

REVIEW

Functional characterizations of Ellenberg indicator values – a review on ecophysiological determinants

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Summary

1. Ellenberg indicator values (EIVs) can be used as a numerical system to classify species' habitat niches and their peak occurrence along gradients. By finding correlations of EIVs with morphological or ecophysiological properties, it is possible to identify determinants of species distributions with respect to environmental factors.
2. We surveyed existing literature containing species comparisons from controlled experiments and combined them with EIVs.
3. The picture emerging is that multiple determinants can be identified for nutrient numbers (N), soil reaction numbers (R) and also soil moisture numbers (M), while only few can be found for light numbers (L) and especially for continentality (C) and temperature numbers (T). Functional characterizations of the different EIV can thus be deduced which help to understand the mechanisms and processes driving the ecological niche of a plant.
4. The described approach is a powerful tool to analyse the ecological significance of different plant properties. Species screenings specifically designed to allow for correlations with EIV have large potential for high explanatory power.

Key-words: controlled experiments, ecological gradients, Ellenberg indicator values, plant traits, species screening

Introduction and scope

Ellenberg indicator values (EIVs) (Ellenberg *et al.* 1991) are extensively used in vegetation science, because of their great merit in allowing for the assessments of environmental variables without direct measurements (Diekmann 2003). Mean EIV derived from vegetation surveys integrates over longer time periods to reflect environmental conditions that allow or restrict the occurrence of species at a site. Conversely, as pointed out by Silvertown *et al.* (2006), EIV can be used as a numerical system to classify the habitat niche of species. This means we have a system available for Central Europe that enumerates at which points along gradients of light availability (L), temperature (T), continentality (C), soil moisture (M), soil reaction (R), soil fertility (N) and salinity (S) a species has its peak occurrence. EIVs are based on expert knowledge and field observations, and partly on measurements of soil parameters, so that standing on their own they are basically of a descriptive nature. However, functional mechanisms

behind EIVs (or habitat niches) have as yet very scarcely been taken into account, although they can well be obtained from ecophysiological characterizations of EIV. We will show that correlating morphological or ecophysiological properties with EIVs is an excellent possibility to relate functional mechanisms to species occurrence in the field.

Species pool concepts as well as concepts of environmental filtering make clear that the occurrence of a species in a certain habitat is an outcome of how well the species can survive and prosper under the ambient conditions (e.g. Keddy 1992). The success of a species in a habitat depends on a set of ecophysiological or morphological characteristics that can be interpreted as determinants of occurrence along environmental gradients. Two selective processes act in concert so that determinants coincide with specific habitat niches (Zobel 1997): the one is environmental filtering, and the other, once a species is allowed in a habitat, is evolutionary adaptation. Environmental filtering is a relatively strict barrier that allows only species with specific adaptations (indispensable determinants) to pass, that is survive. Once established in a

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habitat, a species will also evolve characteristics that might not be absolutely crucial, but that optimize success in the habitat (accessory determinants). These determinants are in some cases very obvious, but quite obscure in others. Textbooks on plant ecophysiology give very good overviews on how plants react to their environment and partly also on properties favouring survival in certain environments (e.g. Larcher 2003; Lambers, Chapin & Pons 2008). However, exemplary cases with few species are usually presented instead of comparisons of numerous species from different habitats. Yet, the latter approach offers the opportunity to quantify correlations of EIV (representing habitat niches) and the extent to which specific determinants are expressed. Strong and significant correlations of that kind can usually be interpreted in a way that the according plant property has significant importance for the occurrence along the gradient. The point of the matter is that when an ecophysiological characteristic can be identified as a determinant of an EIV, it means that this characteristic has got significant ecological importance for where a species can occur. Hence, correlations with EIV are an outstanding tool that deserves far more attention than is to date the case. Therefore, this review focuses its scope on comparisons within assortments of species occurring along environmental gradients (i.e. a range concerning certain EIV) to pinpoint the plant properties that determine species peak occurrences. The analyses are restricted to data sets generated under controlled experimental conditions to avoid the danger of circular reasoning involved in on-the-spot observations along gradients in the field (compare, e.g., Grime *et al.* 1997). While in principle, EIVs are of ordinal nature, they were conceived by Ellenberg as quasimetric data (Ellenberg *et al.* 1991) and have been extensively used as such (Diekmann 2003). Correlations and regressions of metric data to EIV can therefore be regarded as reliable.

A previous study by Thompson *et al.* (1993) has used a number of examples, where EIVs are correlated with plant properties, aiming to validate the respective EIV and to

show their compatibility to species screening approaches. Three of these examples came from controlled experiments (one in reaction numbers, one in moisture numbers, one in nitrate/nutrient numbers) and are all referenced in this review (see below). Already then, the authors pointed out that it would be important to examine ‘What are the mechanisms underlying Ellenberg numbers?’ For this, it is important to go beyond instructive examples by compiling all available significant information. Species occurrence is usually dependent on multiple determinants. Therefore, the aim of this review was to identify determinants and, where possible, to compare their respective importance for whether a species can occur at a site or not. One intention is also to show which EIVs are already well characterized in terms of their ecophysiological determinants (to thereby reveal mechanisms) and which ones still require more investigations and pose challenges for future. For this, this review assembles the information scattered over literature and statistically processes data sets formerly unassigned to EIVs. For correlations or regressions already presented in publications, the original coefficients (R^2 , Rho or r) were adopted when cited. For all regressions presented in Figs 1–5 and in Table 1, we assigned EIV to published data and calculated the regression coefficient R^2 . This review covers all the different EIVs except for salt numbers (S). The latter were omitted, since data sets with sufficient ranges in S-values are very scarce and because validations for S-numbers are as yet merely based on one single study (Scherfose 1990).

