1	The sixth R: Revitalizing the natural phosphorus pump
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20	Key Points:
21 22 23 24	 Animals increase availability of phosphorus globally, but this role had been minimized through extinctions and population reductions. Humans may be approaching peak phosphorus and need better ways to recycle phosphorus
25 26	 We propose a phosphorus trading system to revitalize the natural animal-mediated phosphorus pump
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29	Abstract – Humans and natural systems face three pressing concerns: the loss of large animal
30	biodiversity, eutrophication of many aquatic systems, and the need to better recycle phosphorus.
31	Here we propose a mechanism to help alleviate these problems. Some have hypothesized that we
32	are approaching "peak phosphorus," where phosphorus may become more expensive as it
33	becomes rarer, thus endangering the green agricultural revolution and the ability to feed
34	ourselves. Animals play a key role in the recycling of phosphorus (P) from the ocean depths to
35	the continental interiors, but this movement has declined by >90% over the past 10,000 years.
36	Prior to this decline, animals played a critical role in the global P budget and the pre-
37	Anthropocene P budget was in steady state only after accounting for animal P inputs. Recently a
38	5R strategy was developed by Withers et al (2015) to Realign P inputs, Reduce P losses, Recycle
39	P in bio-resources, Recover P in wastes, and Redefine P in food systems. Here we suggest a
40	sixth R, to Revitalize the natural phosphorus pump. Countries are starting to mandate P
41	recycling, and here we propose a P-trading scheme based on REDD+, where a country could
42	partially achieve its recycling goals through revitalizing the natural P pump. Accrued money
43	from this scheme could be used to restore or conserve wild animal populations while increasing
44	natural phosphorus recycling.

45 Key words – Biodiversity loss, Eutrophication, Peak P, phosphorus, REDD, RNPP,

Rewilding

47 Introduction

Phosphorus (P) is an irreplaceable element vital to all life, and a steady supply is essential 48 49 for human society. In the past, P was widely transported by animals, from the ocean depths to the continental interiors. However, species extinctions, diminished population abundances and 50 constraints on animal movement have reduced this process by more than 90% since the late 51 52 Pleistocene [Doughty et al., 2016]. Today, anthropogenic use of P in many parts of the world vastly exceeds planetary boundaries, causing eutrophication [Diaz and Rosenberg, 2008] [Steffen et 53 54 al., 2015], whilst there are also concerns about insufficient P supplies for future populations [Edixhoven et al., 2014][Neset and Cordell, 2012] [Geissler et al., 2018] [Scholz and Hirth, 2015a] 55 [Ulrich, 2016a]. The inefficient use of P today in industrial and agriculture systems results in 56 losses of up to 95% along the supply chain [Scholz and Wellmer 2015]. As a result, recent work 57 has focused on developing a circular P economy of efficient recycling [Steiner and Geissler, 2018] 58 forwarding a 5R strategy: 1. Realign P inputs, 2. Reduce P losses, 3. Recycle P in bioresources, 59 4. Recover P in wastes, and 5. Redefine P in food systems [Withers et al., 2015] [Withers et al., 60 61 2018]. Here we suggest a sixth R: Revitalize the natural phosphorus pump.

62 By restoring wild populations of whales, seabirds, anadromous fish, herbivores, scavengers, and filter feeders, we can enhance the retention of phosphorus across ecosystems. 63 64 We emphasize that this is the sixth R, or just one component of a broader system to better 65 mitigate P loss. Human mediated transport of P dwarfs the natural animal mediated movement of P today, but past global P budget was likely only in steady state with animal inputs. In 66 addition, animals can greatly alter the connections, drivers and dynamics of P cycling in wild 67 ecosystems. In this paper, we will first review the important roles animals play in the P cycle, 68 69 show how these vital nutrient arteries have been severed, and put the former role of animals into 70 a global P budget. Then, we review the current state of human P usage and show how our

71 system to revitalize the natural phosphorus pump might work in practice.

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I. Animals can greatly alter the connections, drivers and dynamics of P cycling in ecosystems

All animals are important for nutrient recycling because animal digestion accelerates cycling of nutrients from more recalcitrant forms in plants to more labile forms in excreta [*Hobbs*, 1996]. However, animals are also key in the transport of nutrients such as P across concentration gradients or between different systems (e.g., aquatic to terrestrial). Animals are not just key in increasing concentrations but they move P upstream against gravity, the redistribute it more evenly across the landscape, they filter it, and they increase retention. For example:

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1. Upstream movement: Many empirical studies show animal movement of nutrients against 82 gravity. Many wild animals, including whales, migratory fish, and seabirds, play an important 83 84 role in the phosphorus cycle. Whales transport nutrients laterally, in moving between feeding and breeding areas, and vertically by transporting nutrients from nutrient-rich deep waters to 85 86 surface waters via fecal plumes and urine, where it is available to phytoplankton [Roman et al., 87 2014] [Roman and McCarthy, 2010][Nicol et al., 2010] . Studies in the Gulf of Maine show that cetaceans and other marine mammals deliver large amounts of N and P to the photic zone by 88 89 feeding at or below the thermocline and then excreting fecal N and P near the surface [Roman and 90 McCarthy, 2010] [Roman et al., 2016].

