). We used the BioFlor information on “phytosociological affinity” of the plant species following Schubert et al. (2001) and classified each of the phytosociological classes (i.e. habitat types) either as “wet” or “shaded” with values “yes”, “no”, “indifferent” or “unknown”, respectively. Then we simply counted the number of “yes” and “no” occurrences of the species in the habitat types, because species can occur in several habitats. Knowing the species from extensive field experience, classifying species with more “yes” than “no” counts for “wet” habitats and more or equal counts of “yes” compared to “no” for shaded habitats proved to yield sensible results in classifying them. This gave us a further 55 and 296 species classified as occurring or not occurring on wet soils, 87 and 264 species classified as occurring or not occurring in shaded habitats. Finally, we used the data set of Frenette-Dussault et al. (2013) consisting of 34 species of the Moroccan steppe, close to the Saharan desert, which has very dry and nutrient-poor soils and uniformly low and sparse vegetation growing in full sun. The predicted mean Ellenberg scores (Eq. 1) for all of these species with respect to soil moisture and light were then calculated.

If the prediction equations can be generalized then the predicted mean Ellenberg scores of these species with respect to Ellenberg moisture should be lowest for the

Moroccan species, be higher for the TRY “non-wetland” species, and be highest for the “wetland” species. If the prediction equations can be generalized then the mean Ellenberg scores with respect to irradiance should be lowest for the “shade” species, be larger for the “non-shade” species, and be highest for the Moroccan species. Finally, the mean Ellenberg nutrient scores should be lower in the Moroccan steppe species than in the other species. Since the mean predicted Ellenberg scores for both moisture and light were approximately normally distributed, we tested the hypothesized differences in the latent scores using one-way ANOVA followed by Tukey post-hoc tests.

Results

Table 2 presents the cumulative link models. Two models are presented for each gradient: a “simplified” model (i.e. each trait without interactions between them, but including differences in slopes between plant types) and the model having the best AIC score, which is always more complicated. All coefficients in these models, except for the partial slope associated with seed mass for the Ellenberg nutrient scores, are significantly different from zero ($P < 0.05$). The average predictive error of these models, based on 100 independent cross-validation runs, varied between 1.3 (light) and 1.8 (nutrients, moisture) Ellenberg ranks. Table 3 presents the distribution of errors for each model and Fig. 1 shows the predicted vs observed cross-validated values for the AIC-selected models. Between 70% (soil fertility and moisture) and 90% (irradiance) of the cross-validated predictions were within one Ellenberg rank of the actual value and at least 90% were within two Ellenberg ranks. The prediction errors for the simplified models were very similar to the more complicated models, showing that the more complicated models, while capturing statistically significant effects, provided only minor improvements in predictive ability.

In order to illustrate the trait–environment relationships predicted by the models, we plotted the predicted Ellenberg scores as a function of the levels of variation in each trait for each plant type while fixing the other traits at their mean values. The results are shown in Figs 2–4. In general, both increasing leaf size and decreasing LDMC (i.e. less dense leaf tissues) indicated habitat preferences for soils that were wetter and with more nutrients, i.e. more productive habitats. These two traits did not respond strongly to changing irradiance levels. The only exceptions were in the trees, whose LDMC values increased with increasing habitat productivity, and the graminoids, whose leaf areas decreased with increasing light levels.

Increasing SLAs (panel C of Figs 2–4) coincide with an affinity for habitats having wetter, more fertile soils and also lower light levels. Two partial exceptions were seen in

the graminoid species and the trees. SLA in the graminoid species and trees was relatively unresponsive to soil nutrient levels, and SLA actually decreased with increasing moisture levels in the graminoids.

Seed size was the least informative trait with respect to the three Ellenberg gradients. It decreased with increasing soil moisture (except for the herbs) but was largely unresponsive to soil nutrients, and decreased only slightly (and not at all for the herbs and shrubs) with increasing light levels.

