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Phosphorus availability explains productivity patterns in temperate semi-natural vegetation

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Plant production is a key environmental process affecting resource provision, carbon storage, and (via effects on plant competition) biodiversity. However, factors controlling productivity in semi-natural habitats are poorly understood. Using national-scale survey data, the study assessed the ability of different soil measurements to explain variation in an independent metric of plant productivity based on species composition. Soil carbon and moisture contents were strongly related, and explained the major axis of variation in productivity. Productivity was also clearly related to the stock of plant-available phosphorus, but less so to plant-available nitrogen. Phosphorus limitation may be more fundamental than nitrogen limitation, and should be considered explicitly in models of ecosystem responses to climate change, nitrogen pollution and other anthropogenic drivers.

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Phosphorus availability explains patterns in a productivity indicator in temperate semi-natural vegetation

E.C. Rowe[a], S. M. Smart[b] and B. A. Emmett[a]

Plant production is a key process in semi-natural ecosystems, affecting resource provision, carbon storage, and habitat suitability for species of conservation concern. There is debate over whether nitrogen (N) or phosphorus (P) limits productivity more widely, and whether the pattern of limitation has been affected by widespread atmospheric N pollution. In a national-scale survey, floristic composition was used to derive mean Ellenberg N score (E_N) for use as an independent metric of productivity. Much of the variation in E_N within extensively-managed habitats could be explained by bulk-soil properties such as total C and moisture contents, reflecting the axis from wet, organic, infertile soils to drier, mineral, fertile soils. However, this main axis of variation was also explained well by bicarbonate-extractable P stock, and P stock was included in the best 88 of 255 possible models for all habitats, or the best 55 of 255 models for extensively-managed habitats. The stock of mineralisable N was much less well able to explain variation in the productivity metric, particularly in extensively-managed habitats. This suggests that P availability is a more widespread constraint to the productivity of semi-natural ecosystems in the UK than is N availability.

Keywords: Countryside Survey; fertility; nutrient; eutrophication; NPP.

Introduction

Plant productivity is important in terrestrial ecosystems, affecting agricultural and forest productivity, carbon (C) sequestration and biodiversity. In more productive systems, for example where nitrogen (N) pollution has caused a release from N limitation, light availability at ground level is reduced because of larger standing biomass and increased amounts of litterfall. This favours the growth of taller, competitive species over smaller-growing, stress-tolerant species, and is a key reason [1] for the global loss of biodiversity driven by N pollution [2, 3]. Around half of reactive N inputs into the biosphere are now anthropogenic, causing perhaps the greatest perturbation to date of natural ecosystem dynamics [4]. However, the response to this perturbation depends critically on the degree and prevalence of N limitation in ecosystems. Although many ecosystems have historically been N-limited due to the energetic cost of N fixation and the several pathways by which N can be lost [5], N pollution may be causing a shift from N limitation to P-limitation [6, 7]. In a review of 641 factorial fertilisation studies, most were found to be co-limited by N and P [8]. The current study sought to extend the evidence base for limitation by N and/or P across a range of cold-temperate terrestrial habitats, by exploring which of a suite of soil measurements best explains variation in a trait-based indicator of productivity in a stratified-random national-scale survey.

As well as N and P availability, plant productivity may be determined by factors such as soil moisture, availability of other nutrients, temperature and light availability. The 'fertility' of a site can be seen as a function of all of these productivity-regulating factors. Fertility is widely considered to be a beneficial characteristic of ecosystems, and systems that are more productive have the potential to contribute more to commercial agricultural and forest production. More fertile systems also provide greater C flux into soil pools [9, 10], although greater C stocks are correlated with low productivity [11], principally since decomposition is slower on wet sites. The association of less-fertile habitats with greater biodiversity value means there is commonly a trade-off between production and biodiversity, and low fertility is considered a positive trait in habitats managed for nature conservation.

Direct estimation of plant productivity in terrestrial semi-natural habitats usually requires repeated measurements. To measure net primary productivity directly it is necessary to collect gas exchange data over an extended period and estimate photosynthesis and plant respiration rates. Measurements of peak standing biomass can be used to estimate annual productivity, but only in certain habitats such as hay meadows. In other habitats, measuring productivity requires specialist techniques such as the installation of grazing exclosures or measurements of woody biomass increment.

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Alternative methods for estimating productivity based on remote sensing and spectral analysis are improving, but require ground-truthing and calibration for particular habitats. This makes it difficult to obtain enough productivity measurements to assess variation in relation to environmental axes thought to influence productivity, although assessments of survey [12] and experimental [13] data have shown widespread productivity increases in semi-natural vegetation in response to additional N.

