

# *Organic phosphorus in the terrestrial environment: a perspective on the state of the art and future priorities*

Article

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1 **Organic phosphorus in the terrestrial environment: A perspective on the state of the art and future**  
2 **priorities**

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## 64 **Abstract**

65 **Background:** The dynamics of phosphorus (P) in the environment is important for regulating nutrient cycles in  
66 natural and managed ecosystems and an integral part in assessing biological resilience against environmental  
67 change. Organic P (P<sub>o</sub>) compounds play key roles in biological and ecosystems function in the terrestrial  
68 environment, being critical to cell function, growth and reproduction.

69 **Scope:** We asked a group of experts to consider the global issues associated with P<sub>o</sub> in the terrestrial  
70 environment, methodological strengths and weaknesses, benefits to be gained from understanding the P<sub>o</sub> cycle,  
71 and to set priorities for P<sub>o</sub> research.

72 **Conclusions:** We identified seven key opportunities for P<sub>o</sub> research including: the need for integrated, quality  
73 controlled and functionally based methodologies; assessment of stoichiometry with other elements in organic  
74 matter; understanding the dynamics of P<sub>o</sub> in natural and managed systems; the role of microorganisms in  
75 controlling P<sub>o</sub> cycles; the implications of nanoparticles in the environment and the need for better modelling and  
76 communication of the research. Each priority is discussed and a statement of intent for the P<sub>o</sub> research  
77 community is made that highlights there are key contributions to be made toward understanding biogeochemical  
78 cycles, dynamics and function of natural ecosystems and the management of agricultural systems.

## 79 **Keywords**

80 , Ecosystems services, Method development, Microbiome, Modelling, Organic Phosphorus, Stoichiometry.

## 81 **Abbreviations**

82  $\delta^{18}OP$  – oxygen-18 isotope ratio

83 16S rRNA = 16S ribosomal Ribonucleic acid

84 Al = Aluminium

85 ATP = Adenosine triphosphate

86 C = Carbon

87 DNA = Deoxyribonucleic acid

88 Fe = Iron

89 N = Nitrogen

90 P = Phosphorus

91 Pho = Pho regulon transcription factors

92  $P_i$  = Inorganic orthophosphate

93  $P_o$  = Organic phosphate compounds

94 S = Sulphur

## 95 **The Importance of Phosphorus and Organic Phosphorus**

96 The dynamics of phosphorus (P) in the terrestrial environment is critical for regulating nutrient cycling in both  
97 natural and managed ecosystems. Phosphorus compounds fundamentally contribute to life on earth: being  
98 essential to cellular organization as phospholipids, as chemical energy for metabolism in the form of ATP,  
99 genetic instructions for growth, development and cellular function as nucleic acids, and as intracellular  
100 signalling molecules (Butusov and Jernelöv 2013). Plant growth is limited by soil P availability, so turnover of  
101 organic phosphorus ( $P_o$ ) represents a source of P for ecosystem function and, critically, P supply affects crop  
102 production (Runge-Metzger 1995). Phosphorus deficiency constrains the accumulation and turnover of plant  
103 biomass and dictates community assemblages and biodiversity in a range of natural ecosystems (Attiwill and  
104 Adams 1993; McGill and Cole 1981).

105 Chemically, P is a complex nutrient that exists in many inorganic ( $P_i$ ) and organic ( $P_o$ ) forms in the  
106 environment. Through the utilization of orthophosphate, plants and other organisms drive the conversion of  $P_i$  to  
107  $P_o$ . Death, decay and herbivory facilitate the return of both  $P_o$  and  $P_i$  in plant materials to soil. Inputs of P to soil  
108 through these processes may contribute  $P_o$  directly to soil or indirectly, following decomposition, accumulation,  
109 and stabilization of  $P_o$  by microorganisms (Harrison 1982; Lang et al. 2016; Magid et al. 1996; McGill and Cole

110 1981; Stewart and Tiessen 1987; Tate and Salcedo 1988). In its simplest definition, P<sub>o</sub> is any compound that  
111 contains an organic moiety in addition to P, while a wider definition would include phosphate which is  
112 associated with organic matter. Such discrete P<sub>o</sub> compounds are categorized into similarly structured forms and  
113 these forms and their relative lability in soil is shown in Figure 1, taken from Darch et al. (2014). The P<sub>o</sub>  
114 compounds, which are considered to be biologically relevant include monoesters, inositol phosphates, diesters  
115 and phosphonates. The relative lability and accumulation of these different groups varies in the environment, but  
116 overall the labile monoesters and diesters tend to be less prevalent and the inositol phosphates tend to be less  
117 labile and accumulate in the environment (Darch et al. 2014). In general, soil organic P forms have a smaller  
118 affinity to the soil solid phase than inorganic P forms and a large proportion of the P forms found in leachate are  
119 found to be in organic forms (Chardon & Oenema, 1995; Chardon et al. 1997; Espinosa et al. 1999) and can  
120 therefore have large impacts on ecosystem function (Sharma et al. 2017; Toor et al. 2003). All P<sub>o</sub> compounds  
121 have a range of chemical bonds, and all require specific catalytic enzymes to make them biologically available  
122 in the form of orthophosphate. The hydrolysis of P<sub>o</sub> is mediated by the action of a suite of phosphatase enzymes  
123 which may have specificity for single compounds or broad specificity to a range of compounds (George et al.  
124 2007). Unlike for organic nitrogen, there is no evidence for direct uptake of dissolved P<sub>o</sub> compounds by biology,  
125 apart from the uptake of phosphonates by bacteria in marine systems (Dyhrman et al. 2006). Plants and  
126 microbes possess a range of phosphatases that are associated with various cellular functions, including; energy  
127 metabolism, nutrient transport, metabolic regulation and protein activation (Duff et al. 1994). However, it is the  
128 extracellular phosphatases released into the soil that are of particular importance for the mineralisation of soil  
129 P<sub>o</sub>. Extracellular phosphatase activity is induced under conditions of P deficiency and is either associated with  
130 root cell walls or released directly into the rhizosphere (Richardson et al. 2009).