R-numbers (soil reaction)

The soil reaction gradient ranges from ‘strong acidity, never moderately acidic or alkaline’ (R-number 1) to ‘alkaline and calcareous conditions, only calcareous soils’ (R-number 9). Challenges in acidic habitats are aluminium (Al) toxicity and usually a high ammonium/nitrate ratio (Bogner 1968; Falkengren-Grerup 1995). Challenges in habitats with alkaline and calcareous soil conditions are

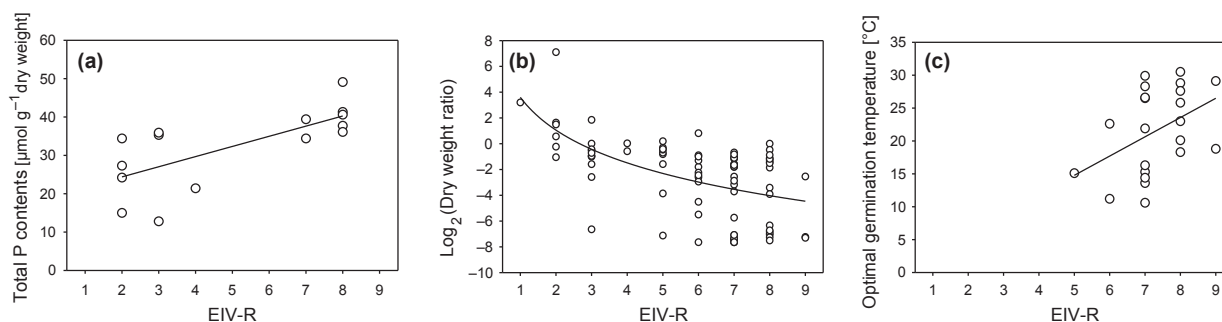


Fig. 1. Regression analysis of Ellenberg indicator values for soil reaction (EIV-R) and different plant properties with (a): the concentration of total phosphorus in plant tissue for plants grown on calcareous soil (data set from Zohlen & Tyler (2004)); (b): the ratio of total dry weight of plants raised with ammonium as compared to nitrate (reanalysis of a data set from Bogner (1968) and Bogner & Dieterich (1968)). The regression line (logarithmic curve, 2 parameters) derives from nonlinear curve-fitting including $N = 85$ species and represents the best fit. Reprinted from Supplemental Materials to Bartelheimer & Poschold (2014); (c): the optimal germination temperature in flood meadow species (data set from Hölzel & Otte (2004)).

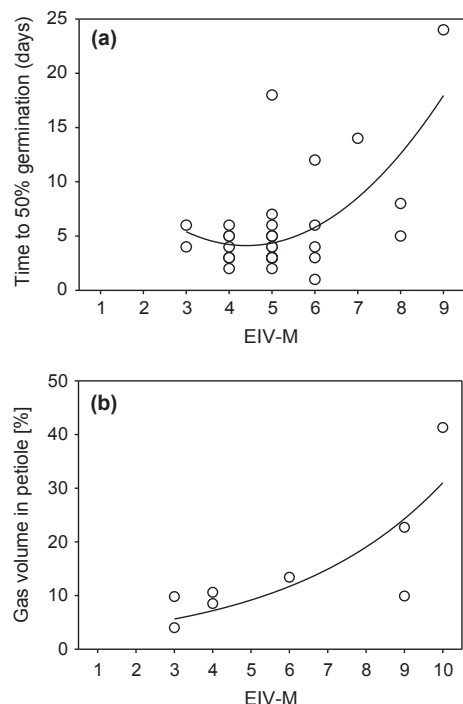


Fig. 2. Regression analysis of Ellenberg indicator values for soil moisture (EIV-M) and different plant properties with (a): the time to 50% germination (t50) in all Asteraceae species ($n = 35$) included in the data set by Grime *et al.* (1981). The nonlinear regression follows a quadratic form (two parameters); (b): the gas volume in petioles of different species in an experiment by Mommer *et al.* (2007). The nonlinear regression follows an exponential growth curve.

thought to be low availabilities of phosphorus (P) and iron (Fe) (Grime & Hodgson 1969; Tyler 1992).

In experiments raising different species on calcareous soils (Zohlen & Tyler 2004), species with low R-numbers have low concentrations of total P in plant tissue, indicating their poor ability to solubilize it from the rhizosphere (Fig. 1a; $R^2 = 0.45$; $P < 0.01$; $n = 15$). A similar result can be inferred for contents in inorganic P ($R^2 = 0.43$; $P < 0.01$; $n = 15$). Many calcifuge species planted to

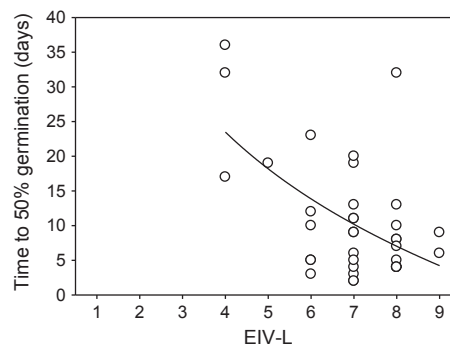


Fig. 4. Regression analysis of Ellenberg indicator values for light (EIV-L) and the time to 50% germination (t50) in all perennial Poaceae species ($N = 36$) included in the data set by Grime *et al.* (1981). The nonlinear regression follows a logarithmic form (one parameter).

calcareous habitats also show lime chlorosis indicating Fe deficiency (e.g. Grime & Hodgson 1969). Gries & Runge (1992) examined 22 grasses for their ability to mobilize Fe (III) from freshly precipitated $\text{Fe}(\text{OH})_3$, presumably by exuding phytosiderophores. Regression analysis revealed that species with high R-numbers had higher Fe-solubilizing capacity than species with low values (reanalysis of data from Gries & Runge 1992; $R^2 = 0.40$; $P < 0.01$). On the other hand, also the toxicity of Fe can pose a challenge: in 11 monocotyledonous species, those with low R-numbers had higher resistance to Fe toxicity (data from Snowdon & Wheeler 1993; analysis by Thompson *et al.* 1993; $r = -0.85$; $P < 0.001$). No such correlation was found for dicotyledonous species, however (Thompson *et al.* 1993; $r = -0.32$; $P > 0.05$; $n = 13$).