As an alternative to direct measurements, the species present on a site can be used to indicate its productivity. Species have particular environmental requirements, which are reflected in their realised niche, i.e. the envelope of environmental conditions within which they occur. To describe and quantify these requirements, trait scores were established for many Central European plant species by Ellenberg *et al*. [14], including the Ellenberg 'N' score (E_N). This score was originally described as indicating nitrogen or more generally nutrient availability. Subsequent authors have concluded that E_N is related to plant productivity [15-18], which is often but not exclusively related to nutrient availability. These studies have mainly been confined to grasslands, presumably because productivity is relatively easy to measure in such ecosystems, but there is no evidence that the relationship between E_N and productivity does not apply to other habitats. It has been argued that trait scores assigned by experts are non-empirical and so should not be used in predictive ecology [19]. However, the E_N score for UK plant species was found to be re-predictable from the presence of associated species using a two-way weighted averaging method, with a correlation of 0.81 between original and re-predicted E_N scores [20].

All methods for measuring productivity are subject to considerable measurement error [21]. Environmental indicators based on the traits of present plant species provide an integrated measure of conditions leading up to the observation date [22], and are less susceptible to short-term variation and observation error than are many physicochemical measurements [23]. For these reasons, and because such indicators are readily derived from floristic datasets even when these lack synlocated abiotic measurements, E_N and other trait-means continue to have a role in ecological description and predictive modelling [24]. We consider that the mean E_N score provides a robust and independent measure of plant productivity that can be used to assess and compare the soil factors that may govern productivity.

A partial test of the validity of trait-mean indicator values is to examine whether these can be related to measurable properties of the site. The relationships between mean Ellenberg 'F' score and soil moisture, and between mean Ellenberg 'R' score and soil pH or calcium concentration, are reasonable, but relating E_N to measurable soil properties has proved more difficult [17]. There is considerable uncertainty as to the best way to measure nutrient availability, and inappropriate measurements are unlikely to be correlated with mean E_N. Bulk soil measures such as total N are often poorly related to nutrient availability, since large proportions are in pools that are not readily plant-available. Instantaneous measurements of extractable soluble nutrients may be strongly affected by previous rainfall and mineralisation events. Rapid plant uptake of nutrients means that soil solution concentrations can be near zero even in systems with considerable plant productivity. Time-integrated measures such as mineralisable N, or N adsorbed onto strong ion-exchange resins, are more likely to reflect plant-available N [25]. In a pilot study [26] we found that mean E_N could be predicted with some confidence from soil moisture content, pH and mineralisable N. Here we assess relationships between soil properties and mean E_N in a much larger dataset, which also includes a measure of phosphorus (P) availability.

The aim of the study was to assess the factors controlling plant productivity, as represented by mean E_N, across a range of habitats. These factors were assessed separately for habitats which are managed extensively and for both extensively-managed and intensively-managed habitats. In the UK nearly all habitats are managed in some sense and so are described as semi-natural. Extensively-managed habitats were defined in the current study as those that are likely to have received no or minimal applications of artificial fertiliser.

Specifically, we aimed to test hypotheses that:

H1: Plant productivity is related not simply to bulk-soil properties such as C content, but also to measures of macronutrient availability in soil.

H2: Available N explains more of the variation in plant productivity than does available P.

Methods

The floristic data and soil measurements used in the study were obtained from a large survey of the British countryside carried out in 2007. The Countryside Survey of Great Britain uses a stratified random design to sample climate and soil classes across Britain [27]. At each location, five plots each of 200 m^2 were randomly located within a 1 km square, of which up to three were used in the current study. All plant species were recorded, and soil samples were taken from within the plot for analysis. Sampling and analytical methods are described in detail elsewhere [28-30].

The vegetation where each plot was located was classified to Broad Habitat, as defined in the Countryside Survey [31]. Only plots where a full set of measurements was available were included. Five plots where C/N ratio was calculated to be implausibly low (< 7.5 g C g^{-1} N) were excluded, giving a total of 582 plots from 231 squares. Additional analyses were carried out on the subset of 221 plots within extensively managed habitats, as identified in Table 1.

Table 1. Numbers of sample plots (*n*) within different Broad Habitats. E = extensively managed.

Broad Habitat	*n*	Broad Habitat	*n*
Broadleaf woodland (E)	39	Bracken (E)	6
Conifer woodland (E)	41	Dwarf-shrub heath (E)	31
Arable	131	Fen / Marsh / Swamp (E)	11
Improved grassland	143	Bog (E)	42

Neutral grassland	72	Urban (e.g. garden)	4
Calcareous grassland (E)	2	Rock or sediment (E)	6
Acid grassland (E)	43	Not determined	11

An independent measure of plant productivity was provided by the mean E_N score for present species. Adjusted E_N scores as calculated for UK species [20] were used. The E_N values for each species were weighted by cover, to reflect the influence of dominant species on overall productivity [17].

