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Measured estimates of semi-natural terrestrial NPP in Great Britain: comparison with modelled values, and dependence on atmospheric nitrogen deposition

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Abstract

Plant growth in nitrogen (N)-limited, unfertilised terrestrial ecosystems should respond to additional N inputs from atmospheric deposition (N_{dep}). We investigated this for sites in Great Britain (GB) by compiling 796 estimates of net primary productivity (NPP) from measured biomass production over the period 1932-2014, although the great majority were for 1995 onwards. The sites were largely vegetated with shrubs, grass and bracken, and had a wide range of N_{dep} (0.5 – 3.3. gN m^{-2} a^{-1} in 2000). The measured NPP estimates were compared with calculated values from the biogeochemical ecosystem model N14CP, which predicts that NPP depends strongly upon N_{dep}. The measured and modelled average total NPP values (gC m^{-2} a^{-1}) from all data were 387 (standard deviation, SD = 193) and 377 (SD = 72) respectively. Measured and modelled averages for vegetation classes followed the sequence: broadleaved trees ~ needle-leaved trees > herbs (rough grassland + bracken) ~ shrubs. After averaging measured values for sites in individual model grid cells (5 km x 5 km) with 10 or more replicates, the measured and modelled NPP values were correlated (n=26, r^2=0.22, p=0.011), with a slope close to unity. Significant linear relationships were found between measured ln NPP and cumulative N_{dep} for both herbs (n=298, p=0.021) and shrubs (n=473, p=0.006), with slopes comparable to those predicted with the model. The results suggest that semi-natural NPP in GB depends positively upon N_{dep}, in a manner that agrees quantitatively with N14CP predictions. Calculations with the model, using modelled temporal variation in N_{dep}, indicate that fertilisation by N_{dep} caused average increases in semi-natural NPP over the period 1800 to 2010 of 30% for shrubs, 71% for herbs, and 91% for broadleaved trees. Combined with previous published results for forests, our findings suggest a general and widespread vegetation response to fertilisation by N_{dep}.

Key words: Net primary production · Nitrogen deposition · Modelling · Grass · Bracken · Shrubs · Long-term change

Introduction

The net primary productivity (NPP) of an ecosystem can be defined as the difference between the annual carbon gain from the atmosphere in plant photosynthesis and the annual carbon (C) loss in plant respiration (Chapin *et al*. 2006; Schlesinger & Bernhardt 2013). It is a key ecosystem flux (gC m^{-2} a^{-1}), equivalent to the net amount of carbon (C) fixed per year, and strongly related to the amount of C, with its associated elements, transferred from living biomass to the soil each year. In agricultural systems it is strongly related to yield. Another important aspect is the association between NPP and plant species diversity; the well-known unimodal model of Grime (1973a,b) postulates maximum species richness at intermediate NPP, although debate about this relationship continues (Adler *et al.* 2012; Fraser *et al.* 2015). The modelling and prediction of NPP is a crucial activity in trying to understand natural and agricultural ecosystems, and to predict how they might respond to environmental change, and models need to be tested against data where possible.

The main factors usually considered to determine, or limit, NPP are vegetation type, light, temperature, and the availability of water and nutrients (Chapin *et al.* 2011; Schlesinger & Bernhardt, 2013). In temperate natural and semi-natural (i.e. managed but not fertilised) ecosystems, N is the nutrient element that is most often limiting, according to evidence from experimental nutrient additions at individual locations (Elser *et al.* 2007; LeBauer & Treseder 2008; Lee *et al.* 2010; Field *et al.* 2017); see also McGuire *et al*. (1992). It therefore follows that additions of N, via atmospheric deposition (N_{dep}, gN m^{-2} a^{-1}), over recent decades and centuries could have brought about increases in NPP, and consequent changes in ecosystem functioning and composition. Observations of temporal changes in the above-ground biomass of woodlands receiving different levels of N_{dep} support this contention (De Vries *et al.* 2006, 2009, 2015; Magnani *et al.* 2007; Kahle *et al.* 2008; Thomas *et al.* 2010). To demonstrate effects of N_{dep} on non-woodland ecosystems is more difficult, because the biomass does not accumulate, and therefore the most straightforward temporal evidence would comprise repeated measurements of annual production over a sufficiently long time period, at locations with different N_{dep}. Such measurements have not been made, but it may be possible to compare data from different locations with the same vegetation, sampled at different times. Another approach is to test whether spatial variations in annual production are related to spatial variations in N_{dep}. This can be supported by comparison with model expectations, which give an idea of the magnitudes of effects over both space and time.

The ecosystem model, N14CP (Davies *et al.* 2016a,b) was developed to link soil and plant processes and explore and predict how changes in nutrient status may affect pools and fluxes of C, N and phosphorus (P), within 5 km × 5 km grid cells, and over a temporal scale focusing on changes over the last several hundred years. The model simulates the stoichiometrically-interlinked cycles of C, N and P in temperate and boreal ecosystems over space and time, driven by climate (mean annual temperature and precipitation, MAT and MAP), N_{dep} and vegetation class. According to N14CP, fertilisation of GB semi-natural ecosystems by N_{dep} over the past two centuries led to increases in NPP, thence to increased rates of input of organic matter into soils, and an increase in soil organic carbon (SOC) pools and concentrations. The modelling results agree, in terms of both SOC changes with time and the dependence of the changes on N_{dep}, with soil survey-resurvey results for samples collected over the period 1959 to 2010 (Tipping *et al.* 2017).

We tested the model's simulations of NPP in GB, focusing on its prediction that N_{dep} has increased semi-natural NPP. GB is well-suited for this test, in view of the substantial variations in N_{dep} across the island (NEGTAP 2001; Smith *et al*. 2000), and plentiful measurements of plant production, which can be used to estimate NPP. We analysed data from a large number (771) of measurements of shrub, rough grass and bracken production made at different sites over recent decades, the majority of the data coming from Pearsall & Gorham (1956), Marrs *et al*. (1998), Le Duc *et al*. (2000), Milne *et al*. (2002), Rowe *et al*. (2016) and Smart *et al*. (2017). Additional, although relatively few (27), individual site data for woodlands were also analysed, and tree growth data published by the Forestry Commission (2002) for the United Kingdom were also used to estimate average NPP values.