Al toxicity is known to increase with soil acidity and by impacting on root growth as well as by inducing changes to the entire root architecture (Kochian, Hoekenga & Piñeros 2004). When analysing 15 calcicoles to calcifuge species for seedling tolerance to Al, Abedi, Bartelheimer & Poschlod (2013) found strong Al tolerance in species with low R-numbers ($R^2 = 0.66$; $P < 0.001$). Likewise, when

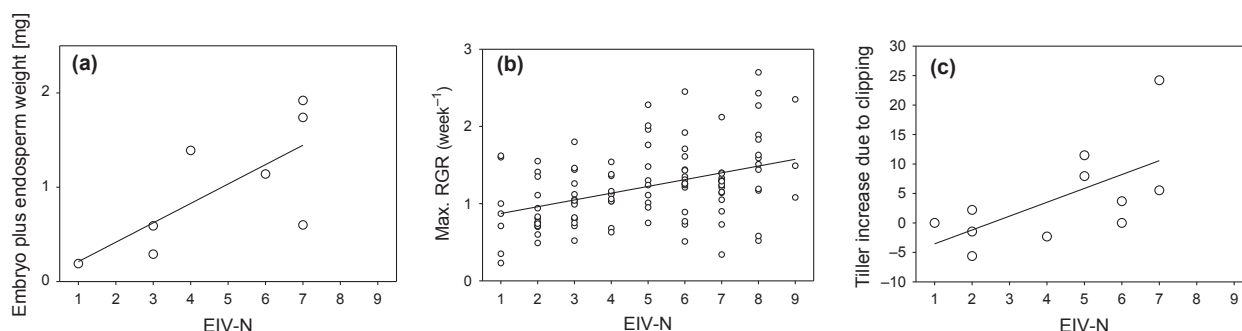


Fig. 3. Regression of Ellenberg indicator values for nutrients (EIV-N) and different plant properties with (a): the weight of embryo plus endosperm in eight grass species from different habitats. Analysis on data from Elberse & Berendse (1993); (b): the maximum relative growth rate (RGR) in 109 species from different habitats. Analysis on data from Grime & Hunt (1975); (c): the growth response of various grasses to defoliation. Clipping response (number of tillers 35 days after removal of 75% of above-ground biomass as compared to unclipped controls) was deduced from Bossard & Hillier (1993).

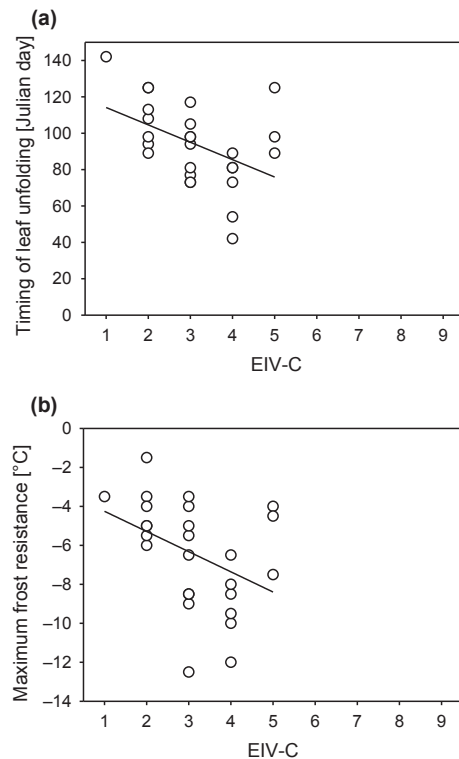


Fig. 5. Regression analysis of Ellenberg indicator values for continentality (EIV-C) vs. timing of first leaf unfolding in spring of the year 1953 (panel a) and frost resistance of these leaves (panel b), respectively (data from Till (1956)).

they reanalysed data from Grime & Hodgson (1969), they found a similar result for nine grassland species ($R^2 = 0.82$; $P < 0.001$). Yet, there are further determinants that must not be overlooked. The predominant form of available nitrogen is dependent on soil pH, because biotic oxidation of ammonium to nitrate needs the presence of the soil bacteria *Nitrosomonas* and *Nitrobacter* which are only active at pH values higher than 5 (e.g. Gigon & Rorison 1972). Hence, preference for either ammonium or nitrate was identified as a possible precondition for the occurrence on either acidic or calcareous soils (Bogner 1968; Falkengren-Grerup 1995). Bartelheimer & Poschold (2014) recently established that in a common garden experiment with seven species from sandy grasslands, the more

calcifuge species had stronger preference for ammonium over nitrate ($R^2 = 0.69$; $P < 0.05$). They also presented similar results for a greenhouse experiment on 12 species from sandy grasslands ($R^2 = 0.51$; $P < 0.01$). In addition, they reanalysed data from Bogner (1968) and from Bogner & Dieterich (1968) and found the same pattern for 85 woodland species ($R^2 = 0.31$; $P < 0.001$; $n = 85$) (Fig. 1b). Also, plant growth parameters were found to be determinants of occurrence along the soil reaction gradient. In a data set from Poorter & Remkes (1990) originally examining plant/soil fertility relations in a controlled experiment, we found ten species with R-numbers. Specific leaf area (SLA) was found to be a determinant of R-numbers ($R^2 = 0.70$; $P < 0.01$), indicating that hardy leaves are more common in species originating from acidic soils, but less so in species originating from calcareous soils. It is not straightforward why plant properties such as SLA should correspond with soil reaction. However, acidic habitats tend to be harsh environments, for example in terms of availability of certain nutrients such as calcium, magnesium and, in certain cases, also phosphorus (Stevens, Dise & Gowing 2009) and in terms of availability of toxic ions. This might explain why sturdiness appears to be correlated with low R-numbers. Likewise, the related parameters leaf area ratio (LAR) and leaf weight ratio (LWR) also correlated significantly or marginally significantly with R-numbers ($R^2 = 0.58$; $P < 0.05$ for LAR; $R^2 = 0.33$; $P < 0.1$ for LWR). Calcifuge species also had more root biomass per total dry weight (root weight ratio (RWR)), indicated by a significant regression coefficient of $R^2 = 0.52$. Also relative growth rate (RGR) was reduced in calcifuges ($R^2 = 0.43$; $P < 0.05$). Concerning seed ecological characteristics, Otte, Bissels & Waldhardt (2006) found a significant correlation between R-numbers and seed mass in annual arable weeds (Spearman's $\rho = 0.35$; P -value not further specified; $n \leq 130$), where species with higher R-numbers tended to have heavier seeds. Also, in a data set by Hölzel & Otte (2004), a correlation between R-numbers and optimal germination temperature could be discovered ($R^2 = 0.18$; $P < 0.05$; $n = 22$) with high R-numbers corresponding to higher germination temperatures (Fig. 1c). A possible explanation is that this reflects an adaptation to the physical properties of calcareous soils. These are usually well