Seabirds act as nutrient vectors by transporting nutrients from marine foraging areas to terrestrial
breeding colonies (*Otero et al. 2018*). Studies have shown that soil P concentrations on seabird

93 islands were greater than on non-seabird islands [*Mulder et al.*, 2011]. In some sites, increased
94 soil P more than doubled plant P concentrations [*Mulder et al.*, 2011].

Many fish species, such as salmonids and river herring, provide an important link between 95 96 marine and freshwater systems (*Tiegs et al. 2011, West et al. 2010*). Sea turtles move marine P to beaches through their eggs during nesting season (Bouchard and Bjorndal 2000). Other species, 97 including pelagic or bottom feeders such as the redhorse (*Moxostoma* spp.), potentially provide 98 99 important nutrient transport during migration to upstream breeding grounds in freshwater systems (e.g., *Reid 2006*). There is still uncertainty about how much of the P moved by whales, 100 fish, and seabirds is retained at the surface and further studies will need to quantify this. 101 2. Filtering. In addition to moving and distributing nutrients, animals can absorb and filter 102 103 phosphorus, typically through feeding or engineering ecosystems. Filter feeders, such as oysters, are especially effective at taking up and retaining phosphorus and other nutrients (Dame et al. 104 1989). In contrast to the upstream movement and distribution of P by anadromous fish and 105 106 scavengers, bivalve suspension feeders transfer P from the water column to sediments in the biodeposits, helping to reduce nutrient pollution (Newell et al. 2005). Such filtering can be 107 108 especially important to counter eutrophication (*Diaz and Rosenberg*, 2008).

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3. Retention. Some species, such as beavers, engineer ecosystems in ways that can reduce
phosphorus runoff, although the effectiveness of beaver dams in reducing phosphate levels
continues to be debated. Puttock et al. (2017) found reduced phosphate levels below beaver
dams, and Muskopf (2007) found increased levels of P after the removal of dams near Lake
Tahoe. Other studies have found higher levels of phosphate downstream or no detectable effect

(Rosell et al. 2005). The role of beavers in the phosphorus cycle is an important research topic inrevitalizing efforts.

4. Diffusion and directional transport: Herbivores, scavengers, and carnivores can distribute 117 phosphorus across the landscape. Animal digestion accelerates the cycling of nutrients from 118 more recalcitrant forms in decomposing plant matter to more labile forms in excreta (Hobbs 119 1996). Wide-ranging carnivores can further distribute phosphorus when they prey on ungulates 120 121 and other herbivores. In terrestrial systems, moose (Alces americanus) move aquatic-derived 122 nutrients to terrestrial systems, thus enhancing terrestrial fertility[Bump et al., 2009] [Bump, 2018]. Isotopic evidence has verified that terrestrial predators (such as eagles, bears, and otters) that 123 124 feed on anadromous fish, transport ocean-derived nutrients to terrestrial ecosystems [Reimchen et al., 2003]. Predator effects also include nutrient excretion, translocation within and across 125 ecosystem boundaries after prey consumption, and indirect effects of predator interactions with 126 127 prey (Schmitz et al. 2010). Marine mammals were important in the diet of coastal scavengers, 128 such as condors and polar bears, though dietary shifts occurred after the commercial harvest of 129 cetaceans and pinnipeds (*Chamberlain et al. 2005, Laidre et al. 2018*). Such scavenging likely resulted in the distribution of P and other nutrients across the coastal landscape. Animals can act 130 as dispersal agents moving significant quantities of nutrients from areas of high nutrient 131 132 concentration to areas of lower nutrient concentrations even without mass flow of faeces out of the fertile area. In Amazonia, woolly monkeys (Lagothrix lagothricha) eating and defecating 133 across a floodplain nutrient concentration gradient transported more P than arrives from dust 134 inputs [Stevenson and Guzmán-Caro, 2010]. 135

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Table 1 (see bottom)

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1 Loss of the planet's nutrient arteries

Most ecosystems lost their large animals at the Late Pleistocene and early Holocene, with 142 143 around 150 mammal megafaunal species (here defined as \geq 44 kg body mass) going extinct [Sandom et al., 2014]. Large animals tend to be the most prone to extinctions and range declines 144 145 and such declines continue into the present [Dirzo et al., 2014], yet these same groups are the 146 most important for nutrient dispersal [Wolf et al 2013][Doughty et al 2013]. Similarly, in marine systems, large bodied and upper trophic organisms have undergone 147 steep declines [McCauley et al 2015]. Since the advent of commercial whaling, many species 148 were reduced to near extinction. For instance, the blue whale (*Balaenoptera musculus*), the 149

150 largest animal ever to have existed, remains at about 1% of its prehunting population size in the

151 Southern Ocean [*Branch and Williams*, 2006] [*Christensen*, 2006]. Freshwater megafauna species

such as sturgeons, river dolphins, and turtles have also experienced large declines and 58% of the

153 132 megafauna freshwater species are threatened [*Carrizo et al.*, 2017].

Seabirds and anadromous fish, which transport nutrients from sea to land, have also
declined as a result of overharvesting, invasive species, and habitat modification. Global seabird
abundance declined by 69.7% between 1950 and 2010 [*Paleczny et al., 2015*]. Populations of
anadromous fish have declined by more than 90% of their historical numbers in the Pacific
Northwest [*Gresh et al., 2000*] and in the northeastern and northwestern Atlantic [*Groot, 2002*]
[*Limburg and Waldman, 2009*]. Anadromous fish in freshwater systems are currently at about
6.7% of the biomass capacity [*Mattocks et al., 2017*].

