

1 **Impact of plant invasion and increasing floods on total soil**
2 **phosphorus and its fractions in the Minjiang River estuarine wetlands,**
3 **China**

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20 **Abstract**

21 Plant invasion and increased flooding intensity projected by climate change models can
22 change the soil capacity of marine wetland to store P. This is a key question to the nutrient
23 balances and eutrophication processes of coastal areas, especially in China coastal area that
24 is receiving the freshwaters of a country in fast economical developing process. We studied
25 the impact of changes in flooding intensity and plant invasion on total soil-P concentrations
26 in the Minjiang River estuarine wetland. Flooding had a weak positive effect on soil P-
27 fractions concentrations, but this effect was largely counteracted by the negative effect of
28 salinity. Soil clay concentration and pH, both of which were related more with species
29 community composition than with flooding intensity, were directly related to the P-fraction
30 concentrations. The replacement of the native mangrove community by the invasive plant
31 *Phragmites australis* was related to a decrease in the soil capacity to store P. A suitable
32 management to maintain this wetland area in optimum conditions to act as a natural
33 eutrophication buffer should tend to favor mangrove communities in the new areas that reach
34 more than 220 days y^{-1} of flooding, and a combination of the three tall-grasses communities
35 below this level of flooding.

36 **Keywords** Clay · flooding · invasive plants · *Cyperus malaccensis* · mangrove · *Phragmites*
37 *australis* · N:P · soil P · soil P fractions · soil pH · soil texture · *Scirpus triqueter*

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41 **Introduction**

42 Phosphorus (P) is a crucial element for all living organisms. Next to nitrogen (N), P is the
43 nutrient that most commonly limits plant production in the terrestrial biosphere (Margalef
44 1997; Aerts and Chapin 2000). Several drivers of global change such as N eutrophication,
45 changes in soil use, species invasion or climate change currently have serious impacts on the
46 P cycle and P imbalances and other important bioelemental cycles, such as that of N (Sardans
47 and Peñuelas 2006; Peñuelas et al. 2012 and 2013). The question now arises whether or not
48 P and its imbalances with other nutrients can alter the capacity of Earth to fix C from
49 anthropogenic emissions of carbon dioxide (Peñuelas et al. 2013).

50 Global warming is affecting ocean levels through its impacts on the global water cycle
51 (Schewe et al. 2011; Mendelsohn et al. 2012; Piecuch and Ponte 2014), and water
52 stoichiometry (Sardans et al. 2012a; Sardans and Peñuelas 2014). These effects of global
53 warming can further affect the global P cycle and its stoichiometric relationships with other
54 nutrients, which can then affect community structure and function (Sterner and Elser 2002;
55 Sardans et al. 2012b; Peñuelas et al. 2012 and 2013).

56 The increase in ocean levels could be especially critical for wetland ecosystems
57 (Ramsar 2013). Flooding in these important ecosystems can alter soil contents and the
58 stoichiometric relationships of C, N, P, and sulfur (S) by changing the aerobic/anaerobic
59 biogeochemical equilibrium, nutrient inputs and outputs, and/or the structures of plant
60 communities (Steinman et al. 2012; Recha et al. 2013; Wang et al. 2013), and by altering
61 water flow and fluxes (Zak et al. 2008; McCray et al. 2012). Wetlands are also frequently
62 affected by other drivers of global change such as species invasions that can interact with the
63 increase in flooding duration and intensity to change the capacity of wetlands to store P

64 and/or to change the proportions of different soil-P fractions. Moreover, the expected
65 increase of typhoon events will increase the flood time, water table, soil salinity and anoxic
66 conditions. Furthermore, typhoon events increase litterfall and nutrient cycling in plant-soil
67 system (Wang et al. 2015 submitted).

68 Estuaries and marshes are sinks for the wastewater from human activities that
69 frequently contain high concentrations of P loaded to rivers (Mustafe and Scholz 2011; Wang
70 et al. 2012). Despite the high priority at a global scale of wetland restoration (Jimenez-
71 Carceles et al. 2008; Mustafe and Scholz 2011; Dunne et al. 2011; Zak et al. 2014), wetlands
72 restored on former agricultural land could potentially release accumulated P and become a
73 source of eutrophication (Kjaergaard et al. 2012; Kinsman-Costello et al. 2014). Under
74 increasing intensities of flooding, we should expect higher levels of anoxic conditions, under
75 which increased Fe^{3+} reduction could increase the release of P from Fe^{3+} phosphates
76 (Jimenez-Carceles et al. 2008; Zak et al. 2008; Kjaergaard et al. 2012).

77 Invasions of alien plant species are currently increasing and are a serious threat to
78 global plant diversity (Vitousek et al. 1987; Funk and Vitousek 2007). Most studies that have
79 investigated alien success have identified nutrient availability and the competitive capacities
80 of nutrient uptake and of coping with low levels of nutrients as the key factors accounting
81 for the success of the alien species (Sardans and Peñuelas 2012a, b; Drenovsky et al. 2012).
82 Moreover, alien plants frequently alter soil nutrient concentrations and availability, the
83 decomposition of organic matter, nutrient cycling, and soil stoichiometry (Sardans and
84 Peñuelas 2012a,b; Drenovsky et al. 2012). Invasive plant species, such as the common reed,
85 *Phragmites australis*, are spreading in several Chinese wetlands (Tong et al. 2011; Wang et
86 al. 2014). The success of *P. australis* has been associated with its higher nutrient-use
87 efficiency and up-take capacity than native species (Wang et al. 2014). We hypothesized that

88 increased flooding could have an impact on its invasive success and its interactions with
89 plant-soil P-cycle, which in turn could affect the effect of flooding intensity on the status of
90 soil P in wetlands.

91 China coastal areas receive great amounts of P (Sharpley and Wang 2014; Gao et al.,
92 2015; Li et al., 2015), that have increased by a factor of 2-5 in the period 1970-2000 and
93 threaten to increase additional 30-200% towards 2050 (Strokal et al. 2014). We hypothesized
94 that total P and P-fractions in soil will change in function of flooding intensity and plant
95 community, and therefore the increase or decrease of wetlands capacity to act as a P sink or
96 source in the next decades can be projected in an scenario of flooding enhancement and
97 reduction of wetland surface and enlighten the management possibilities of improving such
98 capacity.

99 We studied soil-P concentrations under different flooding gradients and under the
100 absence/presence of an invasive species in the Minjiang River estuarine tidal wetland to
101 clarify their effects on P concentrations and fraction variations. We aimed to answer the
102 questions: (i) how do increased flooding and different plant communities, including a
103 successful invasive plant species, affect the concentrations and contents of total soil P and
104 the soil P fractions, and (ii) which physicochemical soil properties are involved in these
105 effects?

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119 **Material and Methods**

120 Study areas

121 This study was conducted in the Minjiang River estuarine wetland in southeastern China, in
122 the transition zone of the mid-subtropical and south subtropical zones (25°50'43"-26°9'42"N,
123 119°5'36"-119°41'5"E). The estuary has an area of 476 km² and a relatively warm and wet
124 climate, with a mean annual temperature of 19.7 °C and a mean annual precipitation of 1346
125 mm (Zheng et al. 2006). Many wetlands are distributed in the estuary and along the river.
126 We conducted three experiments in this study (Figure 1).

127 (1) *P. australis* and the native sedges *Scirpus triqueter* L. and *Cyperus malaccensis* var.
128 *brevifolius* Boeckeler are the plant species that dominate the land surface in the Shanyutan
129 wetland and are typically found in the upper (mid to high) portions of mudflats (Liu et al.

130 2006). These three species can grow in both high-flood and low-flood habitats. We
131 established an experimental setup in this wetland at two flooding intensities and with three
132 species communities. The flooding in the studied areas is based on the tide flood, and
133 therefore depends on the distance to sea. Changes in river flow are also important to control
134 the flood, but the main responsible of the differences of flooding intensity across different
135 wetland areas is sea tidal. The high-flood habitats are flooded by intermediate tides ca. 240
136 d^{-1} and are submerged beneath 10-120 cm of water for 0.5-4 h during each tidal inundation.
137 The areas occupied by each species were ca. 8, 9, and 18 hm^2 for *S. triqueter*, *C. malaccensis*,
138 and *P. australis*, respectively. The low-flood habitats are flooded only during spring tides,
139 ca. 80 d^{-1} , and are submerged beneath 10-50 cm of water for 0.5-2 h during each tidal
140 inundation. The areas occupied by each species were ca. 7, 12, and 6 hm^2 for *S. triqueter*, *C.*
141 *malaccensis*, and *P. australis*, respectively. The soil surfaces of both the low- and high-flood
142 habitats of the entire estuarine wetland are exposed at low tide, but the soil remains flooded
143 in some low areas. We analyzed two flooding intensities \times three communities \times six soil
144 layers \times three replicates, for a total of 108 samples. With this experiment we analyzed how
145 different flood intensities are related with differences in soil P concentrations and P-fraction
146 in soils under each one of the three tall-grasses depending on flooding intensity.

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148 (2) Communities of the invasive *P. australis* in the Shanyutan, Bianfuzhou, and Youxizhou
149 wetlands were selected as high-flood, intermediate-flood, and low-flood habitats,
150 respectively, from the coast inland to test the effects of flooding intensity on the total soil-P
151 concentration and content and different P fractions. The high-flood habitat (Shanyutan
152 wetland) is flooded by tides ca. 240 d^{-1} and is submerged beneath 10-120 cm of water for
153 0.5-4 h during each tidal inundation. The intermediate-flood habitat (Bianfuzhou wetland)

154 is flooded by tides ca. 220 d y⁻¹ and is submerged beneath 10-100 cm of water for 0.5-3 h
155 during each tidal inundation. The low-flood habitat (Youxizhou wetland) is flooded by tides
156 ca. 180 d y⁻¹ and is submerged beneath 10-70 cm of water for 0.5-1.5 h during each tidal
157 inundation. We analyzed three flood intensities (the high-flood intensity was the same as
158 that in the first experiment for *P. australis*) × one community × six soil layers × three
159 replicates, for a total of 54 samples (36 were different from those in the first experiment).
160 With this study we analyzed whether or not soils under the invasive species *P. australis* have
161 different P and P-fractions concentrations at different levels of flooding intensity.

162 (3) *P. australis* in the Shanyutan wetland subjected to high-flood intensity has invaded the
163 wetland over the past 30 years and is now the most prevalent plant species occupying the
164 natural habitat of the native mangroves. *P. australis* has spread occupying sites that
165 previously were covered by mangrove communities. Mangroves had not a high density, and
166 humans tend to reduce its density and to allow *P. australis* spreading. We investigated and
167 compared total soil-P concentration and content and different P fractions in the *P. australis*
168 communities and in the natural mangrove habitat in this high-flood habitat. We analyzed one
169 flooding intensity (high) × two communities (the data for *P. australis* were the same as for
170 the high-flood intensity in the first experiment) × six soil layers × three replicates, for a total
171 of 36 samples (18 were different from those in the first experiment). With this experiment
172 we analyzed the differences in P and P-fractions concentrations between the invasive *P.*
173 *australis* tall-grass and the native mangrove community in the current wetland areas
174 submitted to the high levels of flooding intensity.

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176 Collection and analysis of soil samples

177 Soil samples were collected in October 2007 from the *S. triqueter*, *P. australis*, *C.*
178 *malaccensis*, and mangrove communities in the high- and low-flood habitats. Three replicate
179 plots were randomly established in each community at each flooding intensity. Soil profiles
180 (width, 1 m; length, 1 m; depth, 0.6 m) were excavated, and samples were collected with a
181 small sampler (length, 0.3 m; diameter, 0.1 m) from each of six soil layers (0-10, 10-20, 20-
182 30, 30-40, 40-50, and 50-60 cm) at the centers and both sides of the soil pits. These three
183 samples were bulked to form one sample per layer. A total of 162 soil samples were thus
184 collected (108 for the first experiment plus an additional 36 and 18 samples for the second
185 and third experiments, respectively). In the laboratory, the samples were air-dried, roots and
186 visible plant remains were removed, and the soil was finely ground in a ball mill.

187

188 Soil P analyses

189 Total P (TP) and total inorganic P (Pi) concentrations were determined following the method
190 described by Ruban et al. (1999) (see Appendix 1 in Supplementary Information for details).

191 Total organic P (Po) concentrations were determined by rinsing the residual soil in
192 the above centrifuge tubes twice with 12 ml of deionized water, freeze-drying, ultrasonicing
193 in a bath for 30 s, ashing for 3 h at 450 °C, transferring to 100-ml centrifuge tubes after
194 cooling, adding 20 ml of 3.5 mol L⁻¹ HCl, mixing on the QHZ-98A oscillator at 250 rpm for
195 16 h at 25 °C, and then centrifuging at 2000g for 15 min. The P concentrations of the
196 supernatants were determined colorimetrically as for Pi.

197 We used the continuous extraction procedure of Lu (1999) to determine the P
198 concentrations in the labile Po, moderately labile Po, moderately resistant Po, and highly

199 resistant Po fractions (see Appendix 1 in Supplementary Information for details). We used
200 the continuous extraction procedure of Ruban et al. (1999) to determine the P concentrations
201 in the exchangeable Pi, Fe+Al Pi, and Ca Pi fractions.

202 Residual Pi P concentration was determined by:

203 $[\text{residual Pi}] = [\text{TP}] - [\text{exchangeable Pi}] - [\text{Fe+Al Pi}] - [\text{Ca Pi}] - [\text{total Po}]$.

204

205 Determination of other soil parameters

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207 Total S concentrations were determined by method of Lu (1999) (see Appendix 1 in
208 Supplementary Information for details).

209 Soil bulk density was measured from three 5×3 cm cores per soil layer (Wang et al.
210 2014c), salinity was measured with a DDS-307 conductivity meter (Boqu Scientific
211 Instruments, Shanghai, China), pH was measured with an 868 pH meter (Orion Scientific
212 Instruments, USA), soil particle-size (clay, silt, and sand) contents were determined with a
213 SEDIMAT4-12 particle size analyzer (UGT Scientific Instruments, Müncheberg, Germany),
214 and soil-water content was determined gravimetrically (Lu 1999).

215

216 Determination of soil C, N, and P storage

217 The C, N, and P storages for all soil layers were estimated by following Mishra et al. (2010):

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$$C_s = \sum_{j=1}^n c_m \times \rho_b \times D$$

219 where C_S is C, N, or P storage (kg m^{-2}), j is the soil-depth interval (1, 2, ... n ; 0-10, 10-20,
220 20-30, 30-40, 40-50, and 50-60 cm) c_m is the C, N, or P concentration (g kg^{-1}), ρ_b is the bulk
221 density (kg m^{-3}), D is the thickness of each soil layer (m), and n is the number of soil layers.

222

223 Statistical analyses

224 The statistical significance of differences in the soil parameters among the flooding
225 intensities and soil layers in the communities was assessed with general linear models and
226 Tukey's post-hoc tests. We determined the Pearson correlation coefficients among all
227 pairwise soil studied parameters. We also determined the effects of water content and species
228 on N and P storage. All univariate statistical analyses were performed using SPSS 13.0 (SPSS
229 Inc., Chicago, USA).

230 We performed multivariate discriminant function analysis (DFA) to determine the
231 importance of total C, N, P, and S concentrations; DOC, NH_4^+ , NO_3^- , and available-S
232 concentrations; exchangeable Pi, Fe+Al Pi, Ca Pi, residual Pi, labile Po, moderately labile
233 Po, moderately resistant Po, and highly resistant Po concentrations; exchangeable Pi:labile
234 Po and total Pi/Po ratios; and total C:N, C:P, N:P, C:S, N:S, and P:S ratios in the separation
235 of the chemical components of the soil in the plots at different flooding intensities for the
236 three species (Raamsdonk et al. 2001). The DFAs were performed using Statistica 6.0
237 (StatSoft, Inc., Tulsa, USA). All nutrient ratios were calculated in mass basis.

238 We performed structural equation modelling to determine the best model for explaining the
239 TP concentration, exchangeable Pi concentration, the exchangeable Pi:labile Po ratio, the
240 total Pi:Po ratio, and the recalcitrant P concentration (endogenous variables) as functions of

241 the flooding intensity (as a dummy variable), and the other soil traits such as soil salinity, pH
242 and clay concentrations (exogenous variables). This analysis provided information for the
243 direct, indirect and total effects of the exogenous variables on the endogenous variables and
244 allowed us to determine the direct and indirect relationships of exogenous variables on
245 endogenous variables. For example the direct effect of flooding intensity on total soil P
246 concentrations can be distinguished from the indirect effect of flooding on total soil P due to
247 the effect of flooding intensity on salinity that thereafter has an effect on soil total P
248 concentration. We fitted the models using the sem R package (Fox et al. 2013) and achieved
249 the minimum adequate model using the Akaike information criterion (AIC). Standard errors
250 of the effects were extracted by bootstrapping (1200 repetitions) (Davison et al. 1986;
251 Mitchell-Olds 1986).

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266 **Results**

267 Effects of flooding, soil physicochemical traits and species on soil-P pools (Experiment 1)

268 Flooding increased soil P concentrations of all studied Pi and Po fractions in the *S. triqueter*

269 community but not in soils under the communities dominated by the other two species: the

270 other native species, *C. malaccensis* and the invasive species *P. australis* that did not change

271 P concentrations under higher flooding duration (Figure 2, Table S1). The results of the

272 repeated measures ANOVA (in space) are very similar to those of the GLM analysis of the

273 flooding effect on the variables shown in Figure 2 (Table S1). In the GLM analyses with

274 flooding duration, species and soil depth as independent categorical variables, only the Fe+Al

275 P pools differed, with the Fe+Al Pi pool being higher and the Fe+Al Po (moderately labile)

276 pool lower for *C. malaccensis* than for *P. australis* (Table S2). This asymmetrical effect of

277 increased flooding dependent on species is clearly shown by the PCA with all soil variables,

278 where the PC1 scores for the *S. triqueter* soils subjected to low flooding are very different

279 than those for all other soils (Figure 3). The PCA indicated that bulk density, sand content,

280 and the total Pi:Po ratio were higher in the *S. triqueter* soils subjected to low flooding (Figure

281 3).