Next, we predicted the mean Ellenberg scores for those species that were never classified by Ellenberg. Of the 1134 species in the TRY database for which Ellenberg numbers were missing but for which we had values for the four traits, we were able to classify 125 species as commonly occurring in “wet” soils and 264 species as commonly occurring in drier soils (i.e. not “wet” habitats). Similarly, we could classify 91 species as commonly occurring in “shaded” habitats and 296 species as commonly occurring in non-shaded habitats (i.e. “open” habitats). We further included the 34 species that occur in the Moroccan steppe, which is a very dry, nutrient-poor and open habitat, giving a total of 423 and 421 species classified with respect to soil wetness and habitat light levels, respectively. The average predicted Ellenberg scores for soil moisture increased as predicted (Fig. 5): Moroccan species < dry species (TRY) < wet species (TRY). These mean Ellenberg scores differed significantly ($F_{2,370} = 15.40$, $P = 3.7e^{-07}$) and each was different from the others based on a Tukey post-hoc test. The average predicted Ellenberg scores for light also increased as predicted (Fig. 5): Moroccan species > open species (TRY) > shade (forest) species (TRY). These mean Ellenberg scores differed significantly ($F_{2,370} = 31.99$, $P = 2.2e^{-16}$) and each was different from the others based on a Tukey post-hoc test. Finally, the average predicted Ellenberg scores for nutrients were significantly lower in the Moroccan steppe species than for those of the other species ($F_{1,371} = 80.62$, $P = 2.2e^{-16}$).

Discussion

Trait–environment relationships

Our models predicted that herbaceous species having very small, dense leaves with a low SLA plus (to a lesser degree) larger seeds are more likely to be found on the driest and the most infertile soils. In fact, the models for soil moisture and soil nutrients (Ellenberg’s N) were quite similar even though the two sets of Ellenberg scores are only moderately correlated (Spearman $r = 0.36$). Although these qualitative trait–environment trends have been repeatedly reported in the literature, the trees – and especially the graminoids – responded rather differently. Increasing SLA in these species was indicative of drier sites (decreased

Table 2. Results of the cumulative link model (Eqs. 1 and 2), giving the probabilities that a species with given ln-transformed values of leaf area (LA, mm²), leaf dry matter content (LDMC, g·g⁻¹), specific leaf area (SLA, mm²·mg⁻¹) and seed mass (SM, mg) would be classified in each of the nine ordinal Ellenberg classes for site irradiance level (light), site soil nutrients and soil moisture level.

Simplified Model without Interactions

Term	Ellenberg Nutrients				Ellenberg Light				Ellenberg Soil Moisture			
	G	H	S	T	G	H	S	T	G	H	S	T
Intercept	0	0.5	0.47	3.83	0	-3.57	-8.36	-8.41	0	-7.14	-3.95	-3.23
ln(LA)	0.67	0.44	0.59	0.38	-0.77	-0.17	-0.21	-0.75	0.16	0.21	0.06	0.37
ln(LDMC)	-1.52	-0.65	0.04	1.33	-0.48	-0.39	-2.84	1.03	-0.48	-0.18	0.41	0.53
ln(SLA)	0.73	1.4	1.45	0.82	-2.16	-2.15	-1.41	0.9	-0.63	1.32	1.22	0.42
ln(SM)	0.1	0.09	-0.14	-0.12	0.04	-0.09	-0.18	-0.08	-0.3	-0.15	-0.14	-0.17
Threshold coefficients												
1 2	5.27				-18.41				-7.41			
2 3	7.2				-16.45				-4.41			
3 4	8.12				-15.09				-2.68			
4 5	8.88				-13.72				-1.43			
5 6	9.68				-13.11				-0.37			
6 7	10.37				-12.05				0.18			
7 8	11.41				-10.41				0.74			
8 9	13.18				-8.45				1.6			
AIC	3568.02				3061.75				3773.2			
MEP	1.81				1.3				1.8			

