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3 **Dependence of ombrotrophic peat nitrogen on phosphorus and climate**

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28 **ABSTRACT**

29 Nitrogen (N) is a key, possibly limiting, nutrient in ombrotrophic peat ecosystems, and enrichment
30 by pollutant N in atmospheric deposition (N_{dep} , $g\ m^{-2}\ a^{-1}$) is of concern with regard to peatland
31 damage. We collated data on the N content of surface (depth ≤ 25 cm, mean 15 cm) ombrotrophic
32 peat (N_{sp}) for 215 sites in the UK and 62 other sites around the world, including boreal, temperate
33 and tropical locations (wider global data), and found N_{sp} to range from 0.5 % to 4%. We examined
34 the dependences of N_{sp} on surface peat phosphorus (P) content (P_{sp}), mean annual precipitation
35 (MAP), mean annual temperature (MAT) and N_{dep} . Linear regression on individual independent
36 variables showed highly significant ($p < 0.001$) correlations of N_{sp} with P_{sp} ($r^2 = 0.23$) and MAP ($r^2 =$
37 0.14), and significant ($p < 0.01$) but weaker correlations with MAT ($r^2 = 0.03$) and N_{dep} ($r^2 = 0.03$). A
38 multiple regression model using log-transformed values explained 36% of the variance of the UK
39 data, 84% of the variance of the wider global data, and 47% of the variance of the combined data, all
40 with high significance ($p < 0.001$). In all three cases, most of the variance was explained by P_{sp} and
41 MAP, but in view of a positive correlation between MAP and MAT for many of the sites, a role for
42 MAT in controlling N_{sp} cannot be ruled out. There is little evidence for an effect of N_{dep} on N_{sp} . The
43 results point to a key role of P in N fixation, and thereby C fixation, in ombrotrophic peats.

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45 **Key words:**

46 peat; ombrotrophic; nitrogen; phosphorus; climate; nitrogen deposition; global; nutrient cycling

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58 **INTRODUCTION**

59 The role of nitrogen (N) in peatland ecosystem dynamics has received much recent attention,
60 primarily due to concern about the effects of anthropogenically-driven elevated atmospheric N
61 deposition (N_{dep}) on carbon sequestration (Turunen et al. 2004; Bragazza et al. 2006; Wu et al. 2014;)
62 and biodiversity (Berendse et al. 2001; Chapman et al. 2003; Limpens et al. 2011). Ombrotrophic
63 peats can have a range of N contents; for example in northern peatlands the range is 0.2% to 3%
64 (Loisel et al. 2014). Such variation likely has implications for carbon fixation, peat functioning and
65 sensitivity to increased N inputs.

66 Peat N contents depend upon inputs from N fixation and atmospheric deposition, and losses by
67 burial into the anaerobic catotelm, leaching, erosion and microbial processing including
68 denitrification. Data compiled by Loisel et al. (2014) imply an average long-term (i.e. thousands of
69 years) burial rate of N in northern peatlands of the order of $0.5 \text{ g m}^{-2} \text{ a}^{-1}$. Since N_{dep} values of this
70 magnitude are a phenomenon of only the last half-century (Vitousek et al., 1997; Fowler et al.,
71 2004), this accumulation is due almost entirely to inputs by N fixation, which must also account for
72 losses by processes other than burial. Nitrogen fixation rates of the required magnitude, or even
73 greater, have indeed been reported for ombrotrophic bogs (Martin and Holding, 1978; Hemond
74 1983; Vile et al., 2014).

