A global meta-analysis of soil phosphorus dynamics after afforestation

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Summary

- Afforestation significantly affects soil chemistry and biota, but its effects on the potentially growth-limiting nutrient phosphorus (P) had not to our knowledge been analyzed globally.
- We conducted a comprehensive meta-analysis of 220 independent sampling sites from 108 articles to evaluate global patterns and controls of soil P change following afforestation.
- Overall, total P concentration decreased by 11% and total P stock by 12% in the top 20 cm of mineral soil following afforestation, with no change in available P. Time since afforestation had no consistent effect on total P, while available P tended to increase with time. Prior land cover was the most influential factor for soil P change after afforestation, with available P increasing on native vegetation but decreasing on cropland. Afforestation increased available P by 22% without decreasing total P on formerly 'degraded' land, but depleted total P by 15% at nondegraded sites. Climate also influenced soil P response to afforestation, with larger P loss in the tropics.
- Afforestation did not appear to directly induce P limitation, as available P only decreased on cropland. However, substantial declines in total P may drive tropical plantations toward greater P limitation as the capacity to replenish available P decreases.

Introduction

Afforestation, the conversion of nonforested lands to plantation forests, increases terrestrial biomass and contributes to ecosystem restoration, wood and fiber production, and climate change mitigation (Canadell & Raupach, 2008; IPCC, 2013). Accordingly, the scope of afforestation has rapidly increased in recent decades. As of 2015, *c.* 278 million ha, equivalent to 7% of global forested area, are grown as plantations, including afforestation and reforestation (Keenan *et al.*, 2015; Payn *et al.*, 2015). However, the high growth rates and biomass stocks of plantations compared with previous vegetation types can also lead to higher demand for soil nutrients (Mendham *et al.*, 2003; Merino *et al.*, 2004), which are sequestered in biomass and possibly removed in harvest. The long-term productivity of afforested systems is still uncertain, as a result in part of nutrient limitation of tree growth (Berthrong *et al.*, 2009; Li *et al.*, 2012; IPCC, 2013). Therefore, it is essential to quantify soil nutrient dynamics with afforestation and understand the factors controlling these dynamics, in order to sustain biomass production and mitigate climate change.

Afforestation significantly affects soil water, acidity, and nutrients crucial to plant growth (Jackson *et al.*, 2005; Berthrong *et al.*, 2009; Li *et al.*, 2012). For instance, a global meta-analysis by Berthrong *et al.* (2009) found significant decreases in the nutrient cations magnesium (Mg), calcium (Ca), and potassium (K) after afforestation, which could impair long-term soil fertility and productivity of some plantations. By contrast, the soil nitrogen (N) pool tends to increase with time after afforestation (Li *et al.*, 2012). Globally, phosphorus (P) strongly limits plant growth, particularly in the tropics (Vitousek & Howarth, 1991; Elser *et al.*, 2007). Sequestration of P in slow-cycling pools such as tree biomass could be a major cause of P limitation of plant growth (Vitousek *et al.*, 2010; Goll *et al.*, 2012). In plantation ecosystems where tree biomass is repeatedly harvested, increased P uptake following afforestation could induce P limitation of plant growth over decades as P is removed in biomass, but this has not been tested at a broad scale. To the best of our knowledge, there is no synthesis quantifying global patterns of the dynamics of soil P following afforestation.

Recent progress in implementing mechanistic N and P schemes in terrestrial ecosystem models underscores the importance of P dynamic feedbacks on plant growth (Zhang *et al.*, 2011; Goll *et al.*, 2012; Yang *et al.*, 2014). Despite these advances, model predictions of soil P dynamics following land-use changes, such as afforestation, remain largely uncertain, as multiple factors regulate the availability of P in the soil (Vitousek

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et al., 2010; Zhang *et al.*, 2011; Goll *et al.*, 2012). On one hand, afforestation increases plant nutrient uptake, potentially reducing the quantity of total P and readily available P in soil (Vitousek *et al.*, 2010), and P limitation may constrain the carbon (C) uptake associated with reforestation and afforestation (Wang *et al.*, 2015). On the other hand, afforestation promotes P mineralization by altering root characteristics and microbial symbioses, increasing P availability (Chen *et al.*, 2008). As a result, afforestation has been reported to either increase (Chen *et al.*, 2000; Lemma & Olsson, 2006), decrease (Armolaitis *et al.*, 2007; Zhao *et al.*, 2007) or have no effect on (Morris *et al.*, 2007; Smal & Olszewska, 2008) total and plant-available soil P. Climate, soil properties, tree species planted, and prior land cover/land use all have been used to explain the inconsistent results in different regions (Chen *et al.*, 2008; MacDonald *et al.*, 2012). Variability in site-specific conditions may limit our ability to quantify the dynamics of soil P following afforestation (MacDonald *et al.*, 2012). Therefore, we seek to identify the most important factors contributing to the change in soil P after afforestation.

