

PRIMARY RESEARCH ARTICLE

Natural forests promote phosphorus retention in soil

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Funding information

China National Science Foundation, Grant/Award Number: 32001166, 42071031 and 42130506; Agence nationale de la recherche (ANR), Grant/Award Number: ANR-16-CONV-0003; Jiangsu Key Laboratory of Agricultural Meteorology Foundation, Grant/Award Number: JKLAM2004; Startup Foundation for Introducing Talent of NUIST, Grant/Award Number: 2019r059

Abstract

Soil phosphorus (P) availability often limits plant productivity. Classical theories suggest that total P content declines at the temporal scale of pedogenesis, and ecosystems develop toward the efficient use of scarce P during succession. However, the trajectory of ecosystem P within shorter time scales of succession remains unclear. We analyzed changes to P pools at the early (I), middle (II), and late (III) stages of growth of plantation forests (PFs) and the successional stages of natural forests (NFs) at 1969 sites in China. We found significantly lower P contents at later growth stages compared to earlier ones in the PF ($p < .05$), but higher contents at late successional stages than in earlier stages in the NF ($p < .05$). Our results indicate that increasing P demand of natural vegetation during succession, may raise, retain, and accumulate P from deeper soil layers. In contrast, ecosystem P in PF was depleted by the more rapidly increasing demand outpacing the development of a P-efficient system. We advocate for more studies to illuminate the mechanisms for determining the divergent changes, which would improve forest management and avoid the vast degradation of PF ecosystems suffering from the ongoing depletion of P.

KEYWORDS

growth stage, natural forests, phosphorus, planted forests, successional stage

1 | INTRODUCTION

Phosphorus (P) is a nearly fixed resource in natural ecosystems, as new P is supplied only at rates much smaller than biological demand from the weathering of parental material and atmospheric deposition (Ruttenberg, 2019). As a result, P is one of the main limiting mineral nutrients for plants (Kochian, 2012). The conceptual model proposed by Walker and Syers (1976) described a continuous

trajectory of P depletion during pedogenesis spanning millions of years. Sustained loss of P through leaching, erosion, and occlusion into secondary minerals reduces bio-available P over time (Buendía et al., 2014). Studies investigated changes in P levels during long periods of natural pedogenesis (Buendía et al., 2010, 2014; Crews et al., 1995; Turner et al., 2007; Walker & Syers, 1976) but less so on how ecosystem P contents evolve on successional time scales of a few decades, important for managing and restoring ecosystems. The

classical theory of nutrient strategies established by Odum (1969) states that ecosystems per se develop toward the efficient use of P during succession. But it does not describe if changes in soil P content are discernable already at succession/maturation time-scales. Assessing these changes is fundamental for testing theories on nutrient use strategies.

Odum's theory describes the natural development toward closing or "tightening" of nutrient cycling but planted forests are not included in that theory. Tropical and subtropical regions, where soils are generally poor in P (Du et al., 2020) have seen an expansion of plantations because water availability and warm temperature promote tree growth. Globally, more than 61% (~19 Mha) of newly planted forests (PFs) are in tropical regions since the 1990s (FAO, 2001), and more than 65% (~45.5 Mha) of the PFs in China have been established in tropical and subtropical regions since the 1970s (Liu et al., 2014). Trees require increasing amounts of nutrients as they grow and successive harvests from plantations export nutrients. Both act to reduce soil P contents if not otherwise replenished. Comparably, the re-growth of natural forests (NFs) after human or natural disturbances (Chazdon et al., 2016; Pugh et al., 2019; Watson et al., 2019) places a high demand for P. Unlike agroecosystems that are routinely fertilized (Vitousek et al., 2009) forests receive only limited amounts of P from natural weathering and trivial amounts from streamflow re-infiltration, deposition, and occasionally fertilizers used in plantations (Fox et al., 2011; Newman, 1995; Ruttenberg, 2019; Sohr et al., 2017; Tipping et al., 2014). Both PFs and NFs may, therefore, be exposed to P limitation, which may reduce growth (Ellsworth et al., 2017; Mengel & Kirkby, 2001; Talkner et al., 2015; Thomas et al., 2006), increase seedling mortality (Tng et al., 2014), and undermine the persistence of the recent global greening (Zhu et al., 2016).

A persistent reduction of the total P content of a forest during the succession process can be an indicator of emerging limitations because the natural P cycle at the time scales of forest growth (decades) does not allow for a quick compensation of P losses by new supply (Bouwman et al., 2009). Therefore, we conducted a nationwide field campaign in the forests of China and collected detailed information of forest sites, including total P in vegetation and soil, geographical characteristics, successional/growth stages, disturbances, and human management (Tang, Xu, et al., 2018). We aim to test the hypothesis that P cycling tightens during forest development by examining if the total ecosystem P increases along the growth and successional stages in NF and PF.

2 | MATERIALS AND METHODS

2.1 | Field plot data

The nationwide field campaign was conducted in China during the years 2011–2015 following a standardized protocol (Tang, Xu, et al., 2018) to determine the trajectories of P in different forests within successional time-scales. We first divided mainland China into three

areas with different grid sizes (100, 400, and 900 km²) based on a 1:1,000,000 vegetation map. Specifically, the 100-km² grid size was designed for tropical and subtropical regions where species diversity was high, and the 400- and 900-km² grid sizes were for temperate and alpine regions, where species diversity was lower (Tang, Xu, et al., 2018). We then overlaid the grid maps with administrative maps and randomly chose 3%–5% of the grids for the field survey by considering forest origin, age, and type. The locations of the sites in each grid were determined by referring to the available forest information. We set up a 1000 m² plot consisting of ten 10 × 10 m² subplots for the field survey at most sites (600 m² for few plantations). We also set up a 1 × 1 m² quadrat in each subplot to measure litterfall. The field data were collected from June to September to minimize bias. Fertilized sites and sites with missing measurements in any depth of 0–100 cm soil matrix were filtered, and in total of 1969 sites were retained for analysis (Figure 1).