282 Bulk density was lower (higher silt and lower sand contents) under high flooding
283 intensity, and soil-water content, salinity, and C and N concentrations were higher (Table
284 S2). We observed a significant interaction flooding intensity x species, due to that these
285 effects were particularly observed for *S. triqueter* soils and much less in the other two species.
286 Higher NH_4^+ and lower NO_3^- concentrations were found at high flooding than at lower
287 flooding intensities (Table S2). TP concentration and the concentrations of most P pools were
288 positively correlated with clay and silt contents, total C and N concentrations, DOC
289 concentration, and NO_3^- concentrations and negatively correlated with sand content, bulk
290 density, and S concentration (Table S3). These correlations were stronger in Pi fractions than
291 in Po fractions. Consequently, clay and silt contents and total C, N, and DOC concentrations
292 were negatively correlated with the total Pi/Po ratio, and sand content and bulk density were
293 positively correlated with the total Pi:Po ratio (Figure S1). These effects were mainly due to
294 the large differences between the *S. triqueter* soil under low flooding intensity and all other
295 soils (Figure S1).

296 The total N:P ratios were higher under flooding in the wetlands of the three species
297 at most soil depths (Table S2, Figure 4). Moreover, this ratio was highest for the invasive *P.*
298 *australis* soils (Table S2, Figure 4).

299 The structural models that best explained (lower AIC) the different P fractions and
300 their Pi:Po ratios are shown in Figures 5-7. The best model for TP and exchangeable Pi
301 (Figure 5) concentrations showed that clay content and soil pH had direct positive significant
302 effects on these P variables and that flooding had an indirect negative effect through its
303 positive effect on salinity that subsequently had a negative effect on these P variables
304 (Figures 5-7).

305 The best structural model for total recalcitrant P (Pi+Po) and total Po concentrations
306 indicated a direct effect of clay content but not of soil pH, while an indirect effect of flooding
307 by increasing salinity was also observed (Figures 6 and 7). This relationship is consistent
308 with the expected according to clay properties. The indirect negative effect of flooding on
309 the exchangeable Pi:labile Po ratio was best explained by the direct effect of flooding on
310 higher total S concentrations that subsequently had a negative effect on the exchangeable
311 Pi:labile Po ratio (Figure 7).

312 Soil pH and mainly clay content thus had strong positive relationships with P-fraction
313 concentrations, and these effects were stronger in the Po than the Pi fractions, and both
314 consequently decreased the total and exchangeable Pi:labile Po ratios (Figure 5 and 7).
315 Flooding had no significant direct effects on clay content or soil pH. These results were
316 consistent with those of previous univariate analyses where the variability of clay content
317 and soil pH were slightly related with flooding intensity when comparing overall soils. The
318 relationships between clay content and soil pH with flooding intensity were positive in soils
319 under *S. triqueter* and negative in soils under the other two species (Figure 8).

320

321 Effects of flooding on the soil-P pools in the invasive *P. australis* communities (Experiment
322 2)

323 The *P. australis* soil in the mid-flood habitat had the highest TP concentrations and stored
324 more P, mainly in the upper 30 cm of the soil, relative to the low- and high-flood habitats
325 (Figure 9a and 9l), due mainly to the high concentrations of the Pi pools (Figure 9 b-e). The
326 exchangeable Pi:total P ratio in the upper 30 cm of soil were higher in the mid- than the low-

327 and high-flood habitats dominated by this invasive species (Figure 9m). The PCA with all
328 soil variables indicated that PC1 (explaining 44.7% of the total variance) significantly
329 ($P<0.05$) separated the scores of the stands of *P. australis* growing under the three flooding
330 intensities. The concentrations of the Po pools increased from soils under low flooding to
331 soils under high flooding intensities, coinciding with a decrease in sand content and bulk
332 density and with an increase in clay and silt contents (Figure 10). Interestingly, the PC2
333 scores (explaining 27.2% of the total variance) for the soils in the mid-flood habitat differed
334 significantly from the scores for the soils in the low- and high-flood habitats ($P=0.004$ and
335 $P=0.0001$, respectively) (Figure 10). PC2 was significantly loaded by TP concentration, total
336 P stored in the soil, and all Pi pools, with the soil in the mid-flood habitat placed toward the
337 highest values and coinciding with lower C:P ratios (Figure 10). Increased flooding was
338 associated with an increase in total N:P ratios (Figure 11).

339

340 Differences in soil P contents between mangrove and communities dominated by the invasive
341 *P. australis* (Experiment 3)

342 Mangrove soils accumulated more P in the upper 10 cm of the soil than the *P. australis* soil
343 at the same flooding intensity (Figure 12). The mangrove soils had higher bulk densities,
344 sand contents, pHs, salinities, and NO_3^- concentrations and lower water contents, silt
345 contents, total C and N concentrations, and total N:P ratios than the *P. australis* soils (Table
346 S4). The P stored in the upper 60 cm of soil were marginally significantly ($P=0.08$) higher in
347 the mangrove soils than the *P. australis* soils (Table S4).

348 The PCA with all soil variables indicated that the scores of the mangrove soils were
349 significantly ($P < 0.0001$) separated from those of the *P. australis* soils along the PC1 axis
350 (explaining 31.2% of the total variance) (Figure 13). This axis was significantly loaded by
351 sand content, bulk density, pH, salinity, P storage, water content, and NH_4^+ concentration,
352 with the mangrove scores placed toward higher pH, P storage, sand content, bulk density,
353 and salinity and toward lower water content and NH_4^+ concentration (Figure 13).

354

355 **Discussion**

356 Flooding effects versus species effects on the status of soil P

357 The relationships of flooding and the P pools were very asymmetrical, depending on the
358 species. Despite we did not can disentangle if differences in soils P concentrations in soils
359 under the different species were the cause or the effect of the presence of these species, the
360 P pools changed most in the soils depending on the flooding intensity in the native *S. triqueter*
361 wetlands than in the sites dominate by the other two studied species. These differences may
362 be related, at least partially, to the very much lower biomass of the *S. triqueter* community
363 than those of the *C. malaccensis* and *P. australis* communities (Wang et al. 2014b). The TP
364 concentrations of ca. 0.7 g kg^{-1} in the first few centimeters of soil in these wetlands were
365 within the range of $0.3\text{-}1.3 \text{ g kg}^{-1}$ observed in marine and estuarine wetland areas around the
366 world (Carol et al., 2012; Xu et al., 2012; Irick et al. 2013; Gao et al., 2014; Yu et al.
367 2014). The concentrations of most P fractions abruptly decreased at a depth of 30 cm. Most
368 of the P was stored in the first few centimeters of the soil profiles, as in other wetland areas
369 (Wang et al. 2011; Gao et al. 2014). These areas are thus very vulnerable to P losses from

370 any disturbance that could pose a potential risk of an increase in P in the water column, and
371 consequently its potential export to coastal areas.

372 Flooding increased TP accumulation, several P fractions, and the exchangeable
373 Pi:labile Po ratio, but these effects were partially counteracted by the indirect effects of
374 flooding on soil salinity and total S concentration, because these variables had negative
375 effects. Clay content and soil pH, however, were mostly associated with the various soil P
376 fractions concentrations that in turn were more related with the dominant species and with
377 the interaction between species and flooding than with flooding intensity alone. Most of the
378 variability of the P concentrations was explained by the variation of the clay contents of the
379 *S. triqueter* communities, which were lowest under lower flooding intensity, along with the
380 lowest concentrations of all P fractions and especially the Po fractions. Higher clay contents
381 were associated with higher sulfur concentrations (under high redox potential of the media)
382 and lower soil pHs, consistent with the higher anoxic conditions expected in soils with high
383 clay contents (Miller et al. 2001; Oxmann et al. 2009). The unique important and general
384 effect of flooding intensity on the P fractions was due to its effect on soil salinity. Pore-water
385 salinity in wetlands has been associated with flooding intensity and thus with species
386 composition and P concentration (Mendoza et al. 2012). These associations may be due to
387 the effects of soil salinity on plant P uptake and thus on the P concentrations and contents in
388 the leaves and litter, together decreasing the capacity of P retention in the ecosystem with
389 increasing salinity (Mendoza et al. 2012).

390 In our studied sites, settling rates depend partially of the number of hours of flooding.
391 Thus the longer times that water covers the soil as flooding intensity increases should permit
392 higher particle sedimentation, which should be more relevant for clay particles than for the

393 larger sand particles. Moreover, higher clay contents and anoxic conditions should produce
394 lower pHs. But higher flooding intensity was associated with higher clay contents, within the
395 range of flooding intensities of this study only in the wetlands dominated by *S. triquetra*. Our
396 results, thus, suggested that soil clay content could be related with the specific-species cover
397 at some extent. Anyway, the study design was not aimed to disentangle whether the high
398 clay soil concentrations under *S. triquetra* in specially at high flooding intensity is a cause of
399 the occurrence of this species in rich-clay soils or they are the consequence of the existence
400 of this species increasing the capacity to trap clay particle. In another study, exchangeable Pi
401 increased and labile Po decreased under flooding (Newman and Pietro 2001). The clay
402 concentrations were negatively correlated with the total ($R^2=0.44$, $P<0.00001$) and
403 exchangeable Pi:labile Po ratios ($R^2=0.22$, $P<0.00001$), suggesting that Po mineralization
404 was hindered by high clay contents. Clay content was also negatively correlated with soil
405 pH, but this relationship was not associated with flooding intensity; soil pH was thus not
406 clearly associated with flooding. In contrast to the expected decrease in pH with the more
407 anoxic soil conditions under higher flooding intensity, some studies have observed that soil
408 pH increased with flooding intensity (Saint-Laurent et al. 2014).

409 Previous studies in wetlands have also reported relationships between clay content
410 and P storage (Chapuis-Lardy et al. 2006; McGrody et al. 2008; Wang et al. 2013), due
411 mostly to high Fe-Al P and Ca P fractions and to the higher adsorption capacity of the soil,
412 because high clay contents provide more solid and large surface per unit weight (Wang et al.
413 2013). In fact, and consistent with these observations, the Fe+Al Po fraction was the fraction
414 best correlated with clay content ($R^2=0.62$). Our results thus demonstrate that these effects
415 were mainly related to the species, despite the effects of flooding intensity on the P fractions
416 in the soil profile. Xu et al. (2012) have also suggested that the vegetation could significantly

417 influence P dynamics and availability in the Yellow River delta. However, we can not
418 disentangle whether the different soil texture under the different studied species-communities
419 is the cause or the effect of these species distribution.

420 The concentrations of TP and in the P fractions mostly did not differ significantly
421 between the *P. australis* and *C. malaccensis* soils. We only observed differences in the Fe+Al
422 P fractions, with higher Fe+Al Pi and lower Fe+Al Po concentrations in the *C. malaccensis*
423 soils, consistent with the slightly higher rates of litter mineralization observed in *C.*
424 *malaccensis* soils than in *P. australis* soils (Tong et al. 2011). The lack of general differences
425 in the status of soil P between these two species was consistent with the small differences in
426 litter elemental composition in the same wetlands (Tong et al. 2011). But despite the little
427 differences observed in litter composition, we have observed some stoichiometrical
428 differences between these two species in litter C:P (555 ± 1 and 473 ± 1 , $P < 0.0001$,
429 respectively) and N:P (12.8 ± 0.04 and 10.3 ± 0.12 , $P < 0.0001$, respectively) ratios. These
430 results are consistent with some observed results regarding soil P. For example, the lower
431 soil recalcitrant Po and higher labile Pi/Po ratio in soils under *P. australis* than in soils under
432 *C. malaccensis* suggest higher decomposition rates of organic P consistent of litter with lower
433 N:P ratio related with higher microbial growth rates and activity such as expected in the
434 frame of ecological stoichiometry approach (Mooshammer et al., 2012; Zechmeister-
435 Boltenstern et al., 2015).

436

437 Differences among species of flooding effects on P status

438 Concentrations in the Pi fractions in the upper 30 cm of the *P. australis* soils were higher at
439 the highest flooding intensity than at the lowest and intermediate flooding intensities,
440 whereas concentrations in the Po fractions were lowest at the lowest flooding intensity. The
441 TP stored in soil and the exchangeable Pi:TP ratio in the upper 30 cm of soil were both
442 highest at the intermediate flooding intensity. The intermediate flooding intensity thus
443 produced the highest accumulation of P and the highest proportion of plant-available P in the
444 *P. australis* soils. The biomass of the invasive *P. australis* was thus higher than those of *S.*
445 *triqueter* and *C. malaccensis* ($P<0.05$) in the high-flood habitat but was only higher than that
446 of *S. triqueter* ($P<0.05$) in the low-flood habitat (Wang et al. 2014b). The higher
447 exchangeable Pi: labile Po ratio in the upper 30 cm of soil at the intermediate flooding
448 intensity in the *P. australis* wetlands suggested that the mineralization rates would be higher
449 at the intermediate flooding intensity, within the range tested in this study.

450 The N:P ratios in the *P. australis* soils increased with flooding intensity, as also
451 observed when comparing the three species at two flooding intensities. A higher N:P ratio
452 should mitigate the N limitation observed in other studies in this same wetland area (Wang
453 et al. 2014c). N:P ratios of 5.4-5.7 have been considered as indicating that a wetland is a P
454 sink (Jiménez-Cárceles and Álvarez-Rogel 2008). The range of the total N:P ratio (0.5-3) in
455 this wetland area is thus very low, and N is also probably limiting at the highest flooding
456 intensity. Our results thus also suggest that these wetlands are strong P sinks, with
457 consequently low N:P ratios, and that the N:P ratio increases at higher flooding intensities
458 with increases in N accumulation and not by decreases in P content. The capacity to store P
459 at different flooding intensities is a key question in the estuarine wetlands of China, because
460 cropland soils have very high P concentrations (MacDonald et al. 2011; Wang et al. 2014c),
461 consistent with the large amount of P stored in this estuarine area. This capacity to store P is

462 even more crucial in the wetlands of subtropical China, where the high temperatures produce
463 high rates of P mineralization (Rui et al. 2012) and the strong rains cause severe erosion in
464 the river basins, which increase the transport of P from upriver to estuarine areas (Tian et al.
465 2010).

466 Our results thus suggest that the best management strategy for maximizing the
467 capacity of this wetland area to act as a P sink should favor the combination of *C. malaccensis*
468 and *P. australis* wetlands in areas of low flooding intensity (<180 d y⁻¹ inundation) and the
469 combination of *S. triqueter*, *C. malaccensis*, and *P. australis* wetlands in areas of
470 intermediate-high flooding intensities (>180 d y⁻¹ inundation).

471

472 Effects of mangrove and *P. australis* wetland on the status of soil P

473 In contrast with the previous results suggesting a closer positive relationship between
474 clay content and the different P fractions, especially the Po fractions, the sandier soils in the
475 mangrove community stored higher amounts of P in the upper 10 cm of soil than the less
476 dense soil in the *P. australis* wetlands at similar flooding intensities. The higher soil density
477 in the mangrove community allowed a higher total accumulation of P, despite the higher P
478 concentration in the *P. australis* community. This capacity may thus be responsible for the
479 large structural difference between these two communities. Mangrove ecosystems have a
480 large capacity to retain soil nutrients (Tam and Wong 1996; Silva et al. 1998). The slow
481 decomposition of wood in the upper soil layers could play a large role in this capacity
482 (Romero et al. 2005). Nielsen and Andersen (2003) observed that P in the Bangrong
483 mangrove forest in Thailand tended to be concentrated in the leaf litter during decomposition,

484 which was associated with the high P concentrations in the soils. These results suggest that
485 the maintenance of native mangrove communities to act as P sinks is the best management
486 strategy in wetland areas with high flooding intensities ($>220 \text{ d y}^{-1}$ inundation). Our results
487 strongly suggest that the best management strategy that would both preserve biodiversity and
488 maximize the capacity of the wetland area to act as a P sink for future scenarios of rise in
489 flooding duration, should favor the combination of *C. malaccensis* and *P. australis* wetlands
490 in areas with low flooding intensity ($<180 \text{ d y}^{-1}$ inundation), the combination of *S. triquetra*,
491 *C. malaccensis*, and *P. australis* wetlands in areas with intermediate flooding intensity (180-
492 220 d y^{-1} inundation), and the maintenance of native mangrove communities in areas with
493 high flooding intensities ($>200 \text{ d y}^{-1}$ inundation). In fact, this wetland area has been recently
494 declared as National Reserve and some of the current mangrove areas have been planted by
495 China government. This study thus shows the positive results of this policy of repopulation
496 of native mangrove communities in the higher flooded areas to rise the capacity to store P in
497 soil and to avoid eutrophication.

498

499

500 **Conclusions**

501 Flooding moderately increased TP accumulation, P concentrations in several P fractions, and
502 the exchangeable P_i :labile P_o ratio. Some indirect effects of flooding, such as increases in
503 soil salinity and total S concentrations, contributed to the moderation of the relationship
504 between flooding and the P fractions by counteracting the direct positive relationship with
505 flooding. This moderation occurred because these variables were negatively correlated with

506 total P accumulation, P concentrations in several P fractions, and the exchangeable Pi:labile
507 Po ratio.

508 We observed an interaction between species and flooding on the total-P and P-
509 fraction concentrations. The relationship between flooding and higher P-fraction
510 concentrations depended on the species community. The principal cause of this relationship
511 was the relationship of each species with the increase in clay content as flooding increased.
512 Clay content was the soil variable most positively correlated with the various P-fraction
513 concentrations and was more dependent on the dominant species than on the flooding
514 intensity alone.

515 Higher clay contents were correlated with higher S concentrations and lower pHs,
516 consistent with the higher anoxic conditions expected in soils with higher clay contents. Clay
517 content was also correlated with a higher adsorption capacity. All these soil conditions at
518 high clay contents are consistent with lower Po availability to microorganisms and
519 consequently with conditions unsuitable for mineralization and thus with higher Pi
520 concentrations and especially with higher Po concentrations (low Pi:Po ratio).