Many studies consider the importance of individual species on nutrient movement (see 161 Table 1). However, what is most important is the nutrient movement by all animals over long 162 163 periods of time in an ecosystem. Two studies recently quantified the impact on nutrient distribution of all animals in an ecosystem over long periods of time [Wolf et al., 2013; Doughty 164 et al., 2013]. To address this, they compiled data for terrestrial mammals for various traits such 165 166 as metabolic rate, day range, population density, and lifetime in order to relate nutrient distribution capacity to body mass. They found a size-dependent relationship, with larger 167 168 animals having disproportionately greater importance to the distribution of nutrients across a 169 concentration gradient. They first validated this framework using basaltic/granite concentration gradient in Kruger National park and showed mammal-driven nutrient transport is comparable in 170 magnitude to other (abiotic) nutrient fluxes [Wolf et al., 2013]. Then they estimated that 171 172 following the extinction of megafauna in Amazonia, there was a decrease of >98% of the lateral nutrient flux, with large impacts on ecosystem P concentrations outside of the fertile floodplain 173 174 regions [Doughty et al., 2013].

These studies have been expanded to consider movement of P at a global scale by all 175 animal groups. Following extinctions and animal population losses, there has been a gradual loss 176 177 of animal mediated P recycling over the past 12,000 years (Fig 1). Animals moved phosphorus from the ocean depths to the continental interiors through the bodies and feces of marine 178 179 mammals, anadromous fish, seabirds, and terrestrial animals [Doughty et al., 2016]. For example, whales and other marine mammals formerly moved about 340 million kg P yr⁻¹ from the deep sea 180 to surface waters and anadromous fish moved 150 million kg P yr⁻¹ globally from the ocean to 181 182 land. A recent study used an inventory of global seabird populations and a bioenergetics model to estimate that total phosphorus (P) excreted by seabirds was 99 million kg P y^{-1} [Otero et al., 183

2018]. If global seabird abundance declined by 69.7% [Paleczny et al., 2015] then prior flux of 184 P could have been as high as 330 million kg Py^{-1} . Large terrestrial animals moved nutrients 185 away from these coastal and riverine nutrient hotspots into the continental interior [Doughty et al., 186 2016]. We had previously calculated that the extinctions and population reductions has reduced 187 nutrient movement by about 92% on land and 95% in the ocean. Empirical results comparing a 188 189 world with no tetrapod herbivores (the Carboniferous) to a world with the largest terrestrial 190 herbivores to have ever existed (in the Cretaceous) demonstrated the importance of nutrient 191 movement by animals over long periods of time and at continental scales [Doughty, 2017]. This 192 work suggests that tetrapod herbivores increase P concentrations by 350% (from a median of 81.6 ± 8 to 392 ± 43 ppm in coal deposits). This study also demonstrated animals role in 193 redistributing nutrients more evenly across the landscape with nutrients such a P being 55% more 194 evenly distributed (s.d./median across the landscape) when tetrapod herbivores were present. 195

196 Animals in the context of the global P cycle

197 Animals have traditionally not been considered an important part of the global P cycle, but we contend this is partially because their role has been reduced by >90% (Doughty et al 198 2016). Schlesinger's classic biogeochemistry textbook shows the paradigm of the global 199 phosphorus cycle, but did not include estimates of animal P movement (Schleshinger 1997). 200 201 Here, we put the pre-Anthropocene estimates of animal P movement into the global context. In the Schleshinger work (Table 12.6), dust transports 1 (all units are 10^12 gP/yr) from the land to 202 203 the sea, rivers transport 21 (only 2 available to biota) from the land to sea, mining extracts 12 from rock, and 2 is buried at the ocean bottoms. Our numbers suggest that prior to widespread 204 hunting and extinctions, marine mammals moved 0.34 vertically in the ocean, seabirds moved 205 0.33 from the ocean to the land and migratory fish moved 0.14 from the ocean to the land. The 206

role of all terrestrial animals diffusing P onto land is more complicated, but potentially very
significant, with animals increasing terrestrial plant P concentrations by ~2 (Doughty et al 2013)
to ~3 fold (Doughty 2017).

One would assume that the global P budget was in steady state prior to the Anthropocene. 210 However, this is difficult to ascertain because humans have so thoroughly modified the global P 211 212 budget (mining 12) (Schleshinger 1997). However, we hypothesize that the pre-Anthropocene 213 atmospheric dust transport of P from land to oceans was balanced by animal input of P from 214 ocean to land. For instance, global P deposition has increased 1.4 times compared to 215 preindustrial rates [Brahney et al., 2015]. Therefore, if current P transport from land to ocean is one, then preindustrial loss to the oceans is ~ 0.7 . Here we estimate that the sum of seabirds and 216 migratory fish moving P from oceans to land is 0.47. Since the vertical movement of P by 217 marine mammals would have increased surface water P, 0.47 is likely an underestimate and 218 219 animal transport may have offset dust transport of P into the oceans. Would terrestrial diffusion 220 of nutrients by animals offset pre-Anthropocene river transport (river transport 21- mining 12 =9)? Pre-Anthropocene terrestrial P cycle could have been in steady state if we take into account 221 animal diffusion which increase leaf P approximately two (Doughty et al 2013) to three fold 222 223 (Doughty 2017) (3000 cycled yearly globally between leaves and soil) (Schleshinger 1997). However, further research is needed before these numbers could be added to a global P budget 224 with confidence. 225