The total P contents (g m⁻²) and concentrations (g kg⁻¹ biomass or soil) were measured in leaves, stems, branches, roots, leaf litter, and the total P in soils at different depths intervals of 0–10, 10–20, 20–30, 30–50, and 50–100 cm. Soils below 100-cm were not measured as biological and biochemical processes mostly take place above this depth (Yost & Hartemink, 2020). Specifically, we sampled the organs (stems, branches, leaves, and roots) of the dominant tree species with a diameter at breast height >5 cm, the leaf litter, and the soil (0–10, 10–20, 20–30, 30–50, and 50–100-cm layers) at each site. During the sampling, at least 10 fully expanded sunlit leaves, 3 cores of stems, and 3 pieces of roots were collected from trees for each species. The samples were oven-dried, ground, and analyzed in the laboratory to obtain the P contents and concentrations of the tree organs, litter, and soil. The mean P concentration in a given organ across all plant species in a forest site was calculated based on the relative organ biomass and nutrient concentrations in each tree species (Tang, Zhao, et al., 2018):

$$\text{concentration}_{\text{site},j} = \frac{\sum_{i=1}^n \text{concentration}_{i,j} \times \text{biomass}_{i,j}}{\sum_{i=1}^n \text{biomass}_{i,j}}$$

where $\text{concentration}_{\text{site},j}$ is the P concentration in the j th organ, averaged across all plant species in a forest site, $\text{concentration}_{i,j}$ is the P concentration of the i th tree species in the j th organ, $\text{biomass}_{i,j}$ is the stem, branch, leaf, or root biomass of the i th tree species, and n is the number of tree species in the site. The P content of a forest site was calculated from the organ biomass and nutrient concentrations for each species:

$$\text{content}_{\text{site}} = \sum_{j=1}^4 \sum_{i=1}^n \text{concentration}_{i,j} \times \text{biomass}_{i,j}$$

where $\text{content}_{\text{site}}$ is the P content in the vegetation of a forest site. Litter P content was calculated by multiplying litter dry weight per unit ground area by the P concentration.

Soil bulk density was also measured at all depths to convert soil P concentration into the content. Specifically, we collected at least five soil samples for each layer depth diagonally in each plot. The

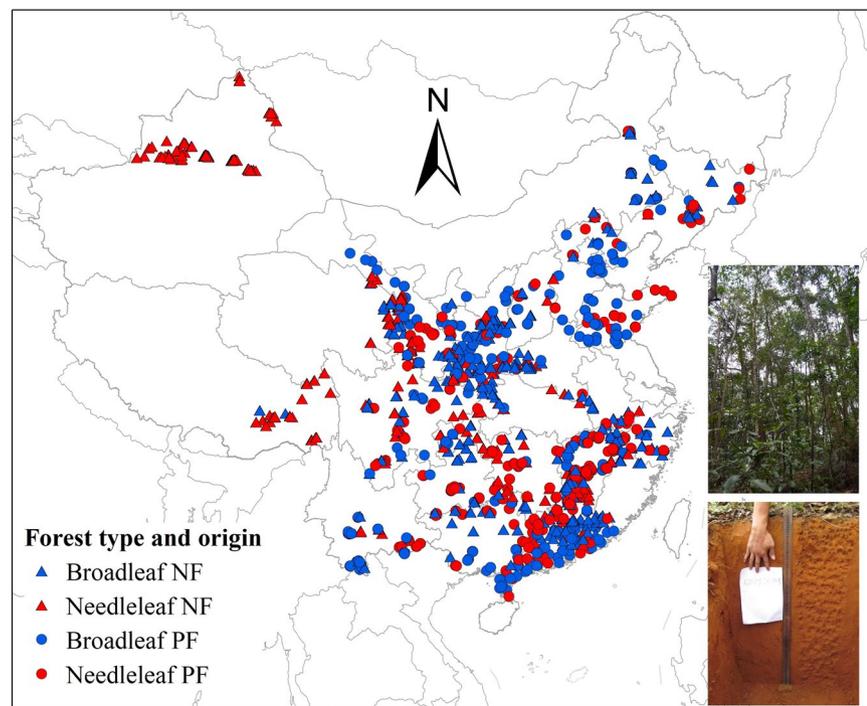


FIGURE 1 Spatial distribution of the forest sites used in this study. (NF, natural forest; PF, plantation forest; the photos were taken from a site sampled)

plant and soil P concentrations in organs and soil were measured using the molybdate/ascorbic acid method after $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2$ digestion (Jones, 2001; Tang, Zhao, et al., 2018). Soil P content was calculated by multiplying soil bulk density by P concentration and summing up the contributions of all sampling depths. More details of the sampling procedures are provided by Tang, Xu et al. (2018).

2.2 | Identification of the successional and growth stages

We divided the surveyed forest sites into three successional stages for the NFs and three growth stages for PFs, early, middle and late, denoted by I, II, and III. The stages of PFs and NFs were determined by classifying tree ages into the age groups defined by the State Forestry Administration (2018) (Table 1; Table S1). This approach allows defining stages differently depending on species (fast-growing species reach stage III sooner than slow-growing species) and on the climatic region (the same species growing under warmer climate reaches stage III sooner than in colder climate). The successional stages of NFs were determined by the ages of dominant tree species in the site. Moreover, NF sites were further scrutinized using criteria adopted in a previous study (Zhou et al., 2014). Specifically, we performed a pre-sampling survey to collect the available historical, anthropogenic, and natural disturbances records. This information is used to ensure that the stage III NF sites had not been subject to disturbance events (landslides, typhoon, forest fires, etc.) for a sufficient time which includes any trace of charcoal in soils and tree stumps with fire scars, footprints of landslides and typhoon and so on. Moreover, soil profiles should be integrated and undisturbed in the NF stage III sites.

2.3 | Grouping analysis and bootstrap sampling

We used two types of statistical analyses to test the robustness of the comparisons of soil P contents among the three successional/growth stages (defined in Table 1). The first type grouped forest sites based on their climatic conditions and biophysical properties. The second type was bootstrap sampling based on the climatic conditions and biophysical properties of the sites. More specifically, the forest sites were grouped or bootstrap-sampled by mean annual temperature (T), mean annual precipitation (P), climatic region (R), leaf type (L), and dryness (D), and each group was further divided into two subgroups, 1 and 2 (Table 2). We then compared differences of soil P among the three successional/growth stages in each subgroup of the NFs and PFs. Significant differences in soil P content were identified using grouping analysis and bootstrap sampling. A total of 33 sample groups were thus available in each approach for the NFs and PFs ([10 subgroups + 1 group pooling all samples] \times 3 successional/growth stages). The sample groups were then used to examine the relationships between the biochemical properties in the NFs and PFs.

