Carpenter, William S ORCID logoORCID: https://orcid.org/0009-0001-9031-5561 and Goodenough, Anne E ORCID logoORCID: https://orcid.org/0000-0002-7662-6670 (2014) How robust are community-based plant bioindicators? Empirical testing of the relationship between Ellenberg values and direct environmental measures in woodland communities. Community Ecology, 15 (1). pp. 1-11. doi:10.1556/ComEc.15.2014.1.1

Official URL: http://dx.doi.org/10.1556/ComEc.15.2014.1.1
DOI: http://dx.doi.org/10.1556/ComEc.15.2014.1.1
EPrint URI: https://eprints.glos.ac.uk/id/eprint/3355

This is a peer-reviewed, post-print (final draft post-refereeing) version of the following published document:

Carpenter, W and Goodenough, Anne E (2014). ***How robust are community-based plant bioindicators? Empirical testing of the relationship between Ellenberg values and direct environmental measures in woodland communities.*** **Community Ecology, 15 (1), 1-11. ISSN 1585-8553**

Published in Community Ecology, and available online at:

http://www.akademiai.com/doi/abs/10.1556/ComEc.15.2014.1.1

We recommend you cite the published (post-print) version.

The URL for the published version is http://dx.doi.org/10.1556/ComEc.15.2014.1.1

Disclaimer

The University of Gloucestershire has obtained warranties from all depositors as to their title in the material deposited and as to their right to deposit such material.

The University of Gloucestershire makes no representation or warranties of commercial utility, title, or fitness for a particular purpose or any other warranty, express or implied in respect of any material deposited.

The University of Gloucestershire makes no representation that the use of the materials will not infringe any patent, copyright, trademark or other property or proprietary rights.

The University of Gloucestershire accepts no liability for any infringement of intellectual property rights in any material deposited but will remove such material from public view pending investigation in the event of an allegation of any such infringement.

PLEASE SCROLL DOWN FOR TEXT

How robust are community-based plant bioindicators? Empirical testing of the relationship between Ellenberg values and direct environmental measures in woodland communities

William Carpenter and Anne E. Goodenough*

School of Natural and Social Sciences, University of Gloucestershire, Cheltenham, UK

* Corresponding author
Anne Goodenough
Francis Close Hall Campus
University of Gloucestershire
Swindon Road
Cheltenham
Gloucestershire
GL50 4AZ UK
aegoodenough@glos.ac.uk

Abstract

There are several community-based bioindicator systems that use species presence or abundance data as proxies for environmental variables. One example is the Ellenberg system, whereby vegetation data are used to estimate environmental soil conditions. Despite widespread use of Ellenberg values in ecological research, the correlation between bioindicated values and actual values is often an implicit assumption rather than based on empirical evidence. Here, we correlate unadjusted and UK-adjusted Ellenberg values for soil moisture, pH, and nitrate in relation to direct environmental measures for 50 woodland sites in the UK, which were subject to repeat sampling. Our results show the accuracy of Ellenberg values is parameter specific; pH values were a good proxy for direct environmental measures but this was not true for soil moisture, when relationships were weak and non-significant. For nitrates, there were important seasonal differences, with a strong positive logarithmic relationship in the spring but a non-significant (and negative) correlation in summer. The UK-adjusted values were better than, or equivalent to, Ellenberg's original ones, which had been quantified originally for Central Europe, in all cases. Somewhat surprisingly, unweighted values correlated with direct environmental measures better than did abundance-weighted ones. This suggests that the presence of rare plants can be highly important in accurate quantification of soil parameters and we recommend using an unweighted approach. However, site profiles created only using rare plants were inferior to profiles based on the whole plant community and thus cannot be used in isolation. We conclude that, for pH and nitrates, the Ellenberg system provides a useful estimate of actual conditions, but recalibration of moisture values should be considered along with the effect of seasonality on the efficacy of the system.

Keywords: vegetation, soil parameters, bioindication, pH, nitrate, moisture

Introduction

Relationships between species and abiotic environmental variables are usually quantified to provide insights into distribution patterns (e.g. Jones, 2001) and spatial differences in species interactions (e.g. Fagan *et al*., 1999), or to inform ecological management (e.g. Thomas *et al*., 1998; Bailey and Thompson, 2009). However, quantification of species-environment relationships also allows opportunities for bioindication. Bioindication is based on organisms having a specific tolerance for multiple environmental parameters. Once tolerance ranges are known, it is possible to use species presence or abundance as a proxy indicator for environmental conditions (Johnson *et al*., 1993; Diekmann, 2003). Bioindicators are advantageous in that data can: (1) often be gathered quickly and without specialist equipment (Cullen 1990; Wamelink *et al*., 2005); (2) supplement laboratory data and provide a long-term insight into environmental parameters rather than the “snapshot” provided by chemical/physical testing (Keeler and McLemore, 1996; Holt and Miller, 2011); and (3) demonstrate effects of an environmental parameter, or change therein, on biota directly (rather than this needing to be quantified separately) (Landres *et al*., 1988).

Given these advantages, numerous bioindicator systems are in use globally, spanning many different environments and utilising many different taxonomic groups. Some systems rely on single species indicators, for example, the plant *Astragalus racemosus* for selenium concentration (Trelease and Trelease, 1938) and the bryophyte *Hylocomium splendens* for heavy metal pollution (Hasselbach *et al*., 2005). However, the majority of indicator systems use community-based approaches whereby the presence (and sometimes abundance) of multiple species is taken into account. These community indices are often more robust than single-species indicators as they combine information from multiple species (Dale and Beyeler, 2001; Diekmann, 2003; Wamelink *et al*., 2005). Examples of community-based biomonitoring systems include the use of aquatic macroinvertebrates as indicators of dissolved oxygen (reviewed by Hawkes, 1998), use of lichens to monitor air quality (reviewed by Conti and Cecchetti, 2001), and use of arthropod community to assess soil acidity (van Straalen and Verhoef, 1997).