Table 1. Regression analyses for Ellenberg indicator values (EIV) and various plant growth parameters from Poorter & Remkes (1990) with RGR: relative growth rate; SLA: specific leaf area; LAR: leaf area ratio (ratio of leaf area and total plant weight); LWR: leaf weight ratio (ratio of leaf weight and total plant weight); SWR: shoot weight ratio; RWR: root weight ratio; NAR: net assimilation rate

EIV	<i>n</i>	Range	RGR	SLA	LAR	LWR	SWR	RWR	NAR
N	23	1–9	0.56***	0.56***	0.46***	ns	ns	ns	ns
R	10	2–8	0.43*	0.695**	0.58*	0.33†	ns	0.52* ↓	ns
M	19	2–6	0.47**	0.29*	0.19†	ns	ns	ns	0.26*
L	23	4–8	0.19* ↓	0.24* ↓	0.32** ↓	0.16† ↓	0.17†	ns	ns

The study by Poorter & Remkes (1990) covers 24 non-woody species grown under constant conditions. Downward arrows indicate negative regressions. All other cases are positive regressions. Note that species numbers of $n < 24$ are due to cases, where species are classified as 'indifferent' towards the respective environmental gradient. Also, note that due to the very short range of T-numbers in the data set, no according regressions were carried out

Given are significant R^2 -values with † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

drained and thus dryer and often warmer than siliceous soils with their higher clay mineral content.

Thus, for R-numbers, it transpires that a number of strong determinants can be identified, some of which might be seen as straightforward (like those related to nutrition), while others might be rather unexpected (such as SLA, seed size), but important nonetheless.

M-numbers (soil moisture)

In terrestrial plants, EIV for soil moisture covers species only growing on dry soils (M-number = 1) to species only growing on wet (hypoxic) soils (M-number = 9). Additionally, M-numbers 10–12 cover aquatic species from those tolerating to fall dry for longer periods to entirely submerge species. Practically, all studies allowing for correlating M-numbers with plant properties restrict their scope to terrestrial species with maximum M-number 9 (but see below for one study with M-number = 10 in Mommer *et al.* 2006). The hydrological gradient is special insofar as two different resources are involved: lack of water at the dry end and lack of soil oxygen at the wet/waterlogged end (Silvertown *et al.* 1999). The major challenges for plants at the dry end are to maintain photosynthesis and growth during drought or to tolerate extended periods without these. Damage from photoinhibition or from onset of the permanent wilting point needs to be avoided (Lawlor & Cornic 2002). Besides, especially during germination and seedling establishment, plants need to cope with higher risk from desiccation. At the wet end, the major challenges are thought to be oxygen supply or tolerance of anoxia (Blom *et al.* 1994). Low diffusion of oxygen can also result in the accumulation of potentially toxic compounds such as H_2S , Mn^{2+} or Fe^{2+} (Crawford 1989). Additionally, in wet habitats, high air humidity can at times hinder transpiration and thereby nutrient transport by water flux (Larcher 2003).

For dry soils, high importance of larger root systems is often assumed, and indeed on a global scale, Schenk & Jackson (2002) found that rooting depth relative to above-ground plant size tended to increase with aridity. However, absolute rooting depth decreased with aridity due to overall smaller plant size. Studies deriving correlations of M-numbers with root size parameters are Thompson *et al.* (1993) and Liu *et al.* (2000). Thompson and co-workers analysed data from Reader *et al.* (1992) and found the responsiveness of rooting depth to drought to be related to M-numbers; that is, species occupying dry habitats are capable of responding to drought by increasing rooting depth, while species with higher M-numbers are less capable of such a response ($r = -0.56$; $P < 0.01$; $n = 29$). No such correlation was found for rooting depth itself. Liu *et al.* (2000) confirmed the responsiveness in rooting depth to drought ($R^2 = 0.56$) and also found root–shoot ratios to increase with drought especially in species with low M-numbers ($R^2 = 0.34$). On a local scale, root elongation rate was shown to be correlated with aridity, but data are

not available for Central Europe (Kos & Poschlod 2010). Germination speed may be a functional adaptation to limited amounts of water. For arid savannas, it was shown that species of open sites germinated faster than subcanopy species, presumably in order to time-efficiently use the ephemeral soil moisture (Kos & Poschlod 2010). Similarly, germination speed measured as t50 (time when half of all seeds have germinated following storage at 20 °C) correlated positively with M-numbers in Asteraceae extracted from an extensive data set by Grime *et al.* (1981) ($R^2 = 0.40$; $P < 0.001$; $n = 35$, Fig. 2a), indicating that species from dryer habitats germinated faster. Other groups of species extracted from the data set of Grime *et al.* (1981) like ‘all forbs’ or ‘all species together’ brought no further correlations of M-numbers with germination speed, however, except for the following two. In annual forbs, there was a weak positive correlation of M-numbers with t50 as well ($R^2 = 0.11$; $P = < 0.05$; $n = 47$, linear regression) and, in contrast to the above, when all grass species were taken together, there was a slightly negative correlation between germination speed (in this case on freshly harvested seeds) and M-numbers ($R^2 = 0.11$; $P < 0.05$; $n = 36$, linear regression).