75 Whereas N can be acquired by fixation from the atmosphere, P cannot, and this may be significant
76 because P is required for N fixation both as a constituent of the responsible organisms and through
77 the ATP energy-transferring function (Sprent and Raven 1985; Elser et al. 2007; Augusto et al. 2013;
78 Batterman et al. 2013; Reed et al. 2013; Vitousek et al. 2013). Although in most soils, the supply of P
79 is primarily from mineral weathering, this is not the case for ombrotrophic peat, which by definition
80 receives most or all of its inputs from the atmosphere in rain, dust, biological debris from other
81 ecosystems, and the activities of insects, birds and mammals (Rydin and Jeglum 2013; Tipping et al.
82 2014). Therefore P acquisition is likely a major determinant of variations amongst peats with
83 respect to nutrition, including N fixation. Indeed, the role of P as a limiting factor of biomass growth
84 and functioning in peatlands has been clearly demonstrated (Fritz et al. 2012; Larmola et al. 2013;
85 Hill et al. 2014). Whilst there have been no studies looking specifically at P effects on biological N
86 fixation in peatlands, the findings that P additions increase both peatland plant N uptake (Limpens et
87 al. 2004) and microbial N processing (White and Reddy 2000) illustrate the importance of P in
88 peatland N cycling.

89 Given the influences of ambient temperature and moisture regimes on biological N cycling (Rustad
90 et al. 2001; Houlton et al. 2008; Ollivier et al. 2011), it is likely that climate also affects N acquisition

91 by peats. Positive effects of temperature on the N dynamics of peat bogs (Weedon et al. 2012) and
92 on biological N fixation by bryophytic symbionts (Houlton et al. 2008; Lindo et al. 2013) have been
93 demonstrated. Moisture has also been shown to be important for feathermoss-associated N fixation
94 (Gundale et al. 2009; Jackson et al. 2011).

95 To obtain a wider picture of the possible controlling effects of P and climate on the variation of the N
96 content of ombrotrophic peats, we conducted a meta-analysis of data for a total of 277 sites across
97 boreal, temperate and tropical regions.

98

99 METHODS

100 We defined three data sets as follows (Table 1): UK-only, wider global (all data except UK), combined
101 (all data). The data were divided between UK and wider global sites because of the much greater
102 number of UK data (see Results). Values for surface peat total N concentrations (N_{sp}) and surface
103 peat total P concentrations (P_{sp}) measured simultaneously at the same ombrotrophic peatland sites
104 were collated from both published literature and previously unpublished data (Table S1). The
105 previously unpublished data were for UK sites from the Centre for Ecology and Hydrology (A F
106 Harrison pers. comm.), Scottish Soils Database (Hudson *et al.* 2012), and for Finnish sites from the
107 University of Helsinki (R Laiho, pers. comm.). In total our database comprises data from 277
108 ombrotrophic peatland sites including 215 from the UK, 14 from other temperate localities, 14 from
109 boreal regions and 34 from the tropics (see Table S1 and Figure 1). 'Surface' peat was defined as
110 peat sampled from starting depths of 0-10 cm from the surface down to a maximum of 25 cm from
111 the surface. The mean sample depth was 15 cm. Analytical methods for measurements of N_{sp} and
112 P_{sp} for each data source are summarised in Table S1. All peat samples had a C concentration $\geq 40\%$,
113 the mean C concentration across all sites being 51%. We assume that both N and P in these organic
114 rich soils are overwhelmingly in organic forms. None of the sites considered have been afforested or
115 fertilised. For the UK, however, some sites may have been subjected to variable intensities of
116 drainage.

117 Values for mean annual precipitation (MAP, m), mean annual temperature (MAT, °C), and total
118 annual N deposition (N_{dep} , $g\ m^{-2}\ a^{-1}$) were collated for each site (Table S1). For the UK sites, MAP and
119 MAT are 1970-2000 means from the UK Meteorological Office, and N_{dep} data are 2006-2008 means
120 derived by the CBED model (Smith *et al.* 2000). For sites not in the UK, MAP and MAT are either
121 values reported in each publication, or 1930-1960 means from the global data set of Cramer and
122 Leemans (2001), with months summed or averaged to give annual values. For all non-UK sites, N_{dep}
123 data are modelled values for 1993 (Dentener 2006).