Plants are tightly constrained by climatic and edaphic factors (Ter Braak and Gremmen, 1987), and plant communities therefore have the potential to be proxies for specific environmental parameters. Several community-based indices have been developed, for example, Zolyomi *et al*. (1967) in Hungary, Landolt (1977) in Switzerland and Bohling *et al*. (2002) in Greece. However, over the last three decades, one indicator system – that developed by Ellenberg (1974) & Ellenberg *et al*. (1992) – has become especially well used, largely because of its comprehensiveness and flexibility. The system comprises values for 2,726 central European vascular plants, with respect to light availability (*L*), soil moisture (*F*), soil fertility (*N*), temperature (*T*), soil reaction pH (*R*), continentality of climate (*K*) and salinity (*S*) (Diekmann, 2003). For all parameters, plants have values indicating the position along the specific environmental gradient at which each, on average, reaches peak probability of occurrence (Smart, 2000; Wamelink *et al*., 2005; Appendix S1). As Ellenberg values were designed originally for use in central Europe, their use elsewhere usually requires location-specific recalibration (previously undertaken for Russia (Maslov, 1996), Italy

(Celesti-Grapow *et al*., 1993), France (Thimonier *et al*., 1994), Estonia (Partel *et al*., 1996; 1999), the Faroe Islands (Lawesson *et al*., 2003) and Great Britain (Hill *et al*., 1999, 2004)). This is important since the reliability of values is likely to be inversely related to distance from initial location, both because species adapt to local conditions (van der Maarel, 1993) and because the ecological optima of specific species depends upon competitor species, which themselves differ spatially (Thompson *et al*., 1993). Indeed Diekmann (2003) notes that recalibration of indicator values for new areas always results in a more reliable system compared to simply using unadjusted values, even where species are very similar. In the UK, recalibration involved comparing original Ellenberg value for a given species to the mean values of species with which it frequently co-occurs in a UK context. Co-occurrence was determined using quadrat data in Barr *et al*. (1993) and species association tables in Rodwell (1991a, 1991b, 1992, 1995). Values were adjusted using a complex algorithm utilising two-way weighted averaging followed by local regression (Hill *et al*., 1999; 2000), which essentially modified values for individual species based on values of co-occurring species (i.e. decreasing the moisture value of species A if co-occurring plants in the UK all have lower values). Information from other published sources on use of plant bioindicators in a UK contest was used where appropriate – for example Palmer *et al*. (1992) for pH in aquatic environments. In cases where there was a large discrepancy between original and recalibrated values, the new value was accepted only after consultation with experts or based on field experience. Original and recalibrated values were highly correlated, especially for soil parameters (Hill *et a*l., 2000).

In order for any community-based bioindicator system, including Ellenberg's, to be used meaningfully and with confidence, there needs to be a strong positive correlation between bioindicated parameters and the actual parameters themselves (Chase *et al*., 2000; McGeoch *et al*., 2002; Smart and Scott, 2004). Worryingly, despite widespread use of Ellenberg values in ecological and environmental research (e.g. Persson 1980; Wittig and Durwen, 1982; Latour *et al*. 1994; Möller 1997; Bunce *et al*., 1999; Ewald, 2000; Smart 2000; Godefroid, 2001; Ling, 2003; Fanelli *et al*., 2006), this correlation is often an implicit assumption rather than being based on empirical evidence. While some work has been done on the robustness of the Ellenberg system, studies have generally focussed upon the relationship with other indicator systems (e.g. Godefroid and Dana, 2007) or the internal consistency in the Ellenberg system by comparing indicator values for species that co-occur (Ter Braak and Gremmen, 1987; Hawkes *et al*., 1997). Somewhat surprisingly, relatively few studies have compared Ellenberg values to actual parameters. Even where the validity of Ellenberg indicator values has been tested using direct measurements, studies have typically: (1) been undertaken using direct environmental measures from just one time period, such that the comparison between these and Ellenberg values might have been compromised by their "snapshot" context (Wilson *et al*., 2001); (2) analysed sites with different habitats in the same analysis, which, according to Ellenberg *et al.* (1992) and Wamelink *et al.* (2002) could seriously bias results (e.g. Ertsen *et al*., 1998; Fanelli *et al*., 2007); (3) have only considered one parameter in isolation from others, such that it is not possible to compare the "fit" between

Ellenberg values and measured values for different environmental variables simultaneously (e.g. Lawesson, 2003); or (4) have only considered a subset of the plant species present (e.g. Hawkes *et al*., 1997). The main detailed studies that have been undertaken have taken place outside of the UK, for example, in Sweden (Diekmann, 1995) and the Netherlands (Schaffers and Sykora, 2000) have given conflicting results as regards the strength of any correlation between Ellenberg and direct measurements for specific environmental parameters. Further studies to quantify the relationship between Ellenberg values and actual measured values are necessary to establish the robustness of Ellenberg values and how the correlation between proxy and actual values can be increased.

In this paper, we provide a detailed comparison between community-derived bioindicator values for moisture, pH and fertility (nitrate) levels using both unadjusted Ellenberg values (Ellenberg *et al*., 1992) and values adjusted for the UK by Hill *et al*. (1999) in relation to direct measures for the same parameters established using laboratory procedures. Our research is based on 50 woodland sites in the UK, which were subject to repeat sampling to avoid the direct environmental measures being a “snapshot” relative to the Ellenberg values and to establish how the relationship between bioindicated values and direct measures might differ seasonally, which has not hitherto been considered. Moreover, this is, to our knowledge, the first time that Ellenberg values for all three soil parameters have been assessed concurrently within woodland communities (other than in the pilot study of Hawkes *et al*., 1997) and the first time that Hill-adjusted values have been correlated with measured parameters in any habitat. Finally, because it has been suggested previously that an unweighted mean (i.e. a mean that take no account of the relative abundance of each plant species) is flawed given that species usually differ in dominance (Hawkes *et al*., 1997; Schaffers and Sykora, 2000), we also address the question of whether it is better to use parameter-specific, site-specific, values that have been generated using an unweighted mean or a weighted mean.

Methods

Study Sites

This study took place during 2011 in Gloucestershire, a county district in the southwest of the United Kingdom centred on 51°46'N 02°15'W. The area has mild-temperate climate (annual mean temperatures around 9°C and 800mm/yr precipitation with considerable intra-annual variation; Met Office, 2012) and a climatic climax vegetation community of *Quercus* spp. woodland.

To obtain 50 random woodland sites within Gloucestershire, the grid references corresponding to the northern, southern, western and eastern county boundaries were defined and a random number generator was used to provide coordinates within this area centred upon woodland habitat and where access was possible (landowner permission had been granted). Of the 50 randomly-selected sites, the majority were mature and relatively unmanaged (i.e. not plantations, under commercial silviculture, or subject to thinning or selective tree removal); six sites had been managed previously with evidence of tree thinning more than a decade before this study. The sites varied both geologically and topographically and were spread across Gloucestershire to give long gradients for the environmental variables (a frequent oversight in this type of study; Diekmann, 2003).Most sites were located on sedimentary substrata, primarily oolitic limestone (42%), sandstone (22%), Carboniferous limestone (some coal bearing) (18%), and mudstone (10%). The remaining 8% of sites were located on shale or glacial deposits. Site elevation ranged from 25 m to 280 m above sea level, while slope angle varied between 0° and ~35°.