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227 II. Human usage of P

Pre-Anthropocene human role in the P cycle - Currently, P efficiently moves from mined
deposits to the bottom of the oceans with few large-scale methods of keeping it within our

natural or agricultural systems (Fig 2a). However, this was not always the case. Early 230 civilisations living in low P environments recycled P for thousands of years. For instance, 231 aboriginal communities in Australia converted P to bioavailable forms using 'firestick' burning 232 ~40,000 years ago, in rural Asia the application of 'night-soil' (faeces and excreta) to fields has 233 been common for at least 5000 years and in Medieval England peasants could graze their sheep 234 235 on the land of nobility, but faced severe punishment if caught removing their droppings [Cordell et al., 2009; Ashley et al., 2011]. More recently, (mid-19th century), people began to mine 236 237 guano mainly from Peruvian and South Pacific islands (Smil 2000). However, guano deposits were almost completely exploited by the end of the 19th century (Stewart et al., 2005), when 238 humans mainly shifted to non-renewable phosphate rock. 239

Modern human P usage – Currently, phosphate is mined in sedimentary (87%) or igneous (13%)
deposits, and guano no longer plays a major role in global markets. More than 80% of P mined
each year is used for human consumption, through the development of chemical fertilizers for
farms for food for human or for animals [*Mew et al.*, 2018].

There are serious concerns that we face a scarcity of phosphorus today. Humans have 244 245 quadrupled P use since the middle of the twentieth century as human population size and meat 246 consumption has increased [Cordell et al., 2009], although phosphorus supply has historically kept pace with population trends over time [*Mew et al.*, 2018]. Recently a debate has emerged about 247 248 whether we are approaching peak P where future price and availability of P might be like the Hubbert curve that popularized the idea of peak oil [Hubbert, 1956]. The combined impact of 249 increasing demand, dwindling reserves, and geopolitical constraints could decrease the supply of 250 251 P and increase its price. In the last 50 years, however, there have been two periods when P prices have increased by more than a factor of 5, during 1974-75 and 2007-08, indicating supply 252

concerns. However, the US Geological Survey (USGS) reported an increase in global P reserves 253 from 16,000 Mt P in 2010 to 67,000 Mt P in 2014 [Van Kauwenbergh, 2010] [USGS, 2014]. 254 255 Based on these results, some have concluded that peak P is not a concern and that P supplies are secure. Others have suggested that such changes to P reserves may have presented an inflated 256 picture of global reserves [Edixhoven et al., 2014]. Several recent special issues have delved into 257 258 this issue more deeply than we can here, and we recommend the following recent special issues 259 for the interested reader [Steiner and Geissler, 2018][Ulrich, 2016b] [Scholz and Hirth, 2015]. 260 Whether P supplies dwindle or become more expensive in coming years, there is 261 widespread agreement that future recycling of P or reducing use is necessary [Steiner and Geissler, 2018]. Agricultural practices could move from a push system – where P is applied liberally in 262 concentrations higher than necessary, with possible detrimental human health effects [Calvo et al., 263 264 2014] – to systems of precision agriculture where animals receive the precise amount of P necessary and soil is analysed to add only the correct amount of P. Even those that argue that 265 266 there is no physical scarcity of phosphorus agree that there are legitimate reasons to ensure future generations' long-term supply [Brundtland 1987] [Steiner and Geissler, 2018]. 267

268 Recent efforts have focused on developing a formal circular P economy, or complete regional recycling of all P inputs [Steiner and Geissler, 2018] and this can lead to surprising results 269 270 such as Denmark imports three-fold more P from animal feed than mineral fertilizers [Klinglmair 271 et al., 2015]. Many countries are starting to develop laws to mandate P recycling [European 272 Commission., 2018] [Mehr et al., 2018]. The Ordinance on Avoidance and Disposal of Waste in Switzerland requires the recovery of P from wastewater, sewage sludge, and sewage sludge 273 ashes and the material utilization of P in meat and bone meal by 2026. Germany obliges 274 wastewater treatment plants in populations of more than 50,000 to implement P recovery within 275

276	the next 12 to 15 years. More countries may follow suit with similar laws in the future [European
277	Commission., 2018]. Recent studies have shown possible complications in achieving the goal of
278	complete P recycling [Mehr et al., 2018]. Today, less P is currently recycled in Switzerland than
279	10-15 years ago despite the above-mentioned laws [Mehr et al., 2018]. P stopped being recycled in
280	bones in Switzerland because of concerns about the spread of Bovine Spongiform Encephalitis
281	(mad cow disease). Health concerns have also led to a ban on sewage sludge import for
282	agriculture. Political decisions made for health reasons are typically enforced more quickly than
283	decisions for environmental reasons, such as the ban of phosphates from laundry detergent [Mehr
284	et al., 2018]. Why is current recycling of P not more widespread? Many water boards indicate
285	that the main barrier to constructing new wastewater treatment plants is the high investment cost
286	with an uncertain return on investment for recovery processes [de Boer et al., 2018]. Future
287	uncertainty in the value of P may also play a role in reducing investment.
288	Given these complications, below we suggest a P trading system may be more efficient,
289	effective, and have long-term ecological benefits.
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292	III. Revitalize the Phosphorus Pump (RPP) trading scheme
293	If it is cheaper and easier to invest in a biodiversity project that recycles a known quantity of
294	P, should countries invest in such projects (Fig 2b)? Switzerland now recycles much less P (Box
295	1) than previously [Mehr et al., 2018] despite laws and enthusiasm to increase P recycling.
296	Switzerland could outsource P recycling to a biodiversity project to help them meet national
297	goals when policy decisions made it difficult (i.e. no bone recycling due to concerns about

