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

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21 **Abstract**

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

42

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

45 Introduction

46 The net primary productivity (NPP) of an ecosystem can be defined as the difference between the
47 annual carbon gain from the atmosphere in plant photosynthesis and the annual carbon (C) loss in
48 plant respiration (Chapin *et al.* 2006; Schlesinger & Bernhardt 2013). It is a key ecosystem flux (gC m^{-2}
49 a^{-1}), equivalent to the net amount of carbon (C) fixed per year, and strongly related to the amount of
50 C, with its associated elements, transferred from living biomass to the soil each year. In agricultural
51 systems it is strongly related to yield. Another important aspect is the association between NPP and
52 plant species diversity; the well-known unimodal model of Grime (1973a,b) postulates maximum
53 species richness at intermediate NPP, although debate about this relationship continues (Adler *et al.*
54 2012; Fraser *et al.* 2015). The modelling and prediction of NPP is a crucial activity in trying to
55 understand natural and agricultural ecosystems, and to predict how they might respond to
56 environmental change, and models need to be tested against data where possible.

57 The main factors usually considered to determine, or limit, NPP are vegetation type, light,
58 temperature, and the availability of water and nutrients (Chapin *et al.* 2011; Schlesinger & Bernhardt,
59 2013). In temperate natural and semi-natural (i.e. managed but not fertilised) ecosystems, N is the
60 nutrient element that is most often limiting, according to evidence from experimental nutrient
61 additions at individual locations (Elser *et al.* 2007; LeBauer & Treseder 2008; Lee *et al.* 2010; Field *et*
62 *al.* 2017); see also McGuire *et al.* (1992). It therefore follows that additions of N, via atmospheric
63 deposition (N_{dep} , $\text{gN m}^{-2} \text{a}^{-1}$), over recent decades and centuries could have brought about increases in
64 NPP, and consequent changes in ecosystem functioning and composition. Observations of temporal
65 changes in the above-ground biomass of woodlands receiving different levels of N_{dep} support this
66 contention (De Vries *et al.* 2006, 2009, 2015; Magnani *et al.* 2007; Kahle *et al.* 2008; Thomas *et al.*
67 2010). To demonstrate effects of N_{dep} on non-woodland ecosystems is more difficult, because the
68 biomass does not accumulate, and therefore the most straightforward temporal evidence would
69 comprise repeated measurements of annual production over a sufficiently long time period, at
70 locations with different N_{dep} . Such measurements have not been made, but it may be possible to
71 compare data from different locations with the same vegetation, sampled at different times. Another
72 approach is to test whether spatial variations in annual production are related to spatial variations in
73 N_{dep} . This can be supported by comparison with model expectations, which give an idea of the
74 magnitudes of effects over both space and time.

75 The ecosystem model, N14CP (Davies *et al.* 2016a,b) was developed to link soil and plant
76 processes and explore and predict how changes in nutrient status may affect pools and fluxes of C, N
77 and phosphorus (P), within $5 \text{ km} \times 5 \text{ km}$ grid cells, and over a temporal scale focusing on changes over
78 the last several hundred years. The model simulates the stoichiometrically-interlinked cycles of C, N

79 and P in temperate and boreal ecosystems over space and time, driven by climate (mean annual
80 temperature and precipitation, MAT and MAP), N_{dep} and vegetation class. According to N14CP,
81 fertilisation of GB semi-natural ecosystems by N_{dep} over the past two centuries led to increases in NPP,
82 thence to increased rates of input of organic matter into soils, and an increase in soil organic carbon
83 (SOC) pools and concentrations. The modelling results agree, in terms of both SOC changes with time
84 and the dependence of the changes on N_{dep} , with soil survey-resurvey results for samples collected
85 over the period 1959 to 2010 (Tipping *et al.* 2017).