131 There have been a number of important advances in our understanding of P<sub>o</sub> dynamics at the ecosystem and  
132 rhizosphere scale in the past decade, with particular advancement in understanding of plant-soil-microorganism  
133 interactions and concomitant advances in techniques used to assess these dynamics. It is now timely to start to  
134 consider how to integrate this information and extract further understanding of the dynamics of P<sub>o</sub> in the  
135 managed and natural environment and this will have a number of potentially important impacts on how we  
136 tackle some of the most pressing global issues of today. Here we summarise the state of the art of P<sub>o</sub> research  
137 and identify priorities for future research, which will help meet these goals.

### 138 **Establishing Priorities for Organic Phosphorus Research**

139 There has been a large increase in the number of publications in the P<sub>o</sub> research field in the last two decades,  
140 with ~400 publications in 2016, compared to 150 in 2000. In September 2016 a workshop on Organic  
141 Phosphorus was held (<https://op2016.com>), gathering together 102 experts in the field of P<sub>o</sub> research from 23  
142 countries to identify research priorities. Contributors were asked, in five groups, to consider the global issues  
143 associated with P<sub>o</sub>, methodological strengths and weaknesses, benefits to be gained from understanding the P<sub>o</sub>  
144 cycle, and priorities for P<sub>o</sub> research. The information from the five groups was collected and the concepts, where  
145 consensus between at least two of the groups was reached, are summarized in Table 1. It is clear from this that  
146 research into P<sub>o</sub> has the potential to have impacts on global biogeochemical cycles of P both in natural and  
147 managed systems and will therefore potentially impact food security, agricultural sustainability, environmental  
148 pollution of both the aquatic and atmospheric environments and will be profoundly affected by environmental  
149 change both in geopolitical terms and through man-made climate change. We are well placed to tackle these as  
150 there are a number of strengths in the way the research is performed and the weaknesses are well understood. It  
151 was considered that P<sub>o</sub> research will have a range of impactful outcomes on our understanding of how natural  
152 and agricultural systems work and has the potential to give society a number of important tools to help manage  
153 the environment more effectively to either prevent or mitigate against some of the major global threats. A  
154 number of research priorities were identified and grouped into specific opportunities which are detailed below.  
155 The key opportunities to improve the effectiveness of P<sub>o</sub> research identified here are similar to those highlighted  
156 in Turner et al. (2005), although it is clear that some progress has been made since that set of recommendations  
157 were made. However, the similarities and consistency between the outcomes of these two studies suggests we  
158 still have some progress to make. A number of new priority areas were identified here that were not identified in  
159 Turner et al. (2005), including the need for greater understanding of the metagenomics and functional microbial  
160 genes involved in organic P turnover, greater understanding of the impact of nanoparticles in the environment  
161 on organic P turnover and the need to integrate the system more effectively in the form of models. It is clear that  
162 P<sub>o</sub> research field is evolving, but some of the issues of a decade ago still persist.

### 163 **1) Opportunities in organic phosphorus analytical methodologies**

164 The core analytical tools for the P<sub>o</sub> discipline are <sup>31</sup>P NMR spectroscopy (Cade-Menun and Liu 2014; Cade-  
165 Menun 2005; Cade-Menun et al. 2005; Turner et al. 2005), which is used to identify P<sub>o</sub> compounds in several  
166 environmental matrices, along with more traditional soil extraction methods, such as those to measure total P<sub>o</sub>  
167 and the fractionation method developed by Hedley et al. (Condon and Newman 2011; Hedley et al. 1982;

168 Negassa and Leinweber 2009). There is discussion and debate focused around the suitability of these analytical  
169 methodologies for characterizing P<sub>o</sub> in soil and terrestrial systems (Liu et al. 2014; Doolette and Smernik, 2011)  
170 and this debate revolves around the identity of the broad base of the inositol hexaphosphate peak on NMR  
171 spectra, which some contest is resolved and other suggest is unidentified (Jarosch et al. 2015). Despite this,  
172 research into P<sub>o</sub> is still limited methodologically and many methods are operationally-defined. Importantly, there  
173 is a need to link the results from these methods to biological and biogeochemical processes in the environment.  
174 In the process of achieving this, there is debate over the benefits of (i) standardization or homogenization of  
175 analytical methods, versus the merits of (ii) promoting diversity of analytical procedures.

176 It is critical to develop non-destructive methods to analyse soil pools and their dynamics without the need for  
177 extraction. Some solid-state methods, such as solid-state NMR or P-XANES (X-ray Adsorptive Near Edge  
178 Structure) spectroscopy are limited by the naturally low concentrations of P<sub>o</sub> forms in soils (Liu et al. 2013;  
179 2014; 2015). Visible Near-Infrared Reflectance Spectroscopy (VNIRS) has shown some promise for  
180 determining total P<sub>o</sub> in soils (Abdi et al, 2016), but further testing is needed. Another priority for P<sub>o</sub>  
181 methodologies is the development of standard analytical quality controls through the use of standardized  
182 reference materials for cross-comparison and checks on analytical methods. These standardized reference  
183 materials will include reference soils and chemicals. There is a need for the community to identify standardized  
184 natural reference materials such as soils and manures, but a large amount of effort would be needed to put  
185 together a collection of appropriate materials as well as a means to share them internationally. Standardization  
186 of P<sub>o</sub> compounds could be achieved through the use of simple, relatively pure, and inexpensive P<sub>o</sub> compounds  
187 (e.g. Na-phytate, glucose 1-P) purchased from a single supplier operating in many countries with a guaranteed  
188 long-term production commitment. And there is a need to develop a commercial supply of other commonly  
189 identified P<sub>o</sub> compounds in soils, such as scyllo-inositol hexakisphosphate, to allow the use of appropriate  
190 substrates for research fully understand the biological and chemical processes controlling the behaviour of this  
191 and other P<sub>o</sub> compounds in the environment. It is a priority for researchers to further develop methods, while  
192 also refining existing P<sub>o</sub> methods and standards, to generate useful and comparable datasets and to build a  
193 consensus with respect to P<sub>o</sub> dynamics and function in agricultural and natural ecosystems.