2.4 | Statistical analysis

All statistical analyses were performed using SPSS v24 (IBM Corp.). The least significant difference test was used to assess the differences in the means among groups (e.g., successional stages). Soil P concentrations were transformed by natural logarithms and the differences were identified using two-tailed *t* tests. Pearson's correlation was used to analyze the association between all parameters studied. The values were considered statistically significant at $p < .05$. All results are reported as means \pm standard errors.

TABLE 1 Growth stage of each age group in each tree species

Forest origin	Forest species	North				South			
		Growth stage				Growth stage			
		Early (I)	Middle (II)	Late (III)	Harvest age	Early (I)	Middle (II)	Late (III)	Harvest age
PF	1	≤40	41–80	>80	81	≤30	31–60	>60	61
	2	≤30	31–60	>60	61	≤30	31–60	>60	61
	3	≤20	21–40	>40	41	≤20	21–40	>40	41
	4	≤20	21–40	>40	41	≤10	11–30	>30	31
	5	≤10	11–20	>20	21	≤5	6–15	>15	16
	6	-	-	-	-	≤5	6–15	>15	16
	7	≤10	11–20	>20	21	≤5	6–15	>15	16
	8	-	-	-	-	≤5	6–15	>15	16
	9	≤20	21–40	>40	41	≤10	11–30	>30	31
	10	-	-	-	-	≤20	21–50	>50	51
	11	-	-	-	-	≤10	11–25	>25	26
NF	1	≤60	61–120	>120	121	≤40	41–80	>80	81
	2	≤60	61–120	>120	121	≤40	41–80	>80	81
	3	≤40	41–100	>100	101	≤40	41–80	>80	81
	4	≤30	31–60	>60	61	≤20	21–40	>40	41
	5	≤20	21–40	>40	41	-	-	-	-
	6	-	-	-	-	-	-	-	-
	7	≤10	11–20	>20	21	≤5	6–15	>15	16
	8	-	-	-	-	-	-	-	-
	9	≤30	31–60	>60	61	≤20	21–50	>50	51
	10	≤40	41–80	>80	81	-	-	-	-
	11	-	-	-	-	-	-	-	-

Note: 1: *Pinus koraiensis* Siebold et Zuccarini, *Picea* spp., *Tsuga* spp., *Taxus* spp.; 2: *Cupressus* spp.; 3: *Larix* spp., *Abies* spp., *Pinus sylvestris* Linn. var. *mongolica* Litv., *Pinus densiflora* Sieb. et Zucc., *Pinus thunbergii* Parlatores, *Abies holophylla* Maxim; 4: *Pinus tabulae*, *Pinus massoniana*, *Pinus yunnanensis*, *Pinus kesiya*, *Pinus armandii* Franch, *Pinus densata* Mast; 5: *Populus* spp., *Salix* spp., *Sassafras* spp., *Paulownia* spp., *Pterocarya* spp.; 6: *Melia* spp.; 7: *Robinia* spp.; 8: *Casuarina* spp., *Eucalyptus*; 9: *Betula* spp. (excluding *Betula dahurica* Pall.), *Ulmus* spp., *Schima* spp., *Liquidambar* spp., *Davidia* spp.; 10: *Quercus* spp., *Castanopsis fargesii* Franch., *Cinnamomum* spp., *Phoebe* spp., *Tilia* spp., *Betula dahurica* Pall.; 11: *Cunninghamia lanceolate*, *Cryptomeria* spp., *Metasequoia* spp.

3 | RESULTS

3.1 | Relationships between vegetation and soil phosphorus

Plant and litter P contents were approximately two orders of magnitudes smaller than the soil P content (Figure 2). Using the averaged data from 33 sample groups, we found that plant P content was negatively correlated with soil P content in PFs ($p < .05$, Figure 2a), while an opposite correlation was found in NF ($p < .05$, Figure 2a). Additionally, litter and soil P contents were more strongly correlated in the NFs than in the PFs (Figure 2b).

3.2 | Soil phosphorus contents in NF and PF

The data unambiguously show that P contents in the top 100 cm of soil decreased significantly with age in PFs, whereas they

increased in NF (Figure 3). In PFs, the net magnitudes of reduction were $138 \pm 37 \text{ g P m}^{-2}$ (–23% compared to just after planting) and $66 \pm 33 \text{ g P m}^{-2}$ (–11%) from stage I to stages III ($p < .05$) and from stage II to stage III ($p < .001$) (Figure 3a). In contrast, soil P content generally increased in the NFs during succession ($p < .05$, Figure 3c), but remained stable between stages I and II ($p > .10$). Soil P content was $102 \pm 43 \text{ g P m}^{-2}$ (+21%, $p < .01$) and $58 \pm 30 \text{ g P m}^{-2}$ (+11%, $p < .05$) higher in stage III than in stages I and II, respectively, indicating a net accumulation of P in the NF soils during succession.

To examine the robustness of distinct P change patterns in different climate regions and biome types, we further applied a grouping approach and bootstrap sampling to test the differences in the soil P content of the three stages in both NFs and PFs. Both analyses found that soil P contents were lower in the PFs at the later growth stages (Figure 3b; Figure S1a), while soil P contents were higher in the NF at the later successional stages (Figure 3d; Figure S1d).

We examined P content distribution vertically and found that P contents in each soil layer did not change consistently in PF at any

TABLE 2 Grouping approach used in the analyses

Group	Subgroup	Details
T	T1	Mean annual air temperature $\leq 11^{\circ}\text{C}$
	T2	Mean annual air temperature $> 11^{\circ}\text{C}$
P	P1	MAP ≤ 980 mm
	P2	MAP > 980 mm
R	R1	Tropical and subtropical region
	R2	Temperate region
L	L1	Needleleaf forest
	L2	Broadleaf forest
D	D1	Dryness index (MAP/PET) ≤ 1
	D2	Dryness index (MAP/PET) > 1

Abbreviations: MAP, mean annual precipitation; PET, potential evapotranspiration.

given maturation stage (Figure 4a). Nevertheless, P content generally increased with depth in NF in all successional stages (Figure 4b). In comparison, the vertical distribution of P concentrations consistently declined with depth in NF and PF (Figure 5). In addition, the declining pattern of P concentrations was more prominent in later successional/growth stages in both forest types (Figure 5).