Waterlogging conditions involve the necessity to cope with low soil oxygen. An analysis of data from Blom *et al.* (1994) found a high regression coefficient ($R^2 = 0.79$; $P < 0.05$; $n = 5$) for M-numbers and the number of adventitious roots per plant in *Rumex* species exposed to 16 days of soil waterlogging. Likewise, the gas volume in petioles (proportion of their total volume), potentially allowing for oxygen conductance to the root, was higher in species with high M-numbers ($R^2 = 0.64$; $P < 0.05$; $n = 8$; see Fig. 2b) when data from a study by Mommer *et al.* (2007) were annotated to EIV. Another data set (deduced from Mommer *et al.* 2006) allowed testing for correlation between M-numbers and the magnitude of aerenchyma, but this yielded no significant regression. However, data from that latter study did yield marginally significant regressions for specific leaf area (SLA) ($R^2 = 0.29$; $P = 0.059$; $n = 10$) after plants were grown in submerged and lighted conditions for 10 days (species with high M-numbers tended to have higher SLAs). The similar relationship of SLA and M-numbers was detected in the data set from Poorter & Remkes (1990) (Table 1), who tested growth parameters in a variety of species raised under controlled conditions ($R^2 = 0.29$; $P < 0.05$; $n = 19$). This data set also revealed that species with higher M-numbers had higher relative growth rates (RGR; $R^2 = 0.47$; $P < 0.01$; $n = 19$) and higher net assimilation rates (NAR; $R^2 = 0.26$; $P < 0.05$; $n = 19$). There was also a marginally significant trend for increased leaf area ratio (LAR; $R^2 = 0.19$; $P < 0.1$; $n = 19$) in species with high M-numbers.

In addition, Bureš *et al.* (2004) found genome size of *Cirsium* species to be negatively correlated with M-numbers (Spearman's $\rho = -0.68$; $P < 0.05$, $n = 10$). One might summarize that the root system's responsiveness to drought, the capacity of plants to form adventitious roots

or air-containing tissue under waterlogged conditions and growth parameters such as RGR and SLA are major determinants of M-numbers. However, comparative studies on adaptations to anaerobic metabolism with considerable numbers of species are lacking.

N-numbers (nitrogen/nutrients)

EIVs for nitrogen/nutrients cover species only growing on the poorest soils (N-number = 1) to species only growing on excessively nitrogen (nutrient)-rich soils (N-number = 9). Ellenberg himself has, in his later works, emphasized that N-numbers may be used in a more general way as nutrient numbers instead of nitrogen numbers (Ellenberg *et al.* 1991). Therefore, N-numbers are increasingly interpreted to reflect general productivity rather than mere nitrogen contents (e.g. Hill & Carey 1997; Wagner *et al.* 2007). Challenges for plants at the oligotrophic end are seed establishment and efficient nutrient use for the maintenance of growth under temporal or permanent conditions of nutrient deficiency. Challenges in eutrophic habitats are connected to high productivity, where plants need to avoid being suppressed (Grime 1973; Grime & Hunt 1975) and seedlings need to be able to establish despite dense vegetation cover (Poschlod *et al.* 2013).

Among all EIVs, N-numbers have been examined most extensively for their determinants. We therefore structure this section to parameters related to germination, to growth and to roots.

Seed weight was correlated with N-numbers ($R^2 = 0.50$; $P < 0.05$, $n = 8$) in a study that compared responses of eight grass species originating from different habitats to nutrient regimes (Elberse & Berendse 1993; also see below) and so was the related parameter of 'embryo + endosperm weight' ($R^2 = 0.52$; $P < 0.05$, $n = 8$; see Fig. 3a). However, in a study with annuals, early seedling weight did not significantly correlate with N-numbers ($r = 0.28$, $P = 0.43$; $n = 10$) (Fichtner & Schulze 1992). Possible interpretations here are that small seeds/seedlings are less competitive under more fertile conditions. For annuals, light (open habitats) may be more important than fertility. Next to the mentioned seed ecological parameters, a relation between N-numbers and temperature requirements for germination could be established by a study by Otte, Bissels & Walhardt (2006). In the respective data set of 130 annual arable weeds, species from habitats with high nutrient levels were found to require higher temperatures for germination. Significant correlations for N-numbers were found for 'optimal temperature' (Spearman's $\rho = 0.46$), 'lowest temperature to generate 5% germination' (Spearman's $\rho = 0.35$) and 'highest temperature to allow 5% germination' (Spearman's $\rho = 0.49$). This might be interpreted in the context of gap detection: germination of annuals often requires vegetation gaps or open vegetation. Higher temperatures can serve seeds to detect such gaps (Washitani & Takenaka 1987), since soil surface temperatures in dense vegetation stands usually tend to be lower than in open gaps.

It was also found that seeds respond differently to nitrogen availability, since species with high N-numbers germinated better with high concentrations in their medium, while species with low N-numbers had optimum germination at lower concentrations ($R^2 = 0.27$; $P < 0.05$; $n = 15$) (Wamelink, van Dobben & van der Eerden 1998). The same set-up was used to test for optimum nitrogen concentrations for the formation of leaves (after 2 weeks) and again the optimum concentration was higher with high N-numbers ($R^2 = 0.30$; $P < 0.05$; $n = 15$) (Wamelink, van Dobben & van der Eerden 1998). Relative growth rate (RGR) and related parameters are often considered by studies dealing with determinants of N-numbers. Poorter & Remkes (1990) found a highly significant regression coefficient for N-numbers and RGR in their growth study ($R^2 = 0.56$; $P < 0.001$; $n = 23$; Table 1). The most extensive study on RGR was carried out by Grime & Hunt (1975), who examined 130 species for their maximum RGR in controlled conditions with high resource supply. One hundred and nine of these species could be annotated with N-numbers. The regression ($R^2 = 0.17$; $P < 0.001$; $n = 109$; Fig. 3b) is highly significant, while the regression coefficient also reflects large variation in the data that might be attributable to the fact that the examined species originated from a large range of habitats not only concerning nutrients, but also other environmental factors (Grime & Hunt 1975). Further, in a study by Fichtner & Schulze (1992), it was the responsiveness in RGR to increased nutrient supply (Δ RGR) rather than RGR itself: in 20 species raised on either 0.1 mM or 6.0 mM nitrogen, species with high N-numbers showed high Δ RGR, while in species with low N-numbers, Δ RGR was low ($r = 0.96$; $P < 0.001$; $n = 10$). The same experiment also revealed that species with high N-numbers were more nutrient-demanding to reach their maximum RGR (nutrient concentration necessary to reach 90% of maximum RGR). Species with high N-numbers required significantly higher concentrations ($r = 0.64$; $P < 0.05$; $n = 10$). Put the other way round this also indicates that nitrophytes are nutrient-limited already at higher nutrient concentrations. A similar result was found in a study by Thompson *et al.* (1993), when 36 species were cultivated with full or with 100-fold diluted nutrient solution. With diluted solution, species with low N-numbers reached high percentage of their maximum yield, whereas species with high N-numbers were strongly nutrient-limited and reached only low percentage of their maximum yield ($r = -0.36$; $P < 0.05$; $n = 36$). Similarly, the aforementioned study by Elberse & Berendse (1993) found the difference between fertilized and unfertilized plants to correlate with M-numbers (Spearman's $\rho = 0.89$; $P < 0.001$; $n = 8$). One exception to this line of evidence is presented by Falkengren-Grerup (1998), who derived biomass ratios from plants raised at high or low nitrogen availability and found this ratio not correlating significantly with N-numbers, neither for herbs (Spearman's $\rho = 0.13$; $P = 0.64$; $n = 15$) nor for graminoids (Spearman's $\rho = 0.26$; $P = 0.39$; $n = 13$). Another determinant of