521 Thus, taking into account future scenarios of flooding intensity rise and the projected
522 scenarios of the amounts of P received by coastal waters from rivers in China (Strokal et al.
523 2014), a suitable management to both preserve biodiversity and to maintain this wetland area
524 in optimum conditions to act as a natural eutrophication buffer should tend to favor mangrove
525 communities in the new areas that reach more than 220 days y^{-1} of flooding, and the
526 combination of the three tall-grasses below this level of flooding.

527

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533

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Figure legends.

Figure 1. Location of the the sampling sites.

Figure 2. Distribution of soil P variables (mean \pm SE, n = 3) in the soil profiles of the wetlands dominated by *S. triqueter*, *C. malaccensis*, and *P. australis* subjected to low and high flooding intensities.

Figure 3. Distribution of variables and cases in the plot of the first two PCs of the PCA analysis conducted with the P fractions and other soil variables in the wetlands dominated by *S. triqueter*, *C. malaccensis*, and *P. australis* subjected to low and high flooding intensities.

Figure 4. Distribution of total N:P ratio (mean \pm SE, n = 3) in the soil profiles of the wetlands dominated by *S. triqueter*, *C. malaccensis*, and *P. australis* subjected to low and high flooding intensities.

Figure 5. Diagrams of the structural models that, by using different physicochemical soil variables and flooding intensity, best explain the variability of total soil P (TP) concentrations and total exchangeable inorganic P (EPi) concentrations in the soil profiles of the wetlands dominated by *S. triqueter*, *C. malaccensis*, and *P. australis* subjected to low and high flooding intensities. The total, direct, and indirect effects of each exogenous variable on the endogenous (TP and TPi) variables are shown in each case with the level of significance (*P* value). Black arrows in the diagram mean positive relationships and red arrows negative relationships. The bar figures show the total direct and indirect relationships of physicochemical soil variables and flooding intensity with total soil P and exchangeable inorganic P (EPi) concentrations.

Figure 6. Diagrams of the structural models that, by using different physicochemical soil variables and flooding intensity, best explain the variability of total soil inorganic P (TPi) concentrations and total organic P (TPo) concentrations in the soil profiles of the wetlands dominated by *S. triqueter*, *C. malaccensis*, and *P. australis* subjected to low and high flooding intensities. The total, direct, and indirect effects of each exogenous variable on the endogenous (TPi and TPo) variables are shown in each case with the level of significance (*P* value). Black arrows in the diagram mean positive relationships and red arrows negative relationships. The bar figures show the total direct and indirect relationships of physicochemical soil variables and flooding intensity with total soil inorganic P (TPi) concentrations and total organic P (TPo) concentrations.

Figure 7. Diagrams of the structural models that, by using different physicochemical soil variables and flooding intensity, best explain the variability of exchangeable-Pi:Labile-Po ratio (EPi:LPO), total Pi:Po ratio (TPi:Po), and soil recalcitrant P (RP) concentrations in the soil profiles of the wetlands dominated by *S. triqueter*, *C. malaccensis*, and *P. australis* subjected to low and high flooding intensities. The total, direct, and indirect effects of each exogenous variable on the endogenous (EPi:LPO, TPi:Po, and RP) variables are shown in each case with the level of significance (*P* value). Black arrows in the diagram mean positive relationships and red arrows negative relationships. The bar figures show the total direct and indirect relationships of physicochemical soil variables and flooding intensity with exchangeable-Pi:Labile-Po ratio (EPi:LPO), total Pi:Po ratio (TPi:Po), and soil recalcitrant P (RP) concentrations.

Figure 8. pH and clay contents (mean \pm SE, *n* = 3) in the soil profiles (0-60 cm) of the wetlands dominated by *S. triqueter*, *C. malaccensis*, and *P. australis* subjected to low and high flooding intensities.

Figure 9. Distribution of soil P variables (mean \pm SE, *n* = 3) in the soil profile of the wetlands dominated by *P. australis* subjected to low, intermediate, and high flooding intensities.

Figure 10. Distribution of variables and cases in the plot of the first two PCs of the PCA analysis conducted with the P-fractions and other variables of the *P. australis* soils subjected to low, intermediate, and high flooding intensities. The arrows indicate the mean of the scores of *P. australis* wetland soils under different duration of flooding and different letters on arrows statistical significant differences (*P*<0.05).

Figure 11. Total N:P ratio (mean \pm SE, *n* = 3) in the soil profiles (0-60 cm) of the wetlands dominated by *P. australis* subjected to low and high flooding intensities.

Figure 12. Distribution of P stored in the soil and total soil P concentrations (mean \pm SE, *n* = 3) in the soil profiles of the wetlands dominated by *P. australis* and the native mangrove community subjected to high flooding intensity.

Figure 13. Principal component analysis of the soil traits as variables and soil samples analyzed in experiment 3 (*P. australis* and mangrove wetland soils in an area of the Shanyutan wetland with high flooding intensity).

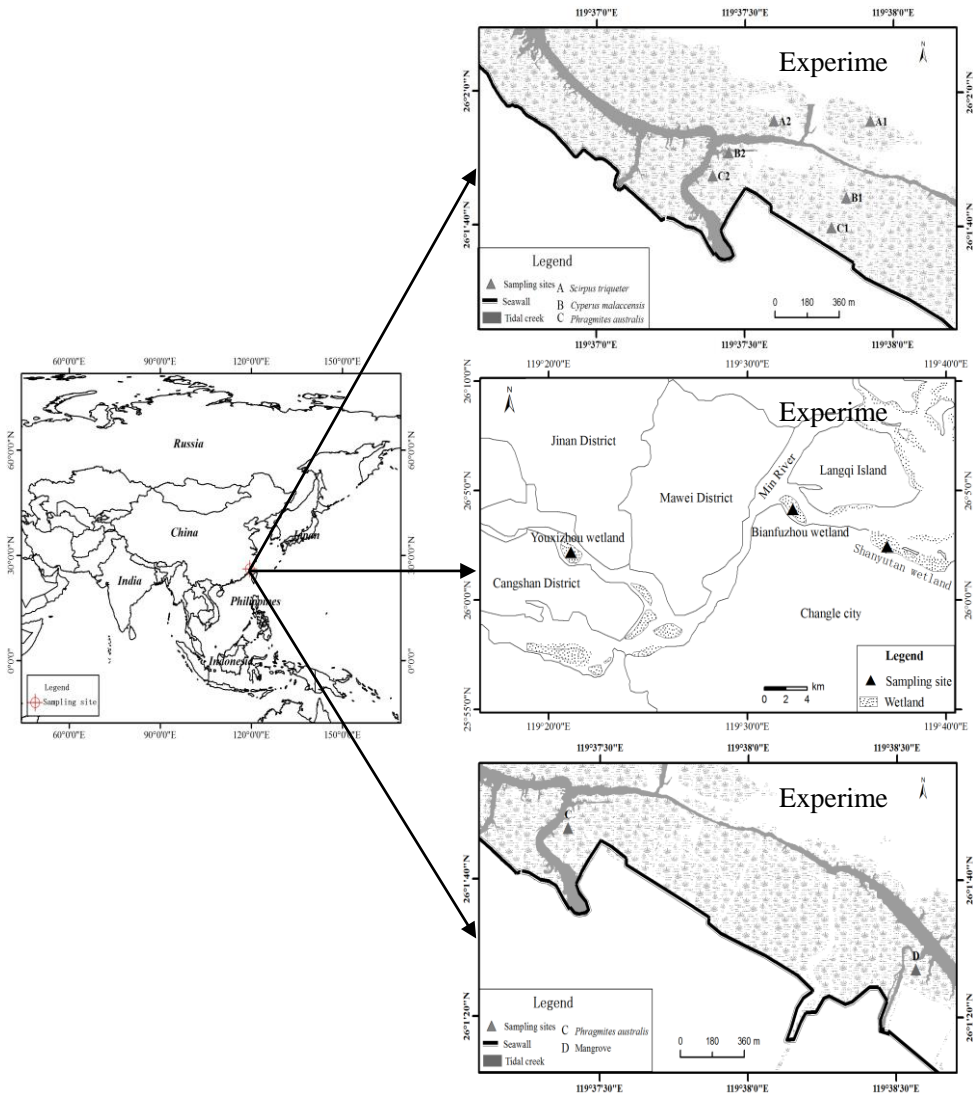


Figure 1

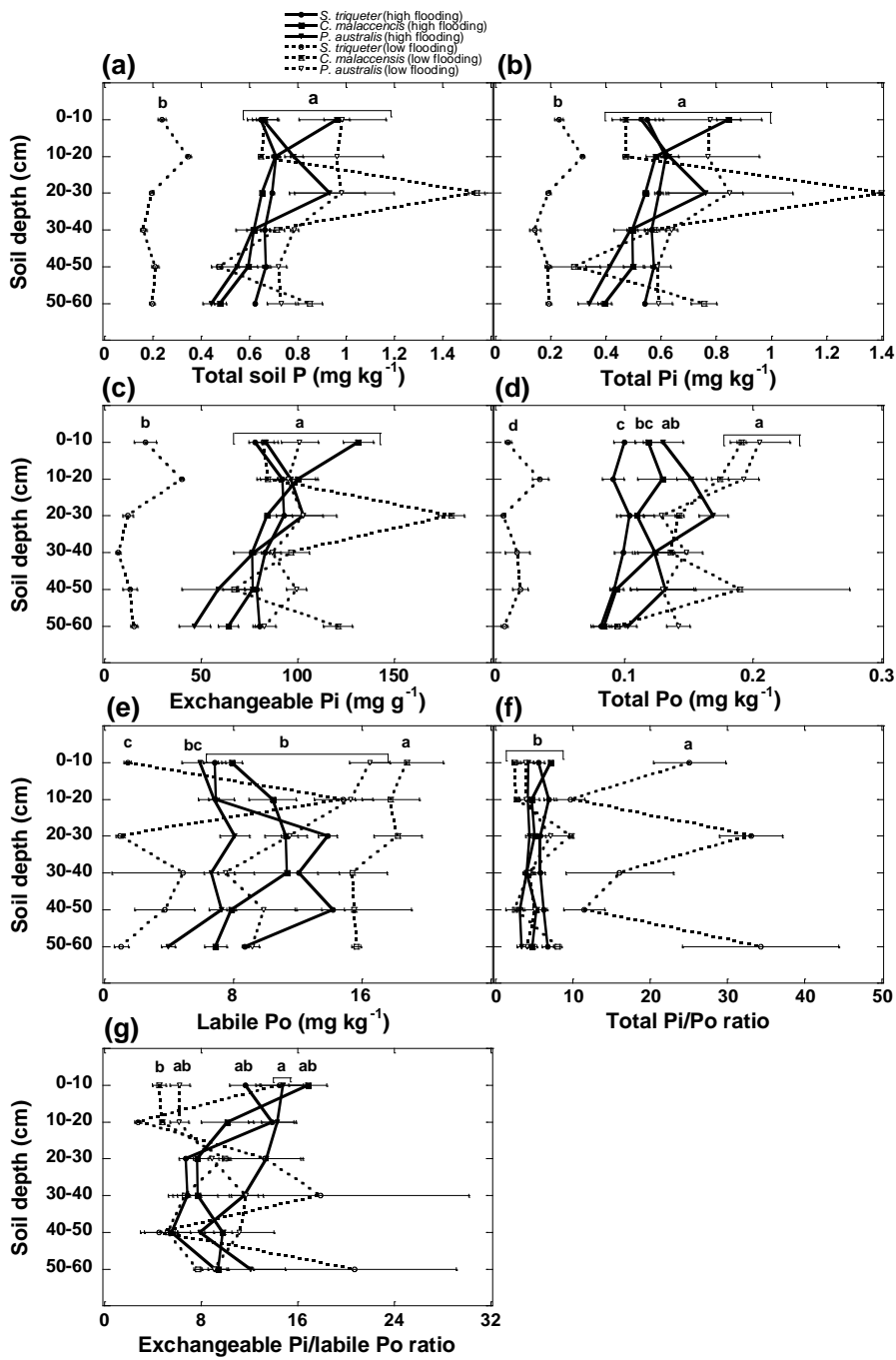


Figure 2

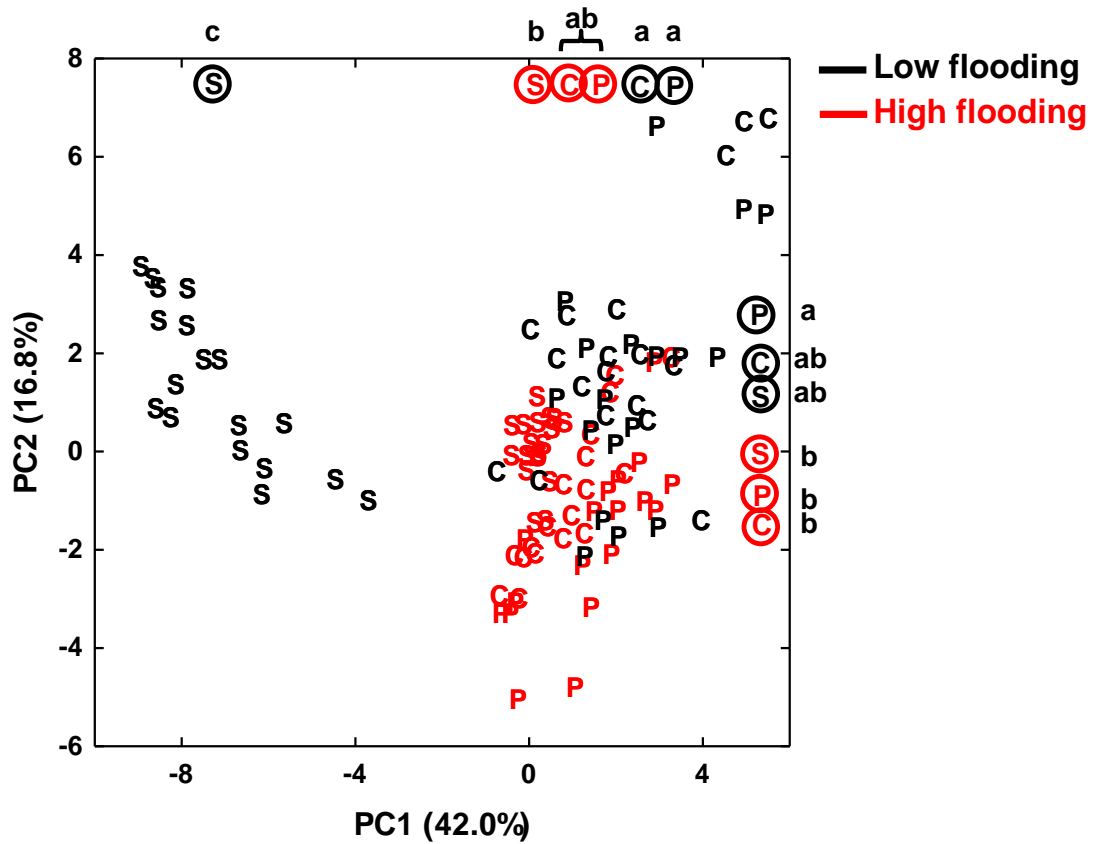
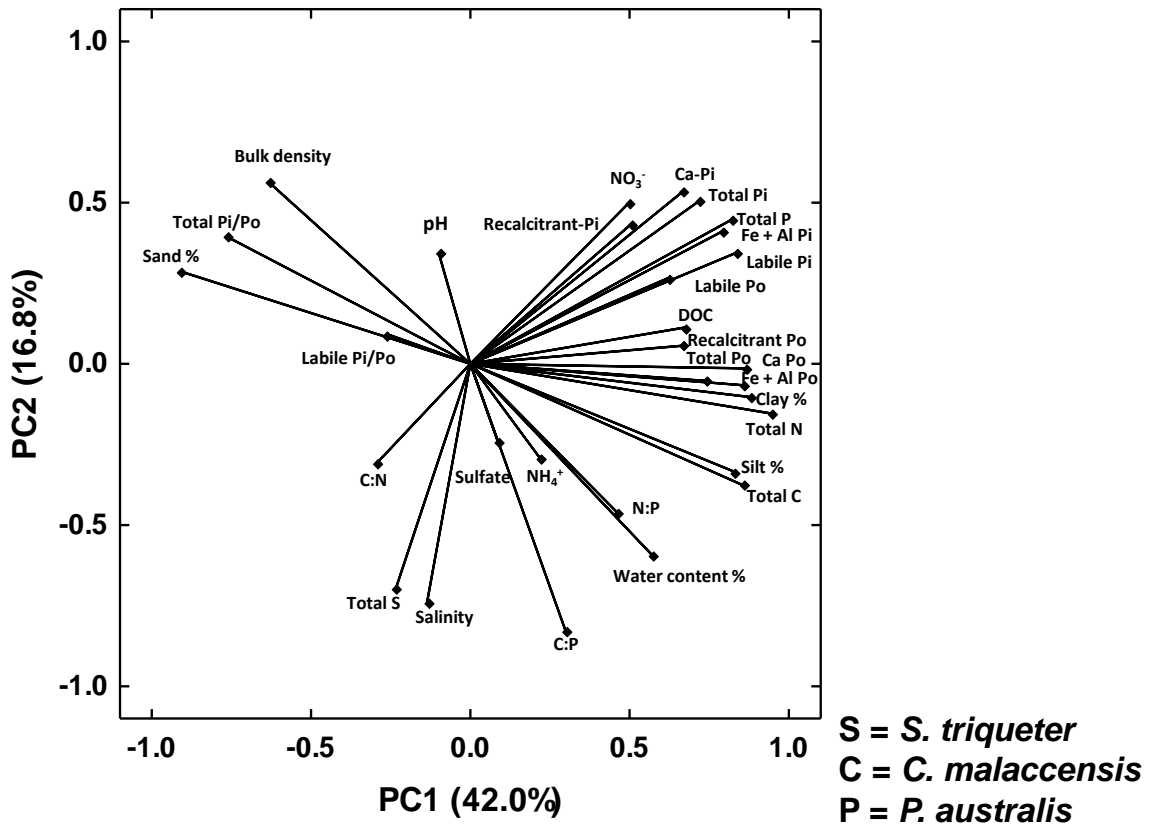