The soil measurements assessed as potential explanatory variates for E_N included quantifications of soil C, N and P and of two properties that are also likely to be related to plant productivity: pH and moisture content (Table 2). Mineralisable N (N_{rm}) was measured in cores that were first flushed with artificial rain solution and then incubated for 28 days at 10 °C, as described in Rowe *et al*. [29]. The concentration of extractable P (P_{ext}) was measured using Olsen's method, i.e. extraction in 0.5 M sodium bicarbonate at pH 8.5 followed by colorimetric analysis [28]. Bulk density measurements were used to express N_{rm} and P_{ext} in terms of stock per hectare in the top 15 cm of soil. The distributions of all variables were inspected and the Box-Cox method applied to assess appropriate transformations [32]. Proportional data (C and N proportion of dry soil, and nitrate proportion of mineralised N) were logit transformed with the exception of moisture content, for which a log transformation gave a more even distribution. Log transforms were also used for N_{rm} and P_{ext}. Soil pH and total N/C ratio were not transformed (the best transform for C/N data was inversion).

Correlations among soil measurements were assessed by Spearman's rank-correlation, using a Bonferroni correction for 28 comparisons. Principal Components Analysis (PCA) was carried out on transformed data, after normalising by subtracting the mean and dividing by the standard deviation. The significance of linear regressions of E_N on each principal component was tested using anova. Mixed models for predicting E_N were fitted using the lme procedure of R version 3.0.1 [33], treating the square within which plots were located as a random effect. Models were evaluated using the Akaike information criterion (AIC), which penalises models with more terms and is minimal for the most parsimonious or efficient model. Additional checks were performed using likelihood ratio tests to assess whether additional terms resulted in significant reduction in residual variance, but in all cases the term was significant when AIC was reduced.

Table 2. Soil and floristic measurements: means, minima and standard deviations, and data transforms applied.

Measurement	Units	Mean	Min	Max	SD	Transform	Name
pH of 10 g fresh soil with 25 g water	-	6.07	3.32	8.75	1.33	None	pH
Moisture content	g water 100 g^{-1} fresh soil	40.0	7.1	94.8	22.6	$\log_{10}$	MC
Total organic carbon concentration	g C 100 g^{-1} dry soil	11.4	0.7	53.3	14.4	Logit (base *e*)	C_{tot}
Total nitrogen concentration	g N 100 g^{-1} dry soil	0.63	0.07	2.71	0.58	Logit (base *e*)	N_{tot}
Total N/C ratio	mg N g^{-1} C	75	10	121	21	None	NC
Mineralisable N	kg N ha^{-1}	17	0	201	19	$\log_{10}$	N_{rm}
Nitrate proportion in mineralised N	g NO_3-N g^{-1} N	0.56	0.00	1.00	0.36	logit(prop ×0.98+0.01)	$PropNO_3$
Bicarbonate-extractable P	kg P ha^{-1}	38	1	499	52	$\log_{10}$	P_{ext}
Mean Ellenberg 'N' score	-	4.8	1.2	7.9	1.8	None	E_N

Results

Correlations among potential explanatory variables

All soil measurements included were significantly correlated (Table 3). Soil total C, total N and moisture content were all strongly positively correlated, reflecting the concurrent changes in these properties along the gradient from wet organic soils to drier mineral soils. Increasing organic matter content was associated with declines in pH and soil total N/C ratio. Mineralisable N, nitrate proportion in mineralised N, and bicarbonate-extractable P all tended to decrease with increasing organic matter content.

Ordination of potential explanatory variables

A PCA plot illustrates the main axes of variation in the full dataset (Figure 1a). The first, second and third axes accounted for 63%, 10% and 9% of the total variance, respectively. The degrees of association between these axes and each variate is shown in Table 4. Mean E_N score was predicted well by the first principal component (P < 0.001), low values of which are associated with high carbon and moisture contents, and high values with large N/C ratios and extractable P contents and high pH values. Mean E_N was not related to the second component, which was strongly related to mineralisable N stock, but was explained by the third component (P < 0.01), which was related particularly to total nitrogen and the nitrate proportion in mineralisable N.