Methods

Production data

The 771 non-woodland sites comprised grassland, shrubland and mixed moorland, most of which are grazed by sheep, managed for grouse shooting, or unmanaged. Except for six sites with more detailed measurements, production estimates were confined to above-ground biomass. The largest single set of results came from Milne *et al*. (2002), who measured above-ground production at 66 sites for shrubs and 17 for herbs in six regions of England and Wales (NE England, NW England, North Pennines, South Pennines, SW England and Wales), giving a total of 597 individual plots. The Milne *et al*. (2002) data form a coherent set, with replication at different sites, eight different dominant plant species or plant development stages, and data for three years (1995-1997). At each site, replicate measurements were made in two or three different years (1995, 1996, 1997) and at between two and nine plots, three in most cases. Other major (results for > 10 sites) non-woodland data sets were from Pearsall & Gorham (1956), Paterson *et al*. (1997), Marrs *et al*. (1998), LeDuc *et al*. (2000), Rowe *et al*. (2016), and Smart *et al*. (2017). The remainder of the data were from studies at fewer than 10 locations each. The sites in these studies refer to areas of representative vegetation, from which quadrats with areas between 0.0625 and 1 m^2 were sampled to quantify above-ground production (g dry mass m^{-2}).

We found NPP data for 27 individual GB woodland sites, obtained by various methods. In three cases, total NPP was estimated from biometric or CO_2 exchange (Reichle, 1981; Morison *et al.* 2012; Fenn *et al.* 2015). In the studies of Ovington & Pearsall (1956), Smart *et al*. (2017) and others, above-ground NPP was determined. We also used data summarising tree wood yields at the national scale (Forestry Commission 2002).

The production measurements were for an initial total of 811 sites, although some were discounted (see Results) so the final total was 796 (see Results). Of the 811 values, 90 were for the period 1932-1989, 646 for 1990-2000, and 75 for 2001-2014. The full collated data set, including information on sampling methods, is given in Table S1, and the geographical distribution of the data is shown in Fig. 1.

Estimation of NPP

The results are expressed and analysed in terms of total net primary production, referred to as NPP, including above and below ground production (ANPP and BNPP), with units of g C m^{-2} a^{-1}, which is what the N14CP model predicts. The literature data included only a few instances in which all components of NPP had been estimated. In the great majority of cases, conversions and assumptions were applied as follows (see Table S1 for the conversion procedure for each sampling site).

(a) For all data reported as dry mass, it was assumed that 50% was C (cf. Schlesinger & Bernhardt 2013).

(b) For herbs, reported production data were mainly measurements of peak above-ground biomass, at sites without grazing or with exclosures erected to prevent grazing (e.g. Milne *et al.* 2002). The above-ground peak biomass was equated with the year's growth, and therefore taken to represent ANPP. The results for *Agrostis-Festuca* grassland reported by Milne *et al.* (2002) were obtained from three clippings per growing season, to simulate grazing. According to Scurlock *et al*. (2002), for grasslands, peak biomass is a "reasonable benchmark indicator of the magnitude of productivity for study sites within a particular sub-biome" (see also Lauenroth *et al.* 1986). The measured above-ground values of dry mass were converted to ANPP (g C m^{-2} a^{-1}), and these were converted to NPP by multiplying by 2.0, this factor being based on measurements (Scurlock *et al.* 2002; Olsen *et al.* 2013; Sims & Singh, 1971) and modelling (Gill *et al.* 2002; Hall *et al.* 1995; del Grosso *et al.* 2008).

(c) For shrubs, sampled at sites without grazing or with exclosures erected to prevent grazing, the current season's new biomass had been identified and isolated after sampling the entire plant by clipping with secateurs, and then quantified. We made the same assumptions as for herbs, i.e. that peak biomass provides a reasonable measure of annual production, and that ANPP can be converted to NPP by multiplying by 2.0.

(d) *Pteridium aquilinum* possesses an extensive rhizome system (Marrs & Watt, 2006), which supplies approximately half of the carbon for the growth of (above-ground) fronds, the rest being obtained by photosynthesis (54 % from rhizome reserves from the data of Williams & Foley 1976). We assumed that the rhizome biomass is essentially the same at the start and end of the year in question (Pakeman *et al*. 1994), which means that the net annual production (dry mass) can be equated with the peak mass of the above-ground standing crop. Thus, NPP was estimated by multiplying the peak dry mass by 0.5 to convert to g C m^{-2} a^{-1}.

(e) In four studies of woodland, total NPP was reported by the original authors, although even in these cases the derivation of NPP involved some assumptions and estimations. In all other cases, we estimated woodland NPP from three partial measures of production, i.e. ANPP, wood increment, and litterfall, using relationships (Fig. S1) derived from data for boreal and temperate woodlands published by Scarascia-Mugnozza *et al*. (2000), Gower *et al*. (2001) and Fenn *et al*. (2015). The calculations yielded an average ANPP/NPP ratio of 0.69 for all the tree plots, which means that 31% of the production is below-ground. This approach ignores the successional state of the woodland, and the tendency for NPP to rise then decline as trees mature (Ovington, 1962; Peterken & Newbould, 1966; Gower *et al.* 2001). Clark *et al*. (2001) discuss in detail the problems inherent in estimating woodland NPP.

Modelling with N14CP

A full description of the N14CP model is available in Davies *et al*. (2016a). A brief summary, with a focus on NPP is provided here. N14CP describes plant-soil pools and fluxes of C, N and P, driven by climate, N_{dep}, sulphur deposition (S_{dep}), base cation deposition (BC_{dep}), weathering of base cations (BC) and P, and known or assumed vegetation history. The model simulates on a quarterly time step the growth and decay of plant biomass, N fixation, the production of litter and its incorporation into soil organic matter (SOM), the immobilisation of nutrients (N, P) by SOM, SOM turnover, leaching losses, and denitrification. N fixation is positively related to temperature and P availability, but does not depend on vegetation type. It is down-regulated by N_{dep} such that no additional N from N_{dep} becomes available until the N_{dep} rate outstrips the potential fixation rate.