4 | DISCUSSION

4.1 | Potential mechanisms in determining vegetation and soil phosphorus content

A sustainable forest ecosystem is expected to replenish P in soil once it is consumed via redistribution to the aboveground biomass as trees grow. We found that the P transferred from the soil was depleted in PFs but was replenished in the NFs (Figure 3a), implying a potentially less sustainable supply of P in PFs than in NFs as the trees grew. We also implemented multiple approaches to validate the robustness of the divergent P content changes in NF and PF (Figures 3 and 4; Figure S1).

To survive and thrive in P limited soils, plants have evolved with different nutrient strategies, which could be classified into two groups, that is, “scavenging” and “mining” (Lambers et al., 2008). The “scavenging” strategy is achieved by rapid root growth, localized root proliferation in enriched zones, development of root hairs, or establishment of symbioses with mycorrhizal fungi, while the “mining” strategy enhances P mobilization through exudation of large amounts of carboxylates from cluster roots specifically developed (Lambers et al., 2008). Thus, the increase in NFs’ P contents from the top to the bottom of the profile could be attained by either strategy with multiple P-efficient processes involved. Due to the lack of leaf manganese concentrations data—an essential indicator of carboxylate-releasing mechanisms in P-utilizations (Lambers et al., 2021)—we are unable to identify the dominant strategy contributing to the P accumulation in China’s NF at the current stage. However, it is likely that the NFs are equipped with more efficient mechanisms

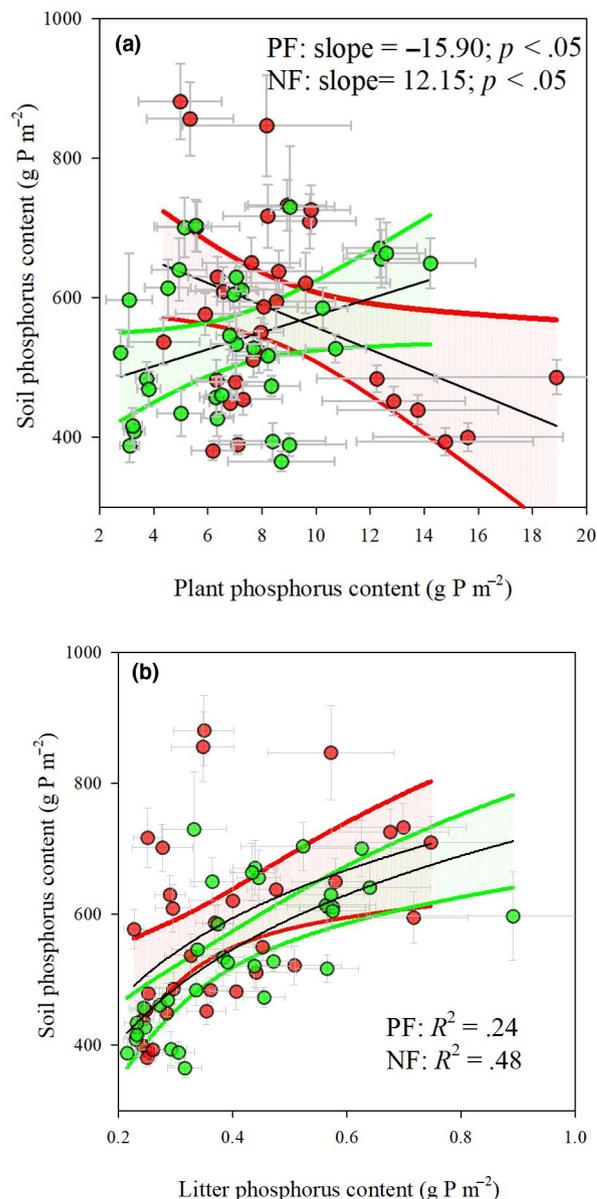


FIGURE 2 Relationships between soil and plant phosphorus contents (a) and soil and litter phosphorus contents (b). The shaded area in red and green indicate the 95% confidence intervals for the plantation forests (PFs) and natural forests (NFs), respectively. Data means and errors were obtained from the grouped samples (see Table 2), with the error bars indicating standard errors of the means

of extraction and recycling from the co-development of biotic and abiotic microenvironments. The hypothesized more efficient mechanisms might include the development of carboxylate-releasing cluster roots (Lambers et al., 2012), higher plant diversity with deeper roots, and more soil animals (e.g., invertebrates) to capture and exploit P from deeper soil (Jobbágy & Jackson, 2001; Mckercher et al., 1979), a more complex canopy structure enabling vegetation to retain P via re-sorption at leaf senescence and to recycle P via organic matter decomposition (Kellman et al., 1982; McGowan & Ledgard, 2005; Powers & Marin-Spiotta, 2017), which in turn might