Best Model Using AIC

Term	Ellenberg Nutrients				Ellenberg Light				Ellenberg Soil Moisture			
	G	H	S	T	G	H	S	T	G	H	S	T
Intercept	0	2.13	6.95	1.13	0	59.57	42.52	173.73	0	-9.15	-7.05	-4.32
A = ln(LA)	0.82	-0.04	-0.66	1.06	8.73	0.17	3.46	17.9	-1.84	-1.84	-1.84	-1.84
B = ln(LDMC)	-8.94	-5.12	0.48	-9.22	-42.12	3.27	4.05	127.52	3.82	3.99	4.66	4.18
C = ln(SLA)	0.25	1.66	1.96	0.54	19.52	-2.04	3.74	-33.31	-4.94	-2.35	-2.31	-3.18
D = ln(SM)	0.52	0.52	0.52	0.52	-28.3	3.54	-11.51	-41.67	-0.08	-0.38	0.25	0.05
A × B	0.64	0.17	-0.46	1.04	6.12	-0.51	-0.03	-17.34	-0.94	-0.94	-0.94	-0.94
A × C	0.24	0.24	0.24	0.24	-3.36	-0.11	-1.44	4.94	0.7	0.7	0.7	0.7
A × D	-0.04	-0.04	-0.04	-0.04	4.02	-0.98	0.47	5.57	-0.07	-0.07	-0.07	-0.07
B × C	1	1	1	1	14.5	-0.8	-1.55	-38.38	-1.56	-1.56	-1.56	-1.56
B × D	-0.24	-0.24	-0.24	-0.24	-26.05	0.95	-18.64	-35.12	-1.32	-1.63	-0.95	-1.02
C × D	-0.19	-0.19	-0.19	-0.19	8.39	-1.26	3.65	13.17	-0.42	-0.42	-0.42	-0.42
A × B × C					-2.16	0.4	-0.1	5.3	0.32	0.32	0.32	0.32
A × B × D					3.52	-0.43	1.7	4.48	0.08	0.08	0.08	0.08
A × C × D					-1.14	0.33	-0.15	-1.79	0.08	0.08	0.08	0.08
B × C × D					7.74	-0.33	6.11	11.39	0.27	0.27	0.27	0.27
A × B × C × D					-1	0.15	-0.56	-1.46				
Threshold coefficients												
1 2	9.54				43				-19.7			
2 3	11.5				44.96				-16.59			
3 4	12.43				46.34				-14.8			
4 5	13.2				47.83				-13.52			
5 6	14.01				48.5				-12.43			
6 7	14.72				49.62				-11.86			
7 8	15.76				51.36				-11.29			
8 9	17.55				53.42				-10.4			
AIC	3559.16				3054.74				3744.86			
MEP	1.77				1.27				1.76			

Shown are the maximum likelihood values for each of four plant types (H = herb, G = graminoid, S = shrub, T = tree) of the partial slopes associated with each of the four ln-transformed traits and their interactions, which together give the latent score. Also shown are the "threshold values" or intercepts; thus "x|y" (e.g. 1|2) gives the value of the latent score, calculated from the partial slopes and trait values, at which a species is more likely to be in Ellenberg state 2 rather than 1. Two sets of models are shown: a simplified model that does not include interactions between traits, and the best model as determined by AIC values. MPE gives the mean predictive error for each model.

Table 3. Levels of prediction error in cross-validated data (100 independent runs, 20% of data for each run) for the Ellenberg scores of soil nutrients, habitat moisture and irradiance, each having 9 levels.

Error	Soil Nutrients		Habitat Moisture		Irradiance Level	
	AIC-Selected	Simplified	AIC-Selected	Simplified	AIC-Selected	Simplified
0	39.5	38.4	45.2	41.6	63.7	59.1
1	34.3 (73.8)	34.9 (73.2)	28.0 (73.2)	29.6 (71.2)	26.1 (89.9)	29.4 (88.5)
2	16.9 (90.7)	16.9 (90.1)	17.1 (90.3)	19.8 (91.0)	6.7 (96.5)	8.0 (96.5)
3	6.8 (97.5)	7.3 (97.4)	7.1 (97.4)	6.8 (97.8)	2.4 (98.9)	2.4 (98.9)
4	2.3 (99.8)	2.4 (99.8)	2.2 (99.6)	2.0 (99.9)	1.1 (100.0)	1.1 (100.0)
5	0.2 (100.0)	0.2 (100.0)	0.4 (100.0)	0.1 (100.0)	0	0

The first column ("Error") is the difference in the observed and predicted Ellenberg score; thus, 1 = the predicted score is within 1 score of the real score, etc. Subsequent columns give the percentage of the cross-validated observations having this level of prediction error (cumulative percentage error). These error rates are given for both the AIC-selected models and the simplified models.

Ellenberg moisture) but changed little with respect to habitat soil nutrients (Ellenberg N). A possible explanation can be found by decomposing SLA into its components (Vile et al. 2005). SLA is approximately equal to $1/(LDMC \times T)$; Shipley & Vu 2002) for typical laminar leaves, where T is leaf lamina thickness; it follows that $\ln(SLA) = \ln(LDMC) - \ln(T)$. The negative relationship between SLA and LDMC can therefore be modulated by changes in lamina thickness and it has already been shown that, although graminoids and herbs have largely overlapping ranges of SLA, the relative importance of LDMC vs T in determining this range is quite different (Pyankov et al. 1999). With respect to increasing Ellenberg nutrients, graminoids decreased LDMC (which would increase SLA) but must have also increased lamina thickness (which would decrease SLA). As a result, SLA was largely insensitive to habitat nutrient levels. With respect to increasing Ellenberg moisture, graminoids did not change LDMC and so the increased lamina thickness actually decreased SLA.