Figure 3

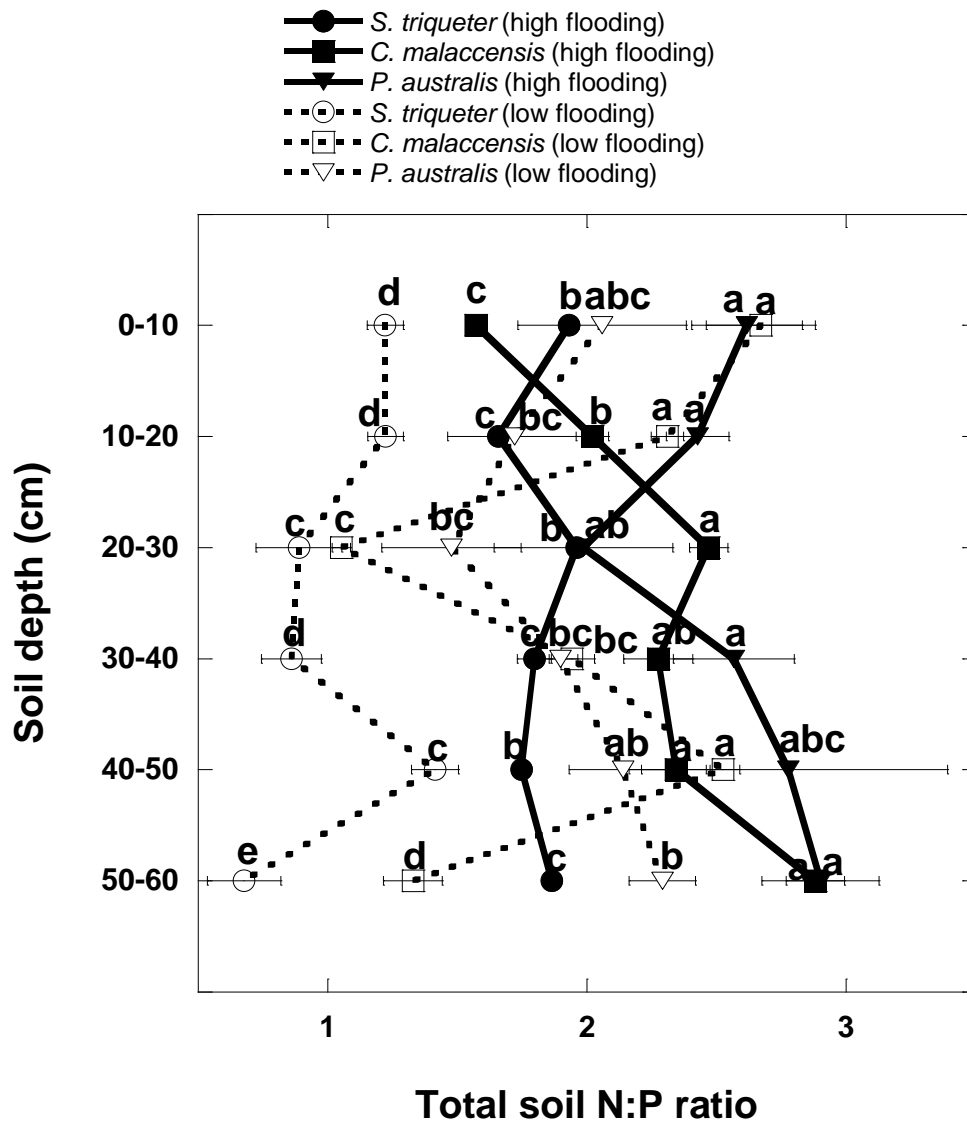
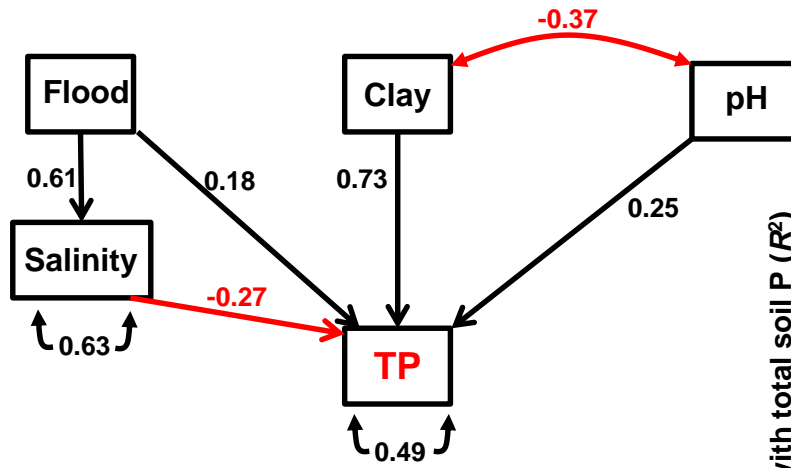
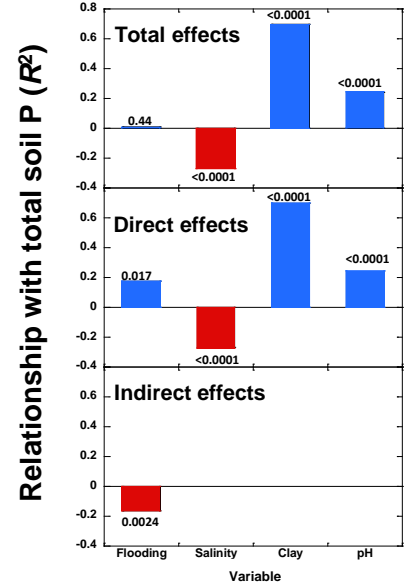


Figure 4

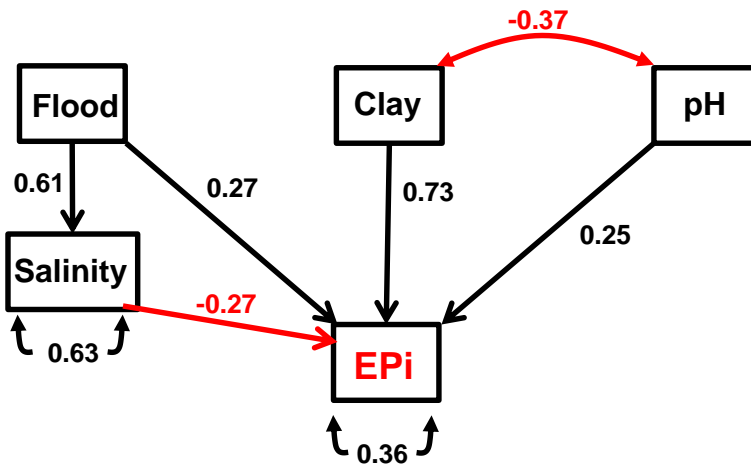
Total soil phosphorus concentration (TP)



R^2 of endogenous variables
 TP = 0.51
 Sal = 0.37



Soil labile inorganic phosphorus (E_{Pi})



R^2 of endogenous variables
 E_{Pi} = 0.64
 Sal = 0.37

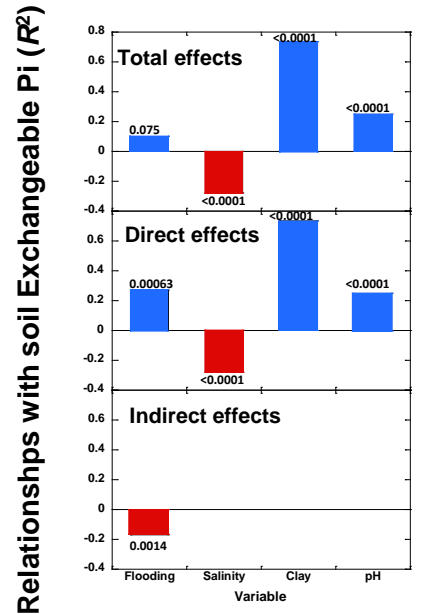
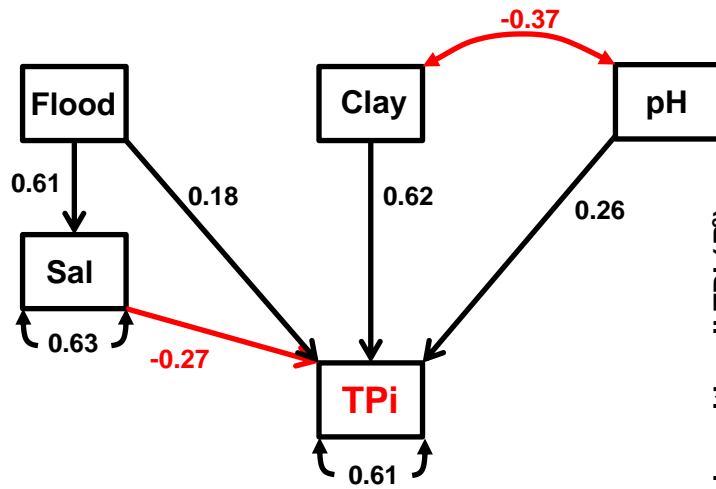
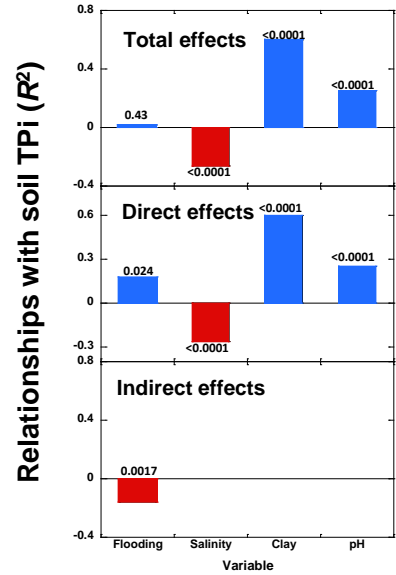


Figure 5

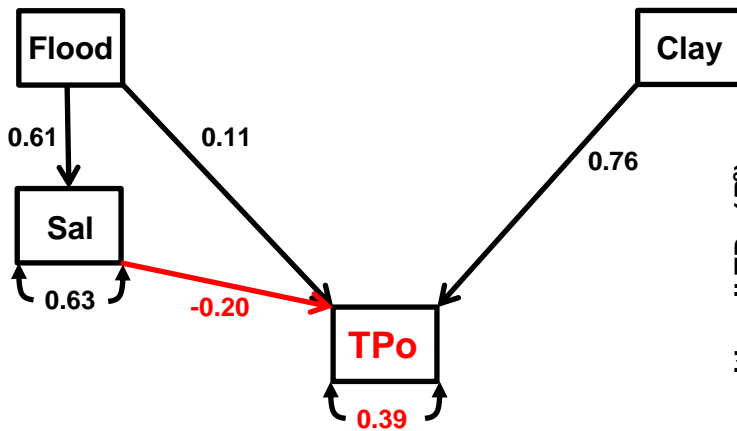
Total soil inorganic phosphorus concentration (TPi)



R² of endogenous variables
 TPi = 0.39
 Sal = 0.37



Total soil organic phosphorus concentration (TPo)