Vegetation data

At each site, a 10m x 10m plot was laid out centred upon the actual coordinates (Sutherland, 2006). All trees and shrubs, as well as vascular ground plants in the field and herb layers, were identified. Species' abundance was recorded using the numerical Braun-Blanquet scale, which is based on defined percentage cover bands (Chytry and Otypkova, 2003). This scale is recommended for studies of species-environment interactions and it is used extensively throughout Europe (Leps and Hadincova, 1992; Chytry and Otypkova, 2003) and the USA (Wikum and Shanholtzer, 1978) because it is both quick and accurate. Both of the previous detailed studies that related Ellenberg values to direct environmental measures (Diekmann 1995; Schaffers and Sykora, 2000) quantified vegetation in this way. Moreover, for reasonably large sample plots (as here), use of Braun-Blanquet is less likely to generate inaccuracies than a finer resolution scale (e.g. cover in 5% bands), when assigning species to the correct band reliably becomes problematic.

There was substantial heterogeneity in the plant communities between the sites: in total 22 woody species were located (including, in order of prevalence, *Fagus sylvatica, Corylus avellana*, *Quercus robur*, *Fraxinus excelsior*, *Acer pseudoplatanus*, *Betula pendula*. A total of 50 non-woody vascular plants was represented (including, in order of prevalence, *Hyacinthoides non-scripta*, *Urtica dioica*, *Anemone nemorosa, Rumex sanguineus*, *Mercurialis perennis*. Each site was surveyed twice, once during the spring (May 2011) and once during the summer (July 2011).

Soil data

A soil sample was obtained from the top of the A horizon in the centre of the plot (as per Hawkes *et al*., 1997). There was very little variability in sample depth between sites, with samples being taken at 10 cm ± 1 cm in all cases. The soil sample was placed in a plastic bag, sealed with as little air as possible, and placed in a cool-box to keep the samples in a cool and dark environment in the field before they were transferred to a fridge at a constant 4°C for a maximum of three days until analysis. To allow for seasonal variation in soil parameters, soil samples were collected from the sample location at each site twice, once during the spring (May 2011) and once during the summer (July 2011).

All laboratory protocols followed Radojevic and Bashkin (2006). To quantify soil moisture content, a sample of each soil was weighed, dried for 24 hours at 105°C and re-weighed. The pH of each sample was obtained by adding deionised water to each soil sample at a ratio of 10:1 (w/v) and agitating the sample using a magnetic flea before allowing it to settle for 30 minutes. The electrode of a digital pH meter (HI 991300, HANNA Instruments, Leighton Buzzard, UK) was then placed in the supernatant and a reading taken. The pH meter was never allowed to come in contact with the settled soil particles during testing and was recalibrated periodically between samples. Quantifying ‘fertility’ was more problematic. Ellenberg *et al*. (1992) loosely defined the fertility values as indicating the amount of nitrogen available during the growing season, but added that the values may also be interpreted as indicating the general nutrient supply. There are many different ways of measuring nitrogen and at least 10 measures, including nitrate, ammonia, nitrification rate, nitrification ratio, mineralization, and plant tissue nitrogen load, have been related to indicator values previously (review by Diekmann, 2003). We quantified nitrate as a proxy for fertility because this has been found previously to correlate the best with Ellenberg values in the Netherlands (Schaffers and Sykora, 2000). Nitrate levels of each soil sample were obtained by preparing each sample as per Radojevic and Bashkin (2006), then using an AutoAnalyser (Sampler 5 system, Bran & Luebbe, Germany) to obtain a nitrate measurement in parts per million (equivalent to mg/kg).

Bioindicator values

Post fieldwork, indicator values were calculated using the vegetation data for the three parameters under consideration (soil moisture, soil pH and soil fertility) using firstly unadjusted Ellenberg values (Ellenberg *et al*., 1992) and secondly the indicator values adjusted for use in the UK by Hill *et al*. (1999). For both schemes, and for each of the three parameters, an unweighted mean was calculated by averaging the indicator scores for all species on a site-specific basis regardless of their relative abundance at that site. Because it has been suggested previously that this unweighted mean is flawed (see above), an abundance-weighted mean was also calculated for each parameter, again on a site-specific basis, using the numerical Braun-Blanquet scale, to establish whether this correlated better with measured parameters (Hill and Carey, 1997). This was done in addition to, rather than instead of, the unweighted mean method, since this has been advocated over the abundance-weighted approach in other studies (Diekmann, 1995). In all cases, a site profile was created firstly using all plant species and secondly using only non-woody vascular species. This was done to establish whether the bioindicated value for a site derived from quick-growing, often seasonal, non-woody species correlated better with direct environmental measures than a bioindicator value based on all species because the former would likely have a reduced lag-time effect. Because non-woody vascular species were also more shallow-rooted, and soil samples were taken from the A horizon, this also ensured that any weak correlations were not an artefact of sampling soils at a different depth from that at which the plant species were rooted. When indictor values were not provided for specific species, these were excluded as per the protocol of Hawkes *et al*. (1997).

Statistical analysis

To determine whether there was a significant difference in site profiles depending on whether Ellenberg's original values or Hill's UK-adjusted values were used, a paired-samples t-test was used. Separate analyses were conducted for moisture, pH, and nitrates. Then, to establish to what extent site profiles generated using the Ellenberg and Hill systems related to site-specific measured values, regression analysis was used. In all cases, separate analyses were undertaken for each of the environmental parameters (soil moisture, pH and nitrates) and for unweighted and abundance-weighted versions of the two indicator systems. Regression was deemed appropriate because although the plant-specific indicator values were actually ordinal, averaging species-specific values to generate a site profile (unweighted or weighted) generated a continuous variable since the averages were not restricted to integer values. Moreover, the data fulfilled all other parametric criteria, being homoscedastic and with normally distributed residuals based on visual evaluation of Q-Q plots. This approach, and a similar rationale, has been used in similar studies (Diekmann, 1995; Schaffers, and Sykora, 2000; Wamelink *et al*., 2002). Because the relationship between indicator values and direct environmental measurements can be non-linear (Diekmann, 1995; Schaffers, and Sykora, 2000), and non-linear relationships were identified here by inspection of scatterplots (Fig. 1 and 2), we used both linear and curvilinear regression approaches. In all cases, the best model (highest r^2, lowest P) was identified and reported. Curvilinear regression was adopted rather than rank-order correlation since: (1) non-linear relationships were logarithmic rather than monotonic; (2) this approach has been used before in studies relating Ellenberg values to environmental conditions (Diekmann, 2003); and (3) models created with linear and curvilinear regression are directly comparable, thereby allowing meaningful comparisons between environmental parameters (in this study) and between countries (comparing this study with others). Finally, to establish whether reliable site profiles could be generated using rare species alone, we repeated the main regression analyses after site profiles had been generated based only upon species with <25% cover. The <25% demarcation was selected since reducing this any further, and thereby generating a profile based on only really rare species, meant that a large number of sites (36 out of 50) had to be excluded. All analyses were conducted in SPSS version 19.