Table 3. Spearman's rank correlation coefficients among soil properties included as potential explanatory factors. All correlations were significant at P < 0.001, with Bonferroni correction for 28 comparisons.

	pH	MC	C_{tot}	N_{tot}	NC	N_{rm}	$PropNO_3$
MC	-0.65						
C_{tot}	-0.65	0.91					
N_{tot}	-0.54	0.85	0.95				

NC	0.65	-0.62	-0.63	-0.41			
N_{rm}	0.25	-0.42	-0.35	-0.27	0.44		
$PropNO_3$	0.45	-0.53	-0.50	-0.42	0.46	0.37	
P_{ext}	0.56	-0.68	-0.65	-0.58	0.54	0.41	0.50

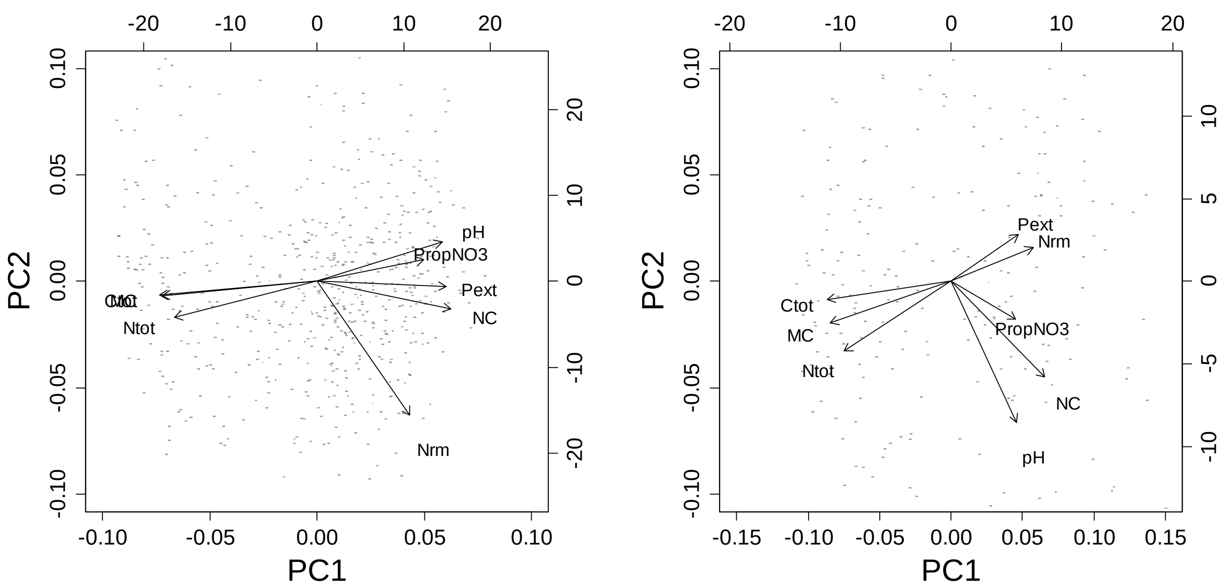
The PCA plot for the subset of sample plots from extensive habitats (Figure 1b) also showed an inverse association of the first principal component with soil C and moisture. Here the variation was less dominated by the first component, with the first three axes accounting for 50%, 13% and 12% of the total variance. Mean E_N was explained by the first component (P < 0.001), and by the second component (P < 0.01) which was related particularly to pH, but not by the third component.

Table 4. Loadings for potentially explanatory variables in relation to the first three principal components of total variation, for all-habitats and extensively-managed habitats.

	All Habitats			Extensive		
	PC1	PC2	PC3	PC1	PC2	PC3
pH	0.34	0.26	-0.25	0.25	-0.70	0.04
MC	-0.41	-0.09	-0.24	-0.46	-0.21	0.01
C_{tot}	-0.42	-0.09	-0.29	-0.47	-0.09	-0.05
N_{tot}	-0.38	-0.24	-0.48	-0.40	-0.35	0.08
NC	0.36	-0.19	-0.26	0.35	-0.48	0.24
N_{rm}	0.25	-0.89	0.06	0.31	0.17	0.55
$PropNO_3$	0.29	0.14	-0.68	0.24	-0.19	-0.75
P_{ext}	0.35	-0.03	-0.14	0.25	0.23	-0.27

Figure 1. Ordination of samples and measurements on first and second principal components of variation: a) all sample plots; b) only sample plots from extensively-managed habitats. MC = $\log_{10}$(% soil moisture); Ctot = logit_e(% soil carbon); Ntot = logit_e(% soil nitrogen); NC = mg total nitrogen g^{-1} total carbon; Nrm = $\log_{10}$(mineralisable N stock, kg ha^{-1}); PropNO3 = logit_e(nitrate proportion in mineralisable N); Pext = $\log_{10}$(bicarbonate-extractable P stock, kg ha^{-1}).

a) b)