In this study, we compiled a database of soil total and available P in afforested and nonafforested (control) sites, with data from 220 independent sampling sites in 108 articles, and conducted a global meta-analysis to evaluate the dynamics of soil total and available P after afforestation. The two major questions we aimed to answer were: (1) how do total and available P in soil change following afforestation; and (2) how do climate, soil properties (soil pH and clay content), prior land cover/use (i.e. vegetation type and degree of anthropogenic degradation) and current land cover (tree species planted) affect the dynamics of total and labile P in soil after afforestation? More specifically, we tested three hypotheses: (1) plantation establishment would decrease total P through sequestration in biomass while increasing available P through accelerated P cycling; (2) total P would become increasingly depleted as plantations aged and more P was extracted from the soil; and (3) prior land cover, climate, and soil properties would contribute significantly to variation in P responses to afforestation.

Materials and Methods

Dataset assembly

We searched for articles reporting the impact of afforestation on soil P using Web of Science and Google Scholar. Searches included combinations of the terms 'tree plantation', 'afforest*', 'reforest*', 'phosphorus', 'soil phosphorus', 'chronosequence', and 'abandoned OR degraded'. We also searched using keywords in Spanish and Portuguese: 'forestación' or 'aforestación' 'fósforo', 'suelo', 'florestal', 'solo', and 'plantaç*'.

We systematically reviewed all results published before March 2015 and included those studies that involved the planting of trees on treeless land; and reported P of mineral soil in the afforested treatment and in a counterfactual control representing similar land in the absence of afforestation. We included studies with two types of controls: nonforest land cover measured at the same time as the afforested site (the most common case), and the site of afforestation measured before tree planting. When studies reported both types of control, we selected the former, in order to compare alternative land use scenarios without assuming that soil conditions would remain unchanged in the absence of afforestation. Controls included primary and successional native vegetation, and active, fallow, or abandoned agricultural land. We excluded studies in which the planting occurred in a recently cleared native forest, but included studies in which trees were planted on historically forested land that had been cleared more than a decade ago and was treeless before afforestation. Our searches yielded a total of 108 articles, comprising 220 independent sampling sites, 353 forest stands, and 1193 observations of soil P (Supporting Information Tables S1, S2). The sites span the world's afforested lands, including data from five continents and Oceania, albeit with emphasis on China, India, and Europe (Fig. 1). In all studies, the comparability between control and afforested sites was established based on either soil characteristics, land use history, or slope, aspect, and relief (Table S2).

Data were either obtained from tables or extracted from figures using WebPlotDigitizer (v.3; Rohatgi 2015) or GetData Graph Digitizer (v.2.24; Moscow, Russian Federation). When data were not included in the publication, we contacted the authors and used the raw data if possible.

We separated reported P into 'total' and 'available' P, based on the authors' designations. Both total and available P were determined by a variety of different procedures, resulting in measurement of different fractions of the soil P pool in different studies. 'Available' P is intended to represent the amount of P availability to plants, either labile or readily dissociated from other minerals. In practice, 'available' P is operationally defined as the amount of total P released into solution by a particular chemical extraction protocol. In all studies, extraction methods were consistent between control and afforested sites. Reported 'labile' P was classified as 'available'.

The compiled database also includes source of data, prior land cover/use, tree species planted, soil characteristics (soil texture and pH), climate zones (mean annual temperature and precipitation), the age of afforestation, and sampling depths at each study site. Prior land covers/uses include grassland, shrubland, savanna, pasture, cropland, and unspecified degraded land; dunes with grass cover and mine spoils were folded into grassland and unspecified degraded, respectively, because of their low number of observations. Additionally, we included a binary categorization of prior land cover as degraded or nondegraded, based on whether the authors used words such as 'degraded', 'overgrazed', or 'wasteland' to describe the site before afforestation, or if the authors noted that agricultural land had been taken out of production because of declining yields. Major species used in afforestation were classified as pine, eucalyptus, other gymnosperms, other angiosperms, and mixed-class stands. We used mean annual temperature and precipitation, latitude, and longitude to determine climate zones, based on the Köppen classification as applied by Kottek *et al.* (2006) and the guidelines of Laganière *et al.* (2010). We partitioned soil texture into sand, loam, or clay, and recorded percent clay where reported. We recorded soil pH at afforested and control sites and assigned alkaline (pH > 8), acidic (pH < 6), or neutral pH (pH 6–8) based on