194 **2) Opportunities from understanding stoichiometry – interactions of organic phosphorus with other**  
195 **element cycles**

196 Comparing element ratios of living organisms and their non-living environment has been at the centre of  
197 scientific debate for many years. In oceans, planktonic biomass is characterized by similar C:N:P ratios as  
198 marine water (106:16:1) (Redfield 1958). While similar characteristic element ratios also exist for terrestrial  
199 ecosystems with much greater heterogeneity across a range of spatial scales (Cleveland and Liptzin 2007). The  
200 comparison of C:N:P ratios in the microbial biomass of soils with that of soil organic matter (SOM) may  
201 therefore help to identify the nutrient status of the soil (Redfield 1958). Following this concept, the  
202 stoichiometric ratios of resources (e.g., SOM) over the microbial biomass has been calculated as a proxy for  
203 nutrient imbalances (Cleveland and Liptzin 2007). An understanding of stoichiometric ratios in soils and their  
204 relationship to those in crop plants and for the decomposition of litter and SOM will provide an important  
205 indicator of nutrient status in terrestrial ecosystems and better management of systems.

206 Until now, the large temporal and spatial heterogeneity of soil systems and the heterogeneous distribution of  
207 SOM constituents have made the analysis and interpretation of ecosystem stoichiometry a challenge because for  
208 microbial decomposers the elemental composition of micro-sites in soils might be more relevant than the overall  
209 element ratio of the soil. For example, by analysing the C:N:P ratio of bulk soils only, information on relevant  
210 and spatially-dependent processes may be lost (e.g., rhizosphere, soil horizons). The most obvious reason for  
211 soil-specificity and heterogeneity among stoichiometric ratios is that part of the SOM is separated from  
212 microorganisms and roots via physical and physicochemical barriers. By re-analysing the results of  
213 C:N:P:Sulphur (S) analyses of SOM obtained from 2000 globally distributed soil samples, Tipping et al. (2016)  
214 demonstrated that there is both nutrient-poor and nutrient-rich SOM, with the latter being strongly sorbed by soil  
215 minerals (Tipping et al. 2016). This may be explained by the incorporation of SOM into aggregates (Stewart and  
216 Tiessen 1987) or the adsorption of P-containing organic and inorganic molecules to mineral surfaces (Celi et al.  
217 2003; Giaveno et al. 2010). Clay and metal (oxy)hydroxide minerals can sequester  $P_o$  and  $P_i$  released by  
218 microbial- or plant-driven processes and/or affect enzyme activities, while limiting P biocycling (Celi and  
219 Barberis 2005). This highlights the need to understand the tight interrelationship between chemical, physical and  
220 biological processes and the potential for stoichiometric assessment as an indicator of P and organic matter  
221 availability in soils. Modern analytical techniques which enable to analyse the stoichiometry of the soil  
222 constituents at a high resolution might help provide this knowledge (Mueller et al. 2012).

223 There are many known mechanisms by which organisms can improve access to  $P_o$  (Richardson et al. 2011), but  
224 there are several novel mechanisms being identified that target key components of SOM, such as polyphenols

225 and tannins, to mobilise P (Kohlen et al. 2011). A priority will be to understand the plant and microbial  
226 mechanisms involved in the accumulation and mobilization of P from organic matter. It is important to attempt  
227 to determine the optimal stoichiometry between C:N:P, and understand the role P<sub>o</sub> plays in this, to allow  
228 sustainable management of P in arable soils and to identify anthropogenic nutrient imbalances in natural,  
229 agricultural and forest ecosystems (Frossard et al. 2015).

### 230 **3) Opportunities from understanding interactions of organic phosphorus with land management**

231 An ability to utilise P<sub>o</sub> to sustain agronomic productivity with declining conventional fertiliser inputs drives  
232 research into interactions among P<sub>o</sub>, land use and management (Nash et al. 2014; Stutter et al. 2012). The  
233 conditions to better utilise P<sub>o</sub> may bring benefits for other soil quality factors (e.g., SOM status and microbial  
234 cycling), but may require management of potentially adverse effects on wider biological cycles and water  
235 quality (Dodd and Sharpley 2015). Societal drivers for food and timber production underpin much of the  
236 research into P<sub>o</sub> speciation, biological turnover and integration with agronomic systems. Numerous studies have  
237 reported P<sub>o</sub> stocks and changes associated with management; fewer have studied the time-course of  
238 transformations and turnover with management change, linked with soil chemical and biological processes. The  
239 interactions between P speciation, (bio)availability and SOM are of prime importance since land management  
240 greatly affects SOM in space and time (in beneficial or detrimental ways) and exert strong geochemical and  
241 microbial controls on P<sub>o</sub> cycling.

242 The interactions of land cover, use and management are important for understanding the role of P<sub>o</sub> across  
243 ecosystems. In agricultural systems, the information on soil P<sub>o</sub> stocks is well represented have been quantified  
244 by numerous studies in North America (Abdi et al. 2014; Cade-Menun et al. 2015; Liu et al. 2015; Schneider et  
245 al. 2016), Europe (Ahlgren et al. 2013; Annaheim et al. 2015; Keller et al. 2012; Stutter et al. 2015), China (Liu  
246 et al. 2013), South America (de Oliveira et al. 2015), and Australia (Adeloju et al. 2016). In forestry, such  
247 information is available in tropical (Zaia et al. 2012) and temperate systems (Slazak et al. 2010) and orchards  
248 (Cui et al. 2015). However, an important improvement will be to better understand the reasons as to why  
249 particular stocks exist under certain geoclimatic-land cover combinations. Key opportunities exist to understand  
250 P<sub>o</sub> dynamics for sustainable P use in tropical systems and for forests growing on marginal soils, both of which  
251 depend on effective management of P<sub>o</sub> resources.