Four vegetation classes are represented: broadleaved trees, needle-leaved trees, herbs and shrubs, with varying stoichiometric demands and litter characteristics based on literature values (Tipping *et al.* 2012). Bracken was modelled as a herb. Plant biomass is divided into coarse and fine tissues; the C:N:P stoichiometry of the former (wood and coarse roots) is constant, while the stoichiometry of the latter varies with N and P availability. Biomass is not divided into above and below ground fractions, and only total NPP is simulated. Following von Liebig's Law of the Minimum, NPP is determined by one of four factors, MAT, MAP, N availability, or P availability. First, the maximum NPP is calculated dependent upon MAT or MAP, maximum NPP being estimated by quantile regression, taking the 90% quantile of NPP data collated by Chapin *et al*. (2011), as functions of MAP and MAT (Davies *et al.* 2016a). Then, if nutrients are insufficient to meet the stoichiometric requirements of the maximum plant growth, whichever nutrient is in the shorter supply is taken to be limiting. Plant growth occurs in the second and third quarters of each year, and therefore there is no variation in growing season length.

Davies *et al*. (2016a) performed a non-site-specific parameterisation of the model by fitting plot scale soil and soil water C, N and P data (pools and fluxes) for 44 sites vegetated with broadleaved trees, needle-leaved trees, herbs and shrubs in northern Europe, then tested the model against data from a separate set of 44 northern European sites. The model yielded reasonable average values of element pools and fluxes, but inter-site variations could only be reproduced by allowing the weatherable P pool to vary on a site-by-site basis, suggesting that the availability of site-scale P weathering data may improve prediction. However, in the absence of such data, a crude distinction on the basis of current soil type is used. Separate weatherable P pools, available at the start of soil formation, were assigned to podzols and rankers on the one hand (smaller initial P pool), and all other soil types on the other (larger initial P pool). The parameterisation approach did not use measured NPP data as a constraint; instead, the fitting aimed to achieve an overall mean NPP of 75% of the maximum values, which was roughly in line with available data (Tipping *et al.* 2012; Davies *et al.* 2016a). Whilst this was the applied constraint, the non-site-specific parameterisation produced an average value for the 88 sites that was 83% the maximum NPP.

In the present work, modelling was performed as follows.

(a) The parameterisation by Davies *et al.* (2016a) was used to predict NPP on a 5 km x 5 km grid across GB. Simulations started at the beginning of the Holocene (10,000 BCE), at which point soil C, N and P began to accumulate.

(b) The UK Land Cover Map 2007 (LCM2007, Morton *et al.* 2007) was processed to provide fractional covers on this grid scale for the broad habitat types examined here. We modelled both grass and bracken as herbs, and shrubs were modelled as a separate vegetation class. Using the LCM2007 as a contemporary starting point, we defined the history of each land use fraction in each grid cell using a range of sources and assumptions. Spatially resolved land cover data for 1931 and 1600 was available from Stamp (1931) and Thirsk (1989) allowing us to estimate land use change over these periods for each grid cell fraction. It is assumed in the model land use history that all contemporary needle-leaved trees in GB are plantation, as native pine-leaved forests make up ~1% of the existing stand. The planting date for needle-leaved trees was assumed to be either 1920 or 1955 (determined by changing land fractions between the Dudley Stamp and LCM2007), as these were two periods of marked acceleration in planting across GB (P. Crow, Forest Research, personal communication). Fractions with shrubs in 1600 were assumed to have had the same vegetation prior to this date. Land use fractions classed as rough grassland in 1600 were assumed to have been converted to grassland from broadleaf forest at some point in the past, with a clearance date based on data from Roberts (2013). Fractions classed as broadleaf forest in 1600 were assumed to have been ancient woodland at this time and to have developed naturally, having succeeded from herbaceous plant cover in ~6000 BCE. This succession date was also applied to fractions where forest was cleared prior to 1600. The sensitivity of outputs to these forest clearance and succession assumptions has been explored previously (Tipping *et al.* 2017), where the model outputs were shown to be much more sensitive to variation in contemporary N_{dep} than the assumptions about land use in the distant past.

(c) Climate inputs were defined using gridded Meteorological Office data between 1910 and 2011. For earlier dates, MAP at each site was assumed constant, while MAT variation was estimated using a historical anomaly based on the temperature record for northern Europe derived by Davis *et al*. (2003) from pollen records. Inputs of N_{dep}, S_{dep} and BC_{dep} resolved spatially (5 km x 5 km grid squares) over the period 1800-2010, and taking vegetation type into account, were estimated as in previous modelling reported in Tipping *et al*. (2017).

(d) The initial pool of weatherable P was determined by the soil classification (podzols and rankers vs. other soils) as described above; the fraction of the two soil classes in each grid cell, as calculated from soil survey data (National Soil Resources Institute 2013; Soil Survey of Scotland Staff, 1981), yielded a weighted average weatherable P pool. The weathering of BC in a cell was estimated from the local rock mineralogy.

Statistics

Summary statistics and conventional linear regression analyses were computed with Microsoft Excel. Generalised Linear Models (GLMs, McCullagh & Nelder, 1989) were used to model NPP against cumulative N_{dep} for herbs and shrubs. In view of the skewed nature of the data, even after taking logarithms, a gamma distribution of the data was assumed, rather than the Gaussian distribution. A log link function was employed, which dampens large skew whilst also respecting the bounded nature of the observed data, i.e. that NPP values cannot fall below zero. Regressions for each vegetation type were conducted independently and any evidence of spatial autocorrelation, resulting from close proximity of some sites, was assessed in each case. For both herbs and shrubs, the variation between sites separated by large distances was no different to the variation in sites separated by small distances. All GLMs were fitted using the R statistical programming language (R Core Team 2017). This approach does not yield conventional r^2 values because the parameters are estimated via maximum likelihood rather than by minimising variance through ordinary least squares. Rather, pseudo r^2 values can be obtained that are comparable to conventional r^2 in the sense that they quantify the improvement of the fitted model over a null model and work on a 0 to 1 scale. Here we used McFadden's pseudo r^2, which is based on a ratio of model deviance to null deviance.