Results

Differences between bioindicator systems

There was a significant difference in site profiles for all three environmental parameters depending on whether original Ellenberg or adjusted Hill values were used. This was true regardless of whether site profiles were generated using unweighted data (paired-samples t-tests: moisture t = 3.351, p = 0.002; pH t = -6.887, p < 0.001; fertility t = 4.032, p < 0.001) or using an abundance-weighted approach (moisture t = 3.051, p = 0.004; pH t = -5.864, p < 0.001; fertility t = 3.495, p = 0.001) (d.f. = 49). The results remained unchanged in all cases when only field layer species (i.e. not trees and shrubs) were analysed (results not shown).

Relationship between bioindicated values and direct environmental measures

Generally, there were significant relationships between site profiles based on an assessment of plant species using the Ellenberg and Hill indicator systems and direct environmental measurements as derived from laboratory analysis (Table 1; Figs 1 and 2). The relationship was good for pH (average r^2 = 0.371) and reasonable for nitrates (average r^2 = 0.189). There was no correlation between moisture bioindicator values and direct environmental measurements (all tests non-significant; average r^2 = 0.007). Relationships were fairly similar for spring and summer sampling periods (and the average of these) in most cases (Fig 1 and 2 and statistical results thereon). The exception was nitrates, when the correlations for the summer period were non-significant (and actually negative). This was in contrast to the positive correlation that was both expected and seen during the spring period (Fig. 1f, 2f). When only considering analyses with significant – and positive – correlations (spring analyses), average model fit increased substantially compared to all analyses combined (average r^2 = 0.270 versus r^2 = 0.189, respectively). To investigate this further, a paired-samples t-test was undertaken on direct environmental measurement of nitrate level for the spring and summer periods. This confirmed that nitrate levels were significantly lower on a per-site basis later in the year (spring mean = 2.255 mg/kg (± 0.258 se); summer mean = 1.361 mg/kg (± 0.100 se); t = 3.039, d.f. = 49, P = 0.004). There was no difference in the significance of any of these findings when only non-woody (field layer) species were included in analyses (results not shown), suggesting that these results are not affected by the lag time inherent for slow-growing woody species or the fact that soils were only sampled from the A horizon. Likewise, there was no change in the significance of any results when analyses were re-run following removal of managed woodland sites from the data set. However, because so few sites were either currently or recently previously managed (n = 6), this was not unexpected.

All relationships were best described by linear equations except for those for nitrates, when curvilinear regression fitting a logarithmic curve generated a better model (higher r^2 and lower P compared to linear models) (Table 1, Fig. 1 and 2). This was the case for all nitrate analyses except those based on data from the summer period when a non-intuitive negative correlation resulted (see above). In all other cases, linear models were superior. A couple of other general patterns emerged. Firstly, Hill's UK-adjusted bioindicator values either correlated better (higher r^2; lower P) with direct environmental measures than did Ellenberg's original values quantified for central Europe (moisture and pH), or were very similar (nitrate) (Table 1; Fig. 3), confirming the importance of using recalibrated values outside of the original geographic area. Secondly, regardless of whether Ellenberg or Hill-adjusted values were used, unweighted data correlated better with direct environmental measures than when data were weighted by plant abundance, suggesting that presence-only data were actually a better proxy for the environmental parameters than abundance-weighted data (Table 1; Fig. 3). However, repeating the main regression analyses after site profiles had been generated based only upon the rare plant species (defined as those with <25% cover) resulted in models that were substantially poorer than those based on the full community, regardless of whether a weighted or unweighted approach was used in the community analyses (Table 2). Indeed, in the case of moisture, the relationship between indicator profiles and direct measurements became non-significant when only data on rare species was used (Table 2).

Discussion

The results of our study show that within UK woodland: (1) the efficacy of plant community bioindicator values is parameter specific (good proxy for pH, reasonable proxy for nitrates overall (although there were important seasonal differences), but a poor proxy for soil moisture); (2) Hill's adjusted values are better than Ellenberg's original ones for UK woodland; and (3) that unweighted values correlate with direct environmental measures better than do abundance-weighted ones.

Relationship between bioindicated and direct environmental measures

The strength of the relationship between bioindicator values and direct environmental measurements is parameter specific. Values correlate particularly well for pH, possibly because species have narrower tolerance ranges for pH than for other environmental parameters. This is supported by lower variability between plant-specific indicator values on a per-site basis for pH than occurs for other parameters (see below). As regards nitrates, there are strong relationships between bioindicated and direct measurements in spring but not in summer. This, coupled with the fact that nitrate levels are significantly higher on a plot-by-plot basis in spring compared to summer, suggests that indicator values are proxies for annual nitrate maxima (i.e. the amount in spring before it is transferred to biomass of seasonal plants) rather than annual minima or the average. This would be an interesting avenue for future research, especially if ammonia (also used by plants) was quantified alongside nitrate. The lack of relationship between indicator values and direct moisture measurements agrees with research on woodlands in the North of the UK by Hawkes *et al*. (1997), which noted variability in Ellenberg values for co-occurring species (also reported by Major and Rejmanek (1992)). In our study, *Ranunculus repens*, which has an Ellenberg moisture value of 10 (indicating waterlogged soil), co-occurred in all cases with *Pteridium aquilinum* and in 83% of cases with *Corylus avellana*, both of which have a moisture value of 5 (indicating moderate moisture). Although soil moisture is the most variable of the three soil parameters considered here, some reanalysis Ellenberg/Hill moisture values might be advantageous.

It is worth noting that none of the correlations are very strong – the highest r^2 value (unweighted Hill values for pH) was 0.549 – such that in almost all cases the indictor values explained <50% of the variability in direct measurements. Although it is possible that stronger relationships might be identified if a wider range of abiotic environments were studied (i.e. if the environmental gradients were longer), there are several reasons to suppose that the assumed strong positive relationship between indicator and actual parameter might not always occur. Firstly, each individual species has a single indicator value – the hypothetical optimum of the species (Wamelink *et al*., 2005) – despite the fact that species typically occur over a tolerance range, the width of which varies species-specifically. Species tolerance ranges also differ spatially due to spatial genetic variation within species (Bocker *et al*., 1983), and can shift geographically over time (Dierschke, 1994), as well as in relation to changes in community dynamics (Diekmann and Lawesson, 1999). Secondly, Ellenberg values (and values in most Ellenberg-derived systems, including Hill's) are based on expert knowledge, with only a minor part being based on actual field measurements. Thus, although they should correlate with actual conditions – indeed this is the whole premise on which the system is based – It is perhaps unreasonable to assume that the correlation will be near-perfect and this is an inherent weakness of the system (Wamelink *et al*., 2002). Indeed, many authors, including Ellenberg, have stressed that indicator values allow for only quick estimates of environmental conditions and cannot replace field measurements (Ellenberg, 1974; Dzwonko, 2001). Finally, autocorrelation of different abiotic factors might also be problematic. For example, Diekmann (2003) found that light and soil pH are often negatively correlated in forests, such that a site profile for, say, soil pH is shifted not because of a change in actual site pH, but because light levels become limiting as a result of inter-correlated abiotic conditions (Smart and Scott, 2004; Verheyen *et al*., 2012).