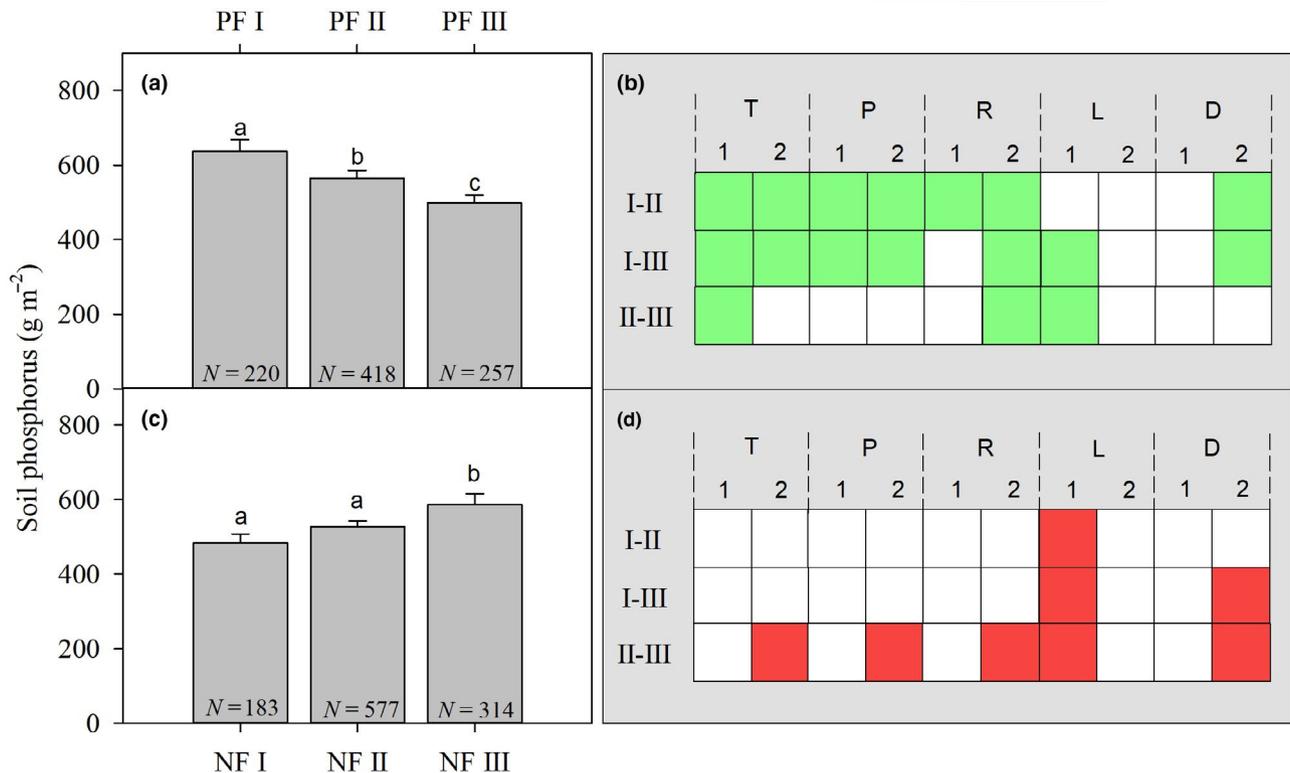


FIGURE 3 Total phosphorus (P) contents of the top 100-cm soil in (a) the plantation forests (PFs) and (c) the natural forests (NFs) in the growth/successional stages. The error bars in (a, c) indicate standard errors of the means. I, II, and III represent the early, middle, and late stages of succession or growth, respectively. *N* indicates the number of forest sites (sample size). The grid charts (b, d) indicate the significant differences among growth/successional stages when grouping sites by temperature (T), precipitation (P), climatic region (R), broadleaf/needleleaf leaf habit (L), and dryness (D), respectively. Comparisons were for the soil P content in the three stages in each subgroup, denoted by 1 and 2. The green and red squares indicate significantly lower and higher contents in the later stage compared to the earlier stage at $p < .05$, respectively, and white squares indicate no significant difference. More details are presented in Table 2

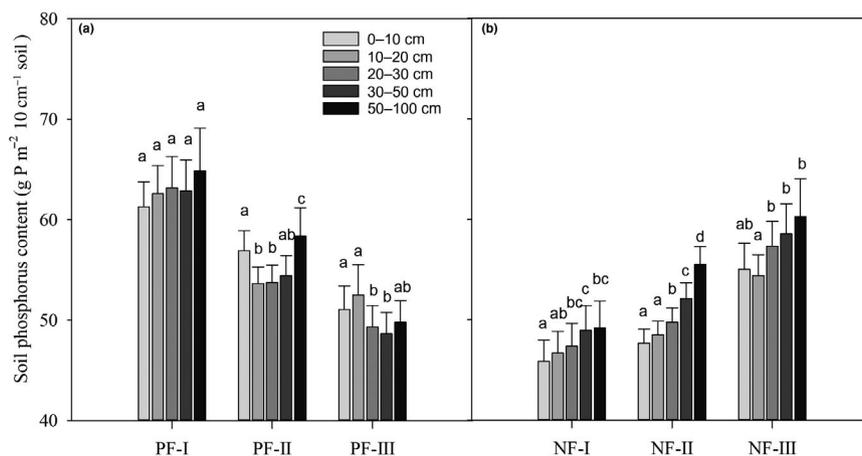


FIGURE 4 Phosphorus contents in the soil layers of the plantation forests [PFs, (a)] and natural forests [NFs, (b)] for the growth or successional stages. I, II, and III represent the early, middle, and late stages of growth or succession, respectively. The error bars indicate standard errors of the means. The numbers of forest sites are 220, 418, 257, 183, 577, and 314 for PF-I, PF-II, PF-III, NF-I, NF-II, and NF-III, respectively. P contents are normalized by a common depth of 10-cm to allow for comparison despite different sampling depth intervals

be allowed by more efficient microbial communities and mycorrhizas (Buendía et al., 2014; Lambers et al., 2008).

Thus, the increase in the P content in the NFs in our study indicated that NFs composed of native species can develop efficient

mechanisms to accumulate P in the ecosystem instead of replenishing P after it is lost, as previously proposed (Filippelli, 2008; Filippelli et al., 2006). This mechanism delays, at least, soil P depletion during long-term soil formation and retrogression. In contrast,

the detectable decreases in P content of PF ecosystems even at successional temporal-scale are mostly attributed to the lack of efficient P retention mechanisms (possibly due to non-native species), which supports the hypothesis that P cycling tightens during succession (Chapin et al., 2011; Walker & Syers, 1976), but only in natural conditions. Moreover, litter and soil P concentrations were more strongly correlated in the NFs than the PFs (Figure 1b), which further corroborates the assumption of more efficient mechanisms for P recycling and retention in the NFs than PFs. Therefore, the divergent trajectories in NF and PF highlight the importance of forest origin in determining nutrient status, supplementing Odum's theory for natural ecosystems.

A recent hypothesis of "co-development of nutrient strategies" claimed that poor P status, but not the ecosystems per se as Odum (1969) asserted, was the main driver of a system increasingly recycling P (Lang et al., 2016). However, our results for the increase in NF's P contents support Odum's theory that instead of the low-P soil hypothesized by Lang et al. (2016), but the ecosystem per se (enhanced P demand from a more complex system at maturity) was likely the main driver of the tightness of the P-cycling system. Odum's theory, however, asserts that nutrients would be gradually depleted if weathering did not increase, implying that ecosystems acclimate to P loss. Nonetheless, P accumulation can be expected if weathering rate exceeds the loss rate. Our results indicate that forests can develop efficient mechanisms to acquire, recycle, and retain P during natural succession. Therefore, a vegetation community more adapted to nutrient scarcity (e.g., NF) is more adapted to accumulate the scarce nutrients than other less adapted communities.