The main response to increasing light levels in the herbs was to decrease SLA even though leaf size and LDMC responded only slightly. Again, a large decrease in SLA without a correspondingly large increase in LDMC means that the decrease in SLA in the herbs was mostly driven by increasing lamina thickness as irradiance levels increased. For the graminoids and trees, the decrease in SLA with increasing light levels was accompanied by an increase in LDMC, and so lamina thickness for these plant types did not change as much. The response of the trees (and somewhat for the shrubs) to levels of habitat irradiance should be interpreted with care since most measurements of SLA in trees are taken on sun leaves. These differences in response between plant types are further complicated by the fact that the number of herb species (691) was much larger than that of the shrubs (44), trees (31) or graminoids (156), and the range of trait variation in the plant types other than the herbs was often quite limited, as seen in Figs 1–3.

Predictive accuracy and generality

Through cross-validation we predicted Ellenberg scores that were within two ranks of the observed values in over 90% of cases. Given that the ranks range from 1 to 9, this means that we could distinguish between low, medium and high scores but not within adjacent ranks. In 40%–64% of cases (depending on the Ellenberg characteristic), the exact score was predicted, with Ellenberg irradiance having the highest accuracy. However, these summary statistics do not provide a complete view of the predictive accuracy of our models.

First, the increased predictive accuracy for Ellenberg irradiance is a consequence of the fact that most species had Ellenberg irradiance scores of 6 or more (plants generally occurring in well-lit places or in only partial shade). As Fig. 1 shows, our equations do a poor job of differentiating between Ellenberg irradiance levels of 5 or less. In part this is because so few species had such scores (Table 1) and that such species had little weight in the model estimation. However, another reason is because there might actually be little real difference in these first five ranks, at least with respect to the chosen traits. An Ellenberg irradiance rank of 5 is a "semi-shade plant, rarely in full light, but generally with more than 10% relative illumination when trees are in full leaf." In other words, ranks 1–5 all indicate species that are generally found in forested understories.

Second, as Fig. 1 shows, our equations predict values that are higher than observed for the lowest Ellenberg scores and values that are lower than observed for the highest Ellenberg scores. In part, this is due to low representation of species at these extremes (Table 1), but it is also due to an unavoidable mathematical bias. Since these are ordinal scales that are bounded by 1 and 9, any prediction error at these bounds must increase the predicted values at the lower bound and decrease them at the upper bound, and this will necessarily generate such a bias. One