R² of endogenous variables
 TPo = 0.61
 Sal = 0.37

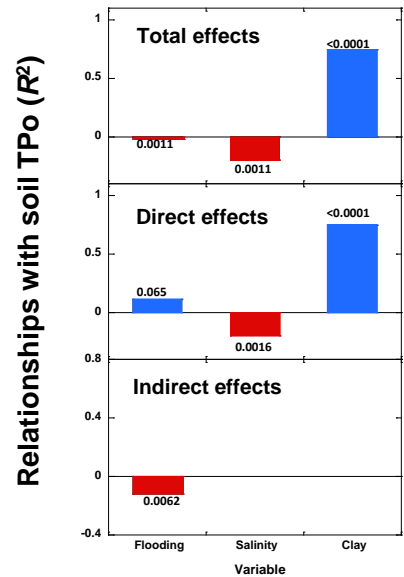


Figure 6

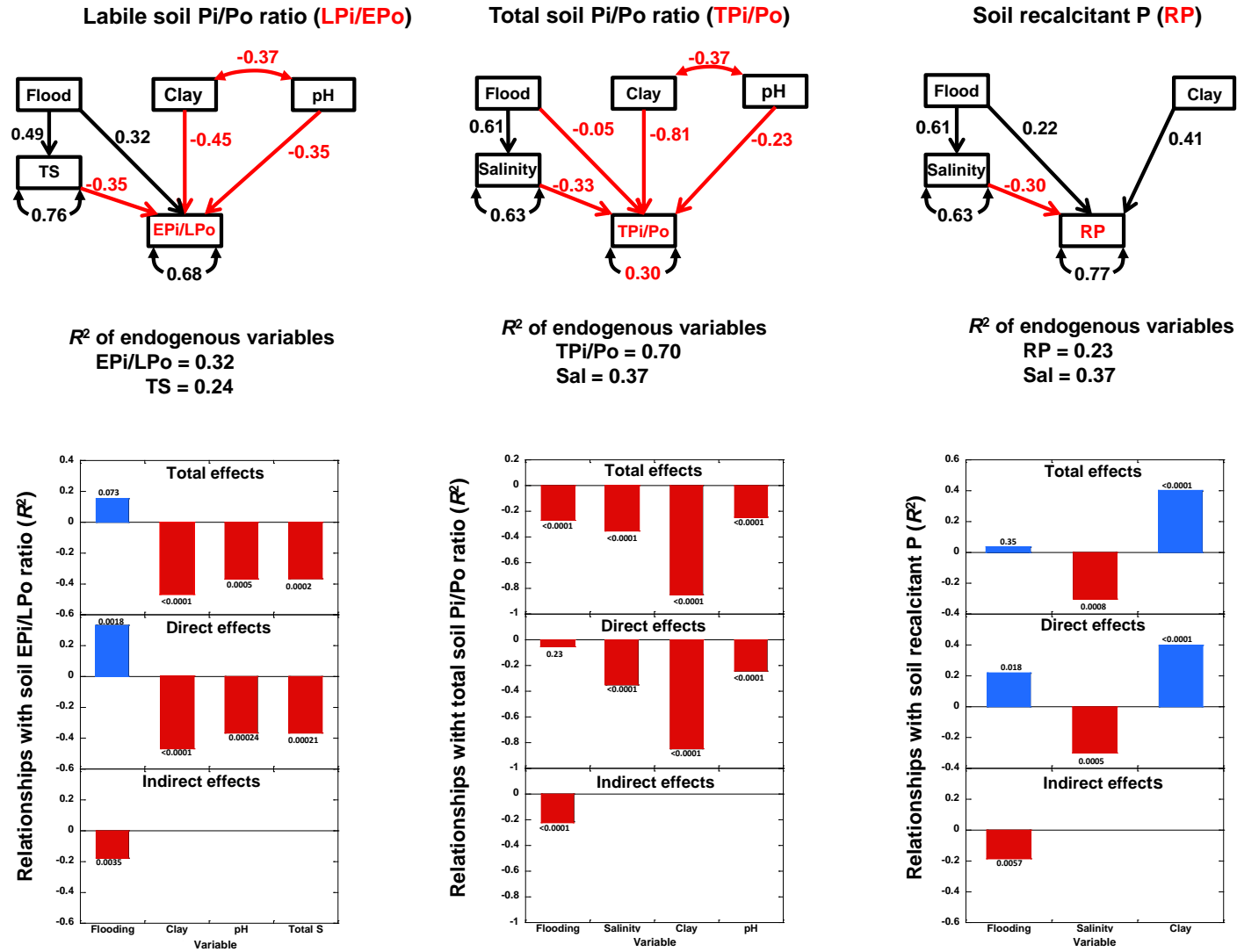


Figure 7

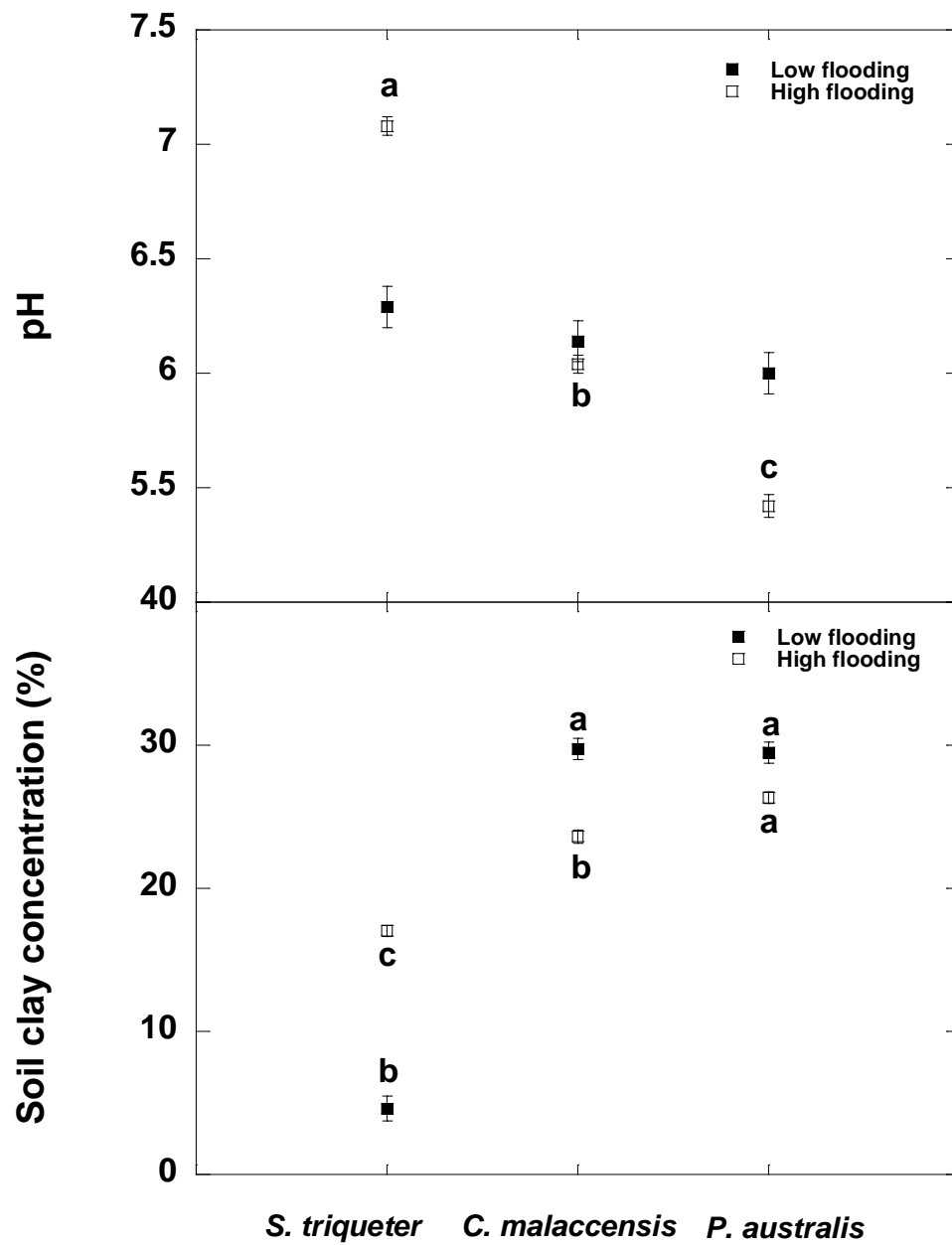


Figure 8

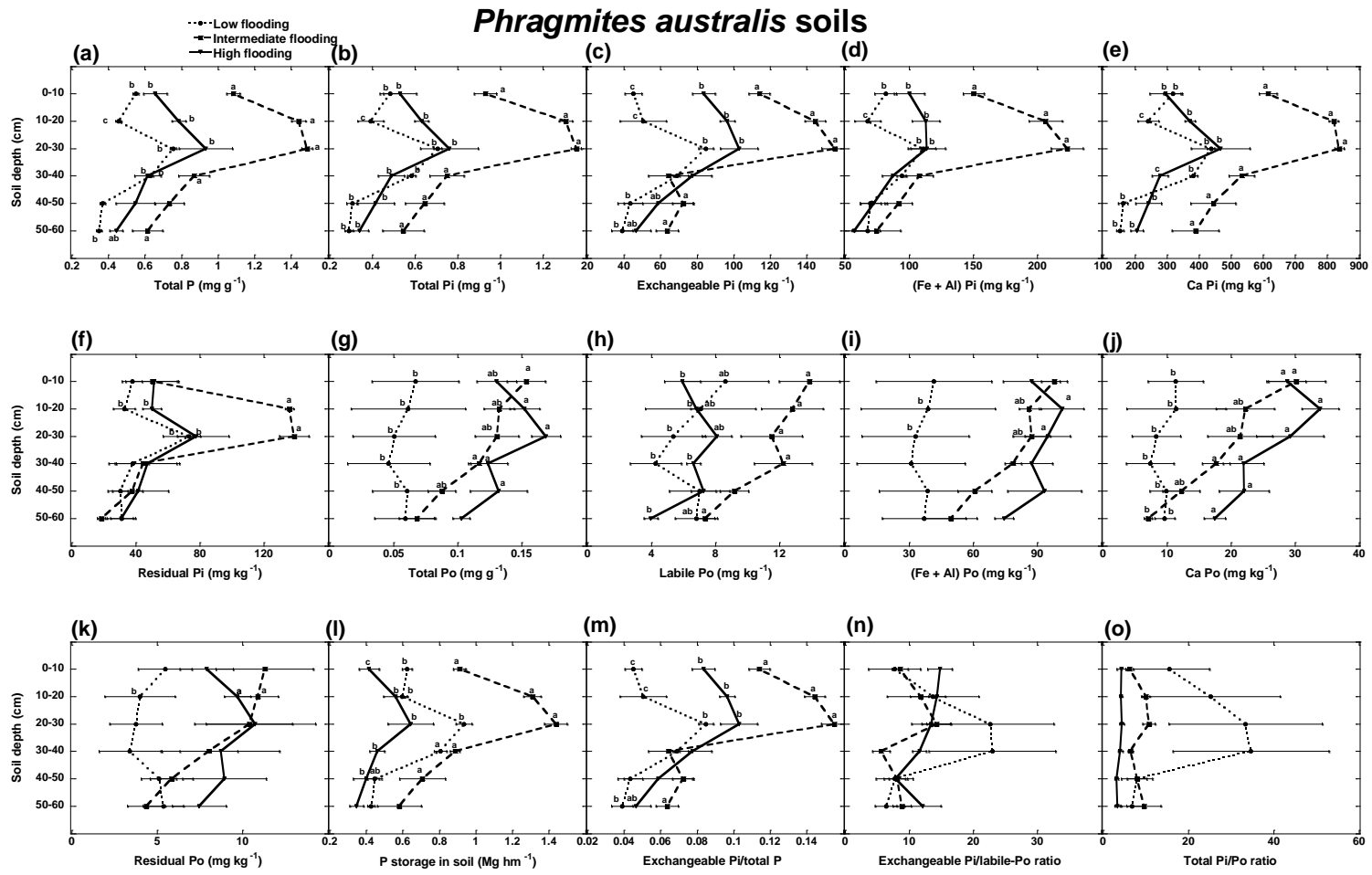


Figure 9

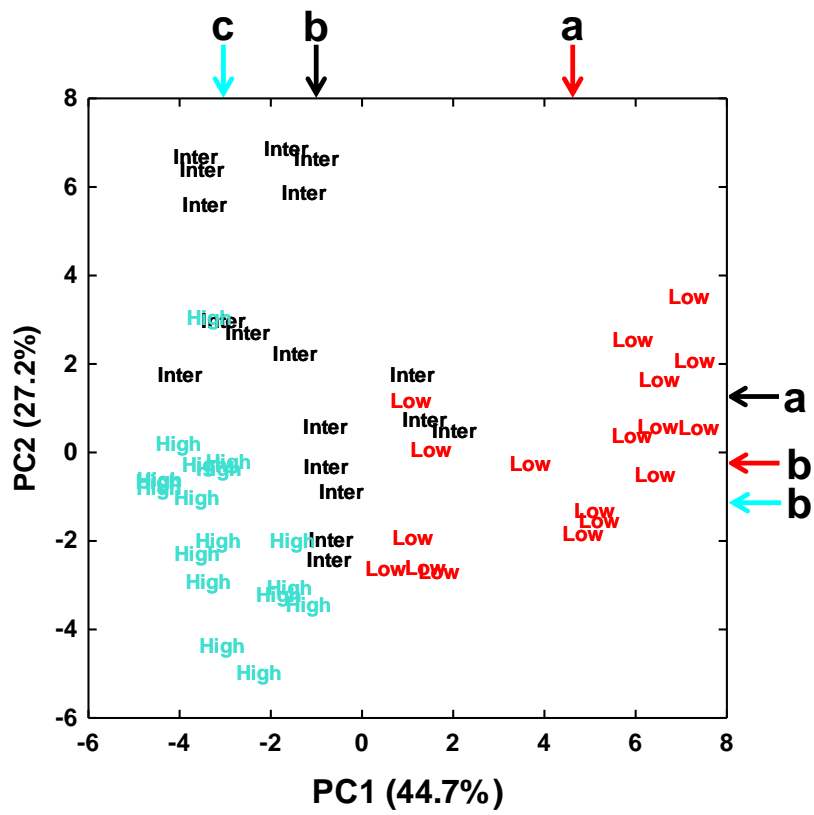
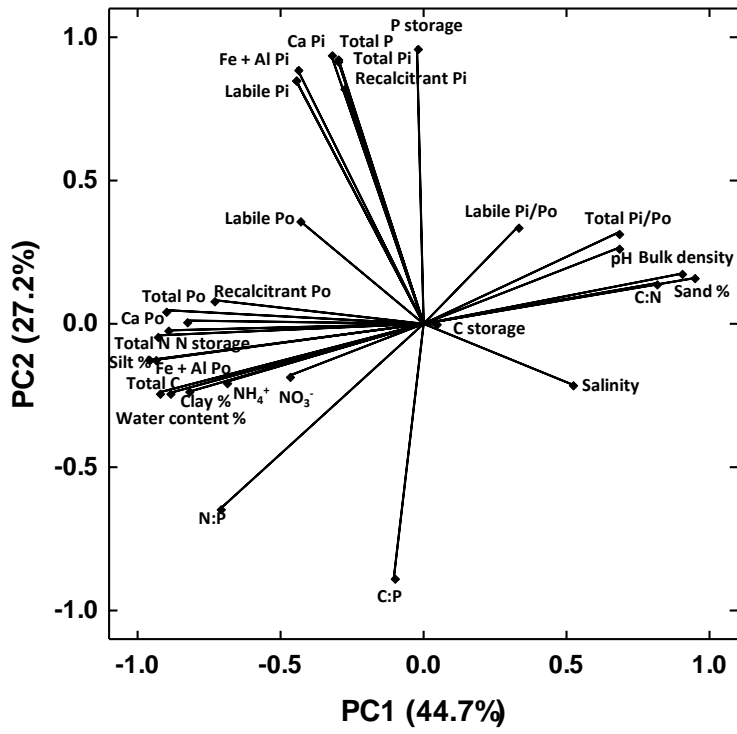


Figure 10

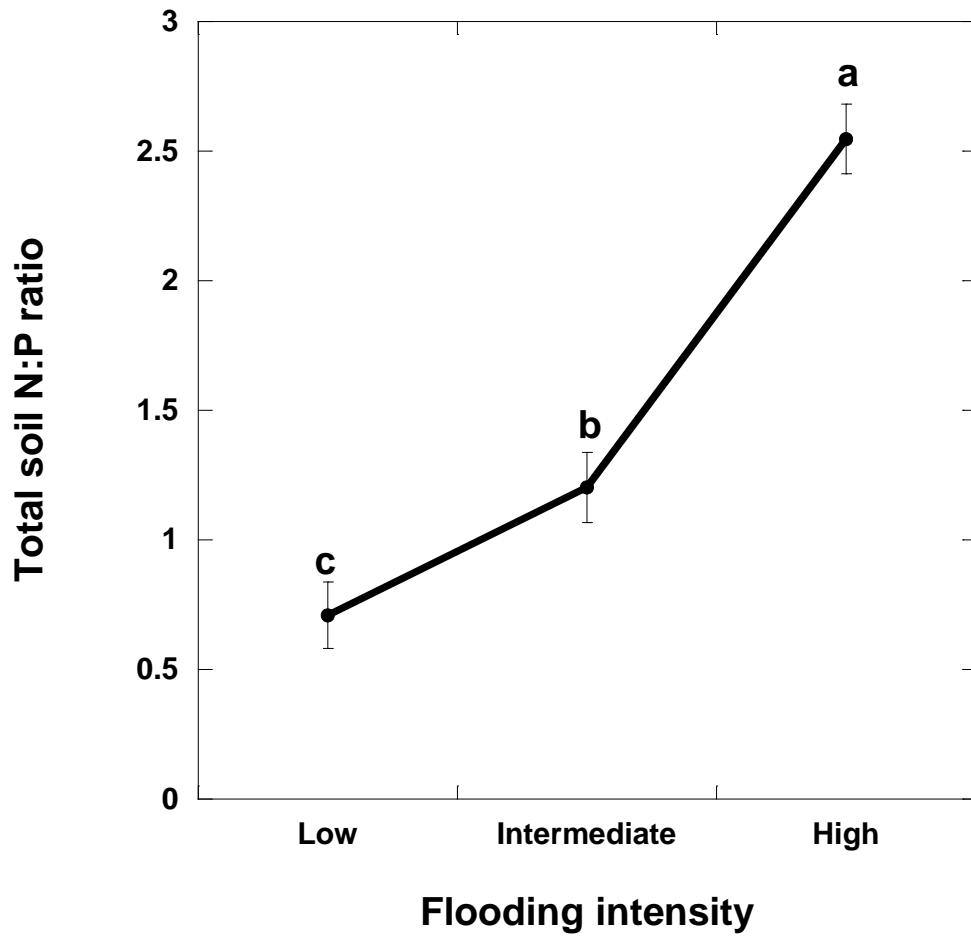


Figure 11

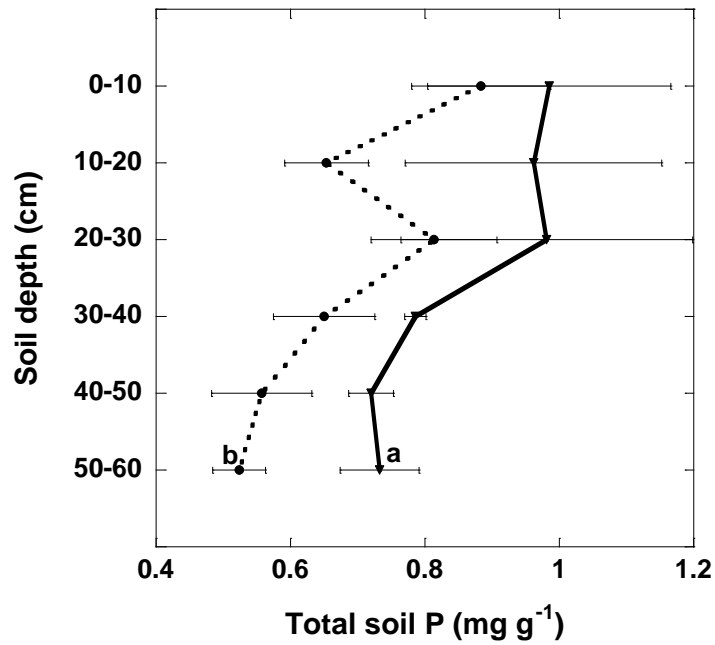
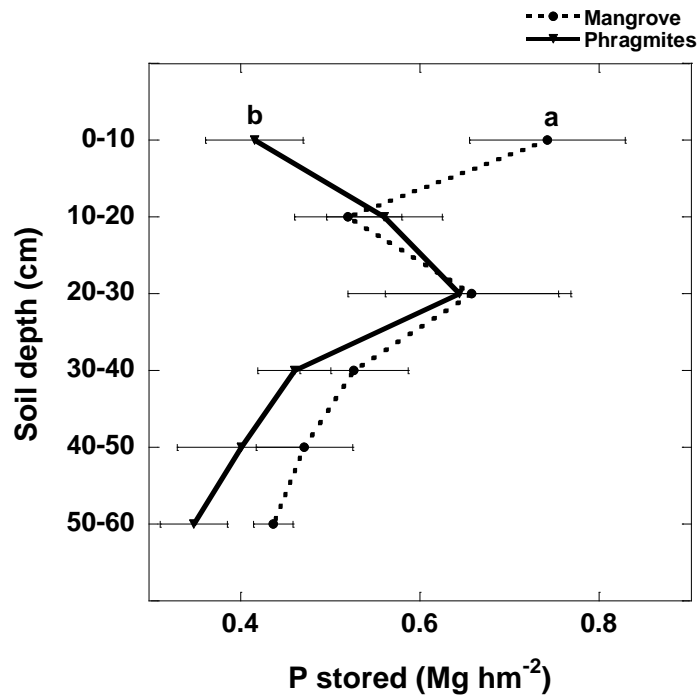


Figure 12

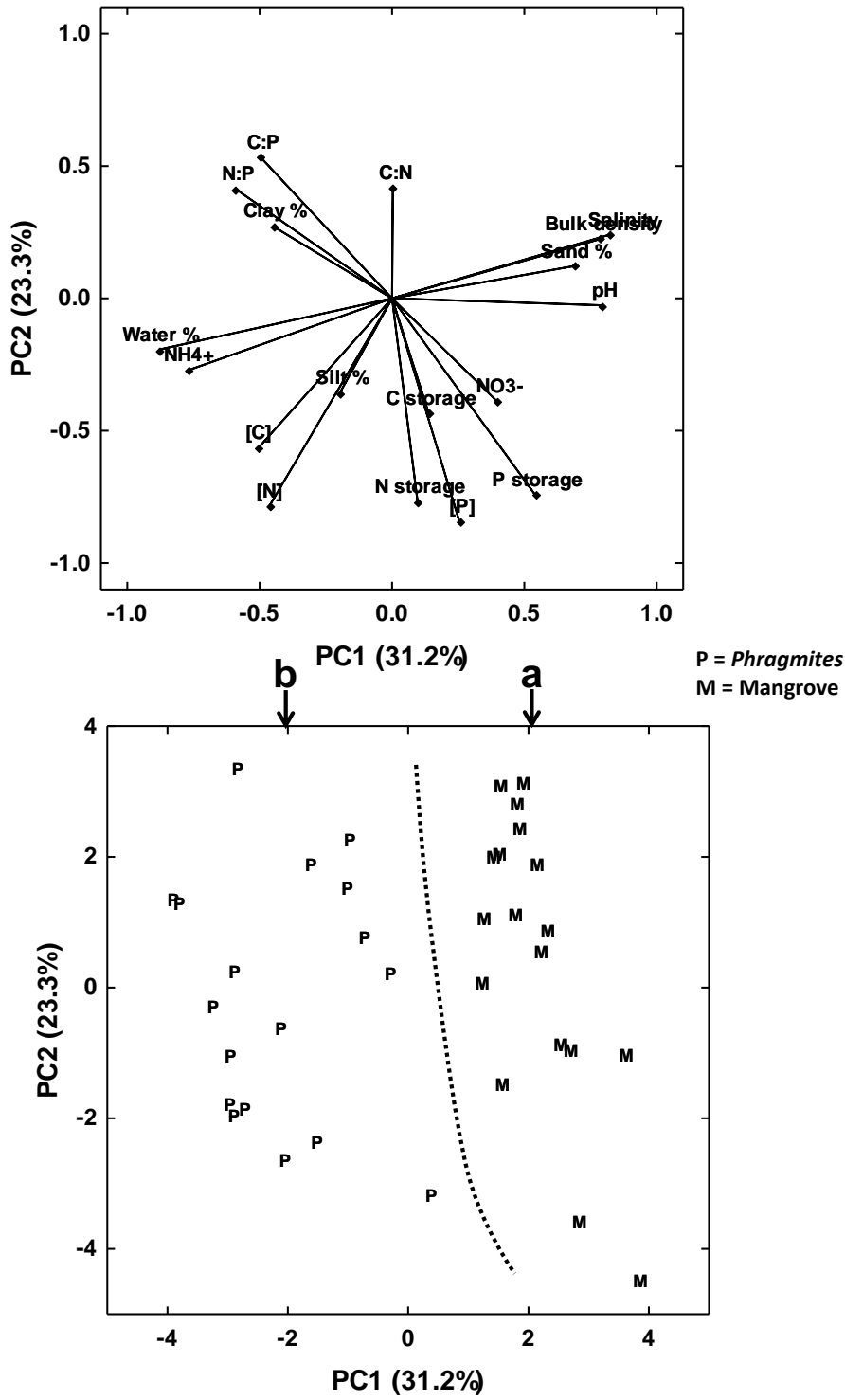


Figure 13

Supplementary information

Appendix 1.