Variations of P content along soil profiles (P abundance in each layer) are rarely reported compared to the widely documented changes in soil P concentrations (Groppo et al., 2015; Lang et al., 2017; Wood et al., 1984). The "nutrient uplift hypothesis" states that contents of minerals most limiting to plant growth increase in the shallower soil layers (Jobbágy & Jackson, 2001). However, we found that P contents in each soil layer increased with depth in NF (Figure 4b), but did not change consistently in PF (Figure 4a) at any given succession/maturation stage. Vertical variations in P concentrations (g kg^{-1} soil) are different and show consistent P concentration

declines with depth across forest types (Figure 5). This result implies that the NF accumulated P in all horizons but PF lost P in the entire soil profile. Soils in NF have also lower bulk density, causing lower overall P contents despite the similar P concentrations of both forest types. These patterns indicate more efficient P retaining mechanisms regardless of depth in NF than PF, which might relate to different species composition, root structure, microbes, invertebrates, and mycorrhizas (Lambers et al., 2008). Previous studies also suggested that plants might slow down P leaching loss by taking up P via roots and mycorrhizal fungi (Rennenberg & Herschbach, 2013; Smith & Read, 2008), but these contributions have not been quantified yet (Bol et al., 2016).

4.2 | Phosphorus budget in NF

The observed accumulation of P through time in the top 100-cm soil in NF is only possible if the input of P is larger than the output from the soil. The P that had accumulated in the top 100 cm of soil may have come from external sources (e.g., deposition and re-infiltration from streamflow) and from below the 100-cm soil, so identifying the dominant source of P is important for clarifying the P change trajectories in the forest ecosystems. In the NFs, such a soil P accumulation with forest age can be due to (i) sustained inputs of external P from stages I to III, (ii) increasing inputs of external P in the later successional stages in sampled sites, and (iii) extraction of P from deep soils to the 0–100-cm zone. To test the first possibility, we collected published deposition data (Du et al., 2016; Wang et al., 2017) and estimated the total P inputs in Chinese forests from 1850 to 2020 (a period of 170 years, similar to the successional time span from stage I to stage III in the NFs) (Table 3). We assumed the most extreme condition, where P from deposition was completely retained, producing the largest P content difference due to deposition from stage I to III. Even under this extreme scenario of a maximum accumulation of deposition during the successional cycle of NF, the estimated increase in P content ($2\text{--}8 \text{ g P m}^{-2}$) was one order of magnitude less than the observed accumulation, implying that deposition was not the dominant driver of P accumulation in the NFs (Table 3). The

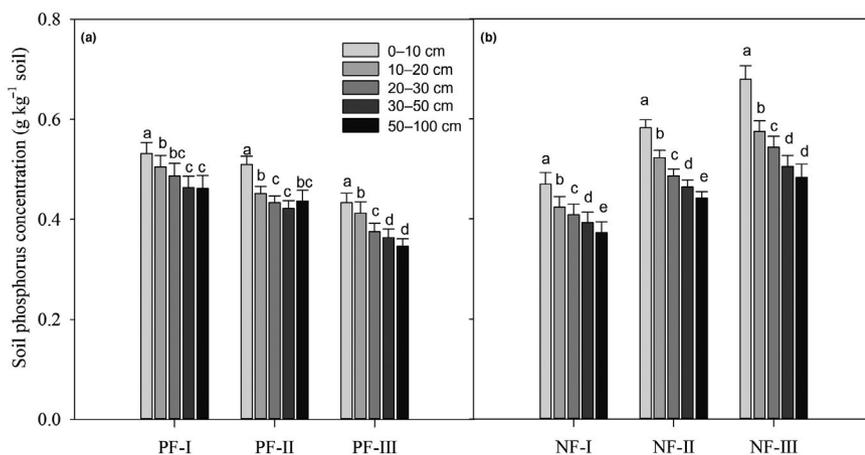


FIGURE 5 Phosphorus concentration in the soil layers of the plantation forests [PFs, (a)] and natural forests [NFs, (b)] for the growth or successional stages. I, II, and III represent the early, middle, and late stages of growth or succession, respectively. The error bars indicate standard errors of the means. The numbers of forest sites are 220, 418, 257, 183, 577, and 314 for PF-I, PF-II, PF-III, NF-I, NF-II, and NF-III, respectively

TABLE 3 Changes in soil P contents and estimated P deposition in the forest types from stage I to III

Estimated parameter	Data source	Total change (g P m ⁻³)
Soil P accumulated in NFs (I to III) ^a	This study	102 ± 43
Soil P accumulated in NFs (II to III)	This study	58 ± 30
Soil P loss in PFs (I to III)	This study	-138 ± 36
Soil P loss in PFs (II to III)	This study	-66 ± 33
Estimated P deposition	Wang et al. (2017)	2–8 ^b
	Du et al. (2016)	7 ^c
Estimated streamflow P loss in NF ^d	Sohrt et al. (2017)	-2 ± 3
Estimated leaching P loss in NF	Sohrt et al. (2017)	-2 ± 3
Estimated weathered P ^e	Hartmann et al. (2014)	0.2–17
	Helfenstein et al. (2018)	0.02–21
	Newman (1995)	0.9–85

^aP accumulated/lost in NF/PF soil from stages I to III in the 0–100 cm layers (all significant at $p < 0.05$).

^bTotal forest P deposition using data for eastern Asia (published number) and China (estimate from the published figure) from 1850 to 2010.

^cTotal forest P deposition using the average of forest sites in China (0.069 g P m⁻² year⁻¹) from 1850 to 2010 [the P deposition in 1850 refers to the data from Wang et al. (2017)].

^dP losses due to streamflow and leaching were estimated from Sohrt et al. (2017) assuming a time-span of 170 years. Specifically, leaching-P was roughly estimated as the amount been vertically transported out of the B horizon (mineral subsoil), which was reported slightly higher than the P in streamflow (Sohrt et al., 2017).

^eWeathered P was estimated from Hartmann et al. (2014), Helfenstein et al. (2018), and Newman (1995) assuming a time-span of 170 years from 1850 to 2010s with soil bulk density at 1.23 g cm⁻³ derived from the average of all forest plots.

loss of dissolved and particulate P in streamflow (i.e., surface and subsurface runoff) is approximately one order of magnitude lower than P deposition (Sohrt et al., 2017). The input of P in streamflow re-infiltration should be of similar magnitude and was thus unlikely the main source of P accumulation in the NFs. These results indicate that external P was a minor contributor, refuting both the first and second possibilities. This leaves us with the third possibility, that the accumulation of P in the NF can be explained by the extraction and retention of weathered P from deep soil.