Results

In the following text, “measured NPP” means total NPP, i.e. ANPP+BNPP, estimated from measurements, e.g. from peak above-ground biomass, as detailed in Methods. Modelled NPP also refers to total NPP.

The measured NPP values were put into perspective by plotting all values against MAP and MAT (Fig. 2), to allow comparison with the theoretical climate-dependent maximum values, from global observations (see Methods) derived by Davies *et al*. (2016a) for the N14CP model. These maxima apply when nutrients are not limiting. Considering all the data (811 points), there were few exceedances; for MAP only 2% of the values exceeded the theoretical maximum, while for MAT 7% showed exceedance. The fact that in the great majority of cases the NPP values fell below the theoretical climate-based maxima is consistent with NPP in GB semi-natural ecosystems being limited by factors other than climate. This agrees with results obtained with the N14CP model, which predicted that N availability was the factor limiting NPP at all but two of the 811 sites, which were P-limited.

Before further analysis of the results, nine outlier points (two for herbs, seven for shrubs) with high NPP (> 1000 gC m^{-2} a^{-1}) were removed. Furthermore, in 6 cases there was not a match with modelled values, because the land cover map (Morton *et al.* 2011) used in the simulations (see below) did not include the relevant vegetation type in the grid cell in question. These sites were also omitted from the analysis. Therefore, the final data set for analysis comprised 796 points. The removed data are indicated in Table S1.

We compared average measured values of NPP with the corresponding averages of the model predictions (Table 1). The measured estimates for herbs and trees tended to exceed the predictions, whereas the opposite was true for shrubs. The overall measured:modelled ratio was 1.03. Only for the small number of needle-leaved sites was the ratio appreciably different from unity, the measurements exceeding the predictions by a factor greater than 2.0. However when the average measured and predicted values for needle-leaved trees in the national forest inventory were compared, the agreement was much closer (Table 1). For each vegetation class the variability in NPP was high (average relative standard deviation, RSD = 0.43), as expected from previous work by Milne *et al*. (2002). The modelled values were appreciably less variable (average RSD = 0.19), which reflects the simple assumptions of the model, i.e. that NPP depends mainly upon nutrient availability and vegetation class.

The average measured and modelled values for different vegetation classes show the expected relationship (Fig. 3), which arises mainly because trees have higher NPP than non-trees. For herbs and shrubs, there were sufficient data to obtain average NPP values for the 5 km x 5 km grid cells used by the N14CP model (see Methods). If cells with 10 or more measurements were used for averaging, data for a total of 26 cells were obtained, covering a reasonably wide geographical range (Fig. S2). As shown in Fig. 4, the average measured values were significantly correlated with the modelled values ($r^2 = 0.22$, $p = 0.011$), and the regression slope is close to unity. A similar relationship was obtained if cells with five or more measurements were used ($n = 40$, $r^2 = 0.16$, $p = 0.010$), but with 15 measurements as the lower limit, the relationship, although positive, was insignificant ($n = 20$, $p = 0.13$).

The main reason for modelled variation in NPP is variation in N_{dep} and therefore the results of Fig. 4 are consistent with N fertilisation causing increases in NPP. To test this further we regressed measured and modelled NPP against modelled cumulative N_{dep} (to the date of sampling) which is a quantitative indicator of the N-enrichment of a site, taking into account both intensity (N_{dep}) and time (cf. Duprè *et al.* 2010). Since herbs and shrubs were modelled separately, and since they have different average measured:modelled ratios (Table 1), separate testing was performed. Both vegetation classes gave significant positive NPP relationships to N_{dep}, with slopes for the measured data between 50-60% of those from modelled values (Table 2, Fig. 5). The pseudo-r^2 value for the herbs plot was 0.018, that for the shrubs plot was 0.023.

We could not establish any temporal trends in the measured values of NPP, principally because there were no instances in which the same vegetation type was monitored at the same site over a sufficiently long period of time. The longest sequences, which apply to bracken, are for less than 25 years, and little change in NPP is calculated with N14CP for the monitoring periods (Fig. S3). Short term variation in NPP is appreciable; for the 67 sites in the database where NPP had been measured at different times, the average RSD was 0.28, which is already greater than the modelled RSD, and more than half the total RSD of 0.45 (from data in Table 1).

Modelled time series (Fig. 6) suggest substantial changes in NPP over the period 1800-2010, almost entirely driven by the increases in N_{dep}. Very modest NPP increases are calculated in the absence of N_{dep}, resulting from slightly faster nutrient cycling due to increasing temperatures (Tipping *et al.* 2017). The model calculations suggest that fertilisation by N_{dep} caused average increases in semi-natural NPP over the period 1800 to 2010 of 30% for shrubs, 71% for herbs, and 91% for broadleaved trees. Results for needle-leaved trees are not shown, since many sites are in conifer plantations, established in the 20th century, which means that modelling long-term variations in NPP is inappropriate.

Discussion

Measured estimates of NPP largely agree with the modelled values, based on overall average values for different vegetation classes (Table 1, Fig. 3), and a significant regression with a slope near to unity for averaged data within model cells (Fig. 4). Significant regressions of measured NPP against cumulative N_{dep} (Fig. 5) are consistent with the major role of fertilisation by atmospherically deposited N being the main reason for NPP variation. Although the slopes from measured data in Fig. 5 are smaller than the model-based values, the standard errors (Table 2) mean that the ranges overlap, and so we cannot conclude that there is significant disagreement. The extra supply of N has increased the flux of N that can cycle through the soil-plant system, permitting more C to be fixed by photosynthesis. Whereas previous field-based work has shown effects of N_{dep} on trees and, to a lesser extent, shrubs, based on temporal increases in standing biomass (see Introduction), this is the first study to do so for herb ecosystems, and to be based on direct measurements of annual production. Taken together with the previous results, the case for a widespread vegetation response to fertilisation by N_{dep} is strong.