Analyses of soil P

Total soil P concentration was determined by ashing 200 mg of dry soil for 3 h at 450 °C, transferring to a 100-ml centrifuge tube after cooling, adding 20 ml of 3.5 mol l⁻¹ HCl, shaking on a QHZ-98A full-temperature oscillator (Taicang Instruments, Taicang, China) for 16 h at 250 rpm and 25 °C, and then centrifuging at 2000g for 15 min. Ten milliliters of the supernatant were transferred to a 50-ml volumetric flask, and the pH was adjusted by adding 4 mol l⁻¹ NaHCO₃ or 0.5 mol l⁻¹ H₂SO₄ until the liquid became yellowish. Five milliliters of molybdenum-antimony anti reagent were added and then deionized water to a volume of 50 ml. The solution stood for 30 min and was then analyzed colorimetrically using a UV-2450 spectrophotometer (Shimadzu Scientific Instruments, Tokyo, Japan) at a wavelength of 700 nm (Ruban et al. 1999). A standard calibration curve was constructed by placing 0, 1, 2, 3, 4, 5, and 6 ml of a 5 mg l⁻¹ P standard solution into 50-ml volumetric flasks, adding 5 ml of molybdenum-antimony anti reagent, and then diluting to 50 ml with deionized water, thereby obtaining 0, 0.1, 0.2, 0.3, 0.4, 0.5, and 0.6 mg l⁻¹ P standard solutions. These solutions were analyzed colorimetrically using the UV-2450 spectrophotometer at a wavelength of 700 nm). Standard calibration curves were constructed by placing 0, 1, 2, 3, 4, 5, and 6 ml of a 5 mg l⁻¹ P standard solution into 50-ml volumetric flasks, adding 5 ml of molybdenum-antimony anti-reagent, and then diluting to 50 ml with deionized water, thereby obtaining P standard solutions of 0, 0.1, 0.2, 0.3, 0.4, 0.5, and 0.6 mg l⁻¹. The solutions were then analyzed colorimetrically using a UV-2450 spectrophotometer (Shimadzu Scientific Instruments, Toyo, Japan) at a wavelength of 700 nm.

Total soil inorganic P (Pi) concentration was determined by adding 200 mg of dry soil to a 100-ml centrifuge tube, adding 20 ml of 1 mol l⁻¹ HCl, shaking on the QHZ-98A full-temperature oscillator for 16 h at 250 rpm and 25 °C, and then centrifuging at 2000g for 15 min. The P concentration of the supernatant was determined colorimetrically as described above.

Total soil organic P (Po) concentration was determined by twice rinsing the residual soil in the above centrifuge tube with 12 ml of deionized water, freeze-drying, ultrasonicing in a bath for 30 s, ashing for 3 h at 450 °C, transferring to a 100-ml centrifuge tube after cooling, adding 20 ml of 3.5 mol l⁻¹ HCl, shaking on the QHZ-98A full-temperature oscillator for 16 h at 250 rpm and 25 °C, and then centrifuging at 2000g for 15 min. The P concentration of the supernatant was determined colorimetrically as described above.

To determine the concentrations in the Po fractions, we used the continuous extraction procedure of Lu (1999). Labile Po was determined by adding 5.0 g of dry soil to a 200-ml flask, adding 0.5 mol l⁻¹ NaHCO₃ (adjust pH to 8.5) and a spoon of 0.05g phosphate-free activated carbon, shaking for 0.5 h at 25 °C, and then immediately filtering with phosphate-free paper into a 100-ml flask. The P concentration of an aliquot was determined colorimetrically as above. This determination is hereafter called the *first measurement*. A 20-ml aliquot of the filtered liquid was transferred to a 50-ml flask and boiled to dryness in a DK-S28 water bath (Jinghong Instruments, Shanghai, China). Three milliliters of 98% H₂SO₄ and 10 drops of 72% HClO₄ were added, and the solution was digested for 0.5 h at 300 °C in a Digiblock EHD36 Digestion System (Zhongzi Instruments, Wuhan, China). The cooled digest was transferred to a 50-ml volumetric flask, deionized water was added to a volume of 50 ml, and the P concentration was determined colorimetrically (hereafter *second*

measurement) as above. The labile Po was obtained by subtracting the first from the second measurement.

Moderately labile Po concentrations were estimated by summing two determinations. For the first determination, we added 2.0 g of dry soil to a 150-ml flask, added 100-ml 1.0 mol l⁻¹ H₂SO₄, extracted for 3 h at 25 °C, and then immediately filtered the solution with phosphate-free paper into a 100-ml flask. We added 0.05g phosphate-free activated carbon to one of two aliquots. The first determination was obtained by subtracting the first from the second treatment. The second determination was obtained by adding the dry residual soil from the first determination to a 150-ml flask, adding 100 ml of 0.5 mol l⁻¹ NaOH, extracting for 6 h at 25 °C, and then immediately filtering with phosphate-free paper into a 100-ml flask (hereafter called liquid A). Twenty milliliters of liquid A was transferred to a 100-ml flask, decolorized with 0.05 g phosphate-free activated carbon, and the P concentration was determined colorimetrically as above.

Moderately resistant Po was analyzed by adding to the soil pellet 20 ml of liquid A to a 150-ml flask, adding HCl to a pH of 1.0-1.8, and standing for 12 h. This solution was filtered. We then prepared two treatments with two aliquots of the filtered solution. A spoon of 0.05 g phosphate-free activated carbon was added to one aliquot, which was shaken for 0.5 h and then immediately filtered with phosphate-free paper into a 100-ml flask. Five milliliters of the filtered solution was transferred to a 25-ml volumetric flask, and the P concentration was determined colorimetrically as above. The second aliquot, 20 ml of the filtered solution, was transferred to a 50-ml flask and boiled to dryness in the DK-S28 water bath. Three milliliters of 98% H₂SO₄ and 10 drops of 72% HClO₄ were added, and this solution was digested for 0.5 h at 300 °C in the Digiblock EHD36 Digestion System (first

measurement). The cooled digest was then transferred to a 50-ml volumetric flask, deionized water was added to a volume of 50 ml, and the P concentration was determined colorimetrically as above (second measurement). The concentration of the moderately resistant Po was obtained by subtracting the first from the second measurement.

Highly resistant Po was analyzed by the following first treatment, subtracting the second treatment, and then subtracting the moderately resistant Po. The first treatment was conducted by adding 20 ml of filtered liquid A to a 50-ml flask, boiling to dryness in the DK-S28 water bath, adding 3 ml of 98% H₂SO₄ and 10 drops of 72% HClO₄, and then digesting for 0.5 h at 300 °C in the Digiblock EHD36 Digestion System. The cooled digest was then transferred to a 50-ml volumetric flask, deionized water was added to a volume of 50 ml, and the P concentration was determined colorimetrically as above. The second treatment was measured by transferring 20 ml of filtered liquid A to a 100-ml flask, decoloring with 0.05 g phosphate-free activated carbon, and the P concentration was determined colorimetrically as above.

To analyze the Pi fractions, we used the continuous extraction procedure of Ruban et al. (1999). Exchangeable Pi was analyzed by adding 200 mg of dry soil to a 100-ml centrifuge tube, adding 20 ml of 1 mol l⁻¹ MgCl₂, shaking on the QHZ-98A full-temperature oscillator for 16 h at 250 rpm and 25 °C, centrifuging at 2000g for 15 min, and immediately filtering the supernatant with phosphate-free paper into a 20-ml flask. The P concentration was determined colorimetrically as above.

Fe+Al Pi was analyzed by adding 200 mg of dry soil to a 100-ml centrifuge tube, adding 20 ml of 1 mol l⁻¹ NaOH, then following the same procedure used for total Pi, shaking

on the QHZ-98A full-temperature oscillator for 16 h at 250 rpm and 25 °C, centrifuging at 2000g for 15 min, transferring the supernatant to a 20-ml flask, adding 4 ml of 3.5 mol l⁻¹ HCl, and then standing for 16 h. The supernatant was immediately filtered with phosphate-free paper into a 20-ml flask, and the P concentration was determined colorimetrically as above.

Ca Pi was analyzed by twice rinsing the residual soil in the above centrifuge tube with 12 ml saturated NaCl solution, adding 20 ml of 1 mol l⁻¹ HCl, then following the same procedure used for total Pi, shaking on the QHZ-98A full-temperature oscillator for 16 h at 250 rpm and 25 °C, and centrifuging at 2000g for 15 min. The supernatant was immediately filtered with phosphate-free paper into a 20-ml flask, and the P concentration was determined colorimetrically as above.

The concentration of the residual Pi was determined by:

$$[\text{residual Pi}] = [\text{total P}] - [\text{exchangeable Pi}] - [\text{Fe+Al Pi}] - [\text{Ca Pi}] - [\text{total Po}].$$

Total S concentrations were determined by put 1.0g dry soil into 50 ml flask, add 2 ml 0.27 mol L⁻¹ magnesium-nitrate digestion (Lu, 1999) and evaporation to dryness at 70 °C on a hot plate and then drying the residue in an oven at 300 °C overnight (Lu, 1999). The 1.0 g dried residue was digested in 5 ml 3.8 mol L⁻¹ nitric acid in a water bath for 2.5 H, oxidizing the S to sulfate. The sulfate concentration was measured by the barium-sulfate turbidity method. The available-S was extracted from 10 g of dry soil. Fifty ml of mixed solution of 8.7 mmol L⁻¹ phosphate and 2 mol L⁻¹ acetic-acid (Lu, 1999) were added to the extract and measured by the barium-sulfate turbidity method (Lu, 1999). Total organic-C content was determined by K₂Cr₂O₇-H₂SO₄ digestion (Sorrell et al. 1997; Bai et al. 2005), dissolved

organic-C (DOC) content was determined by extraction with deionized water and measured using a TOC-V CPH Total Organic Carbon Analyzer (Shimadzu Scientific Instruments, Tokyo, Japan), and total N concentration was analyzed by the K 370 Kjeldahl method (Buchi Corporation, New Castle, DE, USA). NH_4^+ and NO_3^- were extracted with 2 mol L^{-1} KCl. The NH_4^+ concentration was determined by the indophenol-blue method (Wang et al. 2014), and the NO_3^- concentration was determined by the zinc-cadmium reduction method (Wang et al. 2014), using the UV-2450 spectrophotometer.

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Table S1. Repeated measures ANOVA (in space = soil depth levels) with flooding duration as dependent categorical variable and different soil P fraction concentrations as dependent continuous variables.

Variable	Independent variables					
	Flooding duration	Species	Repeated factor (soil depth)	Flooding intensity x species	Repeated factor x flooding intensity	Repeated factor x species
Total soil P	F = 0.801 <i>P</i> = 0.38	F = 29.8 <i>P</i> < 0.0001	F = 21.2 <i>P</i> < 0.0001	F = 30.3 <i>P</i> < 0.0001	F = 5.76 <i>P</i> = 0.0002	F = 6.55 <i>P</i> < 0.0001
Total soil Pi	F = 0.611 <i>P</i> = 0.45	F = 14.9 <i>P</i> = 0.0006	F = 17.9 <i>P</i> < 0.0001	F = 19.6 <i>P</i> = 0.0002	F = 7.17 <i>P</i> < 0.0001	F = 6.3 <i>P</i> < 0.0001
Exchangeable Pi	F = 10.8	F = 68.9	F = 17.8	F = 68.7	F = 7.67	F = 5.74

	$P = 0.0066$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$
Total soil Po	F = 0.216 $P = 0.65$	F = 44.6 $P < 0.0001$	F = 5.4 $P = 0.0004$	F = 20.2 $P = 0.0001$	F = 2.17 $P = 0.069$	F = 1.10 $P = 0.38$
Labile Po	F = 10.2 $P = 0.0077$	F = 22.1 $P < 0.0001$	F = 7.01 $P < 0.0001$	F = 34.4 $P < 0.0001$	F = 10.84 $P < 0.0001$	F = 3.24 $P < 0.0001$
Total Pi/Po ratio	F = 23.5 $P = 0.0004$	F = 30.8 $P < 0.0001$	F = 6.55 $P < 0.0001$	F = 20.8 $P < 0.0001$	F = 6.43 $P < 0.0001$	F = 2.82 $P = 0.0062$
Exchangeable Pi/Po labile ratio	F = 1.42 $P = 0.26$	F = 1.83 $P = 0.20$	F = 1.94 $P = 0.105$	F = 4.29 $P = 0.039$	F = 4.29 $P = 0.0021$	F = 0.966 $P = 0.48$

Table S2. Results of the factorial univariate general linear model with flooding intensity, dominant species of the community, and soil depth (every 10 cm) as categorical independent variables and with the P fractions and other soil variables as dependent variables. A Duncan post-hoc test was used to determine the significant differences (bold, $P < 0.05$) among the dependent variables in each level of the categorical independent variables.

	Flooding duration	Species	Soil depth	Flooding intensity × species	Flooding intensity × soil depth	Species × soil depth	Flooding intensity × species × soil depth
Total P (g kg ⁻¹ soil DW)	Low = 0.633 ± 0.052 High = 0.667 ± 0.020 $P=0.16$	<i>S. triqueter</i> = 0.446 ± 0.038b <i>C. malaccensis</i> = 0.742 ± 0.047a <i>P. australis</i> = 0.762 ± 0.040a $P < 0.0001$	0-10 = 0.692 ± 0.067b 10-20 = 0.693 ± 0.052b 20-30 = 0.833 ± 0.105a 30-40 = 0.593 ± 0.051bc 40-50 = 0.536 ± 0.044c 50-60 = 0.554 ± 0.053c $P < 0.0001$	$P < 0.0001$	$P = 0.0027$	$P < 0.0001$	$P < 0.0001$
Total Pi (g kg ⁻¹ soil DW)	Low = 0.524 ± 0.046 High = 0.554 ± 0.019 $P=0.22$	<i>S. triqueter</i> = 0.392 ± 0.032b <i>C. malaccensis</i> = 0.610 ± 0.048a <i>P. australis</i> = 0.615 ± 0.038a $P < 0.0001$	0-10 = 0.567 ± 0.058b 10-20 = 0.565 ± 0.044b 20-30 = 0.722 ± 0.096a 30-40 = 0.485 ± 0.041bc 40-50 = 0.425 ± 0.041c 50-60 = 0.470 ± 0.046bc $P < 0.0001$	$P < 0.0001$	$P = 0.0005$	$P < 0.0001$	$P < 0.0001$
Exchangeable (labile) Pi (mg kg ⁻¹ soil DW)	Low = 72.6 ± 6.3b High = 83.5 ± 2.8a $P < 0.0001$	<i>S. triqueter</i> = 51.2 ± 5.8b <i>C. malaccensis</i> = 96.9 ± 5.5a <i>P. australis</i> = 86.1 ± 3.9a $P < 0.0001$	0-10 = 83.0 ± 8.3b 10-20 = 84.6 ± 5.6ab 20-30 = 95.7 ± 12.2a 30-40 = 71.2 ± 7.5c 40-50 = 65.6 ± 7.1d 50-60 = 68.3 ± 8.2cd $P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$
Fe+Al Pi (mg kg ⁻¹ soil DW)	Low = 101 ± 8b High = 113 ± 4a $P = 0.0004$	<i>S. triqueter</i> = 79.2 ± 8.2c <i>C. malaccensis</i> = 136 ± 7a <i>P. australis</i> = 106 ± 5.3b $P < 0.0001$	0-10 = 118 ± 11a 10-20 = 117 ± 7a 20-30 = 129 ± 17a 30-40 = 98.6 ± 9.5b 40-50 = 88.7 ± 7.8b 50-60 = 90.5 ± 10.7b $P < 0.0001$	$P < 0.0001$	$P = 0.0001$	$P < 0.0001$	$P < 0.0001$
Ca Pi (mg kg ⁻¹ soil DW)	Low = 317 ± 28 High = 315 ± 11 $P = 0.91$	<i>S. triqueter</i> = 234 ± 16b <i>C. malaccensis</i> = 339 ± 29a <i>P. australis</i> = 375 ± 25a $P < 0.0001$	0-10 = 318 ± 34b 10-20 = 326 ± 30b 20-30 = 438 ± 59a 30-40 = 285 ± 23b 40-50 = 254 ± 21b	$P < 0.0001$	$P = 0.0006$	$P < 0.0001$	$P < 0.0001$