124

125 **RESULTS**

126 The collated data cover appreciable ranges of N_{sp} , P_{sp} , MAP, MAT and N_{dep} (Table 1). The values of
127 N_{sp} vary by a factor of 7 and those of P_{sp} by a factor of 19, while the NP ratio ranges from 6 to 138.
128 The mapped data (Figure 1) show that the wider global data come from a broad range of locations,
129 although remote peatland localities such as northern Canada and Russia are under-represented.
130 From Table S1 it can be seen that tropical and UK locations have the highest values of N_{sp} , while NP
131 ratios are lowest for non-UK temperate and boreal sites, and highest for tropical sites, with UK sites
132 in between. Values of MAP and MAT were not significantly correlated for the UK sites, but for the
133 wider global set we found a strong positive correlation which can be parameterised as $MAP = 0.49$
134 $e^{0.077 MAT}$ ($r^2 = 0.96$, $p < 0.001$), and for the combined data set the relationship is $MAP = 0.93 e^{0.053 MAT}$
135 ($r^2 = 0.53$, $p < 0.001$). For neither the UK nor the wider global data set was N_{dep} correlated to MAP or
136 MAT.

137 Regression analysis of the relationships of N_{sp} to individual potential driving variables for the
138 combined data set revealed highly significant ($p < 0.001$) positive correlations with P_{sp} and MAP, and
139 significant ($p < 0.01$) positive correlations with MAT and N_{dep} (Figure 2). However, none of the
140 relationships explained very much of the variation in N_{sp} ($r^2 \leq 0.23$). The NP ratio varied positively
141 and significantly with both MAT ($r^2 = 0.10$, $p < 0.001$) and MAP ($r^2 = 0.11$, $p < 0.001$).

142 Because increased N_{dep} is a fairly recent phenomenon, and most prevalent in temperate regions, we
143 also conducted a separate analysis of the observations made after 2000 for temperate sites only ($n =$
144 68). This increased the value of r^2 from 0.03 for the combined dataset ($n = 277$) to 0.07, but the
145 significance was lower ($p < 0.05$). Furthermore, we found that neither UK N_{sp} nor the UK NP ratio in
146 surface ombrotrophic peat increased with time between 1963 and 2009.

147 We applied the following multiple regression model to the data;

148
$$\log N_{sp} = c1 \times \log P_{sp} + c2 \times \log MAP + c3 \times \log (MAT+10) + c4 \times \log N_{dep} + c5 \quad (1)$$

149 We used log-transformed data to meet the requirements for a normal distribution of the residuals,
150 and added 10 to the MAT values to make them all positive. Because of the imbalance in the spatial
151 distribution of the data, in particular the large number of UK sites, we conducted separate multiple
152 regression analyses of relationships between N_{sp} and the drivers for UK sites only, wider global data,
153 and combined data. The overall picture was the same in each case, with highly significant
154 dependences on P_{sp} and MAP and weaker ones on MAT and N_{dep} (Table 2, Figure 3). Furthermore,
155 the values of the coefficients $c1$ and $c2$ were similar for the three data sets, whereas $c3$ and $c4$ were
156 variable, and only in two cases are their values significant. The model explained 36%, 84% and 47%

157 of the N_{sp} variance in the UK, wider global, and combined data sets respectively. The standard errors
158 in $\log N_{sp}$ (0.12, 0.09, 0.13) were less diverse than the r^2 values.

159 A simplified model using only P_{sp} and MAP explained 29%, 84% and 44% of the variances in the UK,
160 wider global, and combined data sets respectively, with standard errors of 0.12, 0.09 and 0.13 (Table
161 S2). If MAT was used with P_{sp} , the fits were poorer although still highly significant ($p < 0.001$),
162 explaining 27%, 76% and 31% of the variances, with standard errors of 0.12, 0.11 and 0.15 (Table
163 S3).

164 **DISCUSSION**

165 The results show that ombrotrophic peat N_{sp} depends strongly upon P_{sp} and MAP. The results of the
166 multiple regression analyses are consistent with a multiplicative effect, which can be expressed as;

167
$$N_{sp} = k P_{sp}^{c1} MAP^{c2} \quad (2)$$

168 with values of k , $c1$ and $c2$ of 3.9, 0.35 and 0.44 respectively (Table S2). Because $c1$ and $c2$ are both
169 less than one, N_{sp} is most sensitive to P_{sp} and MAP when the two drivers have low values, and the
170 relative response decreases as they get larger (Figure S1). The dependence on P_{sp} is consistent with
171 the need for this element in N fixation (see Introduction), and raises the question as to whether
172 ombrotrophic peats might be P-limited. Indeed P has been found to limit Sphagnum growth at sites
173 receiving high N deposition (Aerts et al. 1992; Gunnarsson and Rydin 2000; Bragazza et al. 2004) and
174 increased investment in P acquisition via phosphatase activity has been observed with peatland N
175 additions (Phuyal *et al.*, 2008).