298 Bovine spongiform encephalitis). We note that laws mandating phosphorus recycling have

similarities to laws mandating reducing carbon emissions and will explore this further below.

Box 1 – P trading

Switzerland has reduced P recycling from ~6e6kg yr⁻¹ in 1989 to ~2e6kg yr⁻¹ in 2015 despite goals to increase P recycling over time. If Switzerland decided it wanted to maintain a constant P recycling rate (i.e. make up the 4e6kg yr⁻¹ shortfall), could it do so through biodiversity projects? We had previously calculated that in the past marine mammals likely recycled 340e6 kg yr⁻¹ P and migratory fish recycled 140e6 kg yr⁻¹ P and therefore to make up this 4e6 kg yr⁻¹ shortfall, Switzerland would need to increase whale P recycling (from the historic baseline) by (combined) 0.33%, fish by 1%, and seabirds by 0.33%[*Doughty et al 2016*][*Otero et al.*, 2018] (Fig 3).

300 One way of addressing phosphorus scarcity and pollution is by restoring wild terrestrial and

aquatic animal populations. We have described several broad ways including increasing

302 upstream movement, distribution, filtering and retention of P (Table 1).

303 Restoration and conservation projects are expensive and here we propose a REDD+ type 304 (Reducing Emissions from Deforestation and Degradation) type trading scenario to provide funds for such projects [Miles and Kapos, 2008]. REDD+ is a mechanism to encourage carbon 305 306 removal from the atmosphere either by reducing CO₂ pollution from factories or by keeping forests intact and their carbon sequestered. If it is too expensive for a factory to upgrade its 307 pollution control, then it can essentially pay a country to keep its forests intact. In a parallel 308 system, if expense or bureaucratic issues make industrial P recycling difficult, the locality would 309 310 have the option to invest in the natural system of animal-mediated phosphorus recycling. Here 311 we propose a trading system that could reduce nutrient pollution and redistribute phosphorus by 312 natural means (RNPP – Revitalize the Natural Phosphorus Pump).

Money to restore sustainable recycled phosphorus could come from a global phosphate tax on mined phosphorus (for instance, a phased in 10% tax on phosphate revenues could raise \$4.5 billion annually – assuming a 2017 revenue of \$45 billion) or individual projects funded

through voluntary P credits (bought like carbon credits). We estimate the pre-hunting value of 316 the phosphorus moved by marine mammals to surface waters at \$0.85 to 3.5 billion per year, 317 318 based on the variations in P price over the past 15 years. Likewise, we calculate the peak estimated transport of phosphorus from sea to land by anadromous fish at between \$0.37 and 319 \$1.5 billion per year. On land, P movement by terrestrial herbivores in the Amazon basin alone 320 321 could be valued at \$900 million [Doughty et al., 2013]. From this perspective, land-sharing with animals begins to look more attractive than land sparing, which relies on intensive, industrialized 322 323 replacements of animal mediated fertilization.

Funds might be allotted by calculating the quantity of phosphorus that will be transported 324 325 from ocean to land in the fish biomass at historical populations and multiplying this by an estimated price of phosphorus over a period of time (for instance, a period of 30 years). 326 Countries could be assigned gradually increasing phosphorus mandates that could be achieved 327 328 through conservation projects and the construction of wastewater recycling plants. To oversee 329 such a process, an international framework similar to REDD with the expressed goal of recycling phosphorus and restoring ecosystems could be setup. Any REDD policy must ensure that 330 331 emissions reductions are real, measurable, and verifiable and market-based mechanisms must validate the integrity of both emissions reduction and carbon markets. Likewise, our system 332 333 must also ensure that P recycled through biodiversity conservation is real, measurable, and verifiable. Initially, we can rely on modelled outputs, but later such efforts must be tracked. 334

These funds could be used, for example, to restore migratory fish populations. The restoration of the Elwha River in Washington State, USA, is the largest dam removal project in history, costing ~350 million USD. Following removal, Pacific salmon and trout (*Oncorhynchus* spp.) quickly recolonized the area, restoring ancient phosphorus pathways [*Shaffer et al.*, 2017].