252 It is known that both land cover and management factors (tillage, fertilizer type, application rate and timing)  
253 interact with abiotic factors in controlling P<sub>o</sub> stocks and cycling, such as SOM, stabilizing surfaces [e.g., Fe- and

254 aluminium (Al)-oxides, calcium (Ca) forms, clays] and soil moisture, (Adeloju et al. 2016; Cade-Menun et al.  
255 2015; Stutter et al. 2015). Chemical fractionation studies of  $P_o$  stocks provide a snap-shot in time, missing  
256 temporal aspects of cycling associated with management-induced change at seasonal or to longer term  
257 management. As a result, short periods of rapid change in P speciation and turnover may not be appreciated.  
258 The utilization of ‘legacy P’ (Haygarth et al. 2014; Powers et al. 2016), following declining fertiliser inputs or  
259 altered cropping practices, has been studied following long-duration manipulations. Often these look at the end  
260 point of change (Cade-Menun et al. 2015), but have not ‘followed’ the dynamic. Although powerful methods for  
261  $P_o$  assessment are developing rapidly, studies that preceded these have the opportunity to incorporate them with  
262 archived samples or control soils (Keller et al. 2012; Liu et al. 2015). Long-term understanding of  $P_o$  dynamics  
263 in management systems should be pursued, while short-term seasonal observations (for example Ebuele et al.  
264 2016) will be needed to understand the influence of microbial dynamics on P speciation and turnover under  
265 various land-use and management scenarios. If studies of short-term perturbations (via management, climate etc)  
266 can show benefits for providing greater  $P_o$  resources into available pools then these processes may be  
267 beneficially incorporated in future land management.

268 ‘Organic’ farming brings a commercial stimulus to substitute agro-chemicals (including chemical P fertilisers)  
269 with sustainable management, such as use of organic amendments, for example enhancing soil P cycling with  
270 the aim of better utilizing P already present and moving towards a ‘closed’ system (Annaheim et al. 2015; Gaiind  
271 and Singh 2016; Schneider et al. 2016). The same approaches can be applied to less intensive, or developing,  
272 agricultural systems. Canadian pastures managed under an organic regime, had a greater abundance of  $P_o$  (65%  
273 vs 52% of total P) compared to conventional pastures and were able to maintain yield without inorganic  
274 fertilisers (Schneider et al. 2016). These authors concluded that plants were using  $P_i$  rather than  $P_o$  and supported  
275 by other studies showing no indication that the greater microbial activity under organic farming caused  
276 utilization of stabilized  $P_o$  forms (Keller et al. 2012). Therefore, the management conditions and actions  
277 required to promote better acquisition of  $P_o$  pools remain elusive.

278 The consensus is that a key question remains: How long could the turnover of  $P_o$  sustain crop yields under  
279 scenarios of reduced P inputs and maintained or increased outputs and thus contribute to agricultural production  
280 and feed supplies? The mechanistic understanding required to answer this question lies in the role of biota (in  
281 the context of their abiotic setting) in  $P_o$  turnover and the potential pathways of  $P_o$  loss to be managed (e.g.  
282 runoff). In order to progress, a systems approach is needed to fully assess the opportunities and role of  $P_o$ , as

283 well as the interactions of soil chemical, physical and biological processes and impacts of land use change that  
284 control P availability.

#### 285 **4a) Opportunities from understanding microbial P<sub>o</sub>: functional genes and metagenomics**

286 As our abilities to analyse and interpret the complexity inherent in the soil microbiome improves, interest is  
287 burgeoning around the functional ecology of microorganisms. Organic P dynamics across ecosystems, along  
288 with development of many techniques that will aid in this understanding, are beginning to emerge. Scavenging  
289 of P from P-containing organic compounds by soil microbes is tightly controlled by intracellular P availability  
290 through the Pho pathway in yeast (Secco et al. 2012) and the Pho regulon in bacteria. In both cases, transcription  
291 of phosphatase and phytase, which act to release orthophosphate from phosphate esters, and high affinity  
292 transporters which transport P<sub>i</sub> into the cell, are up-regulated under P<sub>i</sub> limitation, affecting the organisms' ability  
293 to utilise P<sub>o</sub>. The Pho regulon also acts as a major regulator of other cellular processes, including N assimilation  
294 and ammonium uptake (Santos-Beneit 2015). The C:N:P elemental ratios of the soil bacterium *Bacillus subtilis*  
295 range between C<sub>53-125</sub>:N<sub>12-29</sub>:P<sub>1</sub> under N- and P-limited culture conditions (Dauner et al. 2001), although  
296 environmental assemblages may exhibit greater stoichiometric flexibility (Godwin and Cotner 2015). Given this  
297 regulatory cross-talk, nutrient stoichiometry will be important to cellular and community metabolism meaning  
298 that the cycling of P must be considered within the context of other biogeochemical cycles, as highlighted  
299 earlier.

300 Soil type, nutrient inputs, and plant species have been shown to determine microbiota species composition and  
301 function (Alegria-Terrazas et al. 2016). However, plant root exudation drives recruitment of specific microbes  
302 and microbial consortia to the rhizosphere and may outweigh the impacts of soil and its management in shaping  
303 community composition and function (Tkacz et al. 2015). As yet, there is only limited understanding of how  
304 specific root exudates affect microbial recruitment (Neal et al. 2012), let alone specific microbiota responsible  
305 for phosphatase expression and production. A better understanding of interactions between plants and microbes  
306 would facilitate identification of functional redundancy among them, which could ultimately help manage the  
307 availability of P in soils and sediments by selection of the optimal plant rhizosphere complement.