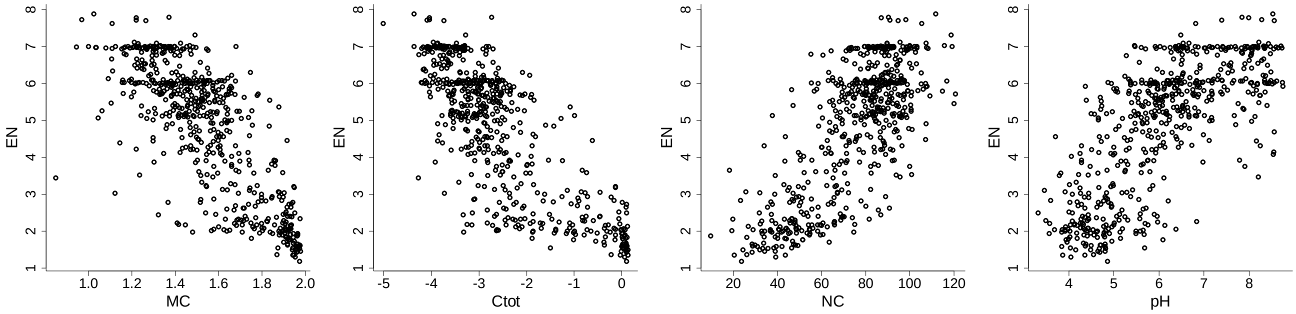


Plots of mean E_N against potential explanatory variables

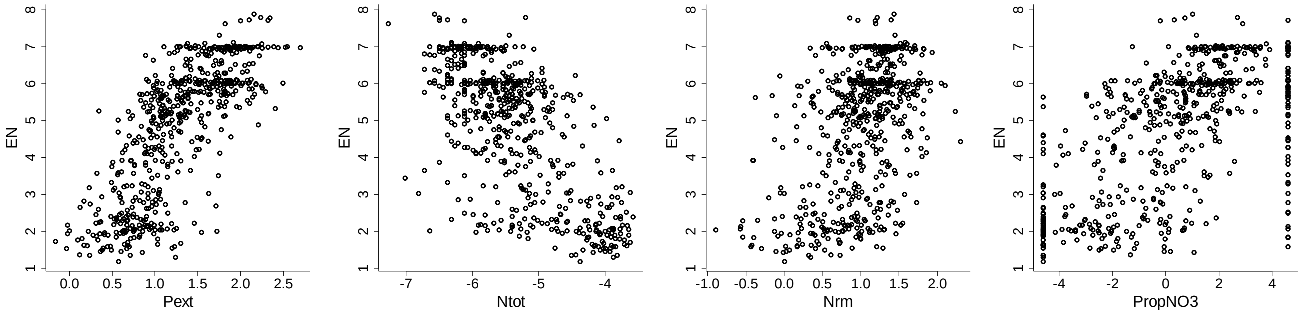
Mean E_N was clearly related to all potentially explanatory variables (Figure 2). Variables related negatively to mean E_N were those that had higher values on more organic soils, in particular C and moisture contents, but also total N content. However, total N/C was positively related to mean E_N, and this is reflected in the weaker relationship of mean E_N with N_{tot} than with C_{tot}. The variables reflecting available nutrient stock (P_{ext} and N_{rm}) were positively related to mean E_N. The relationship was particularly clear for P_{ext}. Soil pH was also positively related, perhaps reflecting greater availability of nutrient cations and/or greater mineralisation rates for N and P at higher pH. The proportion of nitrate in mineralisable N was positively related to E_N.

Figure 2. Plots of mean Ellenberg 'N' score (E_N) against potential explanatory factors: a) $\log_{10}$(% moisture content); b) logit(C proportion of dry soil); c) total N/C ratio; d) pH; e) $\log_{10}$(extractable Pstock); f) logit_e(N proportion of dry soil); g) $\log_{10}$(mineralisable N stock); h) logit_e(nitrate proportion of mineralised N).

a) b) c) d)



e) f) g) h)



Predicting mean Ellenberg N

When applying a single factor to explain the mean E_N signal for all habitats, the C concentration in soil was clearly the best explanatory variate (Table 5). However, using the stock of extractable P as a single predictor gave the second-lowest AIC. Mineralisable N stock, by contrast, was the least well able of the single factors measured to predict variation in mean E_N. The model with the lowest AIC had six terms: pH, C concentration, N/C ratio, nitrate proportion of mineralisable N, mineralisable N stock, and extractable P stock. Extractable P stock appeared in the best 88 of the 255 possible explanatory models. The sum of Akaike weights for models that include a specific variable indicates the relative importance of that variable [34], or more specifically the likelihood that the variable is included in the best model [35]. These sums (Table 7) indicate that mineralisable N has some value in explaining mean E_N when combined with other predictor variables. However, soil pH, nitrate proportion in mineralisable N, and extractable P stock, were all considerably more likely to be included in the best model.

Table 5. Explanatory models for mean Ellenberg N score (E_N) across all habitats (n = 582). Selected linear mixed-effects regression models using soil variables after appropriate transformation. All models included Square (location) as a random effect. AIC = Akaike Information Critrion; AW = Akaike weight.