176 Both temperature and moisture are likely to affect N accumulation, either through N fixation or by
177 affecting other biogeochemical processes in peats (see Introduction). It also seems possible that the
178 MAP effect arises from seasonal variation, with disruption of N cycling processes occurring during
179 times of moisture deficiency - for example, during periods of low temperature and precipitation in
180 boreal winters and periods of low rainfall in temperate summers. Although significant temperature
181 effects appear when only P_{sp} and MAT are used as explanatory variables (Table S3), stronger
182 relationships are found with MAP as the second explanatory variable (Table S2), and when both MAP
183 and MAT are included in the multiple regression model, the former is selected as the more
184 explanatory (Table 2). Interpretation here is confounded by the correlation between MAP and MAT,
185 especially in the wider global data set. However, with the UK data set this correlation is not seen,
186 and it may be significant that this is the one instance where both MAP and MAT are significant
187 predictors (Table 2). Therefore we cannot rule out a separate dependence on MAT of N_{sp} , and it
188 may be that our data are insufficient to draw it out. Nonetheless, it is quite clear that climate exerts
189 a strong effect on the N content of ombrotrophic peats. Furthermore, the positive correlations of
190 peat NP ratio to MAT and MAP suggest that in warmer, wetter regions, proportionally more N is
191 incorporated into surface peat per unit P than in colder, drier regions, which suggests a greater
192 efficiency of P utilisation for N acquisition where climatic conditions favour biological activity.

193 Our results show that N_{sp} does not depend strongly on N_{dep} , even when data are selected to make a
194 fairer comparison by considering only samples collected over a constrained time period, or in a
195 restricted climate zone. There are significant positive responses, but the relationships explain little
196 variation in the data. Although there is evidence that current N deposition influences the N

197 concentration of *Sphagnum* moss (Bragazza et al. 2005), because elevated N_{dep} is a recent
198 occurrence, there probably has not been sufficient time for it to affect N_{sp} as considered here, most
199 of which has instead accumulated via N fixation. Furthermore, it is known that, at least in forest
200 ecosystems, N_{dep} down-regulates N fixation (DeLuca et al., 2008), and this will tend to cancel any
201 effects of deposition.

202 The wider global data set is explained very well by equation (2), but not so well the UK data, in terms
203 of r^2 , and this may partly be a statistical artefact because the wider global data are more evenly
204 spread. The SE values (Tables 2, S2, S3) in predicted N_{sp} are not so different among the three data
205 sets considered, although it is still true that the SE values for the UK-only and combined data sets are
206 higher than that for the wider global set. Whilst to our knowledge the sites included in our analysis
207 were all subject to minimal human disturbance, current and past management practices such as
208 drainage, grazing and burning may have affected their nutrient status (Ramschunder et al. 2009;
209 Jauhiainen et al. 2012; Andersen et al. 2013). This is particularly the case for the UK with its long
210 history of upland management for livestock and grouse rearing (JNCC 2011), and site specific
211 variations in land-management practices may therefore have contributed to the weaker correlation
212 between surface peat N and surface peat P concentrations and climate for the UK sites. Other
213 factors which might account for the unexplained variance in the data include plant type, the effects
214 of atmospherically-deposited contaminants (sulphur, heavy metals, persistent organic pollutants),
215 and the availability of other nutrients.