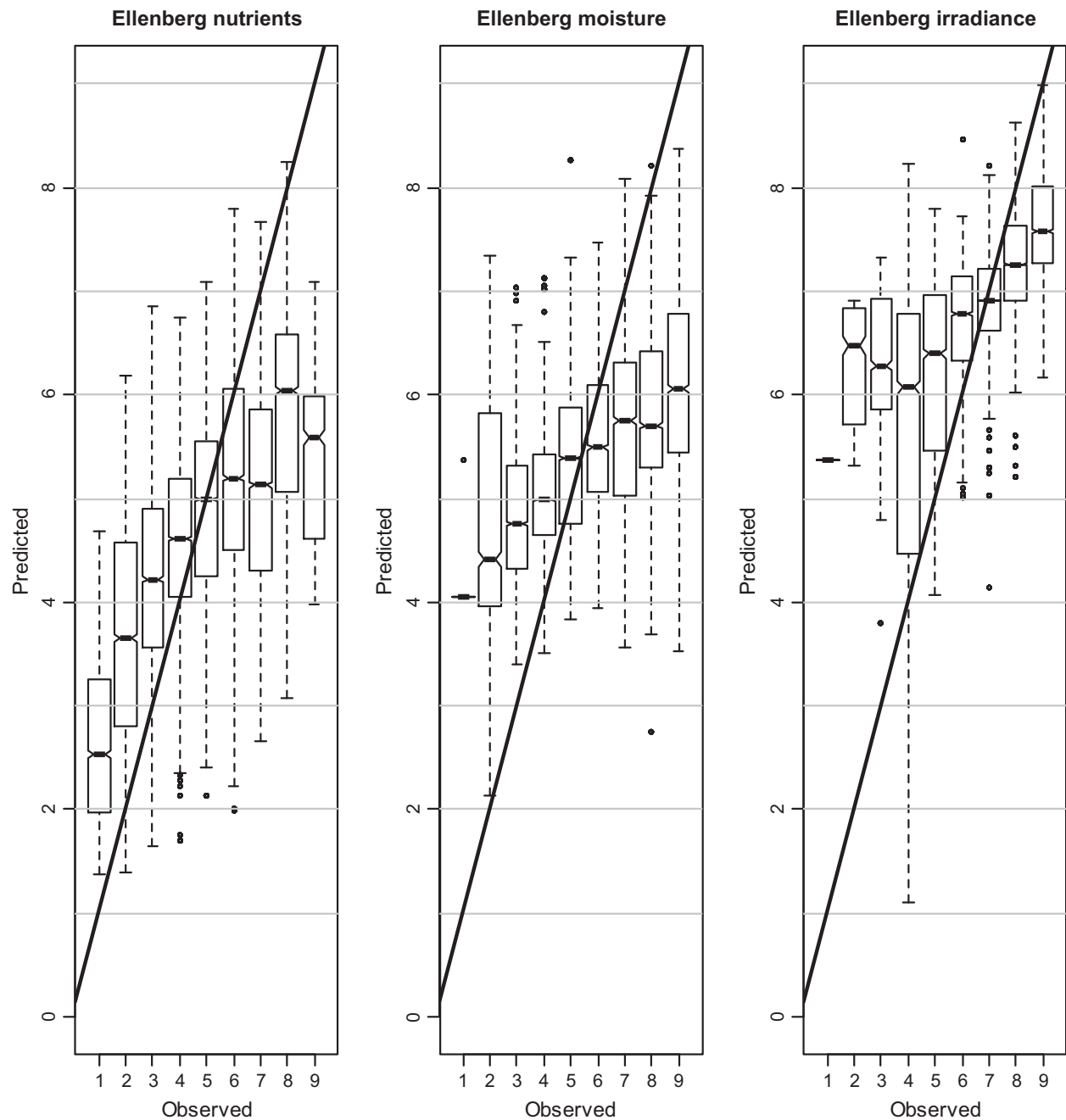


Fig. 1. The observed Ellenberg indicator values for soil nutrients, soil moisture and irradiance plotted against the mean Ellenberg indicator values predicted by four traits: specific leaf area, leaf dry matter content, leaf area and seed mass. Results based on 922 (nutrients), 981 (moisture) and 988 (irradiance) species.

should therefore use Fig. 1 to modify predicted Ellenberg values.

There are some obvious sources of error in these data. First, a substantial proportion of the unexplained variation is probably due the arbitrary nature of the original Ellenberg values, leading to errors in classification of the habitat

affinities of the species. Second, the Ellenberg indicator scores do not include information on niche breadth. Although Ellenberg's classification was based on a lifetime of experience, the habitat descriptions for each class are sufficiently vague, and the field distributions of many species with respect to these habitat descriptions are