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

95 **Methods**

96

97 *Production data*

98

99 The 771 non-woodland sites comprised grassland, shrubland and mixed moorland, most of which are
100 grazed by sheep, managed for grouse shooting, or unmanaged. Except for six sites with more detailed
101 measurements, production estimates were confined to above-ground biomass. The largest single set
102 of results came from Milne *et al.* (2002), who measured above-ground production at 66 sites for
103 shrubs and 17 for herbs in six regions of England and Wales (NE England, NW England, North Pennines,
104 South Pennines, SW England and Wales), giving a total of 597 individual plots. The Milne *et al.* (2002)
105 data form a coherent set, with replication at different sites, eight different dominant plant species or
106 plant development stages, and data for three years (1995-1997). At each site, replicate measurements
107 were made in two or three different years (1995, 1996, 1997) and at between two and nine plots,
108 three in most cases. Other major (results for > 10 sites) non-woodland data sets were from Pearsall &
109 Gorham (1956), Paterson *et al.* (1997), Marrs *et al.* (1998), LeDuc *et al.* (2000), Rowe *et al.* (2016), and
110 Smart *et al.* (2017). The remainder of the data were from studies at fewer than 10 locations each. The
111 sites in these studies refer to areas of representative vegetation, from which quadrats with areas
112 between 0.0625 and 1 m² were sampled to quantify above-ground production (g dry mass m⁻²).

113 We found NPP data for 27 individual GB woodland sites, obtained by various methods. In three
114 cases, total NPP was estimated from biometric or CO₂ exchange (Reichle, 1981; Morison *et al.* 2012;
115 Fenn *et al.* 2015). In the studies of Ovington & Pearsall (1956), Smart *et al.* (2017) and others, above-
116 ground NPP was determined. We also used data summarising tree wood yields at the national scale
117 (Forestry Commission 2002).

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

123

124 *Estimation of NPP*

125

126 The results are expressed and analysed in terms of total net primary production, referred to as NPP,
127 including above and below ground production (ANPP and BNPP), with units of g C m⁻² a⁻¹, which is
128 what the N14CP model predicts. The literature data included only a few instances in which all

129 components of NPP had been estimated. In the great majority of cases, conversions and assumptions
130 were applied as follows (see Table S1 for the conversion procedure for each sampling site).

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

133 (b) For herbs, reported production data were mainly measurements of peak above-ground
134 biomass, at sites without grazing or with exclosures erected to prevent grazing (e.g. Milne *et al.* 2002).
135 The above-ground peak biomass was equated with the year's growth, and therefore taken to
136 represent ANPP. The results for *Agrostis-Festuca* grassland reported by Milne *et al.* (2002) were
137 obtained from three clippings per growing season, to simulate grazing. According to Scurlock *et al.*
138 (2002), for grasslands, peak biomass is a "reasonable benchmark indicator of the magnitude of
139 productivity for study sites within a particular sub-biome" (see also Lauenroth *et al.* 1986). The
140 measured above-ground values of dry mass were converted to ANPP ($\text{g C m}^{-2} \text{ a}^{-1}$), and these were
141 converted to NPP by multiplying by 2.0, this factor being based on measurements (Scurlock *et al.* 2002;
142 Olsen *et al.* 2013; Sims & Singh, 1971) and modelling (Gill *et al.* 2002; Hall *et al.* 1995; del Grosso *et al.*
143 2008).

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

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

156 (e) In four studies of woodland, total NPP was reported by the original authors, although even
157 in these cases the derivation of NPP involved some assumptions and estimations. In all other cases,
158 we estimated woodland NPP from three partial measures of production, i.e. ANPP, wood increment,
159 and litterfall, using relationships (Fig. S1) derived from data for boreal and temperate woodlands
160 published by Scarascia-Mugnozza *et al.* (2000), Gower *et al.* (2001) and Fenn *et al.* (2015). The
161 calculations yielded an average ANPP/NPP ratio of 0.69 for all the tree plots, which means that 31%
162 of the production is below-ground. This approach ignores the successional state of the woodland, and

163 the tendency for NPP to rise then decline as trees mature (Ovington, 1962; Peterken & Newbould,
164 1966; Gower *et al.* 2001). Clark *et al.* (2001) discuss in detail the problems inherent in estimating
165 woodland NPP.