216 The great current interest in the role of peatlands in regional and global carbon cycles has resulted in
217 the publication of major reviews (e.g. Limpens et al. 2008; Lindsay 2010; Yu 2012), and the
218 development of sophisticated models (Frolking et al. 2010; Heinemeyer et al. 2010), but only
219 recently has attention has been focused on the role of nutrients and nutrient stoichiometry in
220 carbon fixation (Wu and Blodau 2013; Wang et al. 2014, 2015). As noted by Vile et al. (2014),
221 ombrotrophic peats are highly efficient at fixing C, having net primary production values typically of
222 several hundred $\text{g m}^{-2} \text{a}^{-1}$ despite their low nutrient status. This is due to the low nutrient contents
223 of their vegetation and high nutrient use efficiency (Small 1972; Wang et al 2014).

224 However, accumulating peats have to combat the loss of nutrients by burial in the catotelm, and
225 while peatland plants may actively hold nutrients in the top layers of peat bogs (Malmer 1998)
226 perhaps by mycorrhizal uptake (Wang et al. 2014), they still bury a good deal of N (Loisel et al. 2014),
227 which necessitates high rates of N fixation. Indeed, the N fixation rates of 1 to 3 $\text{gN m}^{-2} \text{a}^{-1}$ reported
228 for bogs by Martin and Holding (1978), Hemond (1983) and Vile et al. (2014) are comparable to the
229 highest rates estimated for different global ecosystems by Cleveland et al. (1999). Our results

230 strongly suggest that a key factor in the ability of peatlands to carry out N fixation, and thereby C
231 fixation, is P availability, with important modification by climatic conditions, especially precipitation.
232 It seems especially important to understand how peatlands, especially remote ones, acquire P, and
233 how this may have varied over time, given for example Holocene-scale variations in dust transfer
234 (Cockerton et al. 2014) and recent anthropogenic enhancement of this flux (Neff et al. 2008). The
235 incorporation of N and P cycling into models of peat growth is a pressing need.

236

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244

245

246 **SUPPLEMENTARY INFORMATION**

247 Table S1 Surface peat N and P database

248 Table S2 Multiple regression analysis results P_{sp} and MAP only.

249 Table S3 Multiple regression analysis results P_{sp} and MAT only.

250 Figure S1 Predicted dependence of N_{sp} on P_{sp} at different MAP values ($m\ yr^{-1}$)

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470

471 Table 1. Summary of data. See Table S1 for details.

Data source	n	time period	N _{sp} %	P _{sp} %	N:P	MAP m	MAT °C	N _{dep} g m ⁻² a ⁻¹
UK ¹	215	1963-2009	0.5 - 3.6	0.01 - 0.19	11 - 138	0.8 - 2.8	2.7 - 10.8	0.4 - 3.0
Wider global ²	62	1971-2012	0.5 - 2.9	0.02 - 0.15	6 - 85	0.4 - 4.0	-3.8 - 26.4	0.0 - 1.9
Combined	277	1963-2012	0.5 - 3.6	0.01 - 0.19	6 - 138	0.4 - 4.0	-3.8 - 26.4	0.0 - 3.0

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473 ¹ From: Scottish Soils Database; Emmett et al. 2007; Tipping et al. 2003; AF Harrison pers commun;
474 Hayati and Proctor, 1991

475 ² From: Minkinen et al. 1999; Moore et al. 2008; Bragazza et al. 2005; Turetsky et al. 2000;
476 Pakarinen and Gorham 1984; Richardson et al. 1978; Damman 1978; R Laiho pers commun; Keller et
477 al. 2006; Bragazza and Gerdol 1999; Bragazza and Gerdol 2002; Clarkson et al. 2004a; Clarkson et al.
478 2004b; Bridgham et al. 1998; Hill et al. 2014; Cheesman et al. 2012; Page et al. 1999; Anderson 1983;
479 Pajunen 1994

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483 Table 2. Multiple regression analysis results; dependence of N_{sp} on P_{sp} , MAP, (MAT+10) and N_{dep} for
 484 log-transformed data; coefficients c1-c5 refer to equation (1)