For indicator systems to work effectively, the environment must be stable. Plants often lag behind change in environmental parameters, such that it may take years before abiotic change is visible in plant species assemblage (Witte *et al*., 2004). Conversely, one event might have a disproportionate effect; for example, the impact of one dry season may be visible in species composition for many years (Wamelink *et al*., 2005). Species that are either a relic of former conditions or a recent colonist might not make good indicators (Witte *et al*., 2004). This is demonstrated by research by Dzwonko and Loster (1992) and Dzwonko (1993, 2001), which showed that Ellenberg indicator values are good predictors of the environment in ancient woodlands, but much poorer indicators in recent woodlands. Indeed, Dzwonko (2001) showed Ellenberg indicator values correlate only weakly with soil parameters (pH and nitrates) in woodland <70 years old since, until this point, the environment is not floristically stable. This is due in part to ecological succession, coupled with wind-dispersed species being over-represented in relatively recent woodland (Dzwonko and Loster, 1992; Dzwonko, 1993). In this study, however, there was no change in the indicator accuracy once the few currently/recently managed woodlands (n = 6 out of 50) were experimentally removed from analyses. Moreover, correlations between Ellenberg/Hill site profiles and direct measurements were very similar regardless of whether slow-growing woody species were included. Taken together, this suggests that lag time is not a major bias here (and, by extension, suggests lag times at other sites could further reduce the relationship between bioindicated and directly-measured conditions).

Ellenberg *versus* Hill

There were significant differences in the site profiles generated using the Ellenberg and Hill indicator systems, which led to differences in the strength of the correlation between bioindicated and directly-measured values between systems. Correlations between direct environmental measures and indicator profiles were generally weaker when using Ellenberg's original values (formulated for use in

Central Europe: Ellenberg 1974; Ellenberg *et al*. 1992) than when using Hill’s values (adjusted specifically for use in the UK: Hill *et al*., 1999, 2004). This underlines the importance of using regionally-recalibrated values, as highlighted previously by Diekmann (2003), and possibly stems from species having different tolerance ranges in different geographical areas (van der Maarel, 1993) and/or because the ecological optima of specific species depends upon competitor species (Thompson *et al*., 1993). The increase in model fit between using Hill’s values rather than Ellenberg’s was especially high in the case of pH, possibly because the relationship between plants and the pH optima is highly variable spatially.

Unweighted *versus* abundance-weighted approaches

Several studies have suggested that the strictly arithmetic approach of averaging the indicator values of all plant species at a particular site for a given environmental parameter is flawed, given that species are not generally uniformly abundant. Accordingly, it has been suggested that weighting the mean by the abundance of each species in the community might be more biologically meaningful (e.g. Hawkes *et al*., 1997; Schaffers, and Sykora, 2000). This has been advocated over the use of medians (which might be considered to be technically more correct given the ordinal nature of the indicator variables: Kowarik and Seidling, 1989; Seidling and Fischer, 2008) because of the lack of precision that can result from the course scales involved (Smart and Scott, 2004). For our study sites, there was generally a better correlation between direct environmental measures and unweighted indicator values, rather than those weighted by plant abundance, regardless of which indicator system was used. This agrees with Diekmann (1995), who reported similar results in deciduous woodlands in Sweden for both pH and moisture. However, although use of unweighted data was consistently better than abundance-weighted data, the differences in model fit were relatively small for nitrates and moisture. This agrees a review by Diekmann (2003), which concluded that results from presence-absence (unweighted) data compared to those from abundance-weighted data generally show little substantive difference. In the case of pH, however, using unweighted values was substantially better. This is interesting given that in one of the very few other studies to compared bioindicator values with actual measurements, Hill and Carey (1997) found the converse at the long-term UK grassland study at Rothamsted Park. This suggests that the most appropriate approach might be habitat-specific and/or affected by local abiotic conditions, such as soil type or species community structure.

The fact that unweighted values are consistently, and in some cases substantially, better than abundance-weighted values in their agreement with actual values, is interesting. It seems counter-intuitive as it suggests that rare plants are important for obtaining a representative community profile and implies that the presence of species occurring at low abundance can be highly informative. Examining the data revealed that no species were found at low abundance across a range of plots; instead rare species were site-specific. One possible explanation is that plants occurring at a low abundance might be recent colonists and therefore might reflect the current conditions of the plot better than established (and abundant) species (Hawkes *et al*., 1997; Ertsen *et al*., 1998). It is worth noting here that there were very few non-native species found during the entire study, so this pattern is not caused by invasion of non-native flora. Alternatively, it is possible that rare species are more specialist in their ecology. Such species would, almost by definition, have a narrower tolerance range and would, therefore, be better proxies for local environmental conditions than generalist species with wide tolerance ranges (Futuyma and Moreno, 1988; Gilchrist, 1995; Kleshcheva, 2010; Marsh and Kaufman, 2012). Specialist species are still frequently outcompeted by generalist species, even when conditions are optimal, so are often rare (Griffith and Sultan, 2012). However, relating site profiles generated only using rare species to direct environmental measures produced inferior models relative to when site profiles were generated based on the entire plant community (using either unweighted or weighted approaches; Tables 1 and 2) This suggests that although the rare species are a vital part of generating a robust and accurate site profile, they are not very informative on their own. An interesting avenue for future research would be to quantify abundance at a finer resolution than the Braun-Blanquet scale (e.g. using DOMIN or 10% cover categories) to establish whether the increased precision from such an approach might make abundance-weighted measures more useful than suggested here.

Recommendations

This study comparing direct field site measurements and bioindicated values, has indicated some issues particularly for soil moisture. We would recommend further validation studies, in a range of terrestrial ecosystems, ideally using more than the two temporal replicates used in the current study. In the meantime, it is recommended that values are only used if they have been recalibrated for the particular region being studies (i.e. using Hill’s recalibrated values rather than Ellenberg’s original values in the case of Great Britain) and that unweighted values are used since these usually given superior correlation with actual values and also have the advantage of being more straightforward to calculate. We therefore conclude that use of bioindicator values can give useful information on local environmental conditions in some situations, especially for pH, but should not be used without caution.