166

167 *Modelling with N14CP*

168

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

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

191 Davies *et al.* (2016a) performed a non-site-specific parameterisation of the model by fitting
192 plot scale soil and soil water C, N and P data (pools and fluxes) for 44 sites vegetated with broadleaved
193 trees, needle-leaved trees, herbs and shrubs in northern Europe, then tested the model against data
194 from a separate set of 44 northern European sites. The model yielded reasonable average values of
195 element pools and fluxes, but inter-site variations could only be reproduced by allowing the
196 weatherable P pool to vary on a site-by-site basis, suggesting that the availability of site-scale P

197 weathering data may improve prediction. However, in the absence of such data, a crude distinction
198 on the basis of current soil type is used. Separate weatherable P pools, available at the start of soil
199 formation, were assigned to podzols and rankers on the one hand (smaller initial P pool), and all other
200 soil types on the other (larger initial P pool). The parameterisation approach did not use measured
201 NPP data as a constraint; instead, the fitting aimed to achieve an overall mean NPP of 75% of the
202 maximum values, which was roughly in line with available data (Tipping *et al.* 2012; Davies *et al.*
203 2016a). Whilst this was the applied constraint, the non-site-specific parameterisation produced an
204 average value for the 88 sites that was 83% the maximum NPP.

205 In the present work, modelling was performed as follows.

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

209 (b) The UK Land Cover Map 2007 (LCM2007, Morton *et al.* 2007) was processed to provide
210 fractional covers on this grid scale for the broad habitat types examined here. We modelled both grass
211 and bracken as herbs, and shrubs were modelled as a separate vegetation class. Using the LCM2007
212 as a contemporary starting point, we defined the history of each land use fraction in each grid cell
213 using a range of sources and assumptions. Spatially resolved land cover data for 1931 and 1600 was
214 available from Stamp (1931) and Thirsk (1989) allowing us to estimate land use change over these
215 periods for each grid cell fraction. It is assumed in the model land use history that all contemporary
216 needle-leaved trees in GB are plantation, as native pine-leaved forests make up ~1% of the existing
217 stand. The planting date for needle-leaved trees was assumed to be either 1920 or 1955 (determined
218 by changing land fractions between the Dudley Stamp and LCM2007), as these were two periods of
219 marked acceleration in planting across GB (P. Crow, Forest Research, personal communication).
220 Fractions with shrubs in 1600 were assumed to have had the same vegetation prior to this date. Land
221 use fractions classed as rough grassland in 1600 were assumed to have been converted to grassland
222 from broadleaf forest at some point in the past, with a clearance date based on data from Roberts
223 (2013). Fractions classed as broadleaf forest in 1600 were assumed to have been ancient woodland at
224 this time and to have developed naturally, having succeeded from herbaceous plant cover in ~6000
225 BCE. This succession date was also applied to fractions where forest was cleared prior to 1600. The
226 sensitivity of outputs to these forest clearance and succession assumptions has been explored
227 previously (Tipping *et al.* 2017), where the model outputs were shown to be much more sensitive to
228 variation in contemporary N_{dep} than the assumptions about land use in the distant past.

229 (c) Climate inputs were defined using gridded Meteorological Office data between 1910 and
230 2011. For earlier dates, MAP at each site was assumed constant, while MAT variation was estimated

231 using a historical anomaly based on the temperature record for northern Europe derived by Davis *et*
232 *al.* (2003) from pollen records. Inputs of N_{dep} , S_{dep} and BC_{dep} resolved spatially (5 km x 5 km grid
233 squares) over the period 1800-2010, and taking vegetation type into account, were estimated as in
234 previous modelling reported in Tipping *et al.* (2017).

235 (d) The initial pool of weatherable P was determined by the soil classification (podzols and
236 rankers vs. other soils) as described above; the fraction of the two soil classes in each grid cell, as
237 calculated from soil survey data (National Soil Resources Institute 2013; Soil Survey of Scotland Staff,
238 1981), yielded a weighted average weatherable P pool. The weathering of BC in a cell was estimated
239 from the local rock mineralogy.

240

241 *Statistics*

242

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

258 Results

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

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

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

278 We compared average measured values of NPP with the corresponding averages of the model
279 predictions (Table 1). The measured estimates for herbs and trees tended to exceed the predictions,
280 whereas the opposite was true for shrubs. The overall measured:modelled ratio was 1.03. Only for the
281 small number of needle-leaved sites was the ratio appreciably different from unity, the measurements
282 exceeding the predictions by a factor greater than 2.0. However when the average measured and
283 predicted values for needle-leaved trees in the national forest inventory were compared, the
284 agreement was much closer (Table 1). For each vegetation class the variability in NPP was high
285 (average relative standard deviation, RSD = 0.43), as expected from previous work by Milne *et al.*
286 (2002). The modelled values were appreciably less variable (average RSD = 0.19), which reflects the
287 simple assumptions of the model, i.e. that NPP depends mainly upon nutrient availability and
288 vegetation class.