308 Alkaline phosphatase and phytase genes are distributed across a broad phylogenetic range and display a high  
309 degree of microdiversity (Jaspers and Overmann 2004; Lim et al. 2007; Zimmerman et al. 2013), where closely  
310 related organisms exhibit different metabolic activities. It is therefore not possible to determine community  
311 functional potential from 16S rRNA gene abundance – functional gene abundance information is required and

312 this can be provided by employing sequencing techniques to assess the soil metagenome. In marine systems,  
313 there is evidence from metagenomic sequencing of environmental DNA that alkaline phosphatase genes *phoD*  
314 and *phoX* are more abundant than *phoA* (Luo et al. 2009; Sebastian and Ammerman 2009) and the  $\beta$ -propeller  
315 phytase is the most abundant phytase gene (Lim et al. 2007). The dominant alkaline phosphatase gene in  
316 terrestrial ecosystems is also *phoD* (Tan et al. 2013), which is more abundant in soils than other environments  
317 (Courty et al. 2010; Ragot et al. 2015; Fraser et al. 2017). From a functional standpoint, abundance of *phoD*-like  
318 sequences correlate well with estimates of potential alkaline phosphatase activity (Fraser et al. 2015), although  
319 this is not always the case (Ragot et al. 2015). Moreover, in soils there is little information regarding other  
320 phosphatases and little is known about the distribution and abundance of bacterial acid phosphatases, but there is  
321 some information related to *phoX* (Ragot et al. 2016). In contrast, fungi are well known for their capacity to  
322 secrete acid phosphatases (Plassard et al. 2011; Rosling et al. 2016), especially ectomycorrhizal fungi. Since  
323 only a small percentage of soil microorganisms are cultivable, research will need to rely upon culture-  
324 independent approaches to generate a thorough understanding of the abundance and diversity of genes  
325 associated with  $P_o$  turnover. Environmental metagenomic sequencing can form the basis of an efficient  
326 molecular toolkit for studying microbial gene dynamics and processes relevant to  $P_o$  mineralization (Neal et al.,  
327 2017). Such an approach will need to prioritize generating comprehensive understanding of the distribution of  
328 alkaline and acid phosphatase and phytase genes within soils, coupled with activity measurements, and a sense  
329 of their relative sensitivities to edaphic factors. This will allow explicit incorporation of microbial  $P_o$  turnover in  
330 the new generation of soil models, as well as allowing rapid assessment of a soil's capabilities for  $P_o$  cycling.  
331 Improved knowledge will allow the exploitation of microbial activity to sustain and improve soil fertility and  
332 allow the tailoring of new fertilizers based upon the capacity of microbes to exploit  $P_o$ .

#### 333 **4b) Opportunities from understanding microbial $P_o$ : measuring stocks, mineralisation and dynamics of** 334 **turnover**

335 The apparently large diversity of genes associated with  $P_o$ -hydrolysing enzymes suggests that changes in  
336 community composition are unlikely to result in a loss of ecosystem function. This confers resilience to  $P$ -  
337 cycling processes, although many of these genes have very specific functions intracellularly. However, trait  
338 differences are likely to have significant implications for community function in soils, e.g., the contrasting  
339 effects of arbuscular and ectomycorrhizal fungi upon the cycling of  $P$  in forest soils, where it has been shown  
340 that  $P_o$  is more labile in ectomycorrhizal dominated systems than arbuscular mycorrhizal systems (Rosling et al.

341 2016). The fact that enzyme activity in soil appears to be disconnected from soil P status is at odds with the  
342 apparent influence of the Pho regulon or pathway upon gene expression and indicates that much of the observed  
343 activity derives from multiple enzyme sources, which have been stabilised by soil colloids (Nannipieri et al.  
344 2011). This also suggests that soil enzyme activity does not directly represent microbial activity or simply  
345 reflects the complexity in current P requirements of different microbial species. However, visualization of acid  
346 and alkaline phosphatase activity associated with roots by zymography (Spohn and Kuzyakov 2013) does  
347 provide an exciting means to determine regulation of soil phosphatase activity with P availability and illustrates  
348 the clear spatial separation among the activities of physiologically different enzymes. It is a priority to develop  
349 and couple techniques that resolve the distribution of active enzymes in soil with estimates of gene expression  
350 derived from functional genes or meta-transcriptomic studies.

351 The stock of microbial P is an easy-to-determine component in soils, which is widely used to characterize the P  
352 status of microbial communities and ecosystems (Brookes et al. 1982; 1984). Nevertheless, its analysis relies on  
353 many different protocols (Bergkemper et al. 2016). Building on the previous work, further insights into both  
354 microbial-mediated and enzyme-mediated P transformations in soils may now be gained from measurement of  
355 the isotopic composition of oxygen associated with phosphate ( $\delta^{18}\text{O}_\text{P}$ ) (Tamburini et al. 2014; von Sperber et al.  
356 2014) and the use of radiolabelled ( $^{32}\text{P}$  or  $^{33}\text{P}$ )  $\text{P}_\text{o}$  compounds to measure mineralisation and immobilisation rates  
357 directly (Harrison 1982). A powerful tool for quantifying soil P pools and transformation rates is the isotope  
358 dilution technique [reviewed in Bünemann 2015; Di et al. 2000; Frossard et al. 2011]. The decrease in  
359 radioactivity with time is caused by the exchange of the added radiolabelled P (either  $^{32}\text{P}$  or  $^{33}\text{P}$ ) with  $^{31}\text{P}$  from  
360 the sorbed/solid phase and by the release of inorganic  $^{31}\text{P}$  from the organic pool via hydrolysing enzymes  
361 (Bünemann 2015). Determination of gross  $\text{P}_\text{o}$  mineralization rates from  $\text{P}_\text{o}$  to  $\text{P}_\text{i}$  remains a critical approach,  
362 helping understand the processes and rates of P cycling in different soils and under different environmental  
363 conditions (Frossard et al. 2011). These techniques present new opportunities to link P cycling to other  
364 biogeochemical cycles, such as C and N.