	Variable Coefficient	P_{sp} c1	MAP c2	MAT+10 c3	N_{dep} c4	const c5	r^2	SE	p
UK	Value	0.30	0.35	0.89	-0.09	-0.52	0.36	0.12	1.6×10^{-19}
	SE	0.04	0.07	0.21	0.05	0.27			
	p	1.2×10^{-10}	2.9×10^{-7}	4.4×10^{-5}	0.057	0.055			
Wider global	Value	0.43	0.56	0.03	-0.02	0.51	0.84	0.09	8.2×10^{-22}
	SE	0.07	0.11	0.17	0.03	0.23			
	p	8.2×10^{-8}	2.2×10^{-6}	0.87	0.51	0.032			
Combined	Value	0.33	0.37	0.11	0.09	0.44	0.47	0.13	6.2×10^{-37}
	SE	0.04	0.06	0.10	0.02	0.12			
	p	2.0×10^{-14}	4.2×10^{-9}	0.30	6.0×10^{-5}	3.1×10^{-4}			

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489 **Figure captions**

490

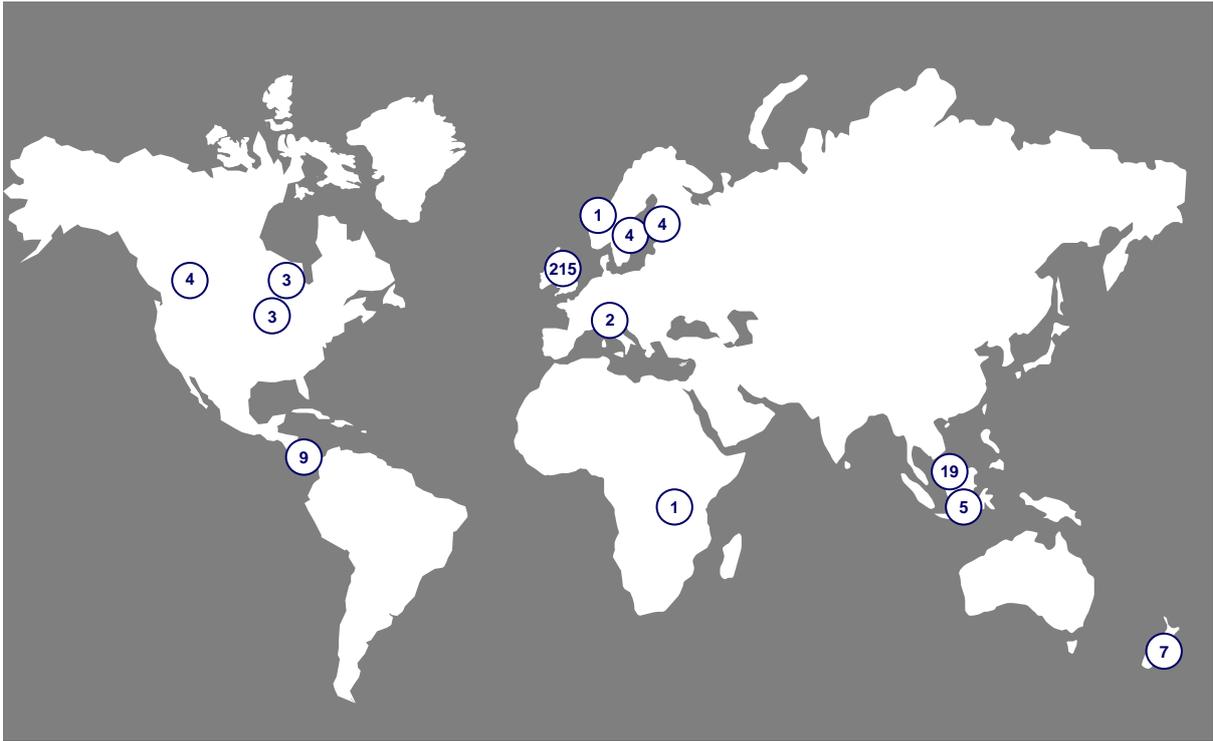
491 **Figure 1.** Map showing ombrotrophic peat sites. The numbers insider the symbols are the numbers
492 of data for each country or region.