289 The average measured and modelled values for different vegetation classes show the
290 expected relationship (Fig. 3), which arises mainly because trees have higher NPP than non-trees. For
291 herbs and shrubs, there were sufficient data to obtain average NPP values for the 5 km x 5 km grid

292 cells used by the N14CP model (see Methods). If cells with 10 or more measurements were used for
293 averaging, data for a total of 26 cells were obtained, covering a reasonably wide geographical range
294 (Fig. S2). As shown in Fig. 4, the average measured values were significantly correlated with the
295 modelled values ($r^2 = 0.22$, $p = 0.011$), and the regression slope is close to unity. A similar relationship
296 was obtained if cells with five or more measurements were used ($n = 40$, $r^2 = 0.16$, $p = 0.010$), but with
297 15 measurements as the lower limit, the relationship, although positive, was insignificant ($n = 20$, $p =$
298 0.13).

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

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

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

323 Discussion

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

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

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

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

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

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

387 Although the measured NPP values analysed in this work cover the period 1932 to 2014, i.e.
388 82 years, 80% referred to the period 1990-2000, and so the agreement achieved with modelled results
389 depends on spatial NPP variation, which according to the model is due to variation in N_{dep} . Therefore,
390 the temporal predictions of Fig. 6 must be justified by time-for-space substitution. However, there is

391 a temporal link through the study of Tipping et al. (2017) who used N14CP to simulate increases in the
392 SOC concentration of GB soils, owing to increased litter inputs associated with increases in NPP caused
393 by N_{dep} fertilisation. Simulated SOC increases over the period 1959 to 2010 agreed with statistically-
394 significant measured changes from sample-resample observations at nearly 2000 field sites (different
395 to those of the present work). Moreover, increases in broad-leaved woodland SOC were highly
396 significantly related to N_{dep} (increases for non-woodland SOC were positively related, but not
397 statistically significant). These results for SOC provide support for the increases in NPP modelled here.
398 Furthermore, the measured and modelled increases in SOC beneath broadleaved trees were found to
399 be greater than those under non-tree vegetation, which is consistent with the larger modelled NPP
400 response of broadleaved trees. Taken together, the present results and the previous SOC modelling
401 provide a coherent quantitative description of GB semi-natural ecosystems, consistent with two large
402 field data sets.

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

411 **Conclusions**

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

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425 Edinburgh) for providing modelled atmospheric nitrogen deposition data. We dedicate this paper to
426 the memory of the late John Milne of the Macaulay Land Use Research (now James Hutton) Institute
427 who pioneered large-scale measurements of plant production across GB and inspired several of the
428 authorship team.

429

430 **Supplementary material**

431 Table S1. The data base

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

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

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

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582 Table 1. Averaged values of NPP ($\text{g C m}^{-2} \text{ a}^{-1}$), estimated from observations and modelled with N14CP.
 583 Numbers of sites are given by n . National averages for woodland are based on Forestry Commission
 584 (2002) data for England, Wales and Scotland.

Vegetation class	dates	n	<u>measured</u>		<u>modelled</u>		<u>measured</u>
			mean	SD	mean	SD	<u>/modelled</u>
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

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

Vegetation class		<u>measured</u>			<u>modelled</u>		
		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

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591 **Figure captions**

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

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

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

601 Fig. 4. Average measured vs modelled NPP for 5km x 5km grid cells with 10 or more observations. The
602 time periods covered for each point were up to 17 years, although most were for 3 years, between
603 1978 and 1997. All but one of the 26 points arise from the Milne *et al.* (2002) data set, the other is
604 bracken data from 1978-1996 (Marrs *et al.* 1998). Cell locations are shown in Fig. S2. The open circles
605 show results for herbs, the closed ones for shrubs. Standard errors are shown. The regression line is
606 $1.01x - 17.7$, $r^2 = 0.22$, $p = 0.011$, $n = 25$.

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

610 Fig. 6. Modelled changes of N_{dep} and NPP over time for herbs (a,d), shrubs (b,e) and broadleaved trees
611 (c,f) in semi-natural land areas of Great Britain. The central line is the mean, dotted lines show 5 and
612 95 percentiles.