### 365 **5) Opportunities in the emerging area of interactions between $\text{P}_\text{o}$ dynamics and nanoparticles**

366 Reactive nanoparticles can take the form of natural soil colloids or man-made particles and are potential  $\text{P}_\text{o}$   
367 carriers, sources and sinks in ecosystems. Up to 90% of P in stream water and runoff is present in nano- and  
368 colloidal sized materials (Borda et al. 2011; Gottselig et al. 2014; Uusitalo et al. 2003; Withers et al. 2009).  
369 Colloidal P may comprise nano-sized aggregates (Jiang et al. 2015) bound to Fe, Al and SOM (Celi and

370 Barberis 2005; Celi and Barberis 2007), including inositol phosphates. However, the influence of nanoparticles  
371 on the dynamics and bioavailability of P in soil-plant systems is unclear (Bol et al. 2016). Nanoparticles such as  
372 C-magnetite, which adsorb and retain P<sub>1</sub> and P<sub>o</sub>, are used to enhance the recovery and recycling of P from P-rich  
373 wastes (Magnacca et al. 2014; Nisticò et al. 2016). It may also be possible to enhance soil enzyme activity with  
374 amendments containing mesoporous nanoparticle materials (Zhou and Hartmann 2012). Phytase encapsulated in  
375 nanoparticles was shown to be resistant to inhibitors and proteases and to promote the hydrolysis of phytate for  
376 P uptake by *Medicago truncatula* (Trouillefou et al. 2015). Nanotechnology has also been used to develop new  
377 fertilizers and plant-growth-enhancing materials (Liu and Lal 2015), representing one potentially effective  
378 option for enhancing global food production. A better understanding of the P<sub>o</sub> nanoparticle interaction may  
379 improve our understanding on P fluxes in natural and agricultural systems, and provide innovative technologies  
380 for fertilizer production and environmental remediation.

#### 381 **6) Opportunities to use modelling of P<sub>o</sub> in soil and ecosystems**

382 The use of all types of modelling approaches to study P<sub>o</sub> is generally overlooked and there is a dearth of P<sub>o</sub>  
383 based models, but development of such models would be extremely beneficial. Modelling should facilitate the  
384 development of a systems-based perspective and help to identify knowledge gaps in the current understanding of  
385 P<sub>o</sub>. Models of all types are needed including those that are conceptual, mechanistic or empirical in nature and in  
386 general there is a lack of focus on all the types of models that exist for P<sub>o</sub>. The potential benefits of advances in  
387 modelling for P<sub>o</sub> include:

- 388 • Prediction of the relationship between soil P<sub>o</sub> and plant uptake, which should be developed in both  
389 conceptual and mechanistic models of P dynamics in the environment.
- 390 • Application at different scales to determine the relationship between P<sub>o</sub> with land use and management  
391 should be possible by building empirical models based on existing data.
- 392 • Application of modelling to help understand the role of microbial traits in soil (Wieder et al. 2015), which  
393 may determine the effects of gene expression, enzyme activities and the stoichiometric ratio of C:N:P in the  
394 microbial biomass relative to that of SOM
- 395 • Application of complete Life-Cycle Analysis for relying on the run-down of soil P<sub>o</sub> as a replacement to  
396 inorganic fertilisers will help us develop adequate conceptual models for management of the system.
- 397 • Modelling could also be used to help in the quantification of soil P pools for estimating flow among P<sub>o</sub>  
398 pools.

399 In general, there is a great opportunity for the development of modelling in all areas of P<sub>o</sub> research and this will  
400 be of considerable benefit to the subject if this can be developed and integrated with all areas. The cooperation  
401 of modellers and empiricists is essential for building models with great potential use to predict changes in P<sub>o</sub>  
402 bioavailability due to land-use and management change and to infer the sustainability of the system as a whole.

403

#### 404 **7) Opportunities to better communicate and translate research**

405 Organic P represents a small, albeit critical component of biogeochemical research. The marginal nature of the  
406 subject to date creates a need to communicate the importance of this science for the future of P sustainability. As  
407 for other scientific disciplines, communication priorities include (1) strengthening communication among  
408 scientists within and outside of the P<sub>o</sub> research community; (2) engagement with stakeholders; and (3)  
409 dissemination of knowledge to the public and specific end-users.

410 Conferences and workshops on the topic of organic P promote the exchange of ideas and forging of new  
411 research partnerships (Sharpley et al. 2015; Turner et al. 2015). Online platforms are also powerful tools to  
412 connect researchers and stakeholders on issues of global P sustainability (e.g., European Sustainable Phosphorus  
413 Platform, [www.phosphorusplatform.eu](http://www.phosphorusplatform.eu), North America Partnership for Phosphorus Sustainability) (Rosemarin  
414 and Ekane 2015). The ‘Soil Phosphorus Forum’ ([www.soilforum.com](http://www.soilforum.com)) provides a platform for the exchange of  
415 information relating to P<sub>o</sub>. Specific protocols and conference presentations are also featured in archived  
416 YouTube channels (<https://www.youtube.com/channel/UCtGI3eUZscCgByewafsQKdw>). A central platform for  
417 P<sub>o</sub> research and communications is still needed, to connect existing forums to global research networks and  
418 would include features such as researcher membership, methodological resources, links to relevant  
419 organizations and platforms, and a clearing house of P<sub>o</sub> data for future meta-analysis and modelling efforts.

420 Key stakeholder groups such as land managers, farmers and extension services are a natural link between  
421 industry, government, and academia (FAO 2016). These key groups hold traditional knowledge on sustainable  
422 farming techniques, which serve as a potential basis for future P<sub>o</sub> research. Industry initiatives such as the 4R  
423 Nutrient Stewardship framework provide feedback from end users and practitioners on research priorities  
424 associated with the management of agricultural nutrients (Vollmer-Sanders et al. 2016). The engagement of P<sub>o</sub>  
425 researchers with existing nutrient initiatives such as these will be critical for bolstering public understanding of  
426 P<sub>o</sub> and its important role in global P dynamics.