Acknowledgements

We thank two anonymous reviewers for their extremely detailed and helpful feedback on an earlier version of this paper.

References

Bailey, H., and P. Thompson. 2009. Using marine mammal habitat modelling to identify priority conservation zones within a marine protected area. *Mar. Ecol-Prog. Ser*. 378: 279–287.

Barr, C.J., R.G. Bunce, R.T. Clarke, R.M. Fuller, M.T. Furse, M.K. Gillespie, G.B. Groom, C.J. Hallam, M. Hornung, D.C. Howard and M.J. Ness. 1993. *Countryside Survey 1990 Main Report*. HMSO, London.

Bocker, R., I. Kowarik and R. Bornkamm. 1983. Studies to use the indicator values after Ellenberg. *Verh. Ges. Okol*. 11: 35-56.

Bohling, N., W. Greuter and T. Raus. 2002. Indicator values for vascular plants in the Southern Aegean (Greece). *Braun-Blanquetia*. 32: 1–109.

Bunce, R.G.H., S.M. Smart, H.M. van der Poll, J.W. Watkins and W.A. Scott. 1999. EcoFact 2: Measuring Change in British Vegetation. *Centre for Ecology and Hydrology*.

Celesti-Grapow, L., E. Pignatti and S. Pignatti. 1993. Ellenbergs indicator values for ecological assessment of archeological zones in Rome. *Phytocoenologia*. 23: 291-299.

Chase, M.K., W.B. Kristan III, A.J. Lynam, M.V. Price and J.T. Rotenberry. 2000. Single Species as Indicators of Species Richness and Composition in California Coastal Sage Scrub Birds and Small Mammals. *Conserv. Biol*. 14: 474–487.

Chytry, M. and Z. Otypkova. 2003. Plot sizes used for phytosociological sampling of European vegetation. *J. Veg. Sci*. 14: 563-570.

Conti, M.E. and G. Cecchetti. 2001. Biological monitoring: lichens as bioindicators of air pollution assessment—a review. *Environ. Poll*. 114: 471–492.

Cullen, P. 1990. Biomonitoring and environmental management. *Environ. Monit. Assess.* 14: 107-114.

Dale, V.H., and S.C. Beyeler. 2001. Challenges in the development and use of ecological indicators. *Ecol. Indicators*. 1: 3–10.

Diekmann, M. 1995. Use and improvement of Ellenberg's indicator values in deciduous forests of the Boreo-nemoral zone in Sweden. *Ecography*. 18: 178-189.

Diekmann, M. 2003. Species indicator values as an important tool in applied ecology – a review. *Basic Appl. Ecol*. 4: 493-506.

Diekmann, M. and J.E. Lawesson. 1999. Shifts in ecological behaviour of herbaceous forest species along a transect from northern Central to North Europe. *Folia Geobot*. 34: 127-141.

Dierschke, H. 1994. *Ecological indicator values. Plant sociology; Principles and Methods*. Ulmer, Stuttgart.

Dzwonko, Z. 1993. Relations between the floristic composition of isolated young woods and their proximity to ancient woodland. *J. Veg. Sci*. 4: 693-698.

Dzwonko, Z. 2001. Assessment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values. *J. Appl. Ecol*. 38: 942-951.

Dzwonko, Z. and S. Loster. 1992. Species richness and seed dispersal to secondary woods in southern Poland. *J. Biogeogr*. 19: 195-204.

Ellenberg, H. 1974. Indicator values of plants in Central Europe. *Scripta Geobot*. 9: 3-122.

Ellenberg, H., H.E. Weber, R. Dull, V. Wirth, W. Werner and D. Paulissen. 1992. Indicator values of plants in Central Europe. *Scripta Geobot.* 18: 1-248.

Ertsen, A.C.D., J.R.M. Alkemade and M.J. Wassen. 1998. Calibrating Ellenberg indicator values for moisture, acidity, nutrient availability and salinity in the Netherlands. *Plant Ecol*. 135: 113-124.

Ewald, J. 2000. The partial influence of Norway spruce stands on under-storey vegetation in mountain forests of the Bavarian Alps. *Mt. Res. Dev*. 20: 364-371.

Fagan, W.F., R.S. Cantrell and C. Cosner. 1999. How habitat edges change species interactions. *Am. Nat*. 153: 165–182.

Fanelli G., S. Pignatti and A. Testi. 2007. An application case of ecological indicator values (Zeigerwerte) calculated with a simple algorithmic approach. *Plant Bios*. 141: 15-21.

Fanelli, G., P. Tescarollo and A. Testi. 2006. Ecological indicators applied to urban and suburban floras. *Ecol. Ind*. 6: 444 –457.

Futuyma, D.J. and G. Moreno. 1988. The evolution of ecological specialization. *Ann. Rev. Ecol. Syst*. 19: 207-233.

Gilchrist, G.W. 1995. Specialists and generalists in changing environments. 1. Fitness landscapes of thermal sensitivity. *Am. Nat*. 146: 252-270.

Godefroid, S. 2001. Temporal analysis of the Brussels flora as indicator for changing environmental quality. *Landscape Urban Plan*. 52: 203-224.

Godefroid, S. and E.D. Dana. 2007. Can Ellenberg’s indicator values for Mediterranean plants be used outside their region of definition? *J. Biogeogr*. 34: 62-68.

Griffith, T. and S.E.Sultan. 2012. Field-based insights to the evolution of specialization: plasticity and fitness across habitats in a specialist/generalist species pair. *Ecol. and Evol*. 2: 778-791

Hasselbach, L., J.M. Ver Hoef, J. Ford, P. Neitlich, E. Crecelius, S. Berryman, B. Wolk and T. Bohle. 2005. Spatial patterns of cadmium and lead deposition on and adjacent to National Park Service lands near Red Dog Mine, Alaska. *Sci. Tot. Environ*. 348: 211–238.

Hawkes, H.A. 1998. Origin and development of the biological monitoring working party score system. *Water Res*. 32: 3: 964–968.

Hawkes, J.C., D.G. Pyatt and I.M.S. White. 1997. Using Ellenberg indicator values to assess soil quality in British forests from ground vegetation: a pilot study. *J. Appl. Ecol*. 34: 375-387.

Hill, M.O. and P.D. Carey. 1997. Prediction of yield in the Rothamsted Park Grass Experiment by Ellenberg indicator values. *J. Veg. Sci*. 8: 579-586.

Hill, M.O., C.D. Preston and D.B. Roy. 2004. *PLANTATT – attributes of British and Irish plants: status, size, life history, geography and habitats*. Centre for Ecology and Hydrology, Huntingdon, U.K.

