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Review

The sixth R: Revitalizing the natural phosphorus pump

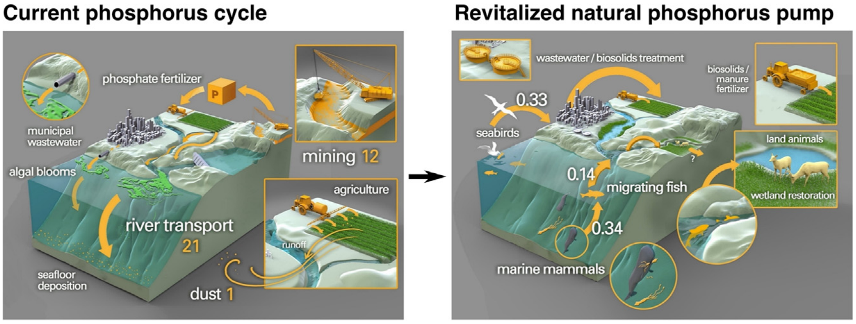
Andrew J. Abraham [a,*,1], Joe Roman [b], Christopher E. Doughty [a,1]

[a] *School of Informatics, Computing, and Cyber Systems, Northern Arizona University Flagstaff, AZ 86011, USA*
[b] *Gund Institute for Environment, Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05445, USA*

HIGHLIGHTS

- Phosphorus (P) is essential for all life on Earth and sustains food production.
- Easily accessible deposits of P-rich rock are becoming rarer.
- Historically, animals increased availability of P but role has been reduced by >90%.
- We propose a nature-based P trading system to revitalize the animal-mediated P pump.
- Biodiversity can help conserve P globally and reduce regional nutrient pollution.

GRAPHICAL ABSTRACT



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ABSTRACT

Phosphorus (P) is essential for all life on Earth and sustains food production. Yet, the easily accessible deposits of phosphate-rich rock, which underpin the green revolution are becoming rarer. Here we propose a mechanism to help alleviate the problem of "peak phosphorus". In the past, wild animals played a large role in returning P from ocean depths back to the continental interiors. In doing so, they collectively retained and redistributed P within the biosphere, supporting a more fertile planet. However, species extinctions and population reductions have reduced animal-mediated P transport >90% over the past 12,000 years. Recently a 5R strategy was developed to Realign P inputs, Reduce P losses, Recycle P in bio-resources, Recover P in wastes, and Redefine P in food systems. Here, we suggest a sixth R, to Revitalize the Natural Phosphorus Pump (RNPP). Countries are starting to mandate P recycling and we propose a P-trading scheme based on REDD+, where a country could partially achieve its recycling goals by restoring past animal-mediated P pathways. Accrued money from this scheme could be used to restore or conserve wild animal populations, while increasing natural P recycling.

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* Corresponding author.
E-mail address: andrew.abraham@nau.edu (A.J. Abraham).
[1] Authors contributed equally.

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1. Introduction

Phosphorus (P) is an irreplaceable element vital to all life, and a steady supply is essential for human society. In living organisms, P is essential for cellular processes (ATP) and structures (e.g., DNA, membranes, seeds, bones) among other important functions. Consequently, the geography of P availability influences the composition and function of terrestrial, freshwater and marine ecosystems throughout the world (Elser et al., 2007; Vitousek et al., 2010). On land, nearly all P is originally derived from the weathering of rocks rich in calcium phosphate minerals (Schlesinger and Bernhardt, 2013). This P leaches into the ocean via rivers where it is eventually buried in deep ocean sediments. In the past, animals played a crucial role in returning P from ocean depths back to the continental interiors (Doughty et al., 2016). In doing so, they collectively retained P within the biosphere, supporting a more fertile planet. Today, however, species extinctions, diminished population abundances and constraints on animal movement have reduced animal-mediated nutrient transport by more than 90% compared to the late Pleistocene (Doughty et al., 2016).

In contrast, anthropogenic use of P in many parts of the world today vastly exceeds planetary boundaries (Steffen et al., 2015). The green agricultural revolution is underpinned by the application of P to nutrient-poor soils, which has driven increasing demand and use of fertiliser globally (Ashley et al., 2011; Liu et al., 2020). However, inefficient use of P in industrial and agriculture systems results in losses of up to 95% along the supply chain (Scholz and Wellmer, 2015) causing deleterious effects of eutrophication in aquatic environments (Diaz and Rosenberg, 2008). At the same time, 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, 2015; Ulrich, 2016). Consequently, whilst global finite P resources are diminishing, some areas of the world experience excessive P pollution and others P depletion. As a result, recent work has focused on developing a circular P economy of efficient recycling (Steiner and Geissler, 2018), forwarding the "Phosphorus 5R" strategy to: 1. Realign P inputs, 2. Reduce P losses, 3. Recycle P in bioresources, 4. Recover P in wastes, and 5. Redefine P in food systems (Withers et al., 2015; Withers et al., 2018). Here we suggest a sixth R: to Revitalize the Natural Phosphorus Pump (RNPP).

By restoring wild populations of animals, we can enhance the retention and distribution of P across ecosystems. We emphasize that this is the sixth R, or just one component of a broader system to better mitigate P loss. Today, human-mediated transport of P dwarfs natural fluxes of redistribution (Schlesinger and Bernhardt, 2013). Unquestionably, continued effort must be placed upon strategies that reduce anthropogenic P losses and pollution. However, our goal is to decrease the flux of P entering the deep ocean, at which point it becomes vastly dispersed and is effectively unrecoverable with current technologies (Cordell et al., 2009). In this paper, we show that restored, interconnected animal communities traversing marine, freshwater and terrestrial ecosystems can provide a viable mechanism to reach this goal. When implemented alongside measures that reduce, recycle and recover anthropogenic P inputs, holistic strategies that utilize animal nutrient transport services can effectively help conserve the global stock of P. Furthermore, wild animals naturally fertilize vast swathes of unmanaged land and ocean (Doughty et al., 2016), which may provide future stocks of available P for anthropogenic use. In the face of climate and ecological breakdown, allochthonous P input by wild animals is also fundamental for ensuring the resilience of many ecosystems over coming centuries (Svenning, 2020).

Here, we first review the important role played by animals as agents of P redistribution and retention, show how these vital nutrient arteries have been severed, and for the first time put the former role of animals within a global P budget. We then review the current state of human P usage and show how our system to revitalize the natural P pump might work in practice. If implemented well, our trading scheme will allow countries to continue using anthropogenically mined P or import P directly from the biodiversity recovery projects under the knowledge that P reserves are maintained at the global scale.