The quantitative agreements between modelled and measured average values, both overall and for different vegetation classes (Table 1, Fig. 3), arise partly because in parameterising the N14CP model Davies *et al*. (2016a) set as a fitting target an average NPP value, at 75% of the mean maximum NPP estimated for the northern European sites for which observations were available (see Methods), and this would tend to generate a modelled average NPP in the right range. Nonetheless, the sites considered in the present work are different from those used for parameterising the model, and so the results provide a partially independent test. The vegetation class variation of Fig. 3 arises because the model assumes the different vegetation classes to have different stoichiometric (C:N:P) compositions.

The NPP-N_{dep} trends of Fig. 5 are obscured by the high degree of scatter in the observations, which leads to low pseudo-r^2 values, and so little of the variance is explained the statistical model. Some of this scatter likely arises because different plant species within a vegetation class have different NPP, as noted by Milne *et al*. (2002), extending to different phases of *Calluna vulgaris*. Milne *et al*. (2002) also noted various dependences among their data on measured physical and soil properties, although not applicable to all species, and not generalisable, since trends that applied to one dominant species did not apply to others. A further contribution to the data scatter is short-term temporal variation, with an RSD of 28%. Scatter could be caused by numerous additional factors including mineral fertilisation (either deliberate or by proximity to other land receiving fertiliser), nutrient deficiencies (P, molybdenum, potassium etc.), herbivory, animal excreta, pests, disease, light availability, ozone levels, soil moisture, soil fauna, and small-scale climatic variation. Scatter could also arise from the approximate nature of the conversion of production values to NPP.

Notwithstanding the high scatter, the trends of Fig. 5 are statistically significant, and provide evidence that N_{dep} affects NPP. This is reinforced by the agreement between measured and modelled averaged NPP (Fig. 4), which arises because the averaging reduces variations among sites and years. Undoubtedly, the best way to investigate variability in NPP would involve a sampling programme that allows appropriate spatial averaging of production data, while covering wide ranges of climatic and biogeochemical factors, and N_{dep}. Although the data assembled here are imperfect in these respects, their large number, and the wide range of N_{dep} covered, justify our meta-analysis.

Milne *et al*. (2002) suggested that the spatial variation of NPP in their dataset reflected the length of the growing season, which would also explain why *Calluna vulgaris* NPP in Scotland, based on data reported by Miller and Watson (1978), Miller (1979) and Grant et al. (1982), was low compared to other parts of GB. However, Milne *et al*. (2002) reported low *Calluna vulgaris* production in SW England, which has the longest growing season in GB. We checked the dependence of measured NPP on latitude (approximately inversely proportional to growing season length) for the averaged data of Fig. 4, and found no relationship. Variations in NPP are better explained by the predictions of N14CP (Fig. 4), which attributes them to variations in N_{dep} and does not take variation in growing season length into account. The model could potentially have predicted that average temperature in the second and third annual quarters was the factor limiting production, but instead it predicted N availability, dependent upon N_{dep}, to be the limiting factor in these unfertilised semi-natural ecosystems.

There have been other studies in GB relevant to the present work. Rowe *et al.* (2012) showed that in semi-natural habitats, readily-mineralisable N (a measure of plant N availability) increased with N_{dep}, which agrees with the assumptions of the N14CP model, and is clearly relevant to plant growth. However, Rowe *et al*. (2014) found that both bicarbonate-extractable P stock and mineralisable N were predictors of Ellenberg N score, taken to be an independent metric of productivity, but that the P variable was superior. In a more spatially-limited study of bracken productivity, Rowe *et al*. (2016) found no dependence on either total soil N or soil organic P. Field *et al.* (2017) found that N additions increased *Calluna vulgaris* growth in an experimental field study. Thus, there is some confirmatory evidence for the limitation of productivity by N, but it is not conclusive. The reason that the N14CP model rarely predicts P limitation is that semi-natural soils in GB are young and calculated still to have significant weatherable apatite.

Although the measured NPP values analysed in this work cover the period 1932 to 2014, i.e. 82 years, 80% referred to the period 1990-2000, and so the agreement achieved with modelled results depends on spatial NPP variation, which according to the model is due to variation in N_{dep}. Therefore, the temporal predictions of Fig. 6 must be justified by time-for-space substitution. However, there is a temporal link through the study of Tipping et al. (2017) who used N14CP to simulate increases in the SOC concentration of GB soils, owing to increased litter inputs associated with increases in NPP caused by N_{dep} fertilisation. Simulated SOC increases over the period 1959 to 2010 agreed with statistically-significant measured changes from sample-resample observations at nearly 2000 field sites (different to those of the present work). Moreover, increases in broad-leaved woodland SOC were highly significantly related to N_{dep} (increases for non-woodland SOC were positively related, but not statistically significant). These results for SOC provide support for the increases in NPP modelled here. Furthermore, the measured and modelled increases in SOC beneath broadleaved trees were found to be greater than those under non-tree vegetation, which is consistent with the larger modelled NPP response of broadleaved trees. Taken together, the present results and the previous SOC modelling provide a coherent quantitative description of GB semi-natural ecosystems, consistent with two large field data sets.

As already pointed out by Tipping et al. (2017), the N14CP modelling shows that the additional storage of SOC, resulting from increased NPP caused by N_{dep}, cannot be regarded as permanent burial, because of SOC turnover. Maintenance of the elevated litter inputs would be needed to prevent the extra SOC returning to the atmosphere over decades to centuries. This implies a need to maintain N_{dep} at present levels, which is undesirable with respect to plant diversity, since that is known to have been reduced by N_{dep} in GB (Stevens *et al* 2004; Maskell *et al.* 2010). Therefore, there is a conflict between the goals of carbon sequestration and the conservation of plant species diversity in semi-natural ecosystems.

Conclusions

- Semi-natural NPP in GB is generally lower than maximum possible values as determined by climate, and modelling with N14CP suggests that this is due to N limitation.
- Mean measured estimates of NPP are in reasonable quantitative agreement with mean modelled values, and the modelled order of NPP by vegetation class (herbs and shrubs < trees) is seen in the data.
- Measured NPP, although displaying high variability, is significantly positively correlated with N_{dep} for both herbs and shrubs, approximately as predicted with N14CP.
- If space-for-time substitution is accepted, there have been substantial (30-100%) increases in NPP in British semi-natural habitats over the past several hundred years, due to N_{dep}.