427

428 **Conclusion - Statement of intent for the P<sub>o</sub> research community**

429 Organic P research has a critical role to play in tackling a number of important global challenges and there are  
430 key contributions to be made toward understanding biogeochemical cycles, dynamics and function of natural  
431 ecosystems and the management of agricultural systems. In particular, we must reduce our reliance on inorganic  
432 P fertilisers and strategies to do this will increase the relevance of soil P<sub>o</sub> for plant nutrition. Secondly, there is a  
433 need to develop a circular P economy and close the P cycle which will likely lead to an increase in the amounts  
434 of organic P “waste” products being recycled to land shifting the P<sub>o</sub>/P<sub>i</sub> balance in the soil. To address these  
435 global environmental changes and challenges, we should concentrate our efforts on understanding the biological  
436 significance of P<sub>o</sub> by considering its interactions with other elements in SOM, soil microorganisms and active  
437 soil surfaces. We should consider these interactions with respect to changes in land use and management and as  
438 a function of geochemical conditions in the wider biophysical and socio-economic environment. We need to  
439 integrate this understanding through the production of models for P<sub>o</sub>, which capture both whole systems and  
440 fine-scale mechanisms. In addition, we need to develop novel and standardised methodologies that can integrate  
441 the dynamics and function of P<sub>o</sub> on appropriate scales in a non-invasive manner. To achieve a step-change in the  
442 impact of P<sub>o</sub> research, we need to engage with researchers outside of the discipline, align the research with  
443 pressing societal issues, and become more global, collaborative, inclusive, interdisciplinary, and longer-term in  
444 nature. The key to fostering this change will depend on logically communicating the importance of P<sub>o</sub> to society  
445 at large, engaging with stakeholders on important global issues, and ultimately pushing this important area of  
446 research up the agenda of policy makers and funding bodies on a global scale.

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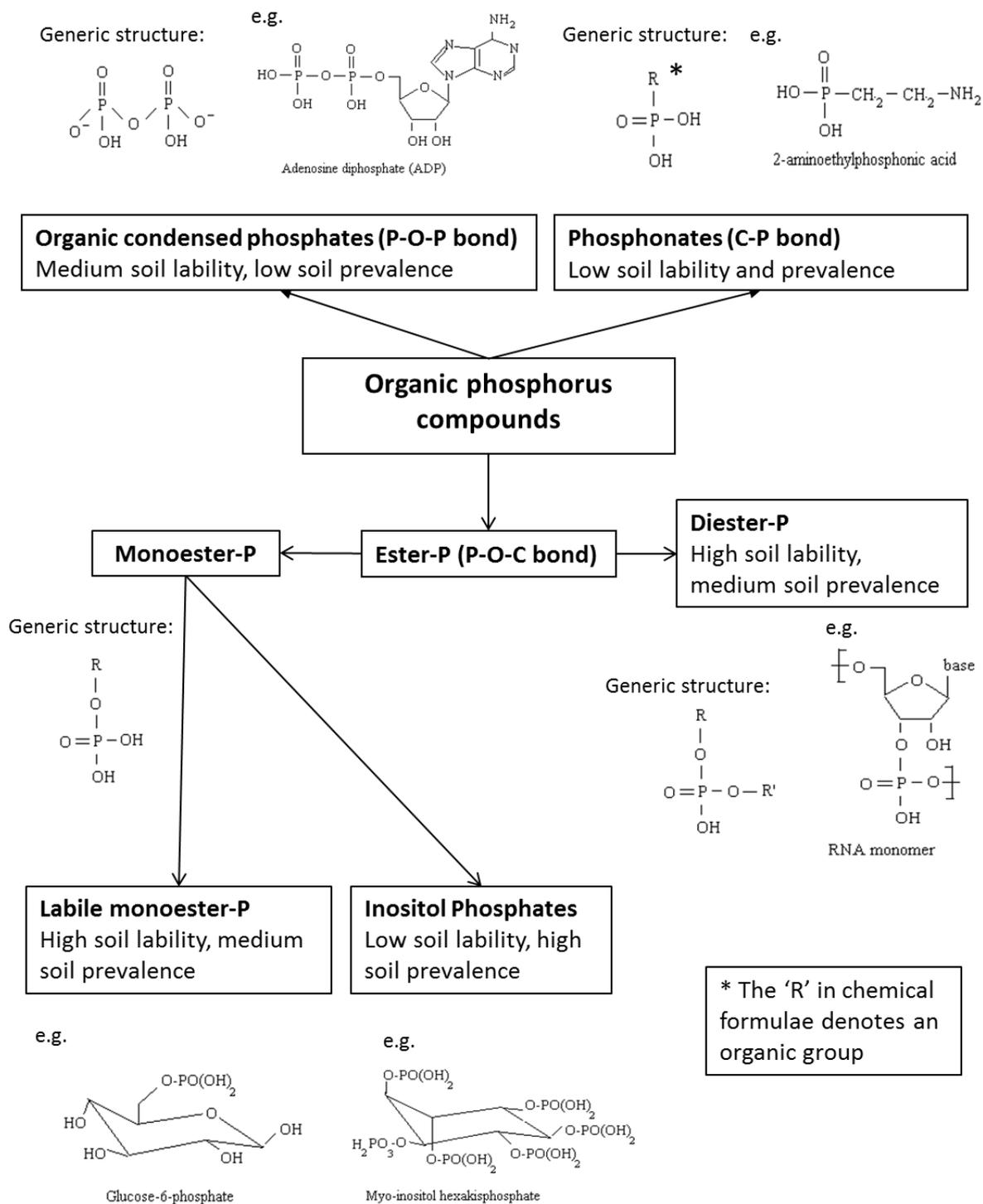
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758

759 FIGURE 1. Organic phosphorus forms with generic and example structures and information on the relative

760 lability and prevalence in soil. (Adapted from Darch et al. (Darch et al. 2014))

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762

763

764 **Table Legend**

765

766 Table 1: Synthesis of expert opinions on the global issues associated with organic phosphorus, how the research  
767 community can potentially contribute to solutions to such issues, and identification of opportunities for research  
768 to allow this to happen.