Hill, M.O., D.B Roy, J.O. Mountford and R.G Bunce. 2000. Extending Ellenberg's indicator values to a new area: an algorithmic approach. *J. Appl Ecol*. 37: 3-15.

Hill, M.O., J.O. Mountford, D.B. Roy and R.G.H. Bunce. 1999. *Ellenberg's indicator values for British plants. ECOFACT Volume 2 technical annex.* Institute of Terrestrial Ecology, Huntingdon, U.K.

Holt, E.A. and S.W. Miller. 2011. Bioindicators: Using Organisms to Measure Environmental Impacts. *Nat. Ed. Knowl*. 2: 87.

Johnson, R.K., T. Wiederholm and D.M. Rosenberg. 1993. Freshwater biomonitoring using individual organisms, populations, and species assemblages of benthic macroinvertebrates.In: D.M. Rosenberg and V.H. Resh (eds.), *Freshwater biomonitoring and benthic macroinvertebrate*. Chapman and Hall, New York, USA.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. *Auk*. 118: 557-562.

Keeler, A.G and D. McLemore. 1996. The value of incorporating bioindicators in economic approaches to water pollution control. *Ecol. Econ*. 19: 237–245.

Kleshcheva, E.A. 2010. Indicator properties of Southern Siberian plants with respect to soil moisture. *Russ. J. Ecol*. 41: 6: 480-485.

Kowarik, I. and W. Seidling. 1989. Ellenberg indicator value calculations: Problems and limitations. *Landscape and City*. 21: 132-143.

Landolt, E. 1977. Ecological indicator values of Swiss Flora. *Veroff. Geobot. Inst. ETH Stiftung Rubel*. 64: 1–208.

Landres, P.B., J. Verner and J.W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. *Conserv. Biol*. 2: 316–328.

Latour, J.B., R. Reiling and W. Slooff. 1994. Ecological standards for eutrophication and desiccation: perspectives for a risk assessment. *Water Air Soil Poll*. 78: 265-277.

Lawesson, J.E. 2003. pH Optima for Danish forest species compared with Ellenberg reaction values. *Folia Geobot*. 38: 403-418.

Lawesson, J.E., A.M. Fosaa and E. Olsen. 2003. Calibration of Ellenberg indicator values for the Faroe Islands. *Appl. Veg. Sci*. 6: 53-62.

Leps, J. and V. Hadincova. 1992. How reliable are our vegetation analyses? *J. Veg. Sci*. 3: 119-124.

Ling, K. 2003. Using environmental and growth characteristics of plants to detect long-term changes in response to atmospheric pollution: some examples from British beechwoods. *Sci. Total Environ*. 310: 203–210.

Major, J. and M. Rejmanek. 1992. *Amelanchier alnifolia* vegetation in eastern Idaho, USA and its environmental relationships. *Vegetatio*. 98: 141-156.

Marsh, W.M. and M.M. Kaufman. 2012. *Physical Geography: Great Systems and Global Environments*. Cambridge University Press.

Maslov, A. A. 1996. Multi-scaled and multi-species pattern analysis in boreal forest communities. In: F. Krahulec, A. Agnew, S. Agnew and H. Willems (eds.), *Spatial Processes in Plant Communities*. Koeltz Scientific Publishers, Koenigstein, Germany.

McGeoch, M.A., B.J. van Rensburg and A. Botes. 2002. The verification and application of bioindicators: A case study of dung beetles in a savanna ecosystem. *J. Appl. Ecol*. 39: 661-672.

Met Office. Historic climate data. Accessed http://www.metoffice.gov.uk/climate/uk/mi/ (12 February 2012).

Möller, H. 1997. Reaction and nitrogen figures by Ellenberg as indicators of the humus form in terrestrial soils in the Hanover area. *Tuexenia*. 17: 349-365.

Palmer, M.A., S.L Bell and I. Butterfield.1992. A botanical classification of standing waters in Britain: applications for conservation and monitoring. *Aquat. Conserv*. 2: 125–143.

Partel, M., M. Zobel K. Zobel and E. van der Maarel. 1996. The species pool and its relation to species richness: Evidence from Estonian plant communities. *Oikos*. 75: 1: 111-117.

Partel, M., R. Kalamees, M. Zobel and E. Rosen. 1999. Alvar grasslands in Estonia: Variation in species composition and community structure. *J. Veg. Sci*. 10: 4: 561-570.

Persson, S. 1980. Succession in a south Swedish deciduous wood: a numerical approach. *Vegetatio*. 43: 103-122.

Radojevic, M. and V.N Bashkin. 2006. *Practical Environmental Analysis.* Second ed. The Royal Society of Chemistry. U.K.

Rodwell, J.S. 1991a. *British plant communities. Vol. 1. Woodlands and scrub*. Cambridge University Press, Cambridge.

Rodwell, J.S. 1991b. *British plant communities. Vol. 2. Mires and heaths*. Cambridge University Press, Cambridge.

Rodwell, J.S. 1992. *British plant communities. Vol. 3. Grasslands and montane communities*. Cambridge University Press, Cambridge.

Rodwell, J.S. 1995. *British plant communities. Vol. 4. Aquatic communities, swamps and tall-herb fens*. Cambridge University Press, Cambridge.

Schaffers, A.P. and K.V. Sykora. 2000. Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *J. Veg. Sci*. 11: 225-244.

Seidling, W. and R. Fischer. 2008. Deviances from expected Ellenberg indicator values for nitrogen are related to N throughfall deposition in forests. *Ecol. Indicators*. 8: 639-646.

Smart, S.M. 2000. Ecological assessment of vegetation from a nature reserve using regional reference data and indicator scores. *Biodivers. Conserv*. 9: 811-832.

Smart, S.M. and W.A. Scott. 2004. Bias in Ellenberg indicator values - problems with detection of the effect of vegetation type. *J. Veg. Sci*. 15: 843-846.

Sutherland, W. 2006. *Ecological census techhniques; a handbook*. Cambridge University Press. U.K.

Ter Braak, C.J.F. and N.J.M Gremmen. 1987. Ecological amplitudes of plant species and the internal consistency of Ellenberg's indicator values for moisture. *Vegetatio*. 69: 79-87.

Thimonier, A., J.L. Dupouey, F. Bost and M. Becker. 1994. Simultaneous eutrophication and acidification of a forest ecosystem in North-East France. *New Phytol*. 126: 533- 539.

Thomas, J.A., D.J. Simcox, J.C. Wardlaw, G.W. Elmes, M.E. Hochberg and R.T. Clarke. 1998. Effects of latitude, altitude and climate on the habitat and conservation of the endangered butterfly Maculinea arion and its Myrmica ant hosts. *J. Insect Conserv*. 2: 39-46.