N-numbers related to growth is regrowth after defoliation. This parameter may represent how well a species can respond to grazing or disturbance and was examined for eleven grasses by Bossard & Hillier (1993). Tiller numbers in clipped plants in excess to control plants were originally plotted by the authors to a dominance index. When plotted against N-numbers instead (Fig. 3c), we find that response to defoliation is also a determinant of N-numbers ($R^2 = 0.39$; $P < 0.05$; $n = 11$). Next to RGR-related parameters, especially SLA appears to determine N-numbers. This parameter was also a determinant of R-, M- and L-numbers (Poorter & Remkes 1990; Table 1), which reflects the multiple challenges and tasks for a plant's leaves in their environment. Here, both data from Poorter & Remkes (1990) and Fichtner & Schulze (1992) indicate SLA to significantly correlate with N-numbers ($R^2 = 0.56$; $P < 0.001$; $n = 23$; for the former study, Table 1), ($r = 0.85$; $P < 0.01$; $n = 9$; for the latter study, who presented specific leaf weight = $1/\text{SLA}$). Further but not unambiguous determinants are the related parameters leaf area ratio (LAR) and leaf weight ratio (LWR). These two parameters might be interpreted in quite a similar way, since one calculates leaf area per total plant mass, the other leaf weight per total plant mass. Yet, the data set by Poorter & Remkes (1990) finds LAR to positively correlate with N-numbers ($R^2 = 0.46$; $P < 0.001$; $n = 23$), while Fichtner & Schulze (1992) identify a negative correlation of LWR with N-numbers ($r = -0.88$; $P < 0.001$; $n = 10$). This might be due to differences in experimental conditions, or it might be related to the choice of examined species (92% perennials in Poorter & Remkes (1990), exclusively annual species in Fichtner & Schulze (1992)), but it certainly stresses that these parameters have to be interpreted with caution. Vertical leaf distribution can be related to N-numbers as well. In the experiments by Fichtner & Schulze (1992), four out of five species growing as rosette plants had M-numbers < 5 , while all five species growing as erect plants had M-numbers ≥ 5 . Also, Ellenberg Jr. (1987) showed a strong correlation between plant height of herbaceous species and the N-value.

Some further determinants of N-numbers are related to the root system. These were all identified in the mentioned study by Elberse & Berendse (1993). The root weight ratio (RWR) is the ratio of root biomass to whole-plant biomass. Following field observations, one might expect to find relatively more roots in species with low N-numbers, but to the contrary, species with lower N-numbers have lower RWR ratios (maximum Spearman's $\rho = 0.92$; $P < 0.001$; $n = 8$), and conversely, leaf weight ratio (LWR) is diminished in species with high N-numbers (minimum Spearman's $\rho = -0.84$; $P < 0.01$; $n = 8$). This might be surprising at first; however, some other determinants related to the root are more intuitive: the authors found specific root length (SRL) to correlate with N-numbers (minimum Spearman's $\rho = -0.72$; $P < 0.05$; $n = 8$). Species from nutrient-poor habitats thus have more root length per dry weight and thereby most likely also more

absorbing surface per dry weight to explore the soil. Species with high N-numbers, on the other hand, had high total N-uptake, especially in fertilized treatments (maximum Spearman's $\rho = 0.85$; $P < 0.01$; $n = 8$), indicating that nutrient saturation lies much higher in nitrophytes than in species with low N-numbers. This compilation makes clear that N-numbers are the EIVs best examined for their determinants, most of which are related to plant growth (also see Table 2 for an overview).

L-numbers (light)

EIV for light covers species only growing in deep shadow with 1–30% of full light available (L-number = 1) to species only growing in full light to minimum 50% of full

Table 2. Summarizing overview of determinants of different EIV, with dots indicating that significant correlations were found in reviewed literature and dots in brackets indicating marginal significance of such correlations. Abbreviations are used as in Table 1

Determinant	EIV					
	N	M	R	L	T	C
Allocation and Morphology						
SLA	•	•	•	•		
LAR	•	(•)	•	•		
LWR	•		(•)	(•)		
SWR				(•)		
RWR	•		•			
SRL	•					
Gas volume in petioles		•				
Growth						
Seed weight	•		•			
Weight of embryo + endosperm	•					
Germination speed (t50)			•		•	
Germination temperature requirements	•		•			
RGR	•	•	•	•		
Nutrient demand for maximum RGR	•					
Responsiveness of RGR to nutrients	•					
Yield response to nutrients	•					
Regrowth after defoliation	•					
NAR		•				
Germination response to NH_4NO_3	•					
Leaf formation response to NH_4NO_3	•					
Timing of leaf unfolding /frost resistance						•
Root Parameters						
Rooting depth response to drought		•				
Root/shoot response to drought		•				
Number of adventitious roots in waterlogging		•				
Nutrition and Toxicity						
Capacity to solubilize P			•			
Capacity to solubilize Fe(III)			•			
Tolerance of Fe toxicity			•			
Tolerance of Al toxicity			•			
Preference for either ammonium or nitrate			•			
Total N-uptake	•					
Others						
Genome size		•				

light (L-number = 9). Challenges at low light intensities are that light compensation points need to be exceeded and/or life cycle has to be finished fast enough to allow avoidance of longer periods with insufficient light. Challenges at high light intensities are connected to damage from UV radiation and, when the ratio of photon flux density to photosynthesis is high, danger of photoinhibition. The latter can be especially the case, when photosynthesis is inhibited due to other stresses such as chilling or drought (Demmig-Adams & Adams III 1992).