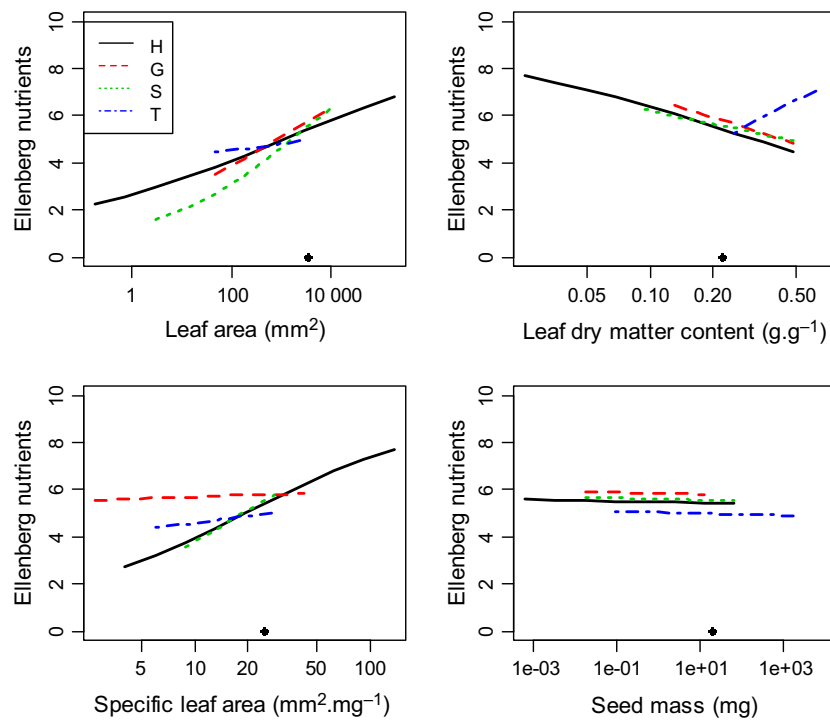


Fig. 2. The predicted Ellenberg indicator values for soil nutrient status as a function of each plant trait. Results are shown for four plant types (H: herbs, G: graminoids, S: shrubs, T: trees). Each line shows the response for that trait when holding constant the other traits at their mean values in the data set. The mean value of each trait is shown by the dot on the x-axis.

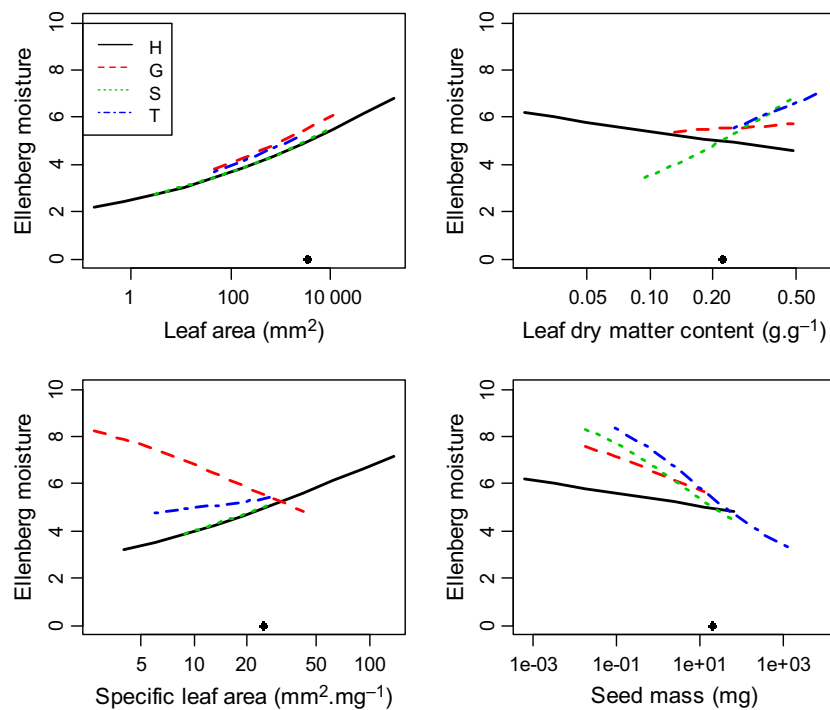


Fig. 3. The predicted Ellenberg indicator values for soil moisture status as a function of each plant trait. See Fig. 1 for details.