Phosphorus weathering rates generally vary widely between 0.001 and 0.5 g P m⁻² year⁻¹ or 10⁻⁴ and 10⁻¹ mg P kg⁻¹ year⁻¹ (Hartmann et al., 2014; Helfenstein et al., 2018; Newman, 1995), which corresponds to approximately 0.02–85 g P m⁻² during a 170-year period with a soil bulk density of 1.23 g cm⁻³ derived from the average of all forest plots (Table 3). The wide range of P inputs from weathering reflects uncertainties of P supply from soil matrix weathering and parent material (Table 3). Thus, the P accumulation in NF might have been contributed from the existing P content below the 100-cm soil or continuously supplied from weathering. This inference, however, should be further examined with more *in situ* measurements of the deep soil P content, the P weathering rate, and the P diffusion rate from parent material (and subsequent transport upwards via root uptake). Despite the uncertainty, our speculation of the P accumulation in NFs supplied from deep soil was also supported by the trend of increasing P contents along the soil profile in the NFs (Figure 4b).

4.3 | Phosphorus budget in PF

In contrast to NF, the significant decline of soil P in PF implies a less efficient P-utilization by these ecosystems. PFs are distinct from NFs in species composition, structure, and human disturbances, and thus may differ in their abilities to absorb, retain, and recycle P. Note that the reduction of P in PF during growth is large and significant, which can be attributed to the loss from erosion, harvesting, and/or inefficient P-retaining system. Erosion-induced P losses were documented at 0.0003–0.1 g P m⁻² year⁻¹ (Farkas et al., 2013; Oyarzun et al., 2007), which might only have a minor contribution to the soil P content decline. Similarly, the loss of P due to logging was previously reported at 10⁻³–10⁻¹ g P m⁻² year⁻¹ with harvesting intervals of 50–100 year (Sohrt et al., 2017). Nonetheless, since the harvesting frequency may be higher in China (i.e., 16–61 years as officially recommended, Table 1), nutrient export from logging could be an essential driver of soil P depletion. To test the possibility, we considered an extreme scenario of logging-induced P depletion where: (i) All PFs were fast-growing species which matured at 16 years (Table 1); 2) the most intensive logging was implemented with the shortest rotation length of 16 years for all PFs (Table 1); (iii) at most four logging events occurred within the time-span of growth from stage I to III, which is 80 years derived from the largest age difference in PF sites; and (iv) the plant and litter P (i.e., total P in leaves, stems, branches, roots, leaf litter) were completely removed during each logging event with the average loss at 7.3 g P m⁻² derived from

stage III PFs (Figures S2 and S3). Therefore, assuming a site was continuously harvested four times, the PF will still reach 16 years (stage III) at the end of 80 years. This scenario is extreme in the sense that we are assuming the highest possible harvest frequency everywhere and the highest P extraction—both assumptions are unrealistic but serve the scope of defining an upper bound of P extraction via harvest. However, even under this extreme scenario, the total P loss estimated was still much lower than the loss detected (29 g P m^{-2} vs. $138 \pm 37 \text{ g P m}^{-2}$).

We suspect that the P loss induced by lateral (i.e., surface and subsurface streamflow) and vertical (i.e., leaching into subsoils) transports in a less P-efficient system also played an essential role, even though the exact contributions of these processes are still unknown (Figure 6). Accurate attribution of the P loss in the top 100-cm soil matrix into lateral and vertical components is challenging. The majority of the previous studies focused on a short period (e.g.,

1–3 years) and the topsoil layers (e.g., 0–20 cm), and the reported losses greatly varied in streamflow and leaching ($0.01\text{--}0.67 \text{ g P m}^{-2} \text{ year}^{-1}$; $0.8\text{--}53.6 \text{ g P m}^{-2}$ for an 80-year period) (Bol et al., 2016; Sohrt et al., 2017; Yu et al., 1989). It should be noted that the leaching of inorganic P is extremely slow. Therefore, if leaching was one of the important loss components, organic P would be the major form contributed to. Nonetheless, a substantial amount of P loss still cannot be explained, even under an extreme scenario. Thus, long-term, persistent observational experiments with a specific focus on forest plantations covering the entire soil profile are required.

4.4 | Implications for forest management

Even though our hypothesis provides explanations for the divergent changes in P in the PFs and NFs, a few uncertainties need to