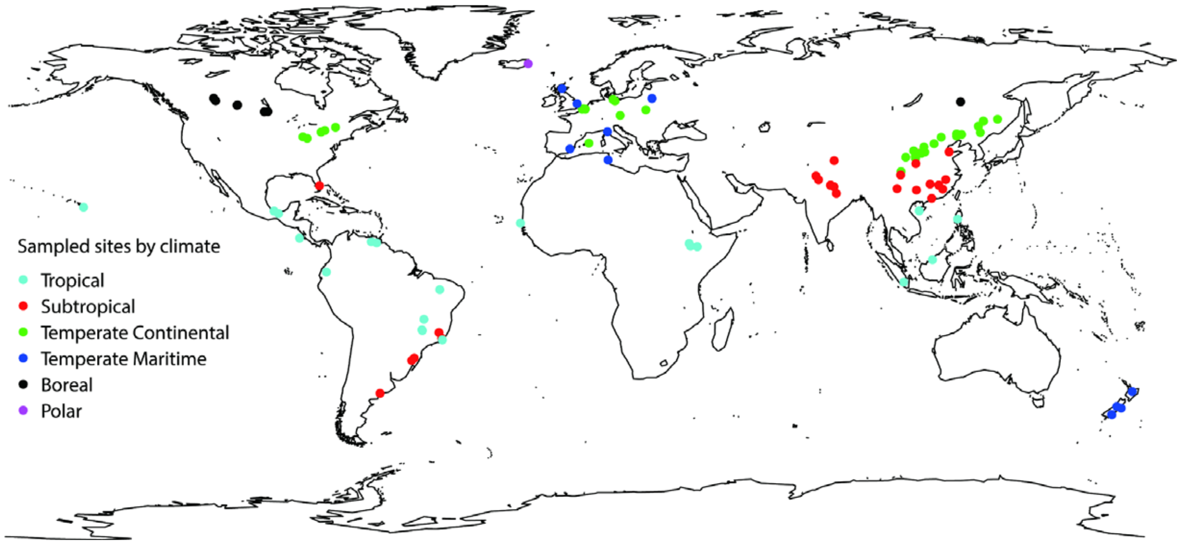

Fig. 1 Global distribution of sites included in the meta-analysis.

pH of the control site. We also recorded the time since afforestation, control and afforested bulk density (or soil organic matter content or soil C content, in that order, if bulk density was not given), P extraction methods, and control and afforested P stock or concentration at each depth increment.

Meta-analysis

We used the log-transformed response ratio, $\log_e(P_{afforested}/P_{control})$, as our metric of effect size. This metric is commonly used in meta-analysis and allows for a symmetrical distribution of effects, equal influence of the test and control values on the total effect size, and comparison of studies with different P extraction techniques (Hedges & Olkin, 1985; Luo *et al.*, 2006).

To compare studies, we calculated a single composited value for the top 20 cm of mineral soil in each afforested stand and the corresponding control area, excluding organic horizons. We averaged the P concentrations from the depth increments to 20 cm, weighting by the mass of soil in each increment. Where multiple samples were taken from the same stand at different times, or from adjacent stands of different ages in a chronosequence, we averaged the composited 20-cm values for the different ages to avoid pseudoreplication. We then used the composited control and afforested P concentrations to calculate the log response ratio. To calculate temporal trends within individual stands or chronosequences, we used the original, noncomposited age data. When studies measured to a maximum depth of < 20 cm, we calculated the average P concentration to the deepest depth available. In the text, we present the results as per cent change ($100\% \times (P_{afforested} - P_{control})/P_{control}$) for ease of visualization, but statistical analyses were performed using the log-transformed response ratio.

Selecting a floor of 20 cm for the analysis allowed us to compare all studies without excluding a large fraction of the data. Seventy-seven studies, representing 67% of independent stands, reported measurments to a depth of at least 20 cm, but only 47 studies, representing 46% of stands, reported measurements below 20 cm (Fig. S1). The 20-cm floor also captures the nutrient changes in a substantial fraction of the zone from which plants access nutrients (Jackson *et al.*