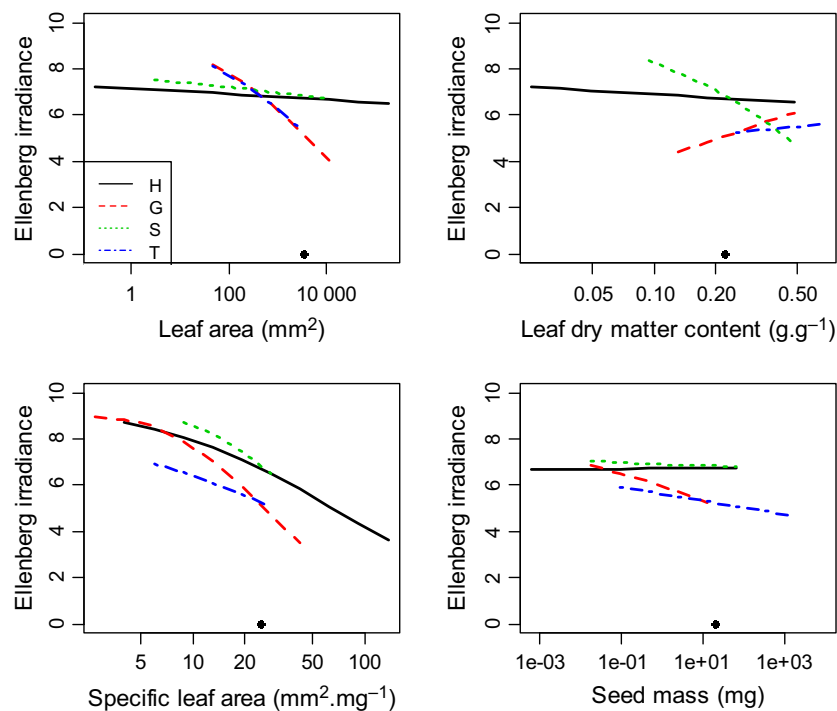


Fig. 4. The predicted Ellenberg indicator values for irradiance as a function of each plant trait. See Fig. 1 for details.

sufficiently difficult to determine, that many species could probably be assigned to several adjacent Ellenberg classes with equal confidence. It is therefore not surprising that our prediction equations cannot discriminate between adjacent Ellenberg classes. Third, the trait values used in the analysis are estimates of species' means obtained from a heterogeneous collection of values uploaded to the TRY database; we do not know how closely the species' trait means calculated from the TRY database correspond to the true species' trait means (Cordlandwehr et al. 2013) and, of course, intraspecific trait variation is completely ignored. A necessary consequence of errors in the predictor variables (i.e. the species' means for each trait) is also to reduce the predictive ability of the model. Finally, these equations treat each environmental gradient separately, but these are correlated in nature and the actual habitat affinities of species would reflect correlated trait adaptations to all environmental gradients. Beyond these sources of error, it is surely true that more (or better) traits would further improve the predictive ability of our equations.

The main goal of this research was to determine the degree to which our easily measured and widely available trait values could be used to predict the habitat affinities of species not already classified by Ellenberg values, and, especially, species for which no habitat affinities are available. Can one use these equations to predict the Ellenberg habitat affinities of species not classified by Ellenberg,

especially of species outside of Central Europe? Strictly speaking, it is impossible to answer this question since these numbers represent Ellenberg's expert opinion rather than some independently measurable attribute. However, if our equations are generalizable, we should be able to correctly differentiate between species that typically occupy clearly different points along the underlying environmental gradients. Our results (Fig. 5) suggest that this is possible. With respect to soil fertility our equations assigned the Moroccan steppe species to Ellenberg levels of 1 ("extremely infertile sites") to 3 ("more or less infertile sites"), while the heterogeneous collection of other species had a median score of around 5 ("sites with intermediate fertility"). With respect to soil moisture and irradiance our equations performed more poorly. Although the order of the predicted ranks for the "wetland", "non-wetland" and "steppe" species was correct, the median moisture score for the "wetland" species was ~5.5 when it should have been around 7 ("plants typically found on constantly moist or damp soils") or more. This level of error was also seen in the cross-validated estimates (Fig. 1). Similarly, although the order of the predicted ranks for the "steppe", "open" and "forest" species was correct, and while the "steppe" and "open habitat" species were assigned reasonable irradiance ranks, the species described as understorey plants were incorrectly assigned Ellenberg ranks of between 6 and 7 when they should have received ranks of 5 or less.