While knowledge on how plants are adapted to their light conditions is extensive (Givnish 1988; Demmig-Adams & Adams III 1992), correlation analyses of species properties to L-numbers are rare. Possibly, the clearest result comes from seed studies. The aforementioned study by Otte, Bissels & Waldhardt (2006) on annual weeds found a significant negative correlation of seed mass with L-numbers (Spearman's $\rho = -0.30$). Hence, in annuals, heavier seeds are more common in species from more shady habitats. A likely advantage to this might be the stronger support of establishing seedlings when energy demand cannot be covered by photosynthesis alone. In the aforementioned data set by Grime *et al.* (1981), we found L-numbers of perennial grasses to negatively correlate with germination speed (t50, time required to reach 50% of maximum germination, $R^2 = 0.31$; $P < 0.001$; $n = 36$; Fig. 4). A possible biological explanation could be that, similar to the mechanism discussed for T-numbers (see below), habitats with high irradiation intensities are prone to drought so that slow germination increases desiccation risks. Interestingly, a data set by Milberg, Andersson & Thompson (2000) on seed mass and on germination responses to light vs. dark conditions provides no significant correlations with L-numbers ($R^2 = 0.00$ and 0.02 , respectively, $n = 50$, data not shown).

As far as morphological and growth parameters are concerned, we found significant regression coefficients for some different parameters in the aforementioned data set by Poorter & Remkes (1990) (Table 1). Species with high L-numbers have hardy leaves, indicated by low SLA ($R^2 = 0.24$; $P < 0.05$; $n = 23$) and low LAR ($R^2 = 0.32$; $P < 0.05$; $n = 23$), which is in line with textbook knowledge and would likely be even more pronounced in studies including species with L-values < 4 . The possible usefulness of SLA as a determinant of L-numbers is corroborated by a study in a different system. When SLA of tropical species is determined under controlled conditions (Markesteijn & Poorter 2009) and regressed to an index similar to Ellenberg's shading intensity (juvenile crown exposure) in the species native habitats, the result is similar to the above. Hardy leaves (low SLA) are found in species originating from habitats with high light availability and vice versa ($R^2 = 0.20$; $P < 0.001$; $n = 59$). Interestingly, in the data set by Poorter & Remkes (1990), RGR is reduced in species with high L-numbers, indicating that high RGR is disadvantageous in habitats with high light intensities ($R^2 = 0.19$; $P < 0.05$; $n = 23$). While the regression coefficient is rather

low, here, it should be stressed that the range in L-number in that data set is quite restricted (from $L = 4$ to $L = 8$), since the experiment was not originally intended for this purpose. For the sake of completeness, it should be noted that when the aforementioned data set by Grime & Hunt (1975) was analysed with L-numbers, a slightly positive regression coefficient occurred (maximum RGR: $R^2 = 0.05$; $P < 0.05$; $n = 116$ and mean RGR: $R^2 = 0.11$; $P < 0.001$; $n = 116$). Clearly, for L-numbers, more controlled studies are needed to identify the strongest determinants. So far, seed mass, germination speed as well as SLA and possibly RGR could be identified (Table 2), but merely with low regression coefficients and, in the case of RGR, apparently inconsistent results. Studies with species comparisons on light compensation points and their morphological/physiological basis as well as on UV protection including xanthophyll cycle suggest themselves.

T-numbers (temperature)

Ellenberg T-numbers predominantly relate to species occurrence at respective elevations above sea level (lower T-numbers correspond to higher elevations) but additionally also include planar/especially warm habitats in Europe. Low temperature poses multiple challenges to plants: the duration of the frost-free vegetation period becomes shorter in habitats at higher elevation levels. Chilling (mostly frost free) temperatures impact on physiological processes including photosynthesis with impacts on energy supply and photo-oxidative damage (e.g. Larcher 2003). Plants may reduce the latter by adapting the levels of antioxidants or by increasing components of the xanthophyll cycle (Öquist & Huner 2003). Frost temperatures lead to damage by ice crystals. Plants may avoid frost (e.g. by their growth form), delay freezing in their tissue (e.g. by solved substances) or tolerate freezing (Larcher 2003). Freezing tolerance in herbaceous species builds up over the course of longer periods with chilling temperatures by the accumulation of carbohydrates (e.g. Chen & Li 1980). In woody species, the build-up of frost resistance consists of multiple phases responding to chilling and first frost events and involves alterations in carbohydrate concentrations, vacuole structures and membranes as well as enzymes (Larcher 2003). High temperatures pose another set of challenges to plants: in the cytosol, physiological temperatures need to be maintained to avoid damage to proteins and membranes, for example by transpiration cooling; at the same time, plants run a desiccation risk. In addition, heat-shock proteins may be formed, which is a highly adaptive process (Vierling 1991).

Rosbakh & Poschlod (2015) found a strong correlation between initial temperature of seed germination (T_{min}) and the mean annual temperature (MAT) at the site of seed collection ($R^2 = 0.57$; $P < 0.001$, $n = 49$). The respective collection sites corresponded to the species respective peak occurrence along an elevation gradient from montane to alpine in the Bavarian Alps. Species from colder

habitats had higher T_{\min} s, interpretable as a safety strategy to avoid the risk of late frost. Considering that small T-numbers relate to the elevational gradient (T_4 = (high) montane, T_3 = subalpine, T_2 = alpine, Ellenberg *et al.* 1991), the correlation found by Rosbakh & Poschlod (2015) derives from a similar analysis strategy as advocated in this review, albeit with the more fine-scale MAT instead of T-numbers. In fact, different to the use of fine-scale MAT, the attempt to correlate T_{\min} with actual T-numbers leads to no significant correlation (S. Rosbakh, personal communication).