			50-60 = 275 ± 25b P<0.0001				
Recalcitrant Pi (mg kg ⁻¹ soil DW)	Low = 37.7 ± 4.9 High = 42.4 ± 3.1 P=0.33	<i>S. triqueter</i> = 28.0 ± 2.3ab <i>C. malaccensis</i> = 43.9 ± 5.6b <i>P. australis</i> = 48.3 ± 5.8a P=0.0024	0-10 = 48.4 ± 7.9ab 10-20 = 37.3 ± 5.1ab 20-30 = 59.2 ± 11.3a 30-40 = 30.5 ± 4.1b 40-50 = 29.1 ± 4.3b 50-60 = 35.7 ± 4.8b P=0.0035	P=0.047	No significant	No significant	P=0.0082
Total Po (g kg ⁻¹ soil DW)	Low = 0.109 ± 0.011 High = 0.113 ± 0.004 P=0.53	<i>S. triqueter</i> = 0.055 ± 0.007b <i>C. malaccensis</i> = 0.132 ± 0.009a <i>P. australis</i> = 0.146 ± 0.006a P<0.0001	0-10 = 0.126 ± 0.016a 10-20 = 0.129 ± 0.014a 20-30 = 0.110 ± 0.013ab 30-40 = 0.108 ± 0.011ab 40-50 = 0.110 ± 0.018ab 50-60 = 0.085 ± 0.010b P=0.0019	P<0.0001	No significant	No significant	No significant
Labile Po (mg kg ⁻¹ soil DW)	Low = 11.0 ± 0.9a High = 8.72 ± 0.43b P<0.0001	<i>S. triqueter</i> = 7.46 ± 0.93c <i>C. malaccensis</i> = 13.1 ± 0.8a <i>P. australis</i> = 9.04 ± 0.64b P<0.0001	0-10 = 9.56 ± 1.53ab 10-20 = 12.0 ± 1.1a 20-30 = 10.7 ± 1.3a 30-40 = 9.64 ± 1.21ab 40-50 = 9.74 ± 1.18ab 50-60 = 7.58 ± 1.12b P=0.0002	P<0.0001	P<0.0001	P=0.01	P=0.0007
Moderately labile Po (mg kg ⁻¹ soil DW)	Low = 69.7 ± 7.1 High = 73.9 ± 2.6 P=0.27	<i>S. triqueter</i> = 33.1 ± 4.5c <i>C. malaccensis</i> = 81.3 ± 4.5a <i>P. australis</i> = 101 ± 4b P<0.0001	0-10 = 81.8 ± 10.7a 10-20 = 82.8 ± 9.6a 20-30 = 68.6 ± 8.1ab 30-40 = 70.6 ± 8.2ab 40-50 = 70.5 ± 10.7ab 50-60 = 56.6 ± 7.3b P=0.0012	P<0.0001	No significant	No significant	No significant
Moderately resistant Po (mg kg ⁻¹ soil DW)	Low = 17.7 ± 2.2 High = 19.6 ± 1.0 P=0.25	<i>S. triqueter</i> = 9.53 ± 1.39b <i>C. malaccensis</i> = 28.9 ± 2.4a <i>P. australis</i> = 23.7 ± 1.2a P<0.0001	0-10 = 22.4 ± 2.9a 10-20 = 22.1 ± 2.8ab 20-30 = 17.5 ± 2.5ab 30-40 = 17.4 ± 2.1ab 40-50 = 19.0 ± 4.5ab 50-60 = 13.6 ± 1.6a P=0.024	P<0.0001	No significant	No significant	No significant
Recalcitrant Po (mg kg ⁻¹ soil DW)	Low = 10.7 ± 1.4 High = 9.62 ± 0.51 P=0.30	<i>S. triqueter</i> = 4.89 ± 0.69c <i>C. malaccensis</i> = 15.1 ± 1.5a <i>P. australis</i> = 10.6 ± 0.9b P<0.0001	0-10 = 12.1 ± 2.0 10-20 = 12.2 ± 1.9 20-30 = 8.96 ± 1.34 30-40 = 9.91 ± 1.46 40-50 = 10.2 ± 2.7 50-60 = 7.62 ± 1.11 P = 0.11	P<0.0001	No significant	No significant	No significant

Labile Pi:Po	Low = 9.21 ± 0.98 High = 10.5 ± 0.5 P=0.18	<i>S. triqueter</i> = 10.6 ± 1.40 <i>C. malaccensis</i> = 8.36 ± 0.61 <i>P. australis</i> = 10.6 ± 0.7 P=0.10	0-10 = 11.4 ± 1.2 10-20 = 8.68 ± 1.17 20-30 = 9.98 ± 0.90 30-40 = 10.4 ± 2.0 40-50 = 7.36 ± 0.85 50-60 = 11.4 ± 1.65 P=0.14	P=0.0059	P=0.0031	No significant	No significant
Total Pi:Po	Low = 10.5 ± 1.5a High = 5.10 ± 0.20b P<0.0001	<i>S. triqueter</i> = 13.9 ± 2.0a <i>C. malaccensis</i> = 5.09 ± 0.39b <i>P. australis</i> = 4.35 ± 0.31b P<0.0001	0-10 = 8.09 ± 2.00abc 10-20 = 5.38 ± 0.65c 20-30 = 10.9 ± 2.5a 30-40 = 6.45 ± 1.44abc 40-50 = 5.64 ± 0.85bc 50-60 = 10.2 ± 3.00ab P=0.0002	P<0.0001	P=0.0003	P=0.017	P=0.063
Water content (%)	Low = 65.1 ± 2.4b High = 99.8 ± 1.8a P<0.0001	<i>S. triqueter</i> = 70.6 ± 4.6c <i>C. malaccensis</i> = 82.7 ± 2.8b <i>P. australis</i> = 94.0 ± 3.2a P<0.0001	0-10 = 88.7 ± 6.7a 10-20 = 82.5 ± 4.6ab 20-30 = 78.7 ± 6.2b 30-40 = 86.3 ± 4.9a 40-50 = 80.5 ± 5.6b 50-60 = 77.9 ± 5.3b P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001
Bulk density (g cm ⁻³ soil DW)	Low = 1.01 ± 0.02a High = 0.748 ± 0.011b P<0.0001	<i>S. triqueter</i> = 0.979 ± 0.038a <i>C. malaccensis</i> = 0.871 ± 0.026b <i>P. australis</i> = 0.789 ± 0.20c P<0.0001	0-10 = 0.841 ± 0.050b 10-20 = 0.889 ± 0.038ab 20-30 = 0.902 ± 0.051ab 30-40 = 0.854 ± 0.033ab 40-50 = 0.889 ± 0.046ab 50-60 = 0.905 ± 0.048a P=0.015	P<0.0001	P<0.0001	P<0.0001	P<0.0001
pH	Low = 6.15 ± 0.06 High = 6.18 ± 0.09 P=0.16	<i>S. triqueter</i> = 6.69 ± 0.08a <i>C. malaccensis</i> = 6.09 ± 0.05b <i>P. australis</i> = 5.71 ± 0.09c P<0.0001	0-10 = 6.33 ± 0.12a 10-20 = 6.40 ± 0.12a 20-30 = 6.30 ± 0.11a 30-40 = 6.12 ± 0.12b 40-50 = 6.00 ± 0.14bc 50-60 = 5.85 ± 0.19c P<0.0001	P<0.0001	P<0.0001	P<0.0001	P=0.012
Salinity (ms cm ⁻¹)	Low = 0.895 ± 0.034b High = 1.21 ± 0.02a P<0.0001	<i>S. triqueter</i> = 1.11 ± 0.04a <i>C. malaccensis</i> = 0.989 ± 0.043b <i>P. australis</i> = 1.06 ± 0.04ab P=0.0061	0-10 = 1.03 ± 0.07ab 10-20 = 1.01 ± 0.06b 20-30 = 0.946 ± 0.06b1 30-40 = 1.08 ± 0.06ab 40-50 = 1.15 ± 0.06a 50-60 = 1.11 ± 0.05a P=0.0029	P<0.0001	No significant	P=0.0013	No significant
Clay content (%)	Low = 21.3 ± 0.2b High = 22.3 ± 0.6a	<i>S. triqueter</i> = 10.8 ± 1.2b <i>C. malaccensis</i> = 26.7 ± 0.7a	0-10 = 20.4 ± 1.92b 10-20 = 22.8 ± 1.8a	P<0.0001	No significant	No significant	P=0.021

	$P=0.031$	<i>P. australis</i> = 27.9 ± 0.5a $P<0.0001$	20-30 = 22.0 ± 2.5ab 30-40 = 22.0 ± 2.4ab 40-50 = 21.6 ± 2.2ab 50-60 = 21.9 ± 2.4ab $P=0.11$				
Silt content (%)	Low = 44.0 ± 3.3b High = 71.1 ± 0.6a $P<0.0001$	<i>S. triqueter</i> = 44.0 ± 5.6b <i>C. malaccensis</i> = 64.9 ± 1.0a <i>P. australis</i> = 63.8 ± 0.6a $P<0.0001$	0-10 = 58.9 ± 5.1ab 10-20 = 60.1 ± 3.8a 20-30 = 54.7 ± 6.0b 30-40 = 57.4 ± 5.5ab 40-50 = 58.6 ± 5.3ab 50-60 = 55.6 ± 5.8ab $P=0.011$	$P<0.0001$	$P=0.0035$	No significant	$P=0.036$
Sand content (%)	Low = 34.7 ± 4.9a High = 6.56 ± 0.21b $P<0.0001$	<i>S. triqueter</i> = 45.2 ± 6.8a <i>C. malaccensis</i> = 8.37 ± 0.5b <i>P. australis</i> = 8.30 ± 0.44b $P<0.0001$	0-10 = 20.7 ± 6.8ab 10-20 = 17.0 ± 5.0b 20-30 = 23.2 ± 8.0a 30-40 = 20.6 ± 7.3ab 40-50 = 19.8 ± 6.9ab 50-60 = 22.5 ± 7.8ab $P=0.034$	$P<0.0001$	$P=0.017$	$P=0.027$	$P=0.0062$
Total C (g kg ⁻¹ soil DW)	Low = 14.4 ± 1.2b High = 19.3 ± 0.4a $P<0.0001$	<i>S. triqueter</i> = 10.0 ± 1.1c <i>C. malaccensis</i> = 18.8 ± 0.4b <i>P. australis</i> = 21.7 ± 0.7a $P<0.0001$	0-10 = 18.6 ± 1.5a 10-20 = 17.2 ± 0.9ab 20-30 = 15.1 ± 1.7c 30-40 = 16.7 ± 1.5c 40-50 = 16.7 ± 1.8c 50-60 = 16.8 ± 2.0bc $P<0.0001$	$P<0.0001$	$P<0.0001$	$P<0.0001$	$P<0.0001$
Total N (g kg ⁻¹ soil DW)	Low = 1.08 ± 0.09b High = 1.42 ± 0.03a $P<0.0001$	<i>S. triqueter</i> = 0.731 ± 0.084c <i>C. malaccensis</i> = 1.44 ± 0.03b <i>P. australis</i> = 1.59 ± 0.04a $P<0.0001$	0-10 = 1.40 ± 0.13a 10-20 = 1.33 ± 0.11ab 20-30 = 1.31 ± 0.13ab 30-40 = 1.19 ± 0.12b 40-50 = 1.16 ± 0.10b 50-60 = 1.12 ± 0.12b $P<0.0001$	$P<0.0001$	$P<0.0001$	$P<0.0001$	$P<0.0001$
Total S (g kg ⁻¹ soil DW)	Low = 1.19 ± 0.13b High = 2.11 ± 0.10a $P<0.0001$	<i>S. triqueter</i> = 1.98 ± 0.15a <i>C. malaccensis</i> = 1.50 ± 0.15b <i>P. australis</i> = 1.46 ± 0.16b $P<0.0001$	0-10 = 1.52 ± 0.22b 10-20 = 1.48 ± 0.24b 20-30 = 1.14 ± 0.17c 30-40 = 1.52 ± 0.18b 40-50 = 2.06 ± 0.21a 50-60 = 2.16 ± 0.24a $P<0.0001$	$P<0.0001$	$P<0.0001$	$P<0.0001$	$P<0.0001$
DOC (mg kg ⁻¹ soil DW)	Low = 34.4 ± 2.7 High = 33.1 ± 1.6 $P=0.38$	<i>S. triqueter</i> = 19.4 ± 0.94c <i>C. malaccensis</i> = 37.4 ± 1.8b <i>P. australis</i> = 44.3 ± 3.0a $P<0.0001$	0-10 = 38.0 ± 4.8b 10-20 = 45.1 ± 5.1a 20-30 = 34.1 ± 3.0bc 30-40 = 31.0 ± 3.0bc	$P<0.0001$	$P=0.0014$	$P=0.0002$	No significant

			40-50 = 28.5 ± 2.7c 50-60 = 25.7 ± 2.1c <i>P</i> <0.0001				
NH ₄ ⁺ (mg kg ⁻¹ soil DW)	Low = 9.09 ± 0.95b High = 22.1 ± 2.2a <i>P</i> <0.0001	<i>S. triqueter</i> = 15.1 ± 3.5b <i>C. malaccensis</i> = 13.9 ± 1.4c <i>P. australis</i> = 17.8 ± 1.6a <i>P</i> <0.0001	0-10 = 14.0 ± 3.2d 10-20 = 12.2 ± 2.3bc 20-30 = 10.5 ± 1.8bc 30-40 = 13.1 ± 1.0bcd 40-50 = 19.6 ± 4.3b 50-60 = 24.3 ± 5.0a <i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> <0.0001
NO ₃ ⁻ (mg kg ⁻¹ soil DW)	Low = 2.85 ± 0.41a High = 1.59 ± 0.14b <i>P</i> <0.0001	<i>S. triqueter</i> = 1.58 ± 0.20c <i>C. malaccensis</i> = 2.30 ± 0.40b <i>P. australis</i> = 2.78 ± 0.48a <i>P</i> <0.0001	0-10 = 3.64 ± 0.78a 10-20 = 3.15 ± 0.70b 20-30 = 2.52 ± 0.50c 30-40 = 1.63 ± 0.25d 40-50 = 1.16 ± 0.27e 50-60 = 1.23 ± 0.24e <i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> <0.0001
Available S (mg kg ⁻¹ soil DW)	Low = 32.5 ± 6.3b High = 59.1 ± 10.8a <i>P</i> <0.0001	<i>S. triqueter</i> = 14.5 ± 0.6b <i>C. malaccensis</i> = 115 ± 13a <i>P. australis</i> = 7.78 ± 0.45b <i>P</i> <0.0001	0-10 = 27.6 ± 6.2c 10-20 = 28.7 ± 7.9c 20-30 = 29.2 ± 9.1c 30-40 = 49.4 ± 17.0b 40-50 = 64.8 ± 19.7ab 50-60 = 75.2 ± 23.3a <i>P</i> <0.0001	<i>P</i> <0.0001	No significant	<i>P</i> <0.0001	No significant
C:N	Low = 14.2 ± 0.8 High = 13.7 ± 0.2 <i>P</i> =0.24	<i>S. triqueter</i> = 15.1 ± 1.2a <i>C. malaccensis</i> = 13.1 ± 0.3b <i>P. australis</i> = 13.7 ± 0.4ab <i>P</i> =0.0035	0-10 = 14.5 ± 0.92b 10-20 = 14.4 ± 1.1b 20-30 = 11.0 ± 0.5c 30-40 = 16.1 ± 1.5a 40-50 = 13.2 ± 0.8b 50-60 = 14.5 ± 0.6b <i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> <0.0001
C:P	Low = 22.7 ± 1.4b High = 30.5 ± 1.3a <i>P</i> <0.0001	<i>S. triqueter</i> = 20.5 ± 1.3c <i>C. malaccensis</i> = 28.2 ± 1.6b <i>P. australis</i> = 31.2 ± 1.9a <i>P</i> <0.0001	0-10 = 27.8 ± 1.4a 10-20 = 25.6 ± 0.8a 20-30 = 18.6 ± 2.1b 30-40 = 28.0 ± 1.6a 40-50 = 29.7 ± 3.1a 50-60 = 30.0 ± 3.8a <i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> =0.00014
N:P	Low = 1.65 ± 0.09b High = 1.86 ± 0.09a <i>P</i> =0.0006	<i>S. triqueter</i> = 1.44 ± 0.08b <i>C. malaccensis</i> = 1.59 ± 0.10b <i>P. australis</i> = 2.24 ± 0.10a <i>P</i> <0.0001	0-10 = 1.99 ± 0.15a 10-20 = 1.79 ± 0.12a 20-30 = 1.45 ± 0.12b 30-40 = 1.69 ± 0.14ab 40-50 = 1.94 ± 0.17a 50-60 = 1.69 ± 0.19ab	<i>P</i> <0.0001	<i>P</i> =0.0015	<i>P</i> =0.0003	<i>P</i> =0.032

			$P < 0.0001$				
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Table S3. Correlation matrix of the soil P fractions and the main physicochemical soil variables.