769

What are the global issues associated with P <sub>o</sub> ?	What are the methodological strengths and weaknesses?	What are benefits of understanding dynamics of P <sub>o</sub> ?	What are the priorities for P <sub>o</sub> research?	Opportunities in P <sub>o</sub> research
<p><b>Food Security and agricultural sustainability</b> P<sub>o</sub> has a role as a source of P for agricultural crops</p>	<p><b>Strengths</b></p> <p>Strong collection of well-developed methods</p>	<p>Management of plant P nutrition</p> <p>Assessment of soil P availability</p>	<ul style="list-style-type: none"> <li>• Use existing datasets more effectively</li> <li>• Avoid repeating experiments by being aware of past research</li> <li>• Better access to shared facilities</li> <li>• Training programmes in P<sub>o</sub> related techniques and concepts</li> <li>• Interdisciplinary and long term research</li> </ul>	<p><b>General advances in the research model</b></p>
<p><b>Nutrient cycling in natural ecosystems</b> P<sub>o</sub> buffers ecosystem function with effects on ecosystem resilience and biodiversity</p>	<p>Wide range of techniques</p> <p>Capacity for multi-disciplinarity</p>	<p>Understanding biological system function</p> <p>Input into climate and biogeochemical models</p>	<ul style="list-style-type: none"> <li>• Link operationally-defined pools with biological processes</li> <li>• Some standardisation of protocols</li> <li>• Development of in situ, non-destructive techniques for P<sub>o</sub></li> <li>• Develop a minimum dataset and an accessible database</li> </ul>	<p><b>Opportunities in organic phosphorus analytical methodologies</b></p>
<p><b>Renewable resources</b> Use of wastes containing P<sub>o</sub> as fertilisers to close the loop</p>	<p>Strong international networks</p> <p>Potential for commercialisation of techniques</p>	<p>Potential to close the P cycle</p> <p>Manage ecosystem services and resilience</p>	<ul style="list-style-type: none"> <li>• Link the P<sub>o</sub> cycle with other biogeochemical cycles</li> <li>• Optimise stoichiometry between P<sub>o</sub> and other elements for system function</li> <li>• Integrate soil physics, chemistry and biology to understand P<sub>o</sub> and how it fits with wider soil fertility</li> </ul>	<p><b>Opportunities from understanding stoichiometry – interactions with other element cycles</b></p>
<p><b>C storage in soils</b> Utilisation of soil P<sub>o</sub> may be counter to our need to store C in organic matter</p>	<p>Range of field based applications</p>	<p>Understand the role of soil biology – fungal vs bacterial dominated systems</p> <p>Assess stability of P forms in soil</p>	<ul style="list-style-type: none"> <li>• Design tailored systems for specific managed environments that optimise use of P<sub>o</sub></li> <li>• Optimise P<sub>o</sub> utilisation over loss</li> <li>• Improve soil P testing</li> <li>• Develop a P credits system</li> <li>• Utilise P<sub>o</sub> more effectively by using what's in soil, what's added to soil and what's lost</li> </ul>	<p><b>Opportunities from understanding interactions with land management</b></p>
<p><b>Environmental pollution</b></p>	<p>'Snap-shot' rather than dynamic</p>			

<p>Need to manage the balance of food security vs environmental P pollution</p> <p><b>Environmental change</b> Warmer temperatures will shift the biogeochemical cycle of P<sub>o</sub></p> <p><b>Biogeochemical cycling from global to cellular scales</b> P<sub>o</sub> compounds are vital for cell function and are moved globally as part of biogeochemical cycles and in the food chain</p> <p><b>Geopolitical stability</b> P<sub>o</sub> as an alternative to mined P resources</p>	<p>techniques</p> <p>Operational methodologies lack biological relevance</p> <p>Lack of standardisation and quality control</p> <p>Methodological limitations (matrix issues)</p> <p>Loss of training/education in soil science</p> <p>Lack of replication and appropriate statistical approaches</p> <p>Limited access to advanced techniques for all</p>	<p>Identify mechanisms from natural systems that can be applied in managed systems</p> <p>Separate plant and microbial contributions to soil functions</p> <p>Develop indicators for tipping points in ecosystem function – identify conditions of resistance, resilience and “points of no return”</p> <p>Allow scaling up in time and space through input to models</p> <p>Extend our understanding of global nutrient dynamics beyond what can be ascertained empirically</p>	<ul style="list-style-type: none"> <li>• Understand which genes and transcripts control the microbial response to P<sub>o</sub></li> <li>• Understand microbial impacts on P<sub>o</sub> cycles</li> <li>• Understand the P limits to plants and microbes</li> <li>• Produce a molecular toolkit for studying microbial structure and function</li> </ul>	<p><b>Opportunities from understanding Microbial Po: Function and dynamics</b></p>
			<ul style="list-style-type: none"> <li>• Understand P<sub>o</sub> interaction with natural and manmade nanoparticles</li> <li>• Assess the utility of nanoparticles to help manage the system</li> </ul>	<p><b>Opportunities from interactions with nanoparticles</b></p>
			<ul style="list-style-type: none"> <li>• Model P dynamics in the environment</li> <li>• Develop conceptual models of cycling at a range of scales</li> <li>• Build empirical models using existing data</li> <li>• Produce a life cycle analysis of P<sub>o</sub></li> </ul>	<p><b>Opportunities to use modelling of Po in soil and ecosystems</b></p>
			<ul style="list-style-type: none"> <li>• Promote discussion of P<sub>o</sub> within the scientific community</li> <li>• Better communication with stakeholders and the public on the importance of P<sub>o</sub></li> <li>• Develop a central platform for knowledge exchange</li> <li>• Understand the needs and motivations of land managers and policy makers with respect to P<sub>o</sub></li> <li>• Emphasise educating the public in issues associated with P<sub>o</sub></li> <li>• Understand the socio-economic factors influencing P<sub>o</sub> dynamics</li> <li>• Improve the translation of research in P<sub>o</sub> to impactful outcomes</li> </ul>	<p><b>Opportunities to better communicate and translate research</b></p>