Bracken productivity is unrelated to nutrient availability

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Introduction

Plant production affects agricultural productivity, carbon storage and biodiversity. Anthropogenic changes are likely to be causing widespread changes in net primary productivity (NPP), but predicting NPP requires an understanding of whether productivity is constrained by nutrient availability. In chronically N-polluted regions such as the UK, a change from N-limitation to other limitations, in particular by P, may be expected.

Measuring NPP in natural and semi-natural habitats is generally time-consuming, requiring multiple site visits. We estimated NPP by measuring peak standing biomass in stands of bracken (*Pteridium aquilinum* (L.) Kuhn). This species is suitable for use as a natural 'phytometer' since it is not affected greatly by herbivory. The aim was to relate NPP to site conditions in terms of soil chemistry and trait-means for co-occurring flora, and so test these hypotheses:

- **H1**: NPP is explained by P availability
- **H2**: NPP is not related to soil N/C ratio
- **H3**: the availability of other nutrient elements (K, Ca, Mg, Mo, Zn, …) does not explain extra variability after considering P.
- **H4**: Concentrations of nutrient elements in bracken leaf tissue are correlated with their availabilities in soil.

Figure 1. Plot locations

Methods

49 unshaded stands with >80 % bracken cover were identified in NW Wales and the Lake District (Figure 1). Biomass was harvested from a 1x1 m plot, dried and weighed. Soil was sampled from 0-15 cm depth and analysed for: pH (in 1:2.5 water slurry); total C and N (Vario elemental analyser); organic P (total P by ICP-OES, minus inorganic P by H_2SO_4 digest and molybdate colorimetry); total K, Ca and Mg by AAS; and total Zn by ICP-OES. Concentrations are stated per g of air-dried, 2mm-sieved soil. Co-occurring plant species were recorded and mean (not cover-weighted) scores on the Ellenberg L, F, R and N axes were calculated. Distributions of all variables were tested using the Shapiro test, and transformed where necessary to achieve normal or near-normal distributions. Measurements potentially explaining the variation in NPP were assessed using ANOVA to compare individual linear-effect models with the null (no-effect) model. For PCA analysis, variables were centred, and normalised to a standard deviation of 1, before ordination.

Results

Of all the nutrient availabilities, other site properties, and floristic trait-means assessed, only one had a significant effect on total biomass: the mean Ellenberg 'F' (water-availability) score (Figure 2). The variation in biomass was largely unrelated to variation in nutrient availabilities or to carbon content (Figure 3a). Variation in site properties as assessed using floristic trait means was more closely related to biomass (Figure 3b), but the ordination shows that the Alkalinity and Fertility scores were orthogonal to biomass and only the water-availability and to a lesser extent light-availability scores were collinear.