Model	AIC	AW
a) Single-term models		
$E_N \sim C_{tot}$	1649	2.6×10^{-79}
$E_N \sim P_{ext}$	1694	5.0×10^{-89}
$E_N \sim MC$	1695	4.0×10^{-89}
$E_N \sim NC$	1708	5.0×10^{-92}
$E_N \sim pH$	1736	3.5×10^{-98}
$E_N \sim N_{tot}$	1801	3.1×10^{-112}
$E_N \sim PropNO_3$	1866	2.8×10^{-126}
$E_N \sim N_{rm}$	1906	5.0×10^{-135}
b) Most-efficient models		
$E_N \sim pH + C_{tot} + NC + PropNO_3 + N_{rm} + P_{ext}$	1290	0.367
$E_N \sim pH + C_{tot} + N_{tot} + NC + PropNO_3 + N_{rm} + P_{ext}$	1291	0.171
$E_N \sim pH + MC + C_{tot} + NC + PropNO_3 + N_{rm} + P_{ext}$	1291	0.171
$E_N \sim pH + MC + C_{tot} + N_{tot} + NC + PropNO_3 + N_{rm} + P_{ext}$	1292	0.097
$E_N \sim pH + C_{tot} + N_{tot} + PropNO_3 + N_{rm} + P_{ext}$	1294	0.041
$E_N \sim pH + MC + C_{tot} + N_{tot} + PropNO_3 + N_{rm} + P_{ext}$	1294	0.037
$E_N \sim pH + N_{tot} + NC + PropNO_3 + N_{rm} + P_{ext}$	1295	0.027
$E_N \sim pH + C_{tot} + NC + PropNO_3 + P_{ext}$	1295	0.024

In extensively-managed habitats, the best single factor explaining the mean E_N signal was moisture content, followed closely by C concentration (Table 6). Extractable P stock as a single factor had slightly less explanatory power within this reduced dataset, but still explained a significant proportion of the variation in mean E_N. Extractable P stock appeared in the best 55 of the possible explanatory models, and the sum of Akaike weights for models that included extractable P stock was 0.999998 (Table 7).

Table 6. Explanatory models for mean Ellenberg N score across less intensively managed habitats (n = 221). Selected linear mixed-effects regression models using soil variables after appropriate transformation. All models included Square (location) as a random effect. AIC = Akaike Information Critrion; AW = Akaike weight.

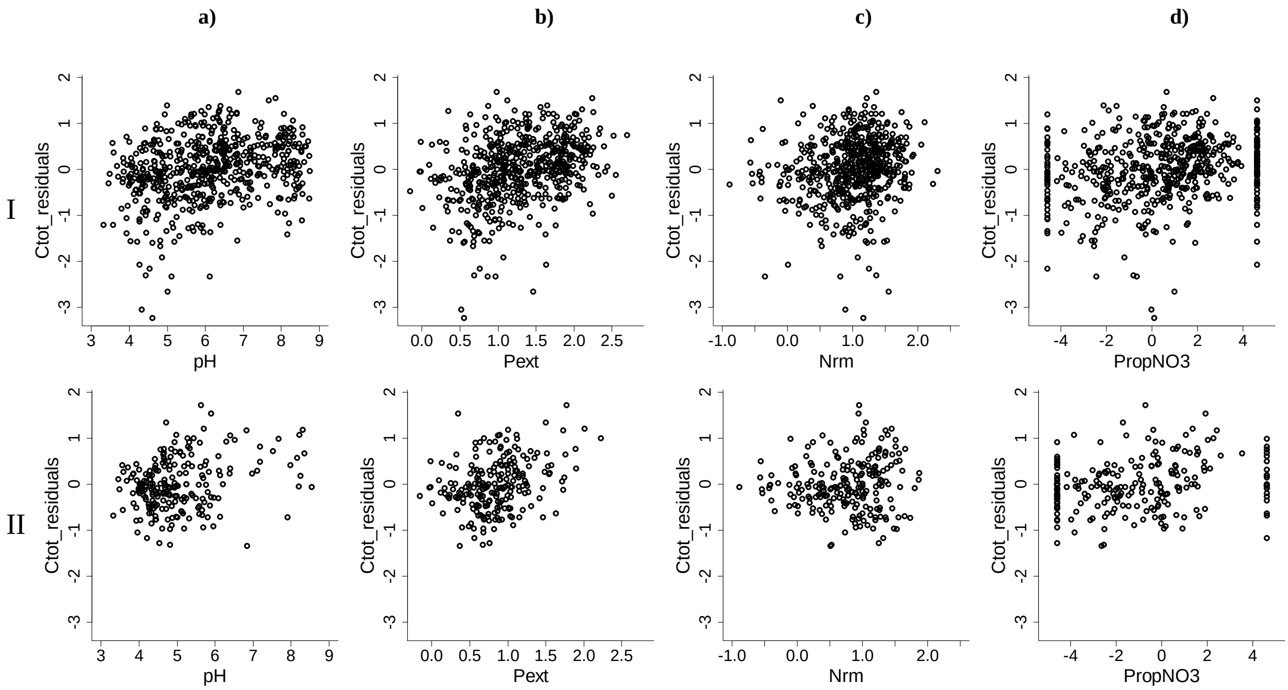
Model	AIC	AW
a) Single-term models		
E_N ~ MC	627	3.1×10^{-22}
E_N ~ C_{tot}	630	7.7×10^{-23}
E_N ~ NC	644	5.1×10^{-26}
E_N ~ pH	649	5.1×10^{-27}
E_N ~ P_{ext}	668	3.0×10^{-31}
E_N ~ N_{tot}	672	5.7×10^{-32}
E_N ~ $PropNO_3$	681	5.2×10^{-34}
E_N ~ N_{rm}	698	8.6×10^{-38}
b) Most-efficient models		
E_N ~ pH + MC + NC + $PropNO_3$ + P_{ext}	531	0.223
E_N ~ pH + MC + NC + $PropNO_3$ + N_{rm} + P_{ext}	532	0.153
E_N ~ pH + MC + C_{tot} + NC + $PropNO_3$ + P_{ext}	532	0.105
E_N ~ pH + MC + N_{tot} + NC + $PropNO_3$ + P_{ext}	532	0.102
E_N ~ pH + MC + C_{tot} + NC + $PropNO_3$ + N_{rm} + P_{ext}	533	0.072
E_N ~ pH + MC + N_{tot} + NC + $PropNO_3$ + N_{rm} + P_{ext}	533	0.071
E_N ~ pH + MC + C_{tot} + N_{tot} + $PropNO_3$ + P_{ext}	534	0.039
E_N ~ pH + MC + C_{tot} + N_{tot} + NC + $PropNO_3$ + P_{ext}	534	0.039