Thompson, K., J.G. Hodgson, J.P. Grime and I.H. Rorison. 1993. Ellenberg numbers revisited. *Phytocoenologia*. 23: 277-289.

Trelease, S.F. and H.M. Trelease. 1938. Selenium as a Stimulating and Possibly Essential Element for Indicator Plants. *Am. J. Bot*. 25: 5: 372-380.

van der Maarel, E. 1993. Relations between sociological-ecological species groups and Ellenberg indicator values. *Phytocoenologia*. 23: 343-362.

van Straalen, N. and H.A. Verhoef. 1997. The development of a bioindicator system for soil acidity based on arthropod pH preferences. *J. Appl. Ecol*. 34: 1: 217-232.

Verheyen, K., L. Baeten, P. De Frenne, M. Bernhard-Romermann, J. Brunet, J. Cornelis, G. Decoq, H. Dierschke, O. Eriksson, R. Hedl, T. Heinken, M. Hermy, P. Hommel, K.J. Kirby, T. Naaf, G.F. Peterken, P. Petrik, J. Pfadenhauer, H. van Calster, G-R. Walther, M. Wulf and G. Verstraeten. 2012.

Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. *J. Ecol*. 100: 352-365.

Wamelink, G.W.W., P.W. Goedhart, H.F. van Dobben and F. Berendse. 2005. Plant species as predictors of soil pH: replacing expert judgement by measurements. *J. Veg. Sci*. 16: 461-470.

Wamelink, G.W.W., V. Joosten, H.F. van Dobben and F. Berendse. 2002. Validity of Ellenberg indicator values judged from physico-chemical field measurements. *J. Veg. Sci*. 13: 269-278.

Wikum D A. and G.F. Shanholtzer 1978. Application of the Braun-Blanquet cover-abundance scale for vegetation analysis in land development studies. *Environ. Manag*. 2: 323-329

Wilson, S.M., D.G. Pyatt, D.C. Malcolm and T. Connolly. 2001. The use of ground vegetation and humus type as indicators of soil nutrient regime for an ecological site classification of British forests. *Forest Ecol. Manag*. 140: 101-116.

Witte, J.P.M., A.F.M. Meuleman, S. van der Schaaf and B. Raterman. 2004. Eco-hydrology and biodiversity. In: R.A. Feddes, G.H. de Rooij and J.C. van Dam (eds.), *Unsaturated-zone modelling: progress, challenges and applications*. Kluwer Academic Publishers. The Netherlands.

Wittig, R. and K.J. Durwen. 1982. Ecological indicator-value spectra of spontaneous urban floras. In: R. Bornkamm, J.A. Lee and M.R.D. Seaward (eds.), *Urban ecology; The second European ecological symposium*. Blackwell Scientific Publications, Oxford.

Zolyomi, B., Z. Barath, G. Fekete, P. Jakucs, I. Karpati, M. Kovacs and I. Mate. 1967. Classification of species of flora in the Hungarian environmental groups to TWR figures. *Fragm. Bot. Mus. Hist. Nat. Hung*. 4: 101–142.

Table 1 – Regression of bioindicator values generated on a site-specific basis using either Ellenberg's original and Hill's UK-adjusted indicator systems against direct environmental measures for the same sites for soil moisture, pH and nitrates. Analyses were conducted for spring and summer periods separately and using data averaged over these two periods using both unweighted and abundance-weighted approaches (n = 50 sites in all cases). * = analysis used curvilinear regression using a logarithmic equation rather than linear regression (as for all other analyses).

	Moisture			**pH**			**Nitrate**		
	F	R^2	*P*	*F*	R^2	*P*	*F*	R^2	*P*
Ellenberg									
Average									
Unweighted	0.300	0.006	0.586	19.560	0.290	<0.001	*16.828	0.260	<0.001
Weighted	0.006	0.000	0.939	10.919	0.185	0.002	*14.000	0.255	<0.001
Spring period									
Unweighted	0.800	0.002	0.778	14.458	0.231	<0.001	*20.178	0.296	<0.001
Weighted	0.086	0.002	0.771	9.780	0.165	0.003	*16.002	0.250	<0.001
Summer period									
Unweighted	0.445	0.009	0.508	18.529	0.279	<0.001	2.154	0.043	0.149
Weighted	0.009	0.000	0.923	9.127	0.160	0.004	0.691	0.014	0.410
Hill									
Average									
Unweighted	0.893	0.018	0.350	58.385	0.549	<0.001	*17.654	0.269	<0.001
Weighted	0.074	0.002	0.787	40.775	0.459	<0.001	*17.177	0.264	<0.001
Spring period									
Unweighted	0.412	0.009	0.524	42.224	0.468	<0.001	*20.006	0.300	<0.001
Weighted	0.010	0.000	0.921	36.049	0.429	<0.001	*17.064	0.262	<0.001
Summer period									
Unweighted	1.050	0.021	0.311	47.070	0.495	<0.001	1.895	0.038	0.175
Weighted	0.130	0.003	0.721	28.824	0.375	<0.001	0.545	0.011	0.464

Table 2 - Regression of bioindicator values generated on a site-specific basis using either Ellenberg's original and Hill's UK-adjusted indicator systems calculated using rare species only (those with <25% cover) against direct environmental measures for the same sites for soil moisture, pH and nitrates. Analyses used data averaged over spring and summer sampling periods and an unweighted approach was used throughout (n = 41 sites in all cases) * = analysis used curvilinear regression using a logarithmic equation rather than linear regression (as for all other analyses)

	Moisture			**pH**			**Nitrate**		
	F	R^2	*P*	*F*	R^2	*P*	*F*	R^2	*P*
Ellenberg	1.254	0.030	0.270	4.551	0.102	0.039	*5.446	0.120	0.025
Hill	1.418	0.039	0.241	4.652	0.104	0.037	*8.953	0.183	0.005

Figure Legends

Figure 1: Relationship between Ellenberg indicator value (unweighted community average) and direct environmental measures for 50 woodland sites in the UK for: (a, b) moisture; (c, d) pH and (e, f) soil nitrate. In all cases the average relationship is shown first, followed by the season-specific relationship. Note that some relationships are curvilinear.

Figure 2: Relationship between Hill-modified Ellenberg indicator value (unweighted community average) and direct environmental measures for 50 woodland sites in the UK for: (a, b) moisture; (c, d) pH and (e, f) soil nitrate. In all cases the average relationship is shown first, followed by the season-specific relationship. Note that some relationships are curvilinear.

Figure 3: Schematic diagram of correlation strength between bioindicated and direct environmental measures for different parameters.