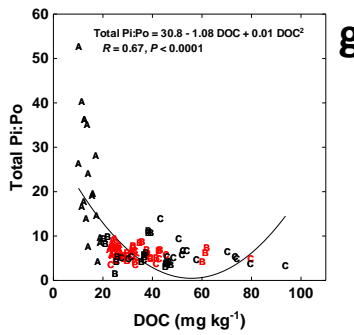
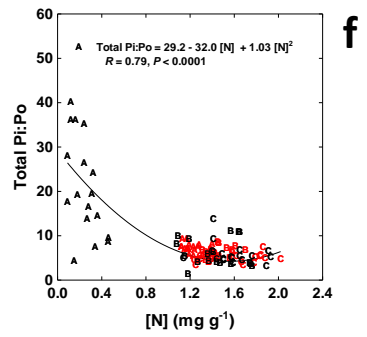
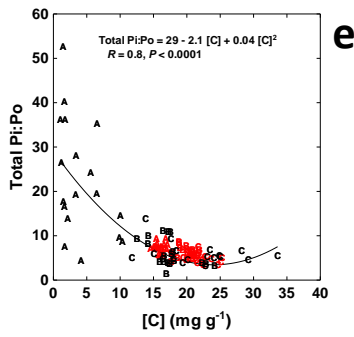
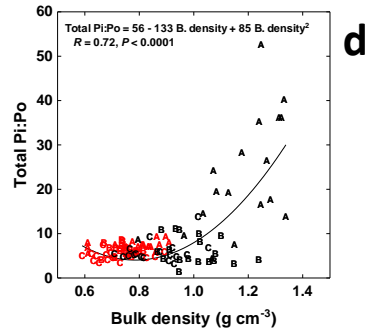
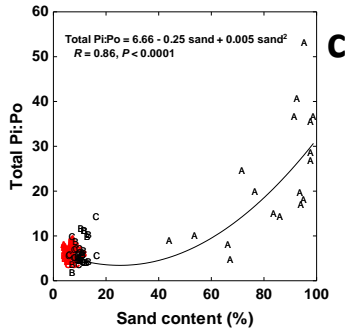
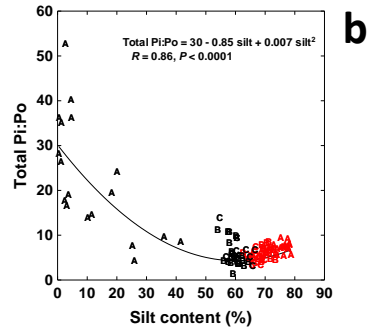
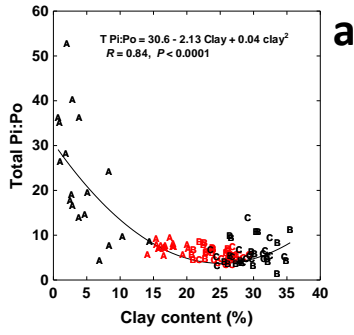
Bulk density			$R=-0.14$ $P=0.14$	$R=-0.49$ $P<0.0001$	$R=-0.52$ $P<0.0001$	$R=-0.79$ $P<0.0001$	$R=0.76$ $P<0.0001$	$R=-0.73$ $P<0.0001$	$R=-0.69$ $P<0.0001$	$R=-0.31$ $P=0.001$	$R=-0.31$ $P=0.001$	$R=-0.45$ $P<0.0001$	$R=0.10$ $P=0.30$	$R=-0.13$ $P=0.18$	$R=0.012$ $P=0.91$	$R=-0.52$ $P<0.0001$	$R=-0.37$ $P<0.0001$
pH			$R=-0.16$ $P=0.095$	$R=-0.37$ $P<0.0001$	$R=0.064$ $P=0.51$	$R=0.068$ $P=0.48$	$R=-0.30$ $P=0.001$	$R=-0.21$ $P=0.030$	$R=0.031$ $P=0.75$	$R=-0.073$ $P=0.45$	$R=0.039$ $P=0.67$	$R=0.37$ $P<0.0001$	$R=-0.13$ $P=0.19$	$R=0.027$ $P=0.78$	$R=-0.35$ $P<0.0001$	$R=-0.29$ $P=0.002$	
Salinity				$R=-0.14$ $P=0.14$	$R=0.22$ $P=0.021$	$R=-0.12$ $P=0.20$	$R=0.11$ $P=0.24$	$R=-0.04$ $P=0.67$	$R=0.75$ $P<0.0001$	$R=-0.31$ $P=0.001$	$R=0.21$ $P=0.032$	$R=-0.55$ $P<0.0001$	$R=0.16$ $P=0.103$	$R=0.17$ $P=0.087$	$R=0.40$ $P<0.0001$	$R=0.074$ $P=0.448$	
Clay content					$R=0.69$ $P<0.0001$	$R=-0.84$ $P<0.0001$	$R=0.80$ $P<0.0001$	$R=0.86$ $P<0.0001$	$R=-0.24$ $P=0.014$	$R=0.62$ $P<0.0001$	$R=0.12$ $P=0.207$	$R=0.31$ $P=0.001$	$R=0.17$ $P=0.076$	$R=0.25$ $P=0.009$	$R=0.40$ $P<0.0001$	$R=0.50$ $P<0.0001$	
Silt content						$R=-0.97$ $P<0.0001$	$R=0.80$ $P<0.0001$	$R=0.82$ $P<0.0001$	$R=0.16$ $P=0.109$	$R=0.43$ $P<0.0001$	$R=0.38$ $P<0.0001$	$R=0.25$ $P=0.009$	$R=0.23$ $P=0.018$	$R=0.23$ $P=0.018$	$R=0.45$ $P<0.0001$	$R=0.45$ $P<0.0001$	
Sand content							$R=-0.85$ $P<0.0001$	$R=-0.89$ $P<0.0001$	$R=-0.043$ $P=0.662$	$R=0.52$ $P<0.0001$	$R=-0.33$ $P=0.001$	$R=-0.29$ $P=0.003$	$R=-0.23$ $P=0.019$	$R=0.25$ $P=0.009$	$R=-0.47$ $P<0.0001$	$R=-0.50$ $P<0.0001$	
Total C								$R=0.92$ $P<0.0001$	$R=0.058$ $P=0.55$	$R=0.57$ $P<0.0001$	$R=0.27$ $P=0.005$	$R=0.26$ $P=0.007$	$R=0.16$ $P=0.11$	$R=-0.044$ $P=0.65$	$R=0.66$ $P<0.0001$	$R=0.56$ $P<0.0001$	
Total N									$R=-0.18$ $P=0.067$	$R=0.69$ $P<0.0001$	$R=0.26$ $P=0.006$	$R=0.40$ $P<0.0001$	$R=0.10$ $P=0.303$	$R=-0.31$ $P=0.001$	$R=0.42$ $P<0.0001$	$R=0.55$ $P<0.0001$	
Total S										$R=-0.42$ $P<0.0001$	$R=0.17$ $P=0.071$	$R=-0.47$ $P<0.0001$	$R=0.28$ $P=0.004$	$R=0.39$ $P<0.0001$	$R=0.51$ $P<0.0001$	$R=0.013$ $P=0.897$	
DOC										$R=0.074$ $P=0.45$	$R=0.59$ $P<0.0001$	$R=-0.022$ $P=0.82$	$R=0.22$ $P=0.024$	$R=0.17$ $P=0.079$	$R=0.29$ $P=0.002$		
NH ₄ ⁺												$R=-0.064$ $P=0.51$	$R=0.031$ $P=0.75$	$R=-0.058$ $P=0.55$	$R=0.16$ $P=0.099$	$R=0.12$ $P=0.210$	
NO ₃ ⁻													$R=-0.29$ $P=0.002$	$R=-0.23$ $P=0.018$	$R=-0.13$ $P=0.181$	$R=0.21$ $P=0.026$	
Sulfate														$R=0.013$ $P=0.89$	$R=0.25$ $P=0.008$	$R=-0.31$ $P=0.001$	
C:N															$R=0.38$ $P<0.0001$	$R=-0.14$ $P=0.145$	
C:P																$R=0.60$ $P<0.0001$	

Table S4. Results of the factorial univariate general linear model with the dominant species of the community and soil depth (every 10 cm) as categorical independent variables and with P fractions and other soil variables as dependent variables. A Duncan post-hoc test was used to determine the significant differences (bold, $P < 0.05$) among the values of the dependent variables in each level of the categorical independent variables.

Variable	Community	Soil depth	Community \times soil depth
Total P (g kg ⁻¹ soil DW)	<i>P. australis</i> wetland = 0.663 \pm 0.049 Mangrove = 0.680 \pm 0.041 $P=0.80$	0-10 = 0.770 \pm 0.075 10-20 = 0.719 \pm 0.044 20-30 = 0.873 \pm 0.082 30-40 = 0.632 \pm 0.047 40-50 = 0.553 \pm 0.058 50-60 = 0.483 \pm 0.030 $P=0.52$	
Water content %	<i>P. australis</i> wetland = 107 \pm 3a Mangrove = 83.8 \pm 0.7b $P < 0.0001$	0-10 = 98.4 \pm 8.5 10-20 = 97.8 \pm 6.6 20-30 = 98.7 \pm 6.6 30-40 = 94.4 \pm 6.5 40-50 = 94.3 \pm 6.6 50-60 = 90.3 \pm 3.6 $P=0.97$	
Bulk density (g cm ⁻³ soil DW)	<i>P. australis</i> wetland = 0.716 \pm 0.020b Mangrove = 0.822 \pm 0.009a $P < 0.0001$	0-10 = 0.735 \pm 0.048 10-20 = 0.751 \pm 0.032 20-30 = 0.743 \pm 0.031 30-40 = 0.783 \pm 0.033 40-50 = 0.794 \pm 0.038 50-60 = 0.809 \pm 0.021 $P=0.69$	
pH	<i>P. australis</i> wetland = 5.42 \pm 0.05b Mangrove = 6.12 \pm 0.02a $P < 0.0001$	0-10 = 5.90 \pm 0.16 10-20 = 5.85 \pm 0.15 20-30 = 5.77 \pm 0.16 30-40 = 5.72 \pm 0.15 40-50 = 5.76 \pm 0.16 50-60 = 5.64 \pm 0.22 $P=0.16$	
Salinity (ms cm ⁻¹)	<i>P. australis</i> wetland = 1.26 \pm 0.03b Mangrove = 1.75 \pm 0.04a $P < 0.0001$	0-10 = 1.48 \pm 0.16 10-20 = 1.43 \pm 0.13 20-30 = 1.48 \pm 0.13 30-40 = 1.53 \pm 0.11 40-50 = 1.53 \pm 0.10 50-60 = 1.57 \pm 0.11 $P=0.43$	
Clay %	<i>P. australis</i> wetland = 26.3 \pm 0.4 Mangrove = 25.2 \pm 0.4 $P=0.061$	0-10 = 24.6 \pm 1.2 10-20 = 26.2 \pm 0.8 20-30 = 25.4 \pm 0.6 30-40 = 26.6 \pm 0.4 40-50 = 25.3 \pm 0.8 50-60 = 26.3 \pm 0.5 $P=0.86$	
Silt %	<i>P. australis</i> wetland = 66.8 \pm 0.4a Mangrove = 65.6 \pm 0.5b $P=0.024$	0-10 = 67.1 \pm 0.6a 10-20 = 66.0 \pm 0.7ab 20-30 = 66.4 \pm 0.9ab 30-40 = 65.5 \pm 1.0b 40-50 = 66.3 \pm 1.2ab 50-60 = 66.0 \pm 0.7ab $P=0.026$	$P=0.026$
Sand %	<i>P. australis</i> wetland = 6.83 \pm 0.29b Mangrove = 9.26 \pm 0.33a $P < 0.0001$	0-10 = 8.29 \pm 0.70 10-20 = 7.78 \pm 0.41 20-30 = 8.20 \pm 1.00 30-40 = 7.89 \pm 1.01 40-50 = 8.41 \pm 0.88 50-60 = 7.68 \pm 0.45 $P=0.72$	

Total C (g kg ⁻¹ soil DW)	<i>P. australis</i> wetland = 22.0 ± 0.4a Mangrove = 18.7 ± 0.7b <i>P</i> =0.0002	0-10 = 22.4 ± 0.8 10-20 = 20.5 ± 0.8 20-30 = 20.6 ± 1.2 30-40 = 20.1 ± 1.1 40-50 = 19.6 ± 1.4 50-60 = 18.7 ± 1.3 <i>P</i> =0.49	
Total N (g kg ⁻¹ soil DW)	<i>P. australis</i> wetland = 1.60 ± 0.06a Mangrove = 1.38 ± 0.05b <i>P</i> =0.0072	0-10 = 1.67 ± 0.08 10-20 = 1.67 ± 0.10 20-30 = 1.60 ± 0.09 30-40 = 1.43 ± 0.07 40-50 = 1.34 ± 0.08 50-60 = 1.22 ± 0.03 <i>P</i> =0.20	
NH ₄ ⁺ (mg kg ⁻¹ soil DW)	<i>P. australis</i> wetland = 20.0 ± 2.4a Mangrove = 6.28 ± 0.30b <i>P</i> =0.00024	0-10 = 20.7 ± 7.4a 10-20 = 16.0 ± 4.4ab 20-30 = 14.1 ± 3.4ab 30-40 = 9.8 ± 2.0abc 40-50 = 7.1 ± 0.6c 50-60 = 11.2 ± 2.1abc <i>P</i> =0.019	<i>P</i>=0.019
NO ₃ ⁻ (mg kg ⁻¹ soil DW)	<i>P. australis</i> wetland = 1.24 ± 0.12b Mangrove = 1.90 ± 0.27a <i>P</i> =0.020	0-10 = 2.52 ± 0.62a 10-20 = 2.02 ± 0.36ab 20-30 = 1.46 ± 0.16ab 30-40 = 1.06 ± 0.11bc 40-50 = 0.86 ± 0.07c 50-60 = 1.50 ± 0.30ab <i>P</i> =0.008	
C storage (Mg hm ⁻²)	<i>P. australis</i> wetland = 15.7 ± 0.4 Mangrove = 15.3 ± 0.6 <i>P</i> =0.63	0-10 = 16.6 ± 1.6 10-20 = 15.4 ± 0.6 20-30 = 15.2 ± 0.3 30-40 = 15.6 ± 0.6 40-50 = 15.4 ± 0.7 50-60 = 15.0 ± 0.9 <i>P</i> =0.60	
N storage (Mg hm ⁻²)	<i>P. australis</i> wetland = 1.13 ± 0.04 Mangrove = 1.13 ± 0.04 <i>P</i> =0.99	0-10 = 1.2 ± 0.1 10-20 = 1.2 ± 0.1 20-30 = 1.2 ± 0.1 30-40 = 1.1 ± 0.1 40-50 = 1.1 ± 0.1 50-60 = 1.0 ± 0.1 <i>P</i> =0.25	
P storage (Mg hm ⁻²)	<i>P. australis</i> wetland = 0.471 ± 0.035 Mangrove = 0.559 ± 0.035 <i>P</i> =0.086	0-10 = 0.579 ± 0.086 10-20 = 0.540 ± 0.040 20-30 = 0.651 ± 0.071 30-40 = 0.493 ± 0.036 40-50 = 0.436 ± 0.043 50-60 = 0.392 ± 0.028 <i>P</i> =0.51	
C:N	<i>P. australis</i> wetland = 14.1 ± 0.5 Mangrove = 13.6 ± 0.2 <i>P</i> =0.40	0-10 = 13.5 ± 0.7 10-20 = 12.4 ± 0.4 20-30 = 13.0 ± 0.4 30-40 = 14.1 ± 0.4 40-50 = 14.7 ± 0.4 50-60 = 15.3 ± 0.4 <i>P</i> =0.49	
C:P	<i>P. australis</i> wetland = 36.1 ± 2.6a Mangrove = 28.6 ± 1.4b <i>P</i> =0.017	0-10 = 30.1 ± 2.1 10-20 = 29.0 ± 1.6 20-30 = 24.5 ± 2.4 30-40 = 32.8 ± 3.3 40-50 = 37.6 ± 4.9 50-60 = 40.0 ± 5.0 <i>P</i> =0.60	
N:P	<i>P. australis</i> wetland = 2.55 ± 0.13a Mangrove = 2.12 ± 0.11b <i>P</i> =0.017	0-10 = 2.26 ± 0.21 10-20 = 2.35 ± 0.13 20-30 = 1.90 ± 0.20 30-40 = 2.31 ± 0.19 40-50 = 2.59 ± 0.35	

		$50-60 = 2.57 \pm 0.19$ $P=0.26$	
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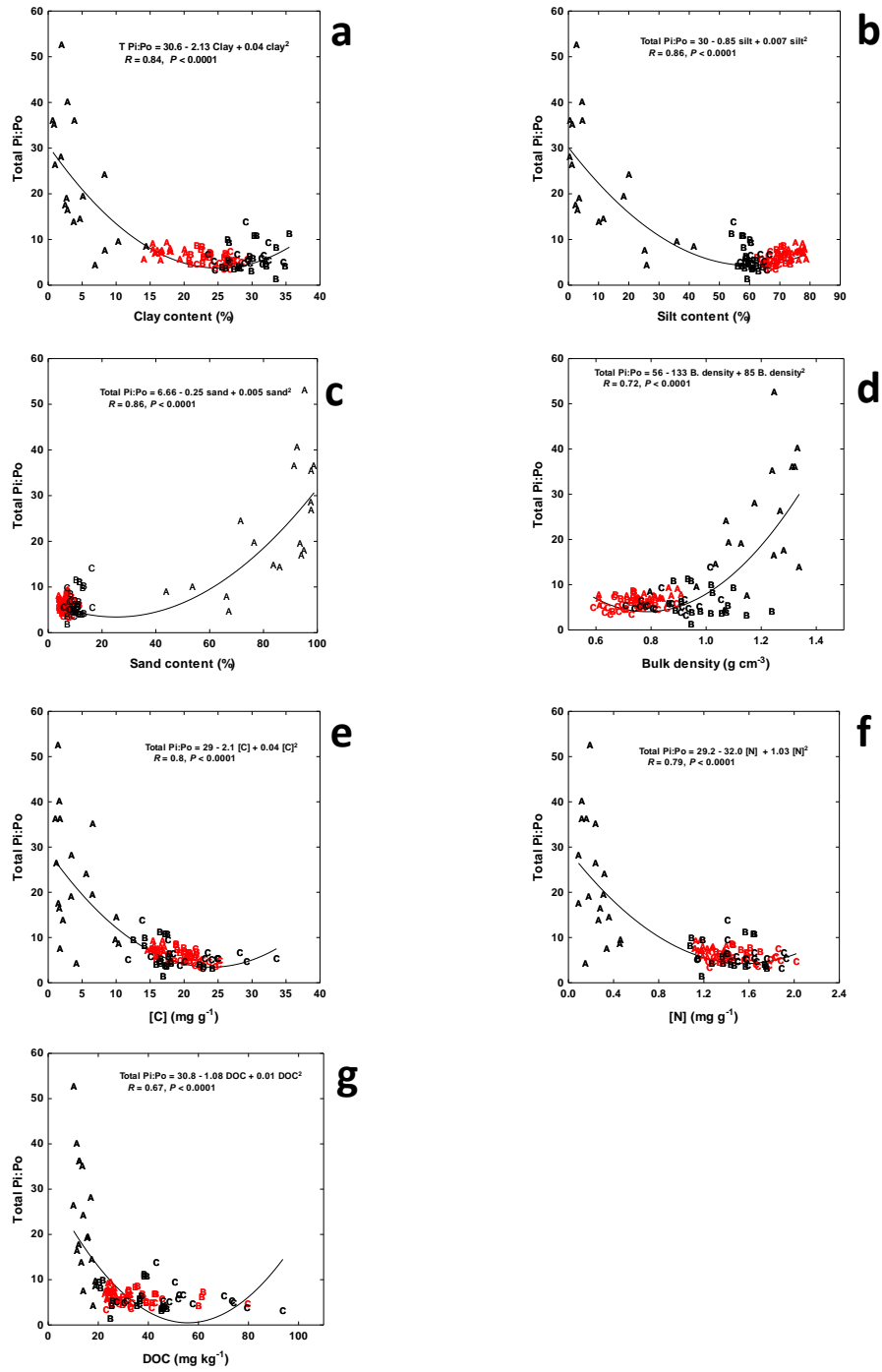


Figure S1. Second-level polynomial regressions between the total soil Pi:Po ratio and clay content (a), silt content (b), sand content (c), bulk density (d), total C concentration (e), total N concentration (f), and total dissolved organic-C (DOC) concentration (g).