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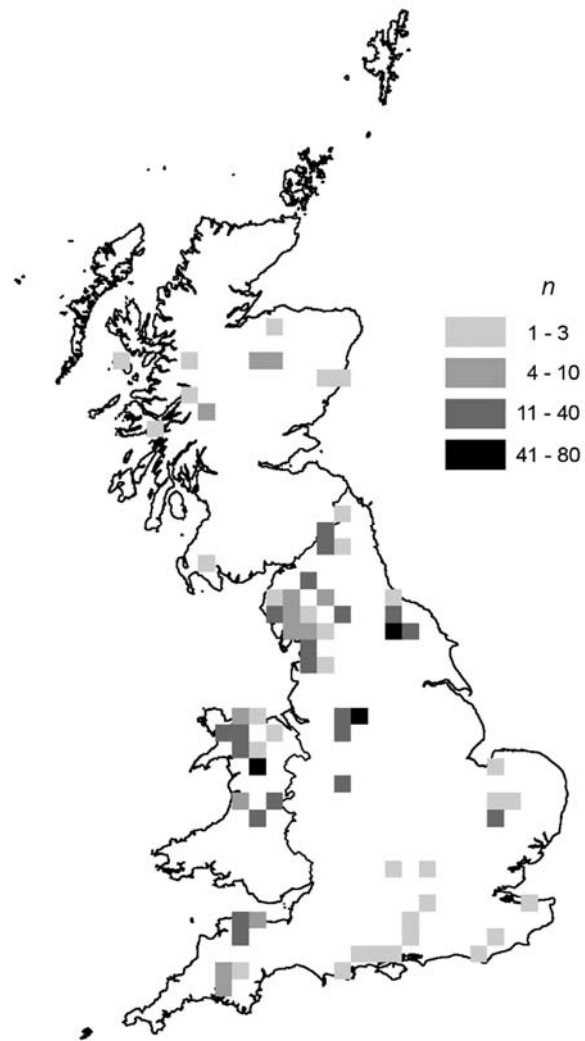
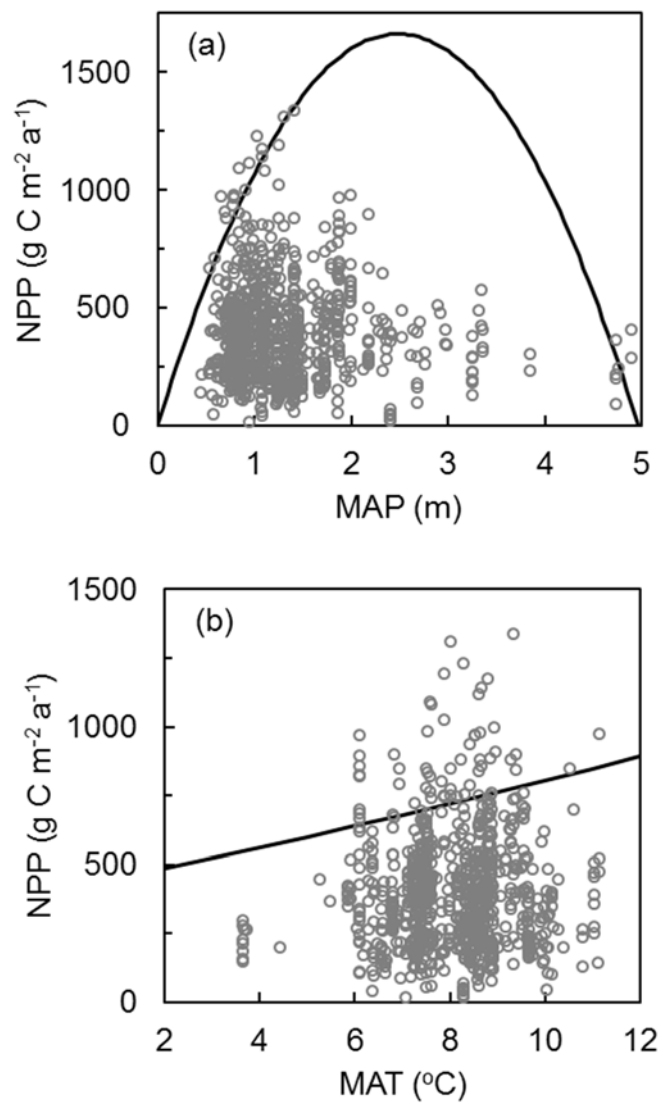
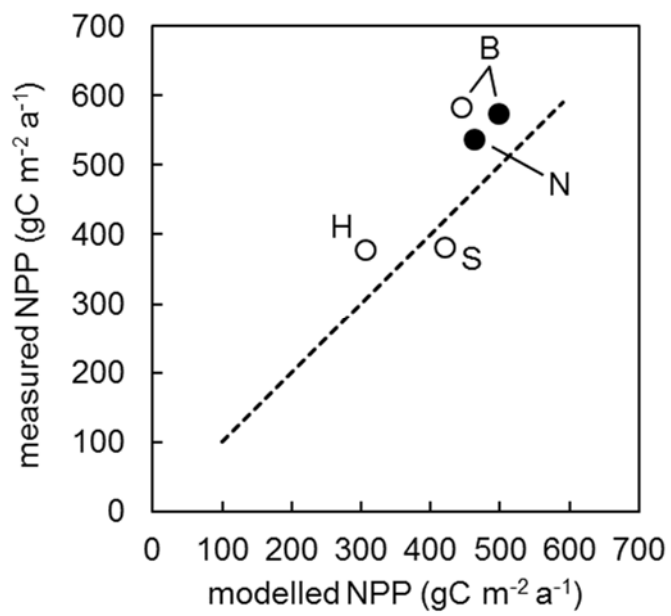