Isotopic data suggest that species such as the Elwha River bull trout, almost entirely landlocked 339 for a century, are rapidly resuming anadromy [Quinn et al., 2017], restoring the flux of marine P 340 to the area. A recent study of the Selune River in Normandy, France, showed that dam removal 341 would reconnect 827 km² of catchment area to the sea [Forget et al., 2018]. Models estimate 342 that migratory fish, such as salmon, would increase suitable habitat three-fold for juveniles and 343 344 greatly increase the mean number of returning salmon. Such models could potentially predict the value of P moved following dam removal. Often restoring one system will increase 345 productivity in others. For instance, one study found total bird and insectivore densities in the 346 summer were strongly predicted by salmon biomass in the autumn [Field and Reynolds (2011)]. 347 Terrestrial restoration projects could include restoring natural movement of P away from 348 aquatic environments, such as bears feeding on migratory fish [Reimchen et al., 2003] or moose 349 consuming aquatic plants [Bump, 2018]. They could include sustainable human consumption of 350 native mussels in waters with too many nutrients. They could include rethinking pasture systems 351 352 to encourage movement of P across concentration gradients or into natural ecosystems. For 353 instance, fenceless, biodiverse native animals in pasture systems could redistribute phosphorus 354 into surrounding ecosystems. Natural pastures could restore a balance in the ratio between domestic and wild mammals. Recently, the dry mass of all domesticated animals was an 355 356 estimated 0.1 Gt of C compared to just 0.007 Gt of C for all wild mammals [Bar-on et al 2018]. 357 Even landlocked areas could benefit from a revitalized phosphorus pump [Box 2]. In Vermont, 358 excess P runoff threatens to cost the state approximately \$25 million per year to reduce P runoff into Lake Champlain. Restoring native mussels, salmon, beavers, bears, and deer could help 359 redistribute phosphorus throughout the Lake Champlain basin, moving some phosphorus 360 upstream and filtering and retaining much of the rest. Such place-based conservation plans are 361

- not a quick fix, but slow conservation can provide more lasting solutions [Draheim et al., 2015]
- 363 [*Roman*, 2016]. The revitalization of the P cycle would have other benefits including carbon
- sequestration, through the feeding, growth, and death of fish and whales [*Roman et al., 2014*,
- 365 http://bluecsolutions.org/fish-carbon]; seed dispersal (large herbivores); and biodiversity
- 366 protection and enhancement.

Box 2 - Revitalizing the Phosphorus Cycle

Case Study: New England

In the eastern US, phosphorus runoff from urban and agriculture lands has resulted in high loads in lakes and other waterbodies. Among the effects are eutrophication in rivers and lakes and repeated cyanobacteria blooms, such as in the shallow bays of Lake Champlain, located between Vermont and New York (*Carpenter et al.* 1998)(*Ghebremichael et al.* 2010). To date, efforts have largely focused on monitoring and reducing phosphorus loads, which will be essential in increasing water quality.

Little attention has been paid to the role that wild animals could play in this system. Worthy of consideration is a holistic approach that would include the upstream movement of P by spawning fish, potential ecological engineering by beavers and their dams, the role of bivalves in filtering phosphorus, and distribution of nutrients by terrestrial herbivores, scavengers, and carnivores.

In Connecticut, alewives, *Alosa pseudoharengus* transport phosphorus from oceans to lake systems. Before widespread habitat alterations—especially in the form of dams, some of which date back more than 300 years—these anadromous fish supplied up to 95% of the phosphorus to coastal lakes in the form of carcasses, gametes, and excretion (*Twining et al. 2013, West et al. 2010*). Other diadromous fish, such as Atlantic salmon, American shad, and sea lampreys, also played important roles in phosphorus and other nutrient cycles before commercial harvest and river alterations in New England (*Saunders et al. 2006*).

Recent research shows that wild and aquaculture filter feeders could be employed to reduce phosphorus pollution. Oyster reefs can uptake 98 g P m⁻² yr⁻¹ (*Dame et al. 1989*). The production of activated oyster shells through pyrolysis shows promise in wastewater treatment, efficiently removing phosphates form wastewater (Kwon et al. 2004). The recent growth of oyster aquaculture in New England could be employed to help further revitalize phosphorus in the region.

Case Study: Amazon Basin

Phosphorus is a key nutrient in tropical forests, and has long been known to significantly limit the productivity of these globally-important ecosystems (*Vituosek, 1984*). Rapid decomposition, a nutrient-poor substrate and intense leaching as a result of high precipitation rates, make these regions particularly prone to P deficiency (*Jordan and Herrera, 1981*). In the Amazon, P is primarily derived from the weathering of rocks in the Andes mountain range to the west and transported to the Amazonia lowlands through an arterial network of rivers and streams. The seasonal flood of these nutrient-rich, or whitewater, rivers deposits large quantities of P onto fertile floodplains (*Queseda et al., 2010*). However, for much of the basin, which is either classified as *terra firme* and lies above the maximum height of the seasonal floods or is fed by nutrient-poor black or clearwater rivers, the ecosystems here remain P deficient.

Animals provide mobile linkages between these P-rich and P-poor landscapes. Fish migrating from nutrientrich whitewater to black or clearwater rivers can transport P to oligotrophic waters, whilst on land terrestrial animals feeding in riparian areas act as key fluxes of lateral P movement. In Columbia, a group of woolly monkeys (*Lagothrix lagothricha lugens*) was found to transport 13.2 g P ha⁻¹ yr⁻¹ to *terra firme* in the seeds of fruits eaten from flooded forests, a quantity of the same order of magnitude as abiotic inputs from atmospheric deposition and weathering processes (Stevenson and Guzman-Caro, 2010). Theoretical modelling studies suggest that lateral P transport by all animals scaled across the whole Amazon basin may have historically provided an ecosystem service worth up to \$900 million yr⁻¹ (Doughty et al., 2013, Doughty et al., 2016).