2. 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 such as in plants to more labile forms in excreta (Hobbs, 1996). However, animals also play important roles in the transport of nutrients such as P both as a diffusive flux (across concentration gradients) or as a directional transport (between different systems). We outline four key areas in which animals help retain P within the biosphere:

A. *Upstream movement*: Many empirical studies show animal movement of P against gravity (see Table 1). Whales transport nutrients vertically from the nutrient-rich deep ocean to surface waters via fecal plumes and urine, where it becomes available for use by phytoplankton in the photic zone (Roman et al., 2014; Nicol et al., 2010; Ratnarajah et al., 2014). P assimilated by phytoplankton travels through the food chain and is eventually consumed by upper-trophic level organisms. Many anadromous fish species, such as salmonids and river herring, then transport ocean-derived P from marine to freshwater systems in their bodies (Tiegs et al., 2011; West et al., 2010). Once in river systems, pelagic or bottom feeders such as redhorse (*Moxostoma* spp.) provide further P transport upstream whilst migrating to their breeding grounds (e.g. Reid, 2006). There is still uncertainty about how much of the P moved by whales and fish is retained in the recipient ecosystem and further studies will need to quantify this.

B. *Aquatic-terrestrial transport:* Animals traversing marine, freshwater and terrestrial habitats provide a mobile P linkage between these ecosystems. For example, sea turtles and crocodilians move marine-derived P to beaches through their eggs during nesting season (Bouchard and Bjorndal, 2000; Subalusky et al., 2009). Similarly, seabirds and pinnipeds transport P from marine foraging areas to terrestrial breeding colonies (Wing et al., 2017; Otero et al., 2018). Studies have shown that soil P concentrations on seabird islands were greater than on non-seabird islands (Mulder et al., 2011). In some sites, increased soil P more than doubled plant P concentrations (Mulder et al., 2011). Isotopic evidence has also verified that land-based predators (such as eagles and bears) that feed on anadromous fish, transport significant quantities of ocean-derived nutrients to terrestrial ecosystems (Reimchen et al., 2003). It should, however, be noted that animals traversing habitats can have complex impacts on ecosystem P budgets (Subalusky and Post, 2019). For example, moose (*Alces americanus*) feeding on P-rich aquatic plants can simultaneously transport P into terrestrial uplands and increase P loss from fluvial sediments via increased turbation (Bump et al., 2009; Bump, 2018).

C. *Lateral redistribution*: Where nutrient concentration gradients exist, animals play an important role in redistributing P via their bodies, faeces and urine (Wolf et al., 2013; Subalusky and Post, 2019). For example, in Amazonia, woolly monkeys (*Lagothrix lagothricha*) provide a net transport of P from fertile floodplains to nutrient-poor upland environments (Stevenson and Guzmán-Caro, 2010). This process is achieved

Table 1

Direct mechanisms by which animals can provide P subsidies for wild ecosystems. Select examples of each mechanism are provided.

Mechanism	Details	Example		
		Biodiversity Group	Location	Reference(s)
Upstream movement	Marine mammal populations return P from ocean depths to surface waters.	Baleen whales	Southern Ocean	Ratnarajah et al. (2014)
		Right whales	Canada	Roman et al. (2016)
		Sea lions	Australia	Lavery et al. (2012)
	Anadromous fish transport P up rivers (a)	Herring	USA	Walters et al. (2009)
		Multiple fish species	North America	Twining et al. (2016)
		Salmon	Canada	Field and Reynolds (2011)
		Salmon	USA	Moore and Schindler (2004)
Aquatic-terrestrial transport	Marine animals bring P ashore at haul-out sites.	Otters	USA	Ben-David et al. (2005)
		Sea lions	Galapagos	Fariña et al. (2003)
		Seals	New Zealand	Wing et al. (2017)
		Turtles	South Africa	Le Gouvello et al. (2017)
		Alligators	USA	Subalusky et al. (2009)
	Seabirds bring P to land in guano	Seabirds	Global	Otero et al. (2018)
		Seabirds	Indian Ocean	Graham et al. (2018)
		Seabirds	USA	Ellis et al. (2006)
	Terrestrial animals feeding in aquatic environments transport P on land	Moose	USA	Bump (2018)
		Insects	Iceland	Dreyer et al. (2015)
		Bears	USA	Hilderbrand et al. (1999)
		Eagles	USA	Gende et al. (2002)
Lateral redistribution	Wild animals redistribute P from P-rich to P-poor ecosystems	Birds	USA	Sturges et al. (1974)
		Deer	Europe	Abbas et al. (2012)
		Deer	Nepal	Moe and Wegge (2008)
		Deer	Switzerland	Flueck (2009)
		Geese	USA	Post et al. (1998)
		Insects	Australia	Green (2011)
		Insects	Global	Landry and Parrott (2016)
		Mammalian herbivores	Amazon	Doughty et al. (2013)
		Mammalian herbivores	South Africa	Veldhuis et al. (2017)
		Megaherbivores	East Africa	Sitters et al. (2020)
		Monkeys	Amazon	Stevenson and Guzmán-Caro (2010)
		Whales	Global	Roman et al. (2014)
Biosphere retention	Removal of animal biomass and faeces leaches P from the ecosystem	Cattle	Kenya	Augustine (2003)
		Cattle	East Africa	Sitters et al. (2020)
		Domestic animals	China	Liu et al. (2016)
		Domestic animals	UK	Withers et al. (2001)
		Terrestrial mammals	Tropical forests	Brodie and McIntyre (2019)
		Mammalian herbivores	South Africa	Abraham et al. (2021)
	P from domestic animal faeces and urine can fertilize wild ecosystems	Humans	Global	Ashley et al. (2011)
		Humans	Uganda	Andersson (2015)
		Domestic animals	Global	Cordell et al. (2009)
	Bone scavengers recycle P from vertebrate carcasses	Hyaenas	Africa	Abraham et al. (2022)
	Natural dams reduce P leaching from ecosystem (b)	Beavers	USA	Muskopf (2007)
		Beavers	UK	Puttock et al. (2017)
	Filter feeders capture P in aquatic environments by zooextraction	Mussels	Sweden	Spångberg et al. (2013)
		Oysters	Australia	Gifford et al. (2005)
		Mussels	USA	Hoellein et al. (2017)

[a] Removal of dams for anadromous fish to swim upstream may lose potential source of P-rich sediments held behind dams. See Maavara et al. (2015) for more details.

[b] Research is inconclusive and could even increase source of nutrients to rivers. See Ecke et al. (2017) for more details.

via variable assimilation of P into the body and excreta, coupled with animal movement between these ecosystems (Wolf et al., 2013). The resulting redistribution of P is a function of the entire food web, whereby all animals from insects (Green, 2011) to mega-herbivores (Veldhuis et al., 2017) contribute to P movement in a way that is similar to that of waves transferring energy over long distances (Buendía et al., 2018). It is not necessary for individual animals to move far, but instead the total action of all animal ingestion and movement that can redistribute P over hundreds of kilometres (Doughty et al., 2013). In some cases, animals may not even need to transport P directly, instead acting as mediating agents between pools of P and abiotic forms of transport (e.g. wind or water flows). For example, in aquatic systems benthivorous animals can redistribute P by disturbing nutrients into the water column, which is then redistributed by water flow (Breukelaar et al., 1994). By influencing animal population size and movement patterns, predators indirectly influence the magnitude and direction of lateral P redistribution (Schmitz et al., 2010). However, in biodiverse systems over long periods of time, P redistribution by animals can be considered as Brownian diffusion, increasing the fertility of entire landscapes (Wolf et al., 2013).

D. *Biosphere retention.* Skeletons of large vertebrates represent significant stocks of P within a landscape (Abraham et al., 2021). Therefore, populations of animals directly act as a store of P, reducing the rate at which P leaches from an ecosystem. If the population of a vertebrate species is increasing, animals may even form a sink of P away from primary producers. Therefore, bone scavengers such as hyaenas play an important role in recycling inorganic P from bone stocks, increasing the bioavailability for other ecosystem components (Abraham et al., 2022). Animals also influence the rate that P leaches from the land via soil erosion (Alewell et al., 2020), fire (Hartshorn et al., 2009) and water (Yuan et al., 2021). For example, studies conducted near Lake Tahoe (USA) and in Devon (UK) measuring P flows in rivers before and after the creation of beaver dams demonstrate substantially reduced P losses (Muskopf, 2007; Puttock et al., 2017). However, other studies have found higher levels of P downstream or no detectable effect (Rosell et al., 2005). The role of beavers as sources and sinks the P cycle is an important research topic in revitalizing efforts. In the ocean, filter feeders such as mussels and oysters, are especially effective at taking up and retaining P (Dame et al., 1989). In contrast to the upstream movement and distribution of P by anadromous fish, bivalve suspension feeders transfer P from the water column to sediments in bio-deposits, helping to reduce nutrient pollution (Newell et al., 2005). Such filtering can be especially important to counter issues of eutrophication (Diaz and Rosenberg, 2008).

Animals are evidently integral to P ecosystem dynamics from local to global scales (Table 1; Fig. 1). However, they are also components of complex ecological networks. As a result, changes to animal community composition can lead to unexpected impacts on different P pools. Nevertheless, empirical results comparing a world with no tetrapod herbivores (the Carboniferous) to a world with the largest terrestrial herbivores to have ever existed (in the Cretaceous) demonstrate an overall net increase of global fertility due to animals (Doughty, 2017). This work suggests that tetrapod herbivores increase P concentrations by 350% (from a median of 81.6 ± 8 to 392 ± 43 ppm in coal deposits), whilst also demonstrating the role of animals in redistributing nutrients more evenly across the landscape. P was found to be 55% more evenly distributed (s.d./median across the landscape) when tetrapod herbivores were present. Continued research is required to understand the complex role animal communities play within the P cycle at local to global scales.

3. Loss of the planet's nutrient arteries

Most present-day terrestrial ecosystems lost their large animals during the late Pleistocene and early Holocene, with around 150 terrestrial mammal megafaunal species (here defined as ≥44.5 kg body mass) going extinct (Sandom et al., 2014). Large animals tend to be the most prone to extinctions and range contractions and such declines continue today (Dirzo et al., 2014). Yet, these same groups are the most important for nutrient dispersal on land, and have been referred to as the planet's "nutrient arteries" (Wolf et al., 2013; Doughty et al., 2013). In marine systems, whilst there have been fewer extinctions, large-bodied and upper trophic populations have undergone steep declines (McCauley et al., 2015). Following the advent of commercial whaling, many cetacean species were reduced to near extinction. For instance, the blue whale (*Balaenoptera musculus*), the largest animal ever to have existed, remains at about 1% of its pre-hunting population size in the Southern Ocean (Branch et al., 2007; Christensen, 2006). Similarly, freshwater megafauna species such as sturgeons, river dolphins, and turtles have also experienced drastic declines and 58% of the 132 megafauna freshwater species alive are considered threatened today (Carrizo et al., 2017). Seabirds and anadromous fish have also declined as a result of overharvesting, invasive species introductions and habitat modification. Between 1950 and 2010, global seabird abundance declined by 69.7% (Paleczny et al., 2015). In the Pacific Northwest and North Atlantic, populations of anadromous fish have declined by more than 90% compared to historical baselines (Groot, 2002; Limburg and Waldman, 2009; Mattocks et al., 2017).

Following extinctions and animal population losses over the last 12,000 years, there has been a significant decrease of large animal-mediated P redistribution globally (Fig. 2). Whales and other marine mammals formerly moved about 340 million kg P yr^{-1} from the deep sea to surface waters. This has now been reduced by 77% (Fig. 3; Doughty et al., 2016). Anadromous fish of the past moved 150 million kg P yr^{-1} from the ocean to land, more than 25× today's flux (Doughty et al., 2016). In some locations, this represented >95% of allochthonous P input for coastal watersheds (Twining et al., 2013). Total P excreted on land by seabirds today equals 99 million kg P y^{-1} (Otero et al., 2018). If global seabird abundance has declined by 69.7% (Paleczny et al., 2015), then the prior flux of P brought to land by seabirds could have been as high as 330 million kg P yr^{-1}. On land, the redistribution of P by large terrestrial animals has been reduced by 92% (Fig. 3; Doughty et al., 2016). Inherently, the impact of animal extinctions and population reductions on P redistribution for any individual ecosystem is dependent upon the specific changes to that ecosystem, including to species composition and barriers for movement.

Although less studied, small organisms also contribute to the movement of nutrients between ecosystems and play a critical role in local nutrient recycling (Subalusky and Post, 2019). If large animals are the nutrient arteries, then small organisms can be considered as the Earth's nutrient capillaries (Doughty et al., 2016). Arthropods account for ~50% of animal biomass (Bar-On et al., 2018) indicating that this group could play a substantial role in mediating P redistribution. For example, dung beetles in African savannahs (Veldhuis et al., 2017) and krill in the Southern Ocean (Ratnarajah et al., 2014) substantially contribute to local and regional P recycling. However, many terrestrial and marine arthropod communities

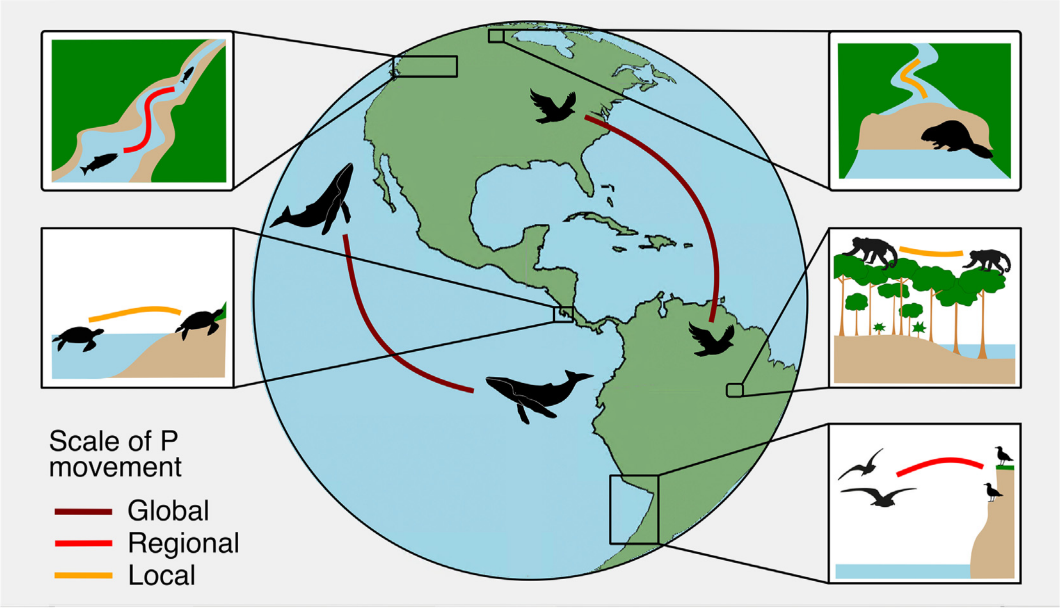

Fig. 1. Scales (global, regional, and local) of P redistribution by wild animal taxa.

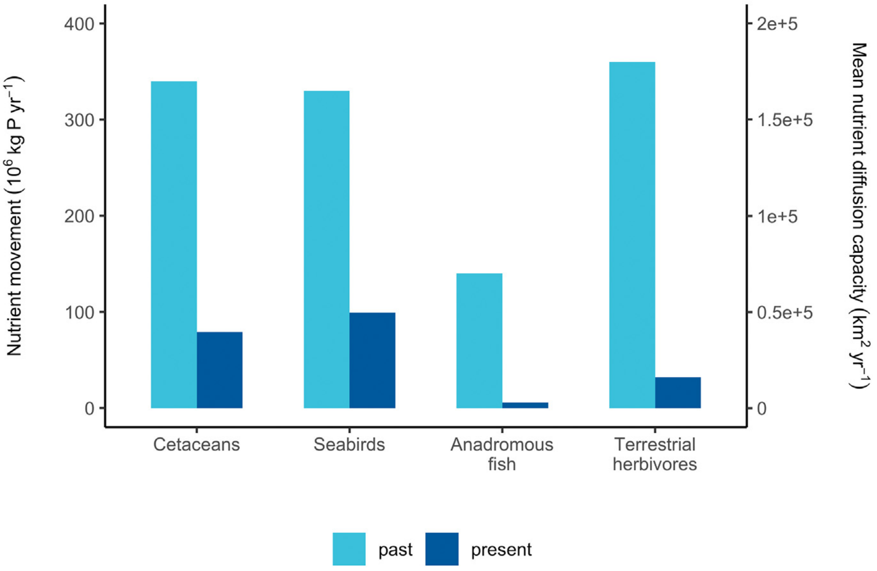

Fig. 2. Prior P redistribution by wild animal taxa compared to current values. Cetaceans, seabirds, and anadromous fish move P directionally (kg P yr^{-1}) against gravity and terrestrial herbivores are calculated as a diffusion capacity (km^2 yr^{-1}) from Doughty et al. (2016). Diffusion capacity is the potential (dependent on the substrate nutrient concentration gradient) of animals in an ecosystem to redistribute nutrients.

are vulnerable to climate change (Hays et al., 2005; Deutsch et al., 2008), or the loss of large herbivores and their excrement, which has led to the downsizing of detritivore assemblages (Schweiger and Svenning, 2018). At present, there are no global estimates of changes to P redistribution by small organisms (e.g. arthropods). Further studies are required to quantify these shifts.

4. Quantitative model putting animals in the global P cycle

Animals have traditionally not been considered an important part of the global P cycle. Instead, biogeochemists have tended to focus on abiotic forces such as fire and water alongside microbes as driving agents within biogeochemical cycles (Schlesinger and Bernhardt, 2013). We contend this is partially because the role of large animals as vectors of nutrient transport has been reduced by >90% (Doughty et al., 2016). However, studies investigating allochthonous nutrient input by diverse clades of animals increasingly demonstrate the importance of animal-mediated P subsidies for structuring the composition and function of ecosystems across the world (see Table 1). The majority of these studies focus on just one species (e.g. Flueck, 2009; Stevenson and Guzmán-Caro, 2010; Abbas et al., 2012; Lavery et al., 2012; Le Gouvello et al., 2017), which is likely driven by certain characteristics of that species which render it particularly important for transport of P. Yet, at the landscape-scale, what is important is the collective impact of *all* animals as agents within P cycling and redistribution. When trying to quantify the role of animals in keeping P from the bottom of the ocean, it is at this scale that we must be concerned.

Inherently, attempts to understand nutrient subsidies by many taxa within an ecosystem are more complex, and there remains a paucity of studies that attempt to do so. In previous studies, we have estimated the magnitude of historic and current P transport by large vertebrate animal groups

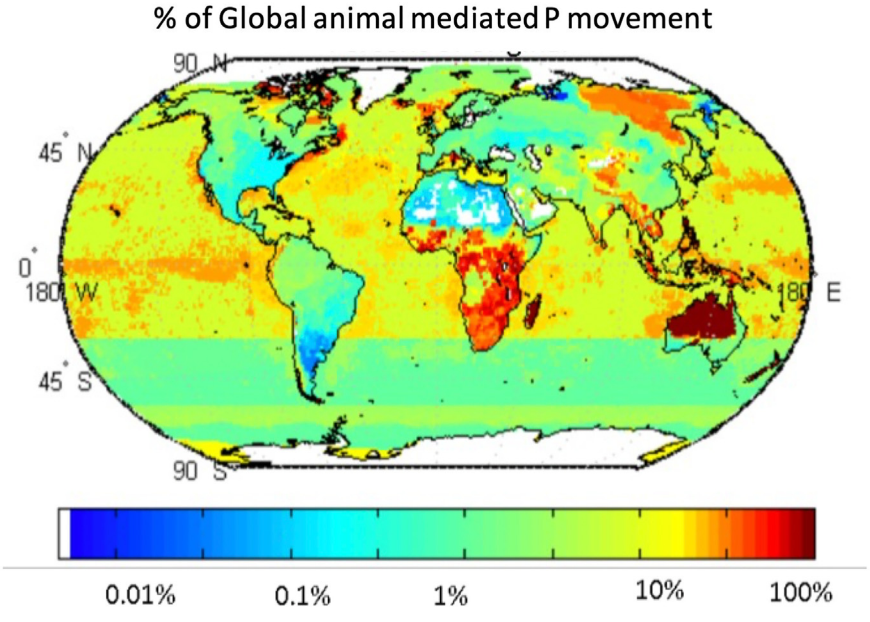

Fig. 3. Present day percent of past (~12,000 years before present) animal-mediated P movement globally for mammalian herbivores on land and great whales in the ocean. Modified from Doughty et al. (2016).

(Wolf et al., 2013; Doughty et al., 2013; Doughty et al., 2016; Roman et al., 2016). We have focused on these groups because allometric scaling of metabolic rate, movement patterns and gut passage time indicate that large animals are disproportionately important for P redistribution (Wolf et al., 2013). Here, we put our pre-Anthropocene estimates of large vertebrate P movement into global context. However, we recognize that due to their abundance (Bar-On et al., 2018) and higher metabolic rate per unit biomass (Deutsch et al., 2008), small organisms may play substantial roles in nutrient redistribution from local-global scales. Consequently, the values presented here represent a conservative estimate for the role of all animals in the global P cycle.

On land, nearly all P is originally derived from the weathering of rocks rich in calcium phosphate minerals (Schlesinger and Bernhardt, 2013). This P eventually follows gravitational pathways and leaches into the oceans where it is buried in deep ocean sediments. Schlesinger and Bernhardt's classic biogeochemistry textbook represents the major abiotic fluxes of the present day global P cycle. In Fig. 12.7 of Schlesinger and Bernhardt (2013) dust transports 1 × 10^{12} gP/yr and rivers 21 × 10^{12} gP/yr (only 2 × 10^{12} gP/yr available to biota) from the land to sea, anthropogenic mining extracts 12 × 10^{12} gP/yr from rock, and 2 × 10^{12} gP/yr is buried in ocean sediments. Our calculations suggest that prior to widespread hunting and extinctions, marine mammals moved 0.34 × 10^{12} gP/yr vertically in the ocean, seabirds moved 0.33 x10^{12}gP/yr from the ocean to the land and migratory fish moved 0.14 × 10^{12} gP/yr from the ocean to the land (Fig. 4). The role of large terrestrial mammals redistributing P on land is more complicated because to understand diffusion of nutrients, all underlying substrate P gradients must be known (Doughty et al., 2013; Doughty, 2017). However, the examples provided in Table 1, suggest that it is likely appreciable in many regions of Earth's land surface.

Globally, the values of animal-mediated transport of biologically available P are therefore of a similar order of magnitude to those from abiotic fluxes such as dust deposition, wildfire and rivers. However, importantly, the net impact of animals is generally to move P directionally against gravity back on land (Fig. 4b). Accordingly, our quantitative model indicates that preindustrial large vertebrate animal-mediated transport of P from ocean depths back on land (0.47 × 10^{12} gP/yr) substantially offset global

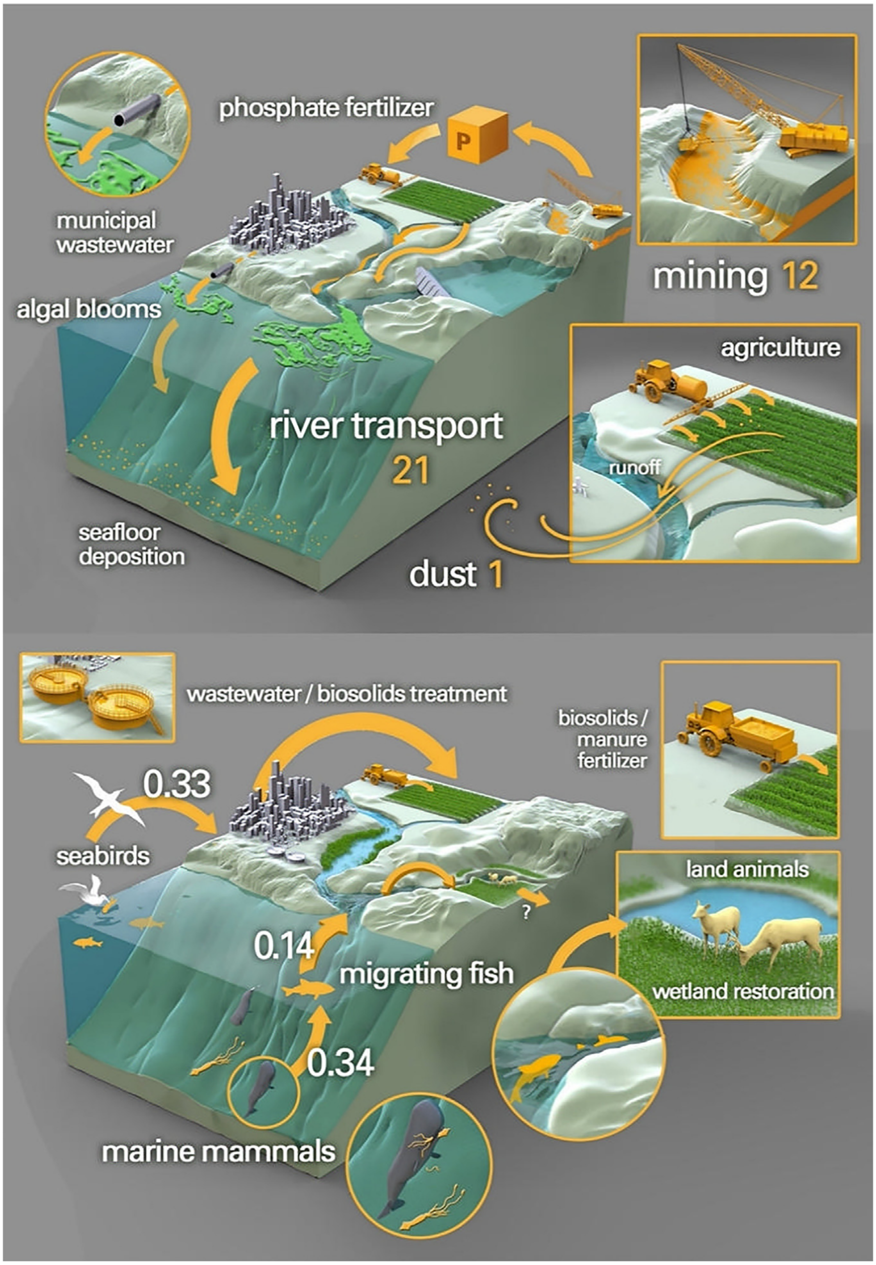

Fig. 4. Present-day abiotic and anthropogenic fluxes of P transport (top) versus historical animal-mediated P transport (bottom). All units are 10^{12} g P yr^{-1}.

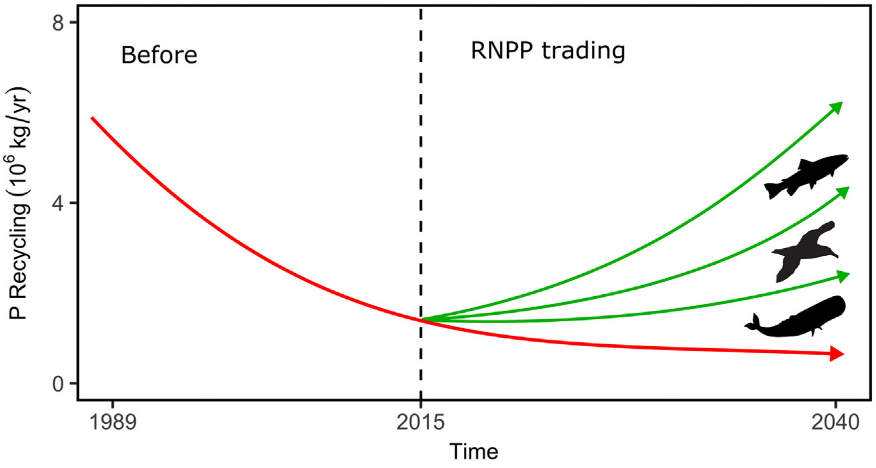

Fig. 5. Possible P revitalisation scenarios for Switzerland, whose P recycling declined from 6×10^6 kg yr^{-1} in 1989 to 2×10^6 kg yr^{-1} in 2015. To make up the 4×10^6 kg yr^{-1} P shortfall, Switzerland could sponsor biodiversity projects in other countries to restore 0.33% of global marine mammal P uplift, 1% of global anadromous fish transport, or 0.33% of global seabird transport. This would be the equivalent of the US sponsoring Costa Rica to keep their forests intact and sequester carbon through REDD+.

P losses to the ocean via atmospheric deposition ($\sim 0.7 \times 10^{12}$ gP/yr; Brahney et al., 2015). Further, since the movement of P by marine mammals and birds would have increased surface water P (Roman et al., 2016; Shatova et al., 2016) and we do not include less studied animal groups (e.g. reptiles or arthropods) in our calculation, this value is likely an underestimate. In this case, animal transport may have balanced dust transport of P into the oceans. Similarly, the lateral redistribution of P from fertile floodplains to uplands by terrestrial animals and the creation of P retention mechanisms by ecological engineers (e.g. beaver dams) may have partially offset pre-Anthropocene losses of P via river transport. It is important to note that in some circumstances, animals may locally transport P in the same direction as gravity, exacerbating P losses from the land. For example, via increased sediment turbation (Bump et al., 2009) or in whale fall carcasses (Roman et al., 2014). Further research is needed to understand where animal-mediated fluxes of P move against and with gravity before these numbers can be added to a global P budget with confidence.

5. Human usage of P

Currently, P moves efficiently from mined deposits to the bottom of the oceans with few large-scale methods of keeping it within our natural or agricultural systems (Fig. 4a; Yuan et al., 2018). However, this was not always the case. Early civilisations living in low P environments recycled P for thousands of years. For instance, aboriginal communities in Australia converted P to bioavailable forms using ‘firestick’ burning ~40,000 years ago, in rural Asia the application of ‘night-soil’ (faeces and excreta) to fields has been common for at least 5000 years, whilst Native Americans fertilized their crops with fish carcasses. In Medieval England peasants could graze their sheep 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 P in guano from Peruvian and South Pacific islands (Smil, 2000) and utilize P stocks in animal bones (Ashley et al., 2011; Someus and Pugliese, 2018). However, guano deposits were almost completely exploited by the end of the 19th century (Stewart et al., 2005), when humans mainly shifted to non-renewable phosphate rock. Currently, P is primarily mined in sedimentary (87%) or igneous (13%) deposits. More than 80% of this P is used for human consumption, through the application of chemical fertilizers for farms that feed humans and domestic animals (Mew et al., 2018).

Today, there are serious concerns that we may face a scarcity of P over coming centuries. Humans have quadrupled P use since the middle of the twentieth century as population size and meat consumption has increased (Cordell et al., 2009). Although P supply has historically kept pace with population trends over time (Mew et al., 2018), a debate has emerged about whether this can continue. We may be approaching peak P, whereby future price and availability of P might follow a Hubbert-like curve, which popularized the idea of peak oil (Hubbert, 1956). The combined impact of increasing demand, dwindling reserves, and geopolitical constraints could decrease the supply of P and thus increase its price. In the last 50 years there have been two periods when market shocks have increased the price of phosphate rock by more than a factor of 5, during 1974–75 and 2007–08. Recently, the US Geological Survey (USGS) has reported an upward estimate in global P reserves from 16,000 Mt. P in 2010 to 71,000 Mt. P in 2022 (Van Kauwenbergh, 2010) (USGS, 2022), although global P reserves are contested (Edixhoven et al., 2014). As a result, several recent special issues have delved into the debate of peak P more deeply than we can here, and we recommend the following recent reviews for the interested readers (Steiner and Geissler, 2018; Ulrich, 2016; Scholz and Hirth, 2015; Scholz and Wellmer, 2015).

Whether P supplies dwindle or become more expensive in coming years, there is widespread agreement that future recycling of P or reducing use is necessary (Steiner and Geissler, 2018). Even those that argue that there is no physical scarcity of P agree that there are legitimate reasons to ensure future generations' long-term supply (Brundtland, 1987; Steiner and Geissler, 2018) and reduce the deleterious consequences of eutrophication (Diaz and Rosenberg, 2008; Yan et al., 2021). Agricultural practices must move from a push system – where P is applied liberally in concentrations higher than necessary (Calvo et al., 2014) – to systems of precision agriculture where crops receive the precise amount of P necessary and soil is analysed to add only the correct amount of P. Recent efforts have also focused on developing a formal circular P economy, or complete regional recycling of all P inputs (Steiner and Geissler, 2018) with many countries developing laws to mandate P recycling (European Commission, 2018; Mehr et al., 2018). For example, the Ordinance on Avoidance and Disposal of Waste in Switzerland requires the recovery of P from wastewater, sewage sludge, and sewage sludge ashes and the material utilization of P in meat and bone meal by 2026. Similarly, Germany obliges wastewater treatment plants in populations of more than 50,000 to implement P recovery within the next 12 to 15 years. More countries may follow suit with similar laws in the future (European Commission, 2018).

However, recent studies have shown possible complications in achieving the goal of complete P recycling (Mehr et al., 2018). For example, today, less P is recycled in Switzerland than 10–15 years ago despite the above-mentioned laws (Mehr et al., 2018). Due to concerns about the spread of *Bovine Spongiform Encephalitis* (mad cow disease), Switzerland has stopped the recovery of P from animal bones, which represents a large stock of concentrated phosphate and has been used as a slow-release fertiliser for centuries (Ashley et al., 2011; Someus and Pugliese, 2018).

Health concerns have also led to a ban on sewage sludge import for agriculture (Mehr et al., 2018). Political decisions made for health reasons are typically enforced more quickly than decisions for environmental reasons, which also often require high initial investment costs. For example, many waterboards indicate that the main barrier to P recovery in wastewater treatment plants is the high investment cost coupled with an uncertain return on investment (de Boer et al., 2018). Given these complications, we suggest a P trading system that may be more efficient, effective and have long-term ecological benefits.

6. Revitalize the Natural Phosphorus Pump (RNPP) trading scheme

If P is considered as a global resource and it is cheaper or easier to invest in a biodiversity project that retains a known quantity of P within the biosphere, should countries invest in such projects (Fig. 4b)? For example, in the above case of Switzerland when policy decisions make it difficult to meet national goals of P recycling (i.e. no bone recycling due to concerns about *Bovine spongiform encephalitis*), they could outsource P recovery and retention to biodiversity projects distributed throughout the world (Box 1). In this way, Switzerland could continue using anthropogenically mined P or import P directly from the biodiversity recovery projects under the knowledge that P reserves are maintained at the global scale. Here, we propose a REDD+ (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 removal from the atmosphere either by reducing carbon dioxide (CO_2) pollution from factories or preventing deforestation. If it is too expensive for a factory to upgrade its pollution control, it can essentially pay a country to keep its forests intact and carbon sequestered. In a parallel system, if expense or bureaucratic issues make industrial P recycling difficult, the locality would have the option to invest in a natural system of animal-mediated P recycling.

Money to recover P could come from a global phosphate tax on mined P. For instance, a phased in 10% tax on phosphate revenues could raise \$6.5 billion annually – assuming a 2019 revenue of \$65 billion (Research and Markets, 2020). Alternatively, bi-lateral agreements between countries or localities could sponsor individual P recovery projects funded through voluntary P credits (bought like carbon credits). If P scarcity increases in coming decades, countries could be assigned gradually increasing P mandates. These funds would then be allotted to biodiversity projects that recover, recycle and redistribute a known quantity of P. For example, by restoring pathways for migratory fish populations. In Washington State, USA, restoring the Elwha River involved the largest dam-removal project in history, costing ~\$350 million. Following its removal, Pacific salmon and trout (*Oncorhynchus* spp.) quickly recolonized the area (Shaffer et al., 2017). Isotopic data suggest that species such as the Elwha River bull trout, almost entirely landlocked for a century, are rapidly resuming anadromy (Quinn et al., 2017) thereby, reviving ancient P pathways. In Europe, dam removal in the Selune River, France, would reconnect 827 km^2 of catchment area to the sea, increasing suitable habitat for juvenile salmon three-fold (Forget et al., 2018). Often restoring one system will increase productivity in others. For instance, when salmon populations increase, so do bird and insectivore densities (Field and Reynolds, 2011).

Box 1
P trading

Switzerland has reduced P recycling from ~6 × 10^9 g yr^{-1} in 1989 to ~2 × 10^9 g yr^{-1} in 2015 despite goals to increase P recycling over time (Mehr et al., 2018). If Switzerland decided it wanted to maintain a constant P recycling rate (i.e. make up the 4 × 10^9 g yr^{-1} shortfall), could it do so through biodiversity projects? We have previously calculated that in the past marine mammals likely recycled 340 × 10^9 g yr^{-1} P and migratory fish recycled 140 × 10^9 g yr^{-1} P globally. Therefore, to make up their 4 × 10^9 g P yr^{-1} shortfall, Switzerland would need to invest in biodiversity projects that increase global P recycling by whales of 0.33%, by anadromous of fish 1% and by seabirds of 0.33% (Doughty et al., 2016; Otero et al., 2018) (Fig. 5). In this trading system, Switzerland could either benefit from animal-mediated P transport directly (e.g. by importing mined bird guano), or indirectly by continuing to use mined rock P but paying for another country to recover P within the global biosphere.

We note that restoration projects of this scale are challenging and require substantial economic, social, and engineering co-operation. As with all conservation endeavours, RNPP projects must also cope with uncertainty and manage conflicts and restrictions (Halme et al., 2013). This is most likely to occur in terrestrial restoration projects, which compete for space with managed land. Whilst wild terrestrial vertebrates only constitute a small fraction of the biomass of domestic animals - the ratio of human biomass and their domestics to other terrestrial vertebrates is approximately 18:1 (Bar-on et al., 2018) – an increase in their population size may cause conflict. Our quantitative modelling, however, suggests that the value of P redistribution by animals may provide justifiable economic incentive. We estimate that the pre-hunting value of vertical P transport by marine mammals was worth between \$0.9–3.5 billion per year, contingent on variations in P price over the past 15 years. Likewise, we calculate the economic value of prior transport of P from sea to land by anadromous fish and sea birds between \$1.2–4.8 billion per year. On land, P movement by terrestrial herbivores in the Amazon basin alone has been valued at \$900 million per year (Doughty et al., 2013). In addition, the revitalization of the animal-mediated P cycle would have ancillary benefits for ecosystems including carbon sequestration, seed dispersal and biodiversity protection (Svenning, 2020; Seddon et al., 2021). From this perspective, land-sharing with animals begins to look more attractive than land sparing, which relies on intensive, industrialized replacements of animal-mediated fertilization.

But how would such efforts function in a working landscape? In many cases, humans and wildlife populations are segregated, and the transport of P would be considered a process most applicable to uninhabited islands or nature reserves. Yet, there are many ways in which biodiversity could help pump or retain P in human-dominated or working landscapes. In recent years, we have seen the restoration of urban and peri-urban wildlife, with attempts to reinvent natural processes (Janis et al., 2016). Initiatives such as the Peri-URban Ecosystem (PURE) are redefining the symbiotic interface between rural and urban environments to allow re-coupling of resource flows (Zhu et al., 2017). For example, Li et al. (2012) estimate that 19% of P transported to Chinese cities remains within the urban environment. Peri-urban biodiversity networks such as PURE could reconnect these environments. Roy (2017) reviewed several ecological engineering techniques for P recovery and recycling by plants, including assimilation of P by macrophytes and algae downstream of urban areas for use as fertiliser in agroecosystems. In a similar way, animal groups such as bivalve molluscs, anadromous fish, and seabirds that concentrate waste P downstream of urban centres in their bodies and faeces may also generate a source of P for human use in agriculture. Beavers could also form part of a natural nutrient-retention network, in the manner of Smart Nutrient Retention Networks that have been proposed for inland waters (van Wijk et al., 2021), though see uncertainties in Section 1 above. In rural environments, fenceless agriculture may allow for hybrid ecosystems shared by domestic and wild animals. Recent research in Kenya demonstrates that mixing megaherbivores with domestic cattle can overturn the negative effects of cattle on soil P loss (Sitters et al., 2020). In some European landscapes, solar-powered GPS collars generate virtual fences for grazing animals and are replacing physical fences, which have stood for hundreds of years (https://www.nofence.no/en/). By allowing wild animals to share the landscape, natural P redistribution across landscapes can occur from both domestic and wild animals (Abbas et al., 2012). Such place-based conservation plans are not a quick fix, and there remain issues with fenceless agriculture, but slow conservation can provide more lasting solutions (Draheim et al., 2015; Roman, 2016). Supplementary text 1 provides two contrasting regional-scale case studies, where a revitalised natural P pump could help conserve P within the biosphere.

In addition to revitalizing degraded ecosystems, protecting threatened natural areas where P is currently recycled is as important and potentially more cost effective. The loss of such existing systems would have a clear and measurable cost in terms of lost P over time. Here we propose that private landowners could sell the P retention capacity for their intact systems to the national government or to voluntary markets.

The cost-benefit of revitalizing the natural P pump may differ spatially and through time depending upon the dynamics of the recipient ecosystem and ability to recover P for anthropogenic use. For example, in tropical regions a recent study quantified P losses via bushmeat hunting in comparison to atmospheric P inputs (Brodie and McIntyre, 2019). Those ecosystems facing the largest P deficit could be specifically targeted by RNPP. In Table 1, we outline multiple possible mechanisms within the RNPP framework. These would each have to be implemented carefully taking into account spatial differences in ecological and social dynamics. Socio-ecological systems are complex and there are many examples of well-intentioned wildlife management strategies that failed their mission statement due to unexpected outcomes. For example, there have been numerous failed biomanipulation experiments by lake managers trying to control phytoplankton biomass due to negative trophic interactions and the plurality of driving variables (deMelo et al., 1992). Furthermore, restoration of some animal groups such as megaherbivores and apex predators requires significant space and could not be done everywhere. Any restoration attempt that uses wild animals to revitalize the natural phosphorus pump will benefit from the four guidelines outlined by Seddon et al. (2021) to maximise the potential of nature-based solutions: (i) RNPP is not a substitute for reducing anthropogenic P losses and pollution, (ii) RNPP should involve a wide range of ecosystems, (iii) RNPP should be implemented with full engagement and consent of Indigenous Peoples and local communities, and (iv) RNPP should be explicitly designed to provide measurable benefits for biodiversity.

We purposefully model our framework on REDD+ to learn from previous lessons experienced during its long history. Any REDD+ policy must ensure that emissions reductions are real, measurable, and verifiable. Likewise, our system 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. Furthermore, care must be taken to prevent issues related to market prices, permanence, leakage, free-riders, indigenous rights and bad incentives, which have all been found to reduce the effectiveness of REDD+ (Reyes and Gilbertson, 2010; van der Gaast et al., 2018). For example, essential in any restoration effort is a focus on returning native species to their historic roles in their ecosystems. Invasive animals, such as the zebra mussel (*Dreissena polymorpha*) cause large problems and should not be viewed as a substitute for native, sustainably harvested filter feeders. 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 biodiversity. Similarly, any P trading scheme should not further push the burden of conservation onto the Global South and indigenous groups (Monsarrat and Svenning, 2021). Instead, our P trading schemes should help incentivise the Global North to disproportionately finance RNPP, supporting the Global South and indigenous groups (Kormann, 2018). REDD+ is not an exact analogy for our P trading idea because issues related to phosphorus and carbon are fundamentally different. CO_2 is a global pollutant as sources of CO_2 quickly become mixed throughout the Earth's atmosphere. In contrast, excessive P use and pollution typically has more localized or regional impacts. Our P-trading scenario addresses the global issue of peak-P, especially in regard to P depletion and losses to the ocean, but it requires local initiatives to address local problems.

The implementation of a RNPP trading scheme will be complex and we do not claim to know all the details. However, similar global-scale P trading frameworks have already been suggested for agricultural and livestock P stocks (Barbieri et al., 2021). Given the substantial body of evidence presented in this study for the important role of animals within P cycles at local-to-global scales, we believe our idea warrants further consideration and encourage other researchers to build upon our broad overview. If implemented well, our proposed trading system could help conserve P globally, reduce regional nutrient pollution and facilitate a sustainable future for socio-ecological systems throughout the world.

7. Conclusion

P is an indispensable element for both human and natural systems, yet we suffer from the effects of excess in some areas and scarcity in others. A defining attribute of animals is their ability to move, connecting the land- and seascapes through which they pass. By restoring animal populations and their habitats across the world, we can revive historical animal-mediated P pathways, which can help address some of the intractable and urgent problems associated with this irreplaceable element. Let us add a sixth R to our future P recycling strategies and Revitalize the Natural P Pump.

CRediT authorship contribution statement

Andrew Abraham: Conceptualization, Writing – Original draft preparation, Writing – Reviewing and Editing. **Joe Roman:** Conceptualization, Writing – Original draft preparation, Writing – Reviewing and Editing. **Christopher Doughty:** Conceptualization, Writing – Original draft preparation, Writing – Reviewing and Editing.

Open research

No data were collected for this study (i.e., theoretical, review, opinion, editorial papers).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.155023.

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