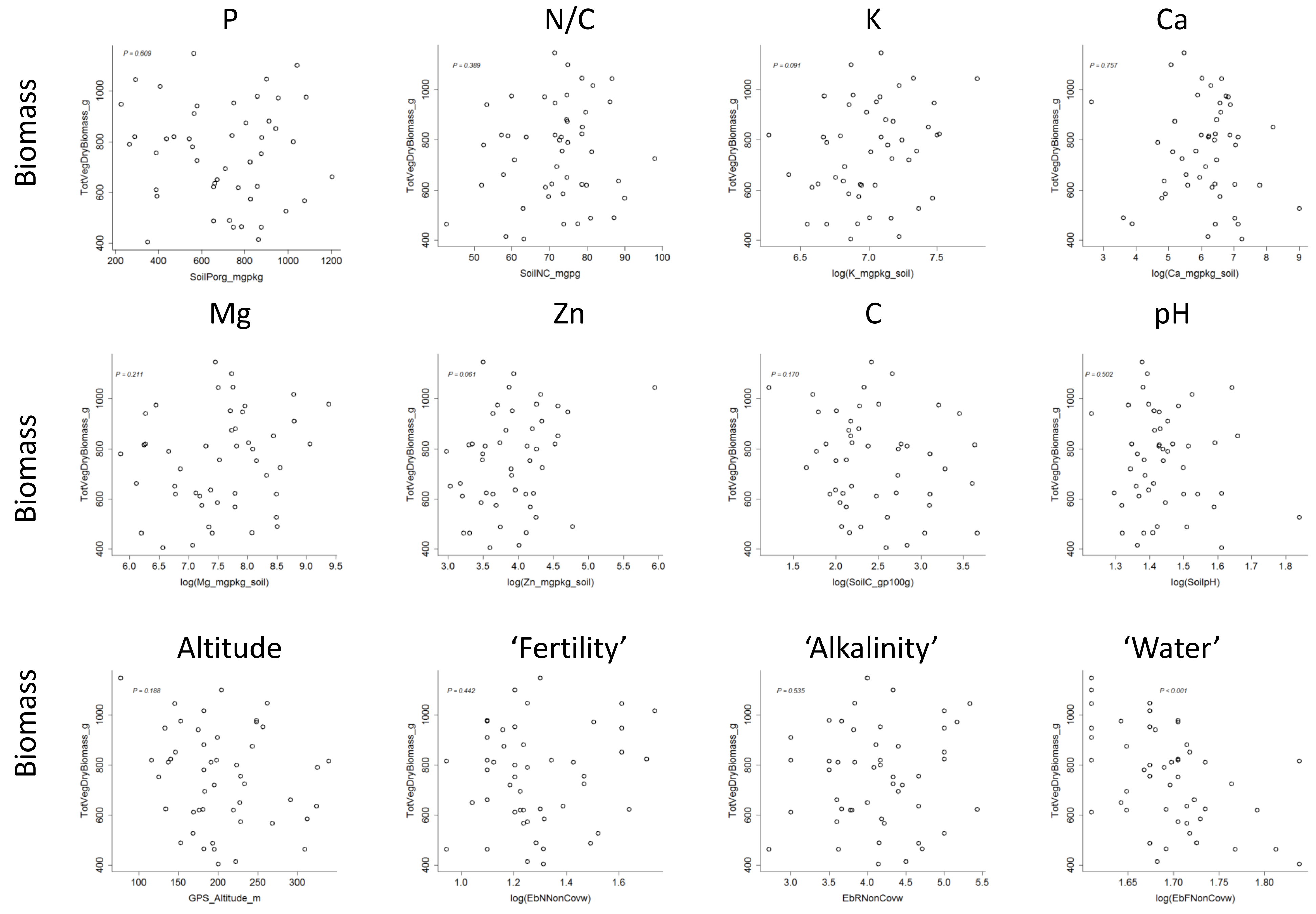

Figure 2. Evaluation of potential predictors of total above-ground vegetation biomass, g m^{-2}, in bracken stands, by comparison of linear models with a null (intercept only) model using anova. Biomass = Total vegetation biomass; P = organic P, mg kg^{-1}; N/C = total mg N g^{-1} C; K = ln(mg K kg^{-1}); Ca = ln(mg Ca kg^{-1}); Mg = ln(mg Mg kg^{-1}); Zn = ln(mg Zn kg^{-1}); C = ln(total C, g 100 g^{-1}); pH = ln(soil pH); Altitude is in m; Alkalinity = Ellenberg R; Fertility = ln(Ellenberg N); Water = ln(Ellenberg F).