Like other tropical forest regions, the Amazon is suffering from defaunation (Dirzo et al., 2014; Abrahams et al., 2017). Where P inputs are low, the removal of animals from tropical forest ecosystems can extract a significant source of P in their bodies (*Brodie and McIntyre, 2018*), as well as considerably reducing lateral P redistribution by wild animals (*Doughty et al., 2013*). Investing in projects that promote wild animal biomass, or that allows these animals to maintain their mobile linkages between environments of high and low P in the Amazon will revitalise phosphorus in this region.

Each of these possibilities could have positive benefits of restoring P flow to terrestrial

ecosystems, but they would have to be done carefully to avoid potential hazards. Restoration of 369 bears and moose require significant space and could not be done everywhere. Many filter 370 371 feeders, such as the zebra mussel (*Dreissena polymorpha*), are invasive, casing large problems, and should not be viewed as a substitute for native, sustainably harvested filter feeders. Essential 372 373 in any restoration effort is a focus on returning native species to their historic roles in their 374 ecosystems. In no sense should our proposal be used to justify the protection or spread of alien and invasive species. Such efforts could come at a large cost to ecological function and regional 375 376 biodiversity. Rethinking pastures would involve major logistical difficulties and fenceless 377 systems have a range of problems.

Some animal groups, such as seabirds, concentrate P, while other animals, such as 378 terrestrial herbivores, disperse P across landscapes. Concentrated P deposits, like cave guano, 379 are more accessible to humans for use in agriculture, whereas the dispersal of P can be more 380 useful to natural ecosystems. We suggest that both systems, indeed any natural vector that keeps 381 382 P away from the ocean bottom and from causing harmful algal blooms, should be considered for 383 P trading. Diffusive processes of P into natural systems, will not improve crop fertility, but they will restore P flows to natural ecosystems that may have lost native animal vectors. Likewise, 384 the concentration of P, such as in guano deposits, can form a point source that can be sustainably 385 386 harvested and added to agricultural fields. Other benefits include subsidies by birds and other animals that can help coastal systems buffer climate change impacts [Graham et al. 2018]. 387 More generally, more P in P limited natural systems could increase growth rates, thus increasing 388 carbon uptake and reducing atmospheric carbon. 389

390 Natural atmospheric P deposition has changed over time, increasing in some regions while
391 decreasing in others (Fig 4). Biodiversity restoration could be more or less valuable in different

places depending on historic changes in P deposition or movement. For example, in tropical
regions, unsustainable bushmeat hunting in terrestrial regions is common, which can greatly
reduce mammal populations [*Lopez et al.*, 2017]. A recent study compared atmospheric P
deposition rates to P loss via hunting on 36 sites on 3 continents and found that in most sites P
input exceeded P output, but at 4 sites, P removal exceeded inputs by factors of 1.7 – 10.4
(Kenya) and 11.0 – 25.0 (Indonesia) [*Brodie and McIntyre 2019*]. Those ecosystems facing a P
deficit could be specifically targeted by RNPP.

How would such efforts function in a working landscape? In many cases, humans and 399 wildlife populations are segregated, and the transport of phosphorus would be considered a 400 401 process most applicable to uninhabited islands or nature reserves. Yet in recent years, we have seen the restoration of urban and peri-urban wildlife, with attempts to reinvent natural processes 402 (Janis et al. 2016). There are many species that could help pump or retain phosphorus in human-403 dominated, or working, landscapes. Protecting threatened natural areas where P is currently 404 405 being transported are as important as revitalizing new ones and potentially more cost effective. The loss of such existing systems would have a clear and measurable cost in terms of lost P over 406 407 time. Here we propose that private landowners could sell the P moving capacity on their intact systems to the national government or to voluntary markets. Our work would be complementary 408 409 to ecological engineering efforts that have been proposed to reduce P loss. Roy (2016) reviewed 410 several ecological engineering techniques for phosphorus recovery and recycling, including 411 assimilation of P by macrophytes, algae, and trees; and aquaculture and aquaponics design that could combine innovations in the P recycling sector with our proposed wildlife restoration 412 efforts. 413

Accounting for P movement in human and natural systems at the country and regional 414 level is necessary prior to any widespread adaptation of P trading. The circular-economy 415 literature for phosphorus has several detailed examples that can serve as a starting point for 416 human systems, such as Switzerland [Mehr et al., 2018]. Likewise, the natural science literature 417 has many empirical case studies (Table 1) and is starting to develop global frameworks to better 418 419 understand P recycling in natural systems [Doughty et al 2016]. However, key future steps will be to link these studies at the regional level and increase our understanding of the movement and 420 retention of P by wildlife following the examples set by Coupled Natural and Human Systems 421 422 (CNHs) [Liu et al 2007], which over the last decade, have begun to overcome the traditional separation of ecological and social sciences. 423

424 Conclusion

Phosphorus is an indispensable element for both human and natural systems, yet we
suffer from the effects of excess in some areas, such as aquatic systems, and from scarcity in
others. A defining attribute of animals is their ability to move. By restoring historic pathways,
and facilitating movement across land and seas, we can take steps toward solving some of
the intractable and urgent problems associated with this irreplaceable element. Let us add a 6th R
to our future phosphorus recycling strategies and revitalize the natural phosphorus pump.