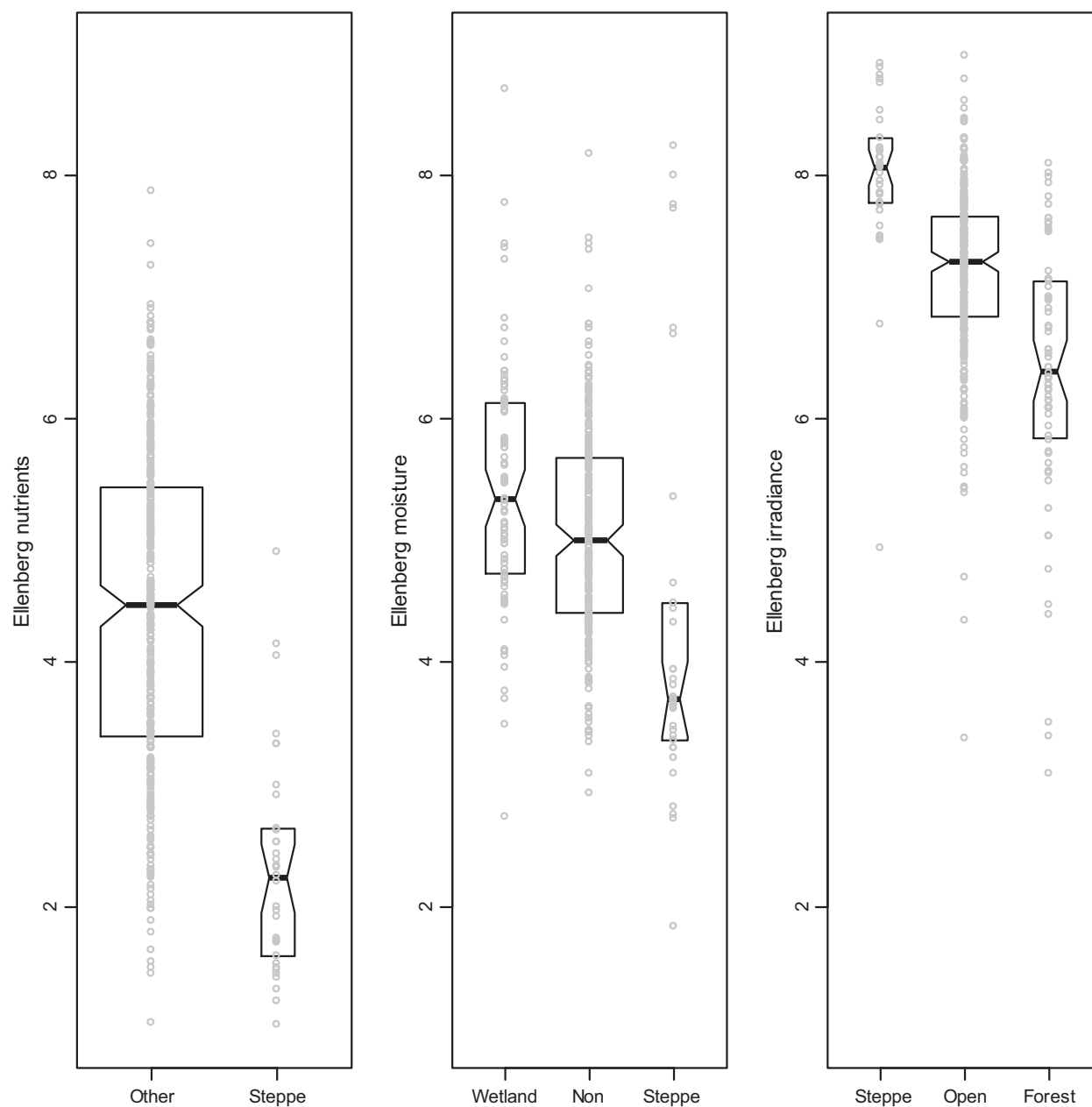


Fig. 5. Predicted mean Ellenberg indicator values for soil nutrient and moisture status, as well as site irradiance. Predictions were obtained for species that had never been classified by Ellenberg. Species classified as being from the dry, infertile Moroccan steppe or not (soil nutrients), as being wetland, non-wetland or Moroccan steppe species (soil moisture), and as being forest understoreys, open habitats or from the Moroccan steppe.

Our equations did particularly poorly when identifying understorey species (Fig. 1).

We therefore propose our equations as a general, but only very approximate, method of describing the likely habitat affinities of soil moisture, soil nutrients and irradiance levels for species lacking such information. When distribution models already exist that include information on the relevant abiotic gradients for a given species then

these would likely provide better predictions than would our equations. Species distribution models (Elith & Leathwick 2009; Peterson 2011) provide an alternate approach for estimating the realized niche of species. Because of the growing availability of species occurrence data and environmental layers (Maldonado et al. 2015), habitat models can now be readily constructed for many species. However, these models tend to be more appropriate at

larger spatial scales and often describe only large-scale climate variables like temperature and precipitation. Currently, such distribution models exist for only a tiny fraction of plant species. Since it is much easier to obtain information on a few static traits than to construct a species distribution model, we expect that our prediction equations will still be useful for the majority of species. Ultimately, as trait databases like TRY continue to accumulate trait information on more species, one may be able to use our equations to predict coarse habitat descriptions for many thousands of species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Ellenberg scores for irradiance level (“light”), moisture and soil fertility, and a worked example of calculations.