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Supplementary material

Table S1. The data base

Fig. S1. Regression relationships in data for temperate and boreal broadleaf and conifer woodlands, taken from Scarascia-Mugnozza et al. (2000), Gower et al. (2001) and Fenn et al. (2015).

Fig. S2. Locations of model grid cells containing >= 10 measurements; (see Fig. 4). Left, herbs; right, shrubs.

Fig. S3. Bracken time series; points are measured values, lines are model predictions. Data at Cannock Chase are from two separate areas.

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Table 1. Averaged values of NPP (g C m^{-2} a^{-1}), estimated from observations and modelled with N14CP. Numbers of sites are given by *n*. National averages for woodland are based on Forestry Commission (2002) data for England, Wales and Scotland.

Vegetation class			*measured*		*modelled*		*measured*
	dates	*n*	mean	SD	mean	SD	*/modelled*
Broadleaved trees	1932-2014	19	585	176	444	59	1.32
Needle-leaved trees	1932-2014	6	688	280	305	125	2.25
Herbs	1952-2014	298	378	199	306	48	1.24
Shrubs	1958-2014	473	382	184	419	42	0.91
All	1932-2014	796	388	195	377	72	1.03
Broadleaved national average	1995-1999	-	574	-	497	84	1.15
Needle-leaved national average	1995-1999	-	538	-	463	141	1.16

Table 2. Summary of regression analysis results, ln NPP (gC m^{-2} a^{-1}) vs cumulative N_{dep} (gN m^{-2}). SE = standard error.

Vegetation class		measured			modelled		
		value	SE	p	value	SE	p
Herbs	intercept	5.73	0.09	0.000	5.35	0.016	0.000
	slope	0.00101	0.00043	0.021	0.00188	0.00008	0.000
Shrubs	intercept	5.72	0.084	0.000	5.67	0.008	0.000
	slope	0.00111	0.00040	0.006	0.00179	0.00004	0.000

Figure captions

Fig. 1. Map showing densities of sampling sites within 20 km x 20 km squares (16 model grid cells). See Table S1 for details.

Fig. 2. Measured NPP compared with (a) MAP limits and (b) MAT limits used in the N14CP model. The limits, shown by solid lines, are fits of the 90% quantiles of reported NPP values collated by Chapin *et al*. (2011). Estimated NPP values at individual sites are shown by open circles.

Fig. 3. Measured vs modelled mean NPP for different vegetation classes, using data from Table 1. Open circles are averages from individual sites (needle-leaved trees omitted), filled ones are Forestry Commission (2002) data. Key: B = broadleaved trees, N = needle-leaved trees, H = herbs, S = shrubs. The 1:1 line is shown.

Fig. 4. Average measured vs modelled NPP for 5km x 5km grid cells with 10 or more observations. The time periods covered for each point were up to 17 years, although most were for 3 years, between 1978 and 1997. All but one of the 26 points arise from the Milne *et al*. (2002) data set, the other is bracken data from 1978-1996 (Marrs *et al.* 1998). Cell locations are shown in Fig. S2.The open circles show results for herbs, the closed ones for shrubs. Standard errors are shown. The regression line is 1.01x – 17.7, $r^2 = 0.22$, p =0.011, n = 25.

Fig. 5. Regressions of ln NPP vs cumulative N_{dep} for (a) herbs and (b) shrubs. The solid lines indicate regressions of the measured values, the dashed lines are modelled trends. See Table 2 for a summary of the regression statistics. All plotted points are open circles.

Fig. 6. Modelled changes of N_{dep} and NPP over time for herbs (a,d), shrubs (b,e) and broadleaved trees (c,f) in semi-natural land areas of Great Britain. The central line is the mean, dotted lines show 5 and 95 percentiles.