493 **Figure 2.** Relationships between surface peat %N (N_{sp}) and surface peat %P (P_{sp}), mean annual
494 precipitation (MAP), mean annual temperature (MAT) and atmospheric N deposition (N_{dep}) for the
495 combined dataset. Trend lines and r^2 are for linear regression ($n = 277$); the regressions are all
496 significant, %P and MAP both $p < 0.001$, MAT and N_{dep} both $p < 0.01$.

497 **Figure 3.** Observed N_{sp} vs. values predicted from linear multiple regressions with P_{sp} , MAT, MAP and
498 N_{dep} as independent variables. The 1:1 lines are shown. Numbers of data points are given in Table 1.

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502 Figure 1

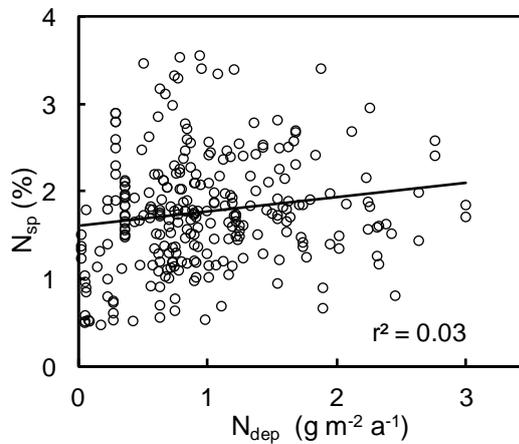
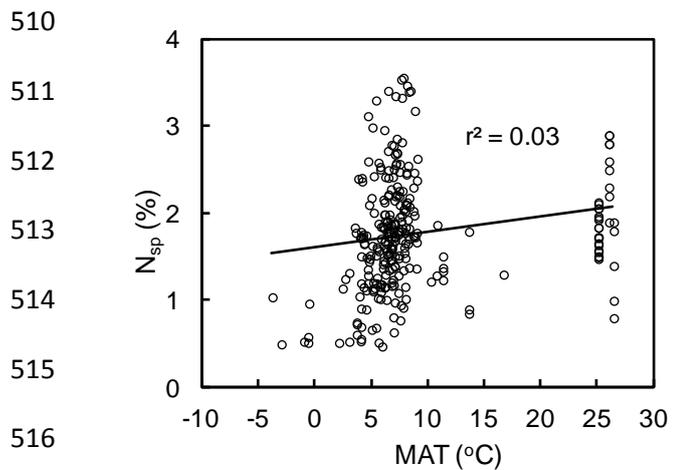
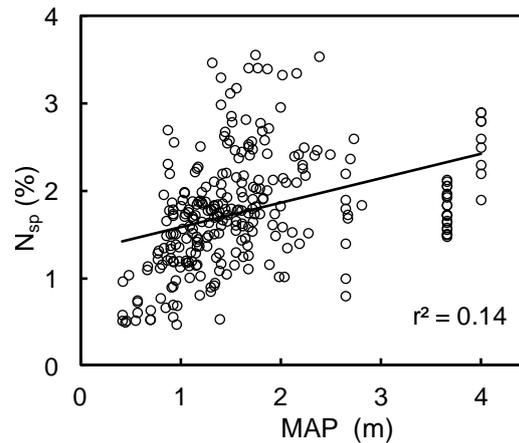
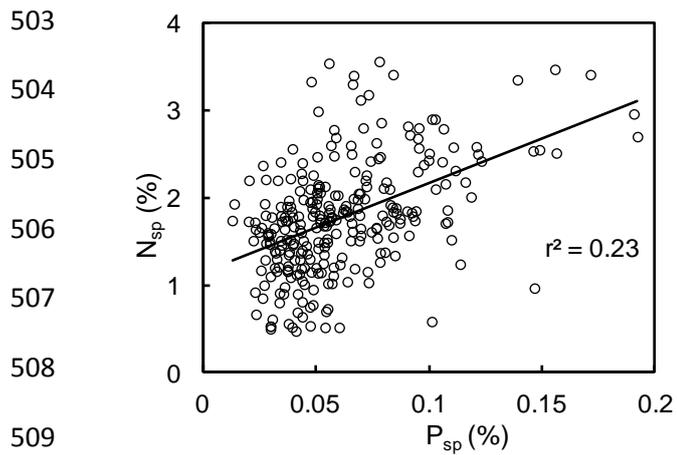
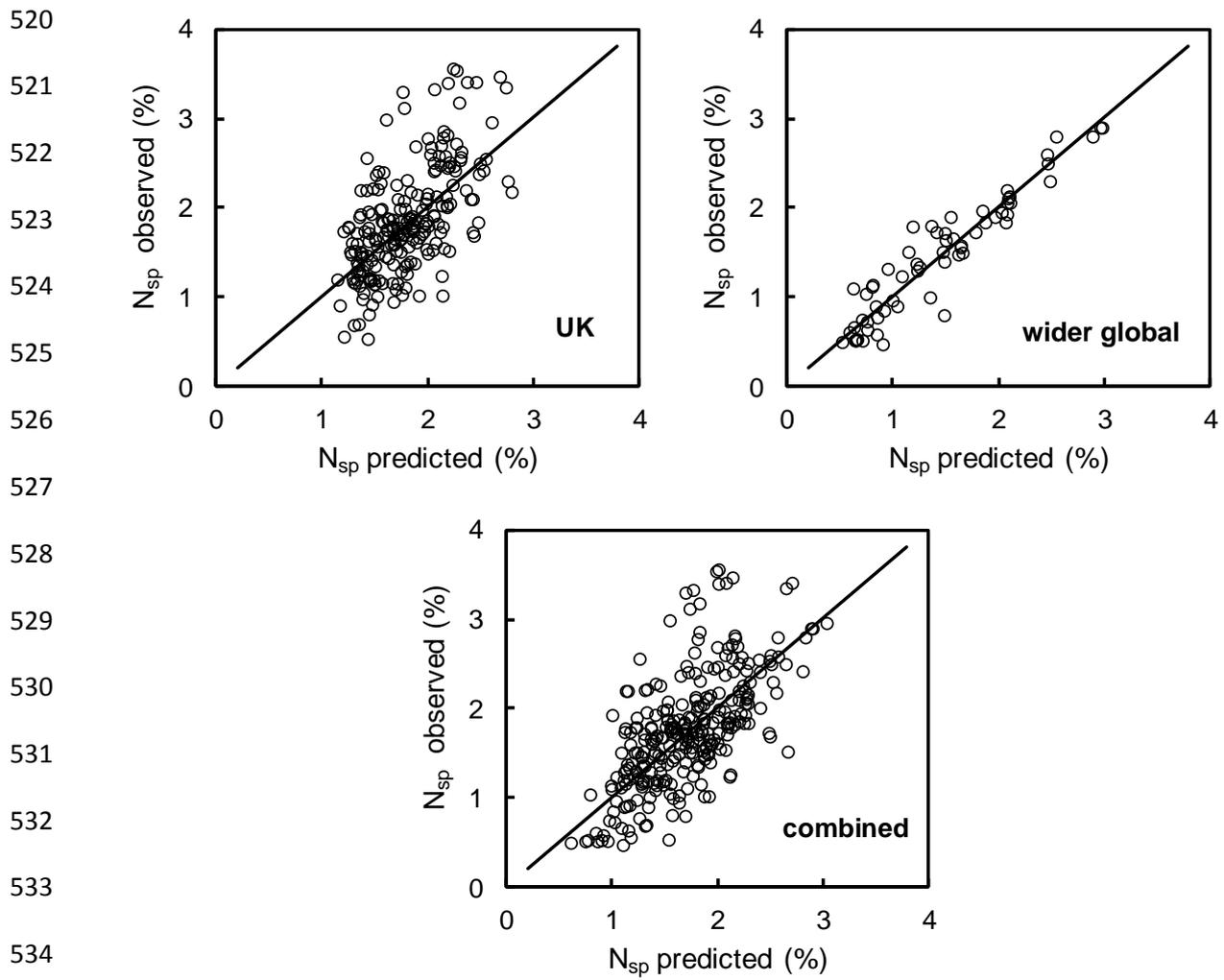


Figure 2



535 Figure 3

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