We found no further data sets that revealed significant correlations of T-numbers with any of the examined parameters. In all likelihood, this is for one part due to the very narrow range of T-numbers in available data, since virtually all reviewed studies include only lowland species. The second likely reason is that the mentioned mechanisms inducing resistance to temperature stress are highly adaptive and therefore complicated to determine. It may well be that the degree to which a plant can adapt, for example by increasing its protective compounds, can be identified as a determinant to the occurrence along a temperature gradient. Large controlled experiments with species representing a broad range of T-numbers would be necessary to examine this hypothesis.

C-numbers (continentality)

Ellenberg C-numbers relate to the distance to the sea in Central Europe, where 'eucontinental' ($C = 9$) represents a species peak distribution at a far distance to the sea and 'euoceanic' ($C = 1$) indicates close proximity to the sea. Continentality steps are related to increasing temperature amplitudes between seasons (cold winters but hot summers in more continental areas) and also to hygric factors (Ellenberg *et al.* 1991). Challenges for plants in more continental habitats are thought to be resistance to severe frost as well as (in the case of wintergreen plants) tolerance of frost desiccation (Walther 1984). The latter occurs, when frozen soil impedes water uptake while leaf temperature already promotes transpiration. Frost resistance is a highly inducible and reversible process (Till 1956), making controlled screening studies with numerous species very complicated. We are aware of merely one data set on frost resistance in herbaceous species with a sufficient range of continentality numbers (from Till 1956). The respective study was not carried out under climate chamber conditions but at the identical outdoor location to infer timing of first leaf unfolding in spring as well as leaf frost resistance of those newly unfolded leaves. C-numbers in herbaceous species correlate with timing of leaf unfolding (Fig. 5a, $R^2 = 0.20$; $P < 0.05$; $n = 26$) as well as with maximum frost resistance of those leaves (Fig. 5b, $R^2 = 0.16$; $P < 0.05$; $n = 26$). It should be noted that there is also strong correlation between the two named determinants ($r = 0.78$; $P < 0.001$; $n = 26$). Hence, it appears that frost resistance (and/or the connected ability to unfold leaves in

relatively cold conditions) can in fact be identified as a determinant of C-numbers.

Conclusions

The outlined analyses make clear that numerous determinants can be found for some, but not all of the different EIVs (also see Table 2). In particular, in N - and R -values, there are more determinants than might be expected (e.g. 16 for N -numbers). While these high number might in part stem from examined parameters being very similar or related (such as LAR and LWR), there is clearly some ecological relevance involved, here. Not unexpectedly, this finding of multiple determinants implies that there is a syndrome of properties rather than one single plant property that allows peak occurrence in a certain habitat. In connection with the concept of environmental filtering (e.g. Keddy 1992), this leads to an interesting point. For simplification, this concept is usually illustrated with just a few levels of filters, selecting only well-adapted species. However, considering how many plant properties are significant determinants of one EIV, or even more than one of them, we need to be aware that environmental filtering includes a multitude of filter levels. For instance, determinants of R -numbers include tolerance to Al and Fe toxicity, preference for either ammonium or nitrate, as well as SLA and RGR. All of these determinants had high regression or correlation coefficients. Though one needs to be cautious not to overinterpret the mere magnitude of regression coefficients (we found R^2 -values tending to be smaller in data sets with more species, likely due to higher total variation), these plant properties might be seen as 'indispensable' determinants; that is, they are subject to environmental filtering. A number of other plant properties might be seen as 'accessory' determinants that might have evolved to provide additional advantages once a species was established in a habitat.

Controlled experiments with species covering vast ranges of environmental factors were found to provide a useful tool to functionally underpin EIVs. The functional background of EIV should provide additional information, for instance when used for the interpretation of vegetation processes. This possibility is all the more remarkable, since the inclusion of EIV in research studies has received impressive increase in popularity (Table 3). The number of studies hit by the search engine 'Web of Knowledge v. 5.16.1' with the search terms 'Ellenberg number 'OR' Ellenberg indicator value' was 277 in the period from 2010 to 2014. Some 25 years earlier (period from 1985 to 1989), merely 20 studies were hit.

It is also informative to consider individual determinants in terms of how universally they may serve as determinants of various EIVs. Some are determinants of one particular EIV only (like gas volume in petioles), while other properties were found to be determinants of more than one EIV (Table 2). The analysis of data from Poorter & Remkes (1990) has now revealed that RGR correlates with four

Table 3. Time course of number of studies listed by the 'Web of Knowledge v.5.16.1' search engine when the search terms 'Ellenberg number OR Ellenberg indicator value' are used in the 'Topic' field

Time period (Gregorian years)	1985	1990	1995	2000	2005	2010
	1989	1994	1999	2004	2009	2014
Number of hits	20	34	58	120	164	277

different EIVs simultaneously, and the same is the case for SLA and LAR. The principle behind this is known from Lepš, Osbornová & Rejmánek (1982) and MacGillivray, Grime & Team (1995) and here receives statistical confirmation: low RGR allows for low rates of nutrient turnover as well as for long-lived organs, which can be advantageous under various kinds of stress. Likewise, low SLA is advantageous under situations of high irradiation, low nutrient availability, drought and soil acidity. The method of correlating species properties to EIV allows defining possible determinants to species peak distribution along environmental gradients. It also allows a more functional characterization of the different EIVs and makes us understand the mechanisms and processes driving the ecological niche of a plant. It transpires that correlation of ecophysiological characteristics assessed for a range of species with their EIVs is a powerful tool to analyse the ecological significance of this characteristic. The explanatory power of future studies could largely profit from set-ups being designed for this purpose.

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Data accessibility

The data presented in this article have come from other studies which should be treated as the primary source with respect to issues of data access.

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