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- **Data Availability statement** This is a review paper with all relevant data available in the cited
- 434 papers.

436 Tables

Theme	Mechanism	Example		
		Biodiversity Group	Location	Reference(s)
Upstream movement	Increase marine mammal populations to return P to surface waters.	Baleen whales Right whales Baleen whales Sea lions	USA Canada Southern Ocean Australia	Roman and McCarthy (2010) Roman et al. (2016) Ratnarajah et al. (2014) Lavery et al. (2012)
	Increase number of seabirds that bring P to land in guano	Seabirds Seabirds Seabirds	Global Indian Ocean USA	Otero et al. (2018) Graham et al. (2018) Ellis et al. (2006)
	Increase number of animals that bring P ashore at haul-out sites	Sea lions Seals Turtles Otters	Galapagos New Zealand South Africa USA	Fariña et al. (2003) Wing et al. (2017) Le Gouvello et al. (2017) Ben-David et al. (2005)
	Remove dams and increase anadromous fish P transport (*)	Herring Fish Salmon Salmon	USA North America Canada USA	Walters et al. (2009) Twinning et al. (2017) Field and Reynolds (2011) Moore and Schindler (2004)
Distribution	Increase terrestrial animals feeding in P-rich riparian environments	Moose Bears Monkeys Insects Alligators	USA N America Amazon Iceland USA	Bump (2018) Hilderbrand et al. (1999) Stevenson and Guzmán- Caro, (2010) Dreyer et al. (2015) Subalusky et al. (2009)
	Increase number of wild animals moving P through terrestrial environments	Mammalian herbivores Mammalian herbivores Mammalian herbivores Tetrapod herbivores Insects Deer	South Africa Amazon Africa USA Global Nepal	Wolf et al. (2013) Doughty et al. (2013) Hempson et al. (2017) Doughty et al. (2017) Landry and Parrott (2016) Moe and Wegge (2008)

	Increase connectivity of land to known P hotspots (floodplains, volcanic soils, etc).	Remove bomas Remove fences Deer	Kenya Serengeti Europe	Augustine (2003) McNaughton (1988) Abbas et al. (2012)
Retention	Reduce P removal in wild animal biomass from ecosystems	Terrestrial mammals	Tropics	Brodie and McIntyre (2018)
	Reduce P consumption in domestic animals	Domestic animals Domestic animals	China UK	Lui et al. (2016) Withers et al. (2001)
	Recycle P in animal faeces and urine	Humans (faeces) Humans (urine) Domestic animals	Global Uganda Global	Ashley et al. (2011) Anderson et al. (2015) Cordell et al. (2009)
	Application of arbuscular mycorrhizae P symbioses	Mycorrhizae Mycorrhizae	Global Serengeti	Roy-Bolduc and Hijri (2011) Stevens et al. (2018)
	Reduce P removed in deforestation/timber production	Trees Trees Trees	Global Borneo Finland	Achat et al. (2015) Imai et al. (2012) Kaila et al. (2015)
	Restore P retention in natural dams (**)	Beavers Beavers	USA USA	Wegener et al. (2017) Correll et al. (2000)
	Allow rivers to flood and deposit P-rich floodplains	Rivers Rivers	USA Neotropics	Noe and Hupp (2005) Small et al. (2015)
Filtering	Capture P in salt marsh and mangrove ecosystems	Mangroves Mangroves Salt marsh Salt marsh	India Australia China USA	Hussain and Badola (2008) Boto and Wellington (1984) Shao et al. (2013) Alexander et al. (2008)
	Capture of P by zooextraction	Mussels Oysters	Sweden Australia	Spångberg et al. (2012) Gifford et al. (2005)
	Capture P by macrophytes and algae	Kelp Duckweed Water hyacinth	China USA Sri Lanka	Xu et al. (2011) Adhikari et al. (2015) Jayaweera and Kasturiarachchi (2004)

438 Table 1: Examples of animal P subsidies.

439 * Removal of dams may lose potential source of P-rich sediments held behind dams. See

440 Maavara et al. (2015) for more details.

441 ****** Research is inconclusive and could even increase source of nutrients to rivers. See Ecke et al.

 $442 \qquad (2017) \text{ for more details.}$

443 Figures





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seabirds, and anadromous fish move P directionally (kg P yr-1) against gravity and terrestrial
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herbivores are calculated as a diffusion capacity $(km^2 yr^{-1})$, from Doughty et al 2016.







time

Figure 3 – Cartoon representing possible P tradeoffs between Switzerland, whose P recycling has declined from 6e6B kg yr⁻¹ to 2e6 kg yr⁻¹ since 1989, and possible biodiversity restoration projects. To make up the 4e6 kg yr⁻¹ P shortfall, Switzerland could sponsor projects to restore

455 0.33% of marine mammal uplift, 1% of anadromous fish, or 0.33% of seabirds.



Figure 4 – Modifications to the global P cycle. (A) The ratio of current to preindustrial P
deposition modified from [*Brahney et al.*, 2015] (B) Percent of animal mediated P movement in

the nutrient diffusion capacity between the late Pleistocene and today for terrestrial mammalsand marine great whales modified from [*Doughty et al.*, 2016].

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