Table 7. Sum of Akaike weights for models that include each of the potential explanatory variates, for all habitats and for extensively-managed habitats.

	All Habitats	Extensive
pH	$1 - 1.8\times10^{-16}$	$1 - 2.2\times10^{-7}$
MC	0.350	0.885
C_{tot}	0.958	0.390
N_{tot}	0.425	0.386
NC	0.913	0.905
N_{rm}	0.924	0.431
$PropNO_3$	$1 - 1.2\times10^{-7}$	0.987
P_{ext}	$1 - 9.1\times10^{-27}$	$1 - 1.2\times10^{-6}$

To separate the effects of indicators of nutrient availability from the major axis of variation along the organic to mineral soil gradient, it is useful to inspect plots of residuals from a simple model, which fitted E_N to only C_{tot}, against indicators of nutrient availability (Figure 3). Soil pH was included among these indicators, since it is directly related to supply of nutrient cations (calcium and magnesium) and is also likely to affect mineralisation and supply of other nutrient elements. Residuals from the C_{tot}-only model showed weak but discernable positive relationships with pH, P_{ext}, N_{rm} and N_{tot}. Patterns of residuals for all habitats (Figure 3.I) and for extensively-managed habitats (Figure 3.II) were broadly similar, except that N_{rm} was not related to these residuals in extensively-managed habitats. This reflects the relatively low Akaike weights for N_{rm} in the latter dataset.

Figure 3. Plots of residuals from a model that fitted mean Ellenberg 'N' score to logit(carbon proportion of dry soil) against selected indicators of soil chemical conditions: a) pH; b) Pext = $\log_{10}$(bicarbonate-extractable P stock); c) Nrm = $\log_{10}$(mineralisable N stock); and d) PropNO3 = logit(nitrogen proportion of dry soil), in: I) all habitats; II) extensively-managed habitats. All terms significantly reduced deviance compared with the carbon-only model (*P* < 0.001), with the exception of Nrm in extensively-managed habitats (*P* > 0.05).



Discussion

All single factors explained a significant proportion of the overall variation in plant productivity as indicated by mean E_N score. The high degree of correlation among the variates makes it difficult to definitively identify which factors fundamentally limit productivity in UK habitats. However, the most parsimonious models selected by AIC included six terms for all habitats and five terms for extensively-managed habitats, reflecting the effects of many interacting factors on plant productivity.

In analyses of both all-habitats and extensively-managed habitats, C content and/or moisture content were shown to be key factors affecting productivity. These two factors were among the best three single explanatory variates for both sets of habitats, and appeared in many of the best two-term models. Clearly a major influence on plant productivity at a site is whether the soil is organic or mineral. Soil organic matter may directly affect the availability of nutrients to plants through immobilisation, and indirectly by decreasing pH through dissolution into organic acids. Soil C content was very strongly correlated with moisture content, and the anaerobiosis associated with wet soils also strongly constrains plant productivity [36].