Fig. 1



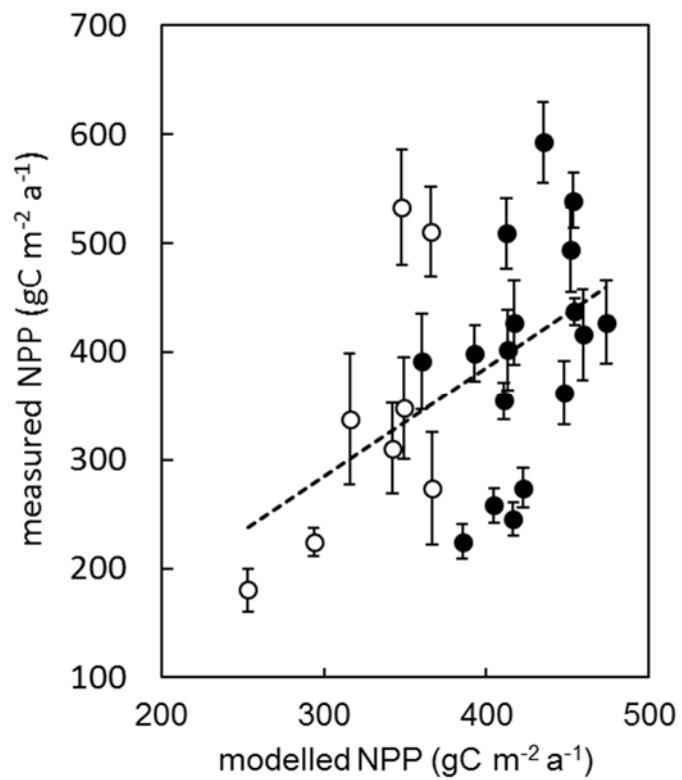
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637 Fig. 2



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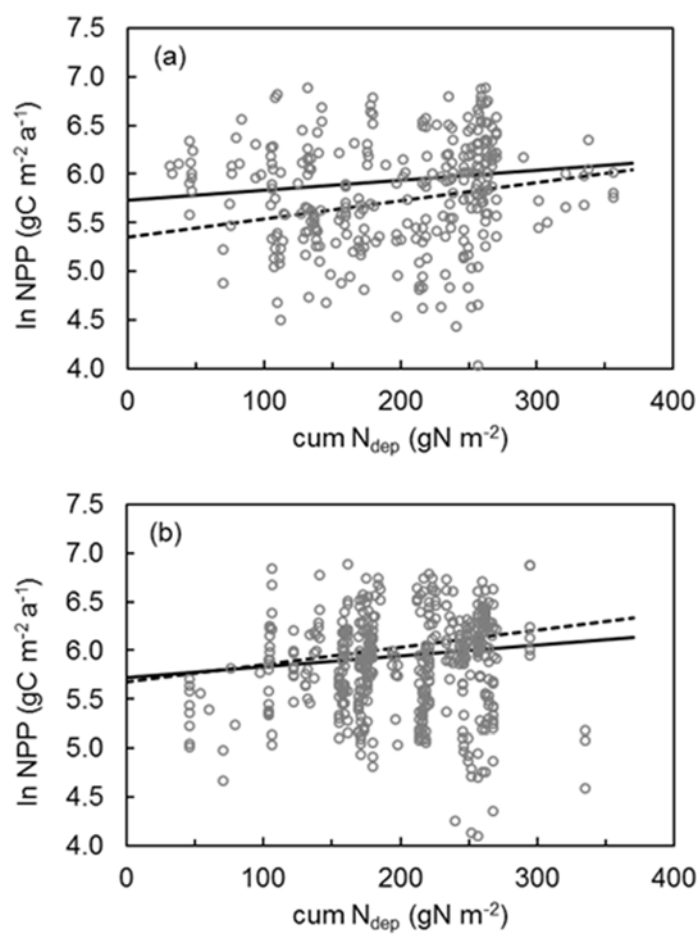
639 Fig. 3