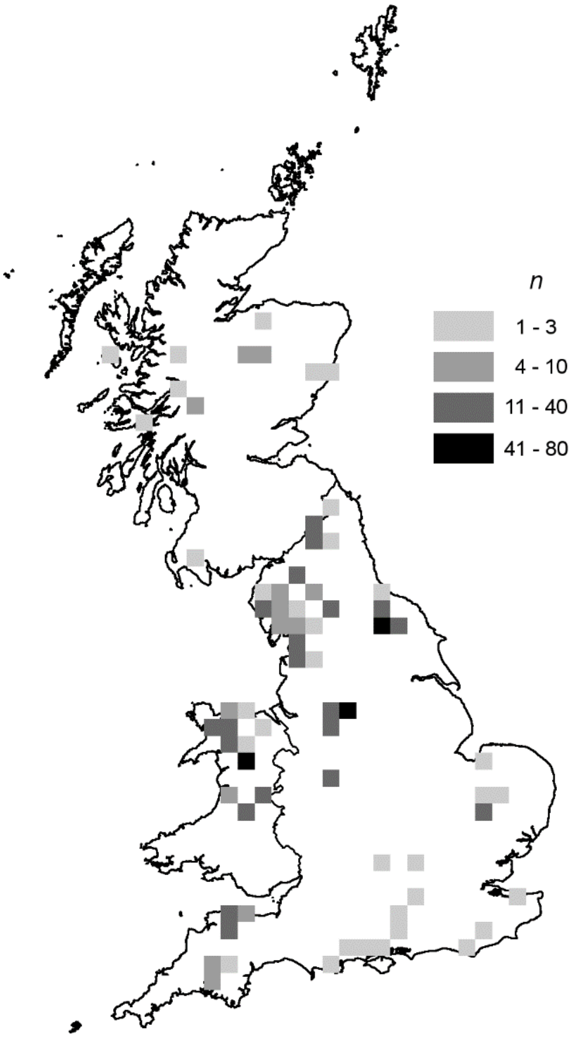

Fig. 1

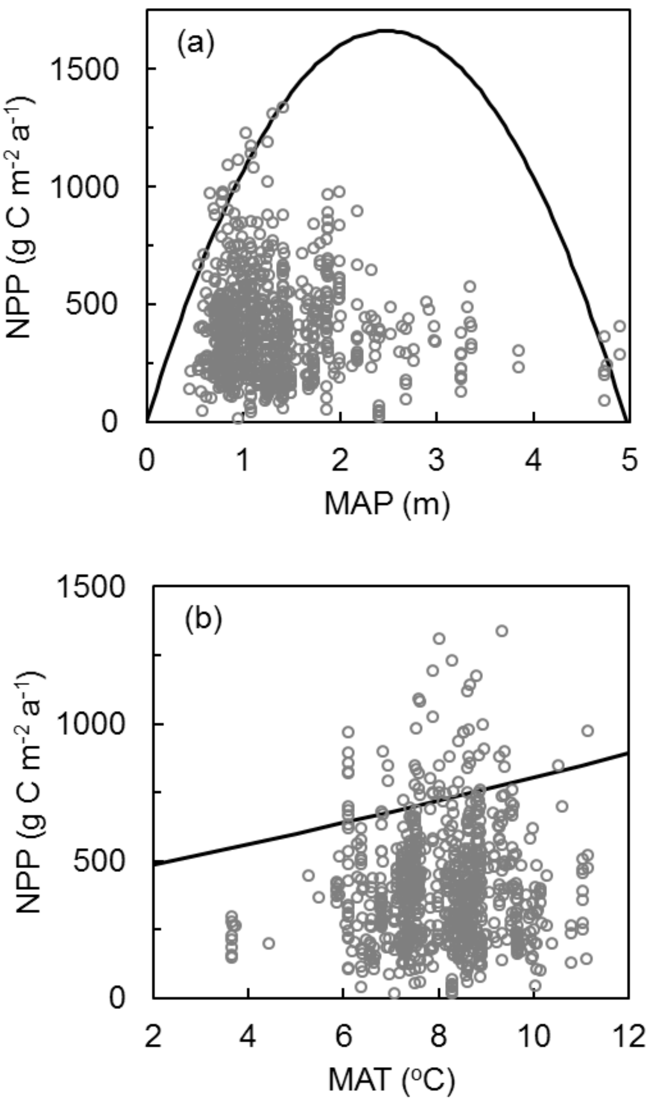
(a)
NPP (g C m^{-2} a^{-1})
0
500
1000
1500
MAP (m)
0
1
2
3
4
5
(b)
NPP (g C m^{-2} a^{-1})
0
500
1000
1500
MAT (^{o}C)
2
4
6
8
10
12

Fig. 2

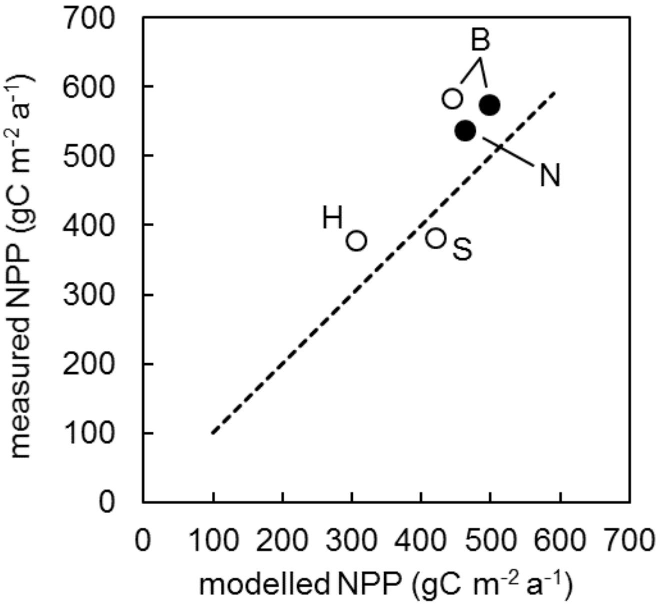
B
N
H
S
measured NPP (gC m-2 a-1)
modelled NPP (gC m-2 a-1)
0
100
200
300
400
500
600
700
0
100
200
300
400
500
600
700

Fig. 3

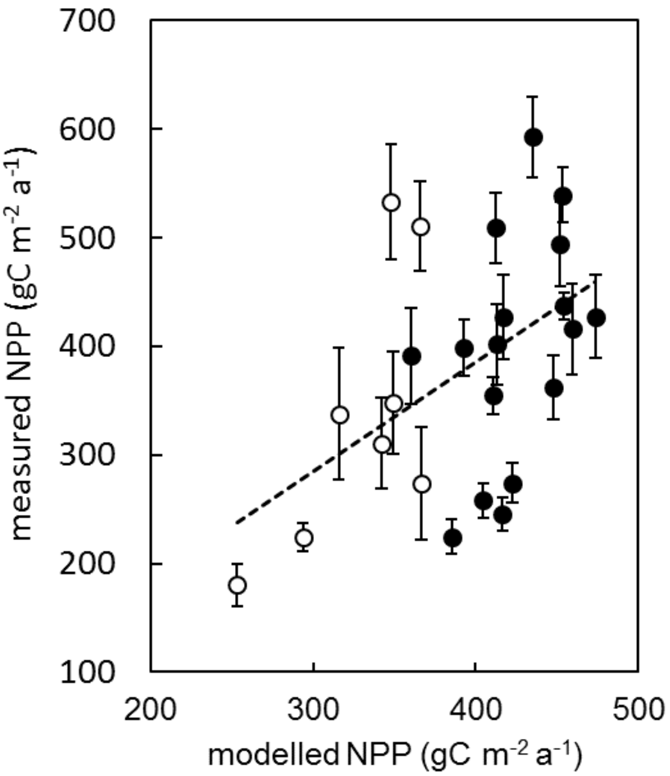
700
600
500
400
300
200
100
200
300
400
500
measured NPP (gC m^{-2} a^{-1})
modelled NPP (gC m^{-2} a^{-1})