Plant productivity was also strongly related to macronutrient availability, measured as mineralisable N and extractable P, and hence the first hypothesis was supported. However, the effect of available N was much less apparent than that of available P, which led us to reject the second hypothesis. Although mean E_N clearly increased with N_{rm} (Figure 2), much of this effect could be explained by the negative correlation between N_{rm} and C content, and N_{rm} alone was the least good of all the single explanatory factors tested. In extensively-managed habitats, N_{rm} added no explanatory power after fitting C content. By contrast, P_{ext} showed a tighter relationship with mean E_N, and was strongly related to residuals of a model with respect to C content in both datasets. The effect of P_{ext} was particularly clear for the all-habitats dataset, in which it was second only to C content as a single explanatory factor for mean E_N, and appeared in all of the best two-term models (data not shown). Within extensively-managed habitats, P_{ext} was also a useful explanatory factor, although in these habitats total N content and the soil pH both explained more of the total variance.

The positive relationship between the proportion of nitrate in mineralisable N and mean E_N may reflect a tendency for plants typical of more fertile environments to be adapted to use nitrate rather than ammonium. However, nitrification during the mineralisation incubation is likely to be determined by soil aeration, with greater nitrate proportions found in more porous, coarse-textured or better-structured soils. This correlation may thus result from better conditions for root growth and greater nutrient availability in more aerated soils, rather from a direct effect of N form.

The analysis provides strong evidence that macronutrient availability limits productivity in many habitats, and some evidence that the effect of available P is stronger than that of available N. An alternative explanation for the weaker statistical effect of N_{rm} might be that it is subject to more measurement error than P_{ext}. However, the N_{rm} measurement clearly has some power to explain the E_N signal, and in a previous study was shown to be related to the rate of atmospheric N deposition [29], so we are confident that the measurement does represent N availability in soil.

A simpler explanation is that P limitation is more widespread than N limitation. The mechanisms by which these elements interact and may become limiting were reviewed by Vitousek *et al.* [5]. Reactive N can enter ecosystems through atmospheric fixation, and N is likely to become limiting when this fixation is restricted or when there are uncontrolled N losses, for example as dissolved organic N [37, 38]. Until recently it was thought that phosphorus limitation prevails in freshwater aquatic ecosystems [39] and nitrogen limitation in terrestrial ecosystems [40], but it is increasingly recognised that phosphorus limitation and N-P co-limitation are also widespread in terrestrial ecosystems [8, 41]. Phosphorus limitation is often related to long-term depletion and/or a low rate of supply from parent material. Relative limitation by N and P can change with time, with a common pattern of N limitation in young soils recently formed from P-rich parent material, progressing to P limitation as P weathering rates decline [41], although which limitation ultimately prevails depends on the balance between input and loss fluxes [42]. The post-glacial soils of the UK are comparatively young, and not as much of their original P content is likely to have been lost as in many tropical soils. However, nearly all apatite and similarly-weatherable mineral P would likely have been transformed into occluded or organic P by around 4000 years after de-glaciation [43]. Additions of P fertiliser to more-intensively managed agroecosystems will have decreased overall P limitation in the UK landscape, but P limitation might be expected in many sites.

The strong relationship between P availability and productivity may also relate to the effects of chronic atmospheric N pollution. Total N deposition rates to the UK range from 3 to 49 kg N ha^{-1} yr^{-1} (CBED model estimates for grid-average vegetation in 2006-8; Rognald Smith, *pers. com.*) and have been elevated for much of the 20th century [44]. Cumulative N deposition since 1945 has been of the order of 500-4000 kg N ha^{-1} [45]. Although elevated N deposition can increase the accessibility and supply of P to plants [46] this effect is likely to be limited to soils with large organic P stocks. In general, stimulation of productivity by increased amounts of N is likely to cause dilution of plant tissue P and an increase in P limitation. Crowley *et al.* [7] interpreted changes in leaf tissue chemistry as indicating a shift from N limitation towards P limitation in the Adirondacks region of northeastern USA. Although analyses of survey data cannot definitively attribute variation in plant productivity to particular factors when these are strongly confounded, the strong association of plant productivity with P availability observed in the current study suggests that N pollution may have changed the pattern of limitation by these two elements at a national scale.

Conclusions

Greater plant productivity, as indicated by higher mean E_N score, is associated primarily with mineral soils with relatively low moisture contents. Plant productivity is also associated with greater availability of N and P, and higher soil pH. It is not possible to fully distinguish the effects of these factors in a survey study, but extractable P was more consistently associated with greater plant productivity than was mineralisable N. This suggests that P is a more fundamental constraint to plant productivity than N in UK terrestrial habitats.

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