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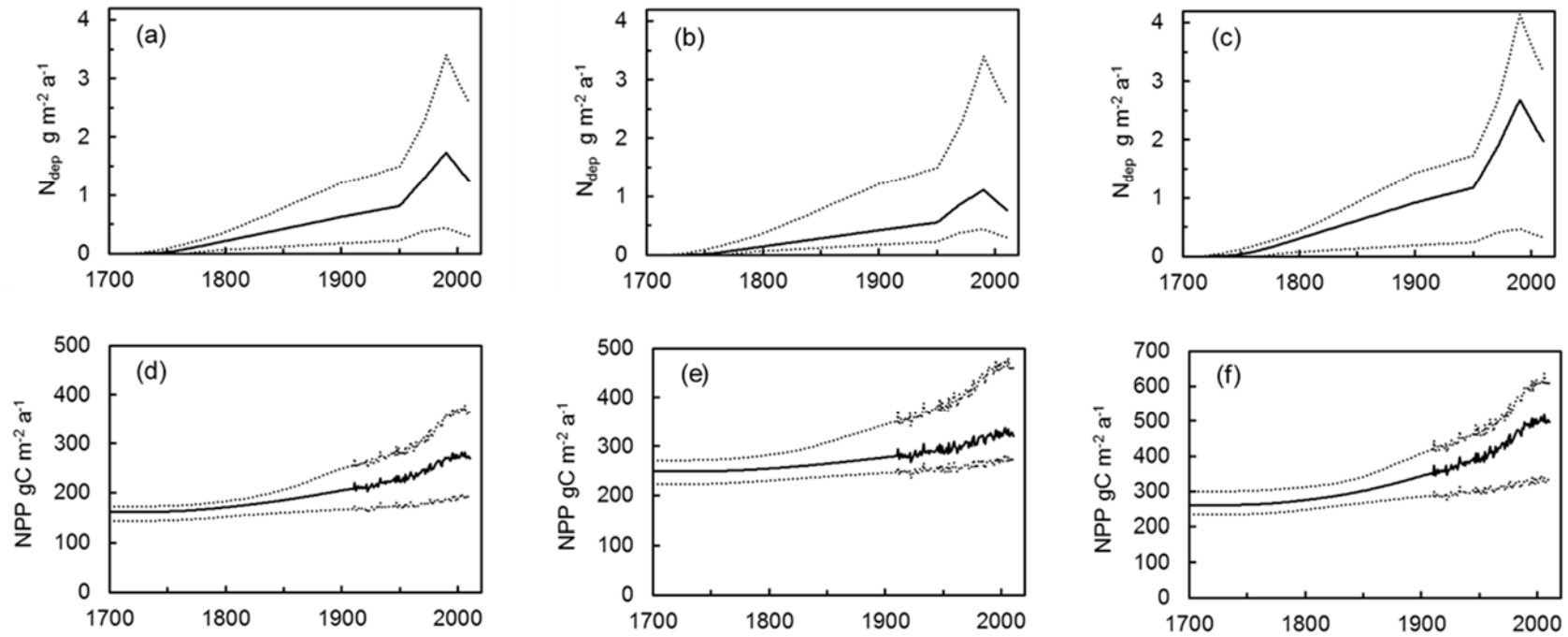
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