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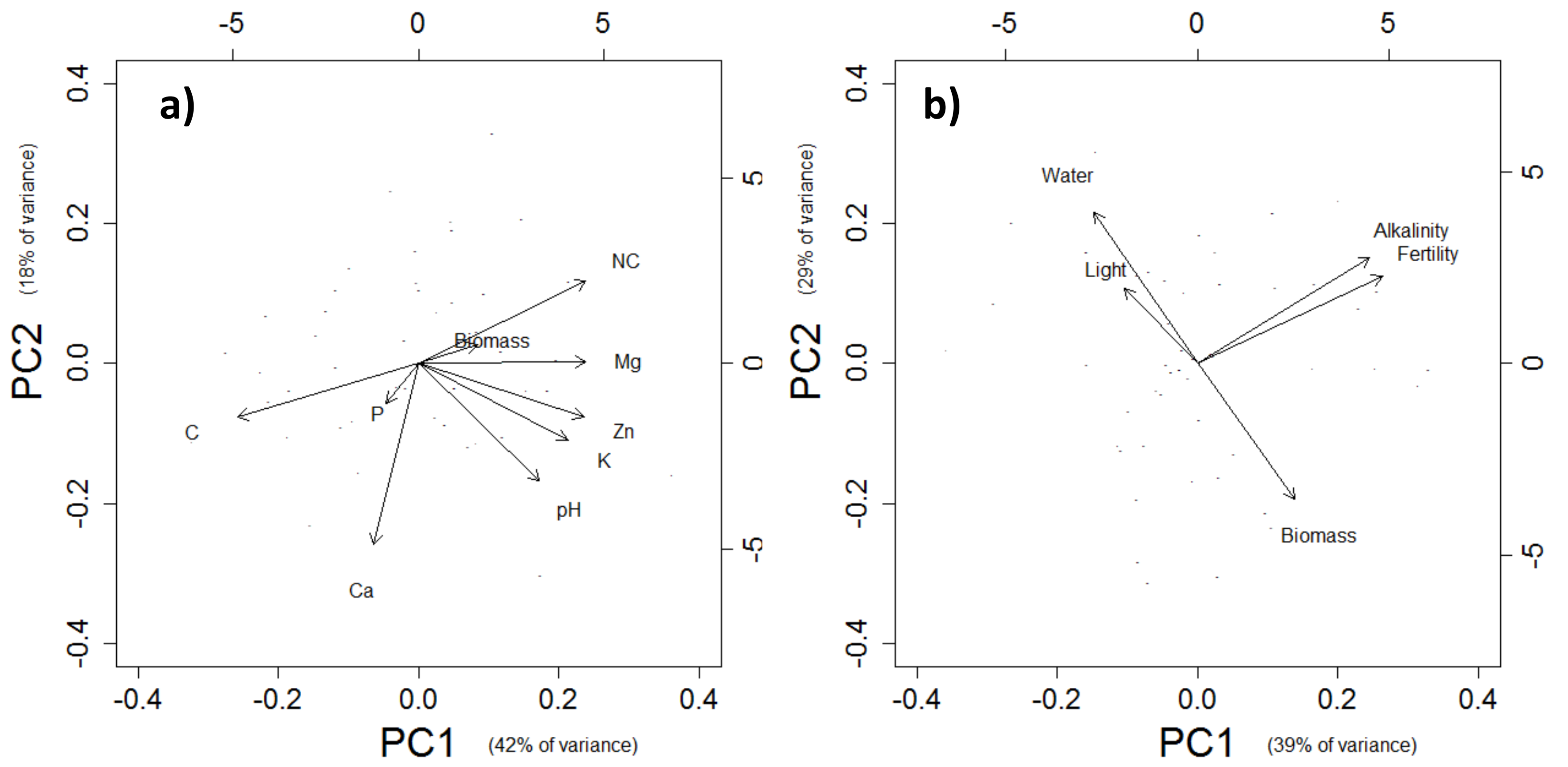

Figure 3. Principal Components Analysis biplots showing relationships between biomass and: a) soil chemical conditions; and b) floristic indicator-scores. Biomass = Total vegetation biomass, g m^{-2}; pH = Ln(soil pH); C = ln(total C, g 100 g^{-1}); NC = total mg N g^{-1} C; P = organic P, mg kg^{-1}; K = Ln(mg K kg^{-1}); Ca = Ln(mg Ca kg^{-1}); Mg = ln(mg Mg kg^{-1}); Zn = Ln(mg Zn kg^{-1}); Light = (Ellenberg L)^2; Water = Ln(Ellenberg F); Alkalinity = Ellenberg R; Fertility = Ln(Ellenberg N).

Discussion

The results were unexpected. Peat standing biomass, a proxy for NPP in these stands, was not explained by any of the soil properties measured. Bracken is known to be restricted to free-draining soils, and so a negative association with the floristic water-availability is explicable. In broader surveys, greater water-availability is associated with high-carbon soils. The lack of an observed response to soil C in this survey may be explained by the sampling of many sites that had thick accumulated humic layers despite being free-draining.

Biomass was not predicted by soil organic P, although this is considered a good proxy for plant-available P. Inorganic P and total P also did not predict NPP (data not shown). Biomass was not related to soil total N/C, although it is possible that better proxies for plant-available N would have been predictive. Thus H1 was unproven, and although H2 and H3 were upheld, the results indicated that plant productivity was not related to availabilities of any of the nutrient elements measured. Applying Liebig's 'law of the minimum', this implies that other resources limit growth in this habitat, such as light availability, growing season length and/or temperature.