Fig. 4

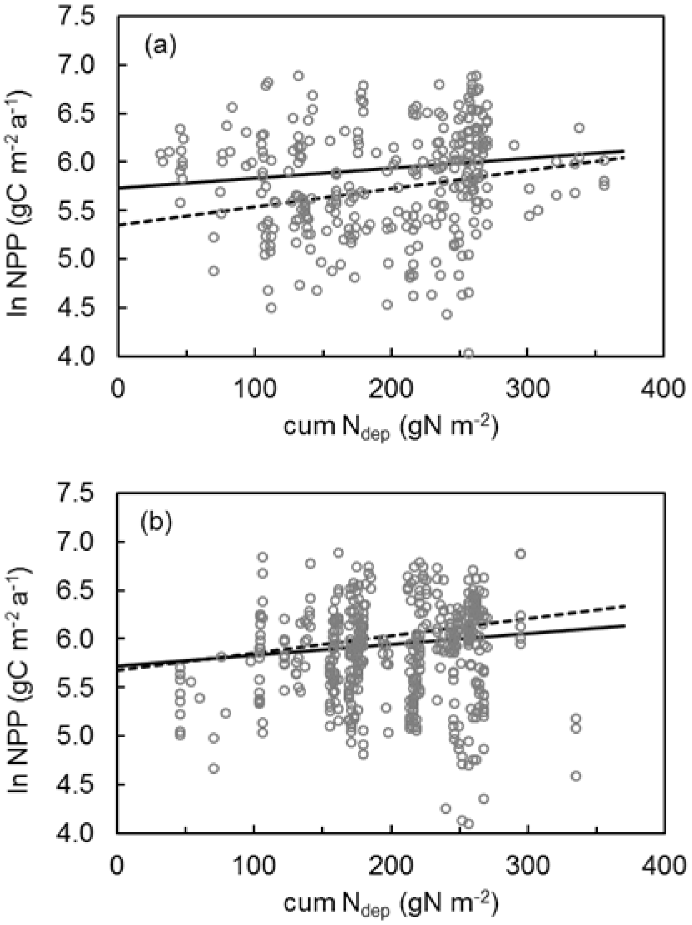
(a)
ln NPP (gC m-2 a-1)
7.5
7.0
6.5
6.0
5.5
5.0
4.5
4.0
0
100
200
300
400
cum Ndep (gN m-2)
(b)
ln NPP (gC m-2 a-1)
cum Ndep (gN m-2)

Fig. 5

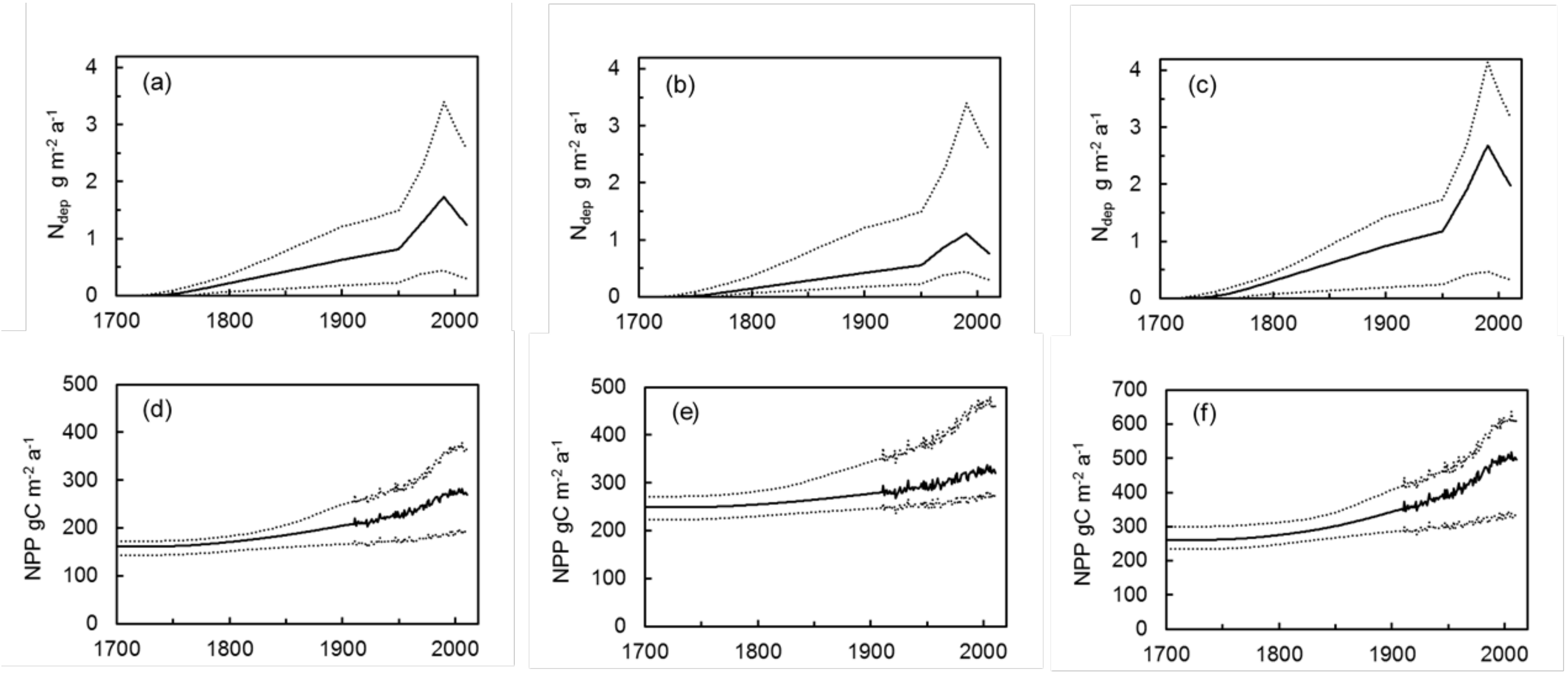
(a)
(b)
(c)
N_{dep} g m^{-2} a^{-1}
0
1
2
3
4
(d)
(e)
(f)
NPP gC m^{-2} a^{-1}
0
100
200
300
400
500
600
700
1700
1800
1900
2000

Fig. 6