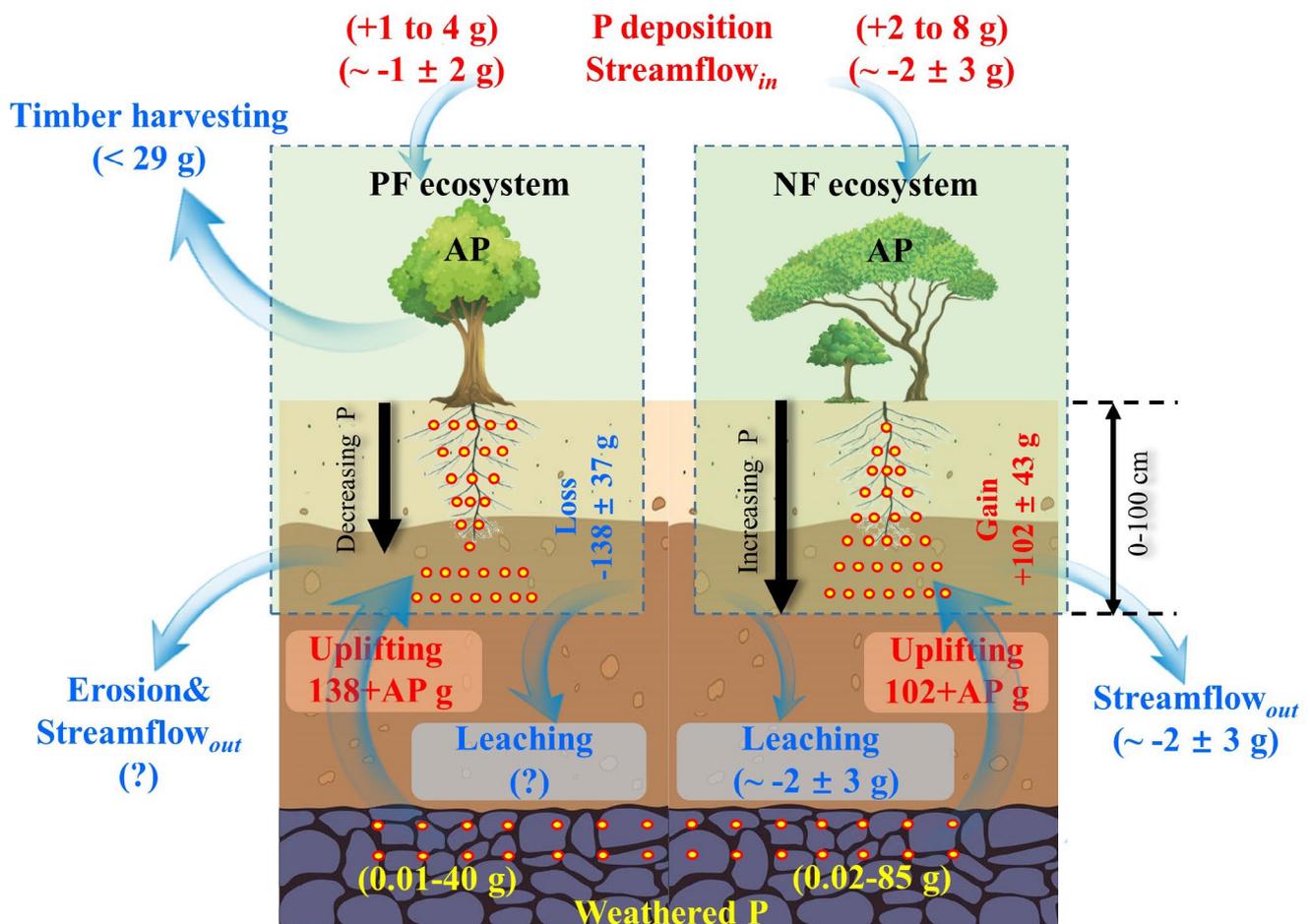


FIGURE 6 The accumulated phosphorus (P) fluxes in the plantation forests (PFs, left) and natural forests (NFs, right) from stages I to III. [The fluxes are the accumulated changes (g m^{-2}) for the time-span of stage I to III, namely 80 and 170 years for PF and NF, respectively. The number of red circles represents the relative differences of P contents between layers. The P flux due to deposition was estimated from Du et al. (2016) and Wang et al. (2017), while the P fluxes in streamflow (i.e., surface and subsurface runoff) and leaching (i.e., vertical loss) were derived from Sohrt et al. (2017). Streamflow_{in} and streamflow_{out} indicate input and output of P in streamflow, respectively. Weathered P was estimated from Hartmann et al. (2014), Helfenstein et al. (2018), and Newman (1995) assuming a time-span of 80 (PF) and 170 (NF) years with soil bulk density at 1.23 g m^{-3} derived from the average of all forest plots. AP represents plant P absorbed from soil in PF and NF, respectively. Changes in P content are estimated from stage I to stage III. Blue and red text indicates P transferred out and into the forest ecosystems, respectively]

be examined, including the role of biotic factors, the conversions of P forms, and the change of P content below the 100-cm soil matrix. For example, our analyses focus on the total P in the top 100-cm soil matrix, while future studies should examine both total P and different forms of P in the entire soil column to illustrate the P-utilization mechanisms in different ecosystems. Thus, more studies are required to elucidate the mechanisms of acquiring, recycling, and retaining P in the two forest types, including examinations of highly reactive factors such as weathering rates, root structure, microbes, invertebrates, soil characteristics, and the history of land use (Lambers et al., 2006, 2008, 2012; Macdonald et al., 2012). We also expect that a continuous decrease in soil P content would decrease PF ecosystem productivity and stability, suggesting that forest management should be improved (e.g., implementing management to promote forest development close to NFs) to slow the depletion of P in the PFs. We thus advocate more studies to illuminate the mechanisms of nutrient use for improving forest restoration in the P-deficient tropics. This is essential for achieving the commitments to global sustainable development, e.g., the New York Declaration on Forests, the United Nations Sustainable Development Goals (particularly Goal-15), and the intended Nationally Determined Contributions to the Paris Climate Agreement (Brancalion et al., 2019; Holl, 2017; Holl et al., 2017).

To summarize, we found that NF ecosystems were capable to accumulate P and promote P retention in soil as succession develops, while PF ecosystems were increasingly suffering from rapid P depletion in China. The negative impacts of P depletion may not be apparent in the short term, but PFs could be prone to long-term P losses slowing down tree growth and increasing seedling mortality induced by the nutrient limitation. Thus, future global biogeochemical models should be improved for a more accurate projection of P distribution and the future growth of forests with different origins.

ACKNOWLEDGMENTS

We thank field data collection efforts from Jingyun Fang, Guirui Yu, Gengxu Wang, Keping Ma, Shenggong Li, Sheng Du, Shijie Han, Youxin Ma, Deqiang Zhang, Shizhong Liu, Guowei Chu, Qianmei Zhang, Yuelin Li. We also thank Shirong Liu and Evgenios Agathokleous for help in language editing and for providing suggestions to improve the manuscript. This work was supported by the China National Science Foundation (No. 42130506, No. 32001166, No. 42071031), Jiangsu Key Laboratory of Agricultural Meteorology Foundation (JKLAM2004), and the Startup Foundation for Introducing Talent of NUIST (No. 2019r059). Daniel Goll and Philippe Ciais benefited from support from the Agence nationale de la recherche (ANR) grant ANR-16-CONV-0003 (CLAND).

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Phosphorus data can be obtained from: <https://doi.org/10.6084/m9.figshare.16917451>. Climate data can be obtained from the

National Ecosystem Research Network of China (<http://cnerp.org.cn/>). Please contact the corresponding authors for permission to use the data.

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How to cite this article: Yu, Z., Guoyi, Z., Liu, L., Manzoni, S., Ciais, P., Goll, D., Peñuelas, J., Sardans, J., Wang, W., Zhu, J., Li, L., Yan, J., Liu, J., & Tang, X. (2022). Natural forests promote phosphorus retention in soil. *Global Change Biology*, 28, 1678–1689. <https://doi.org/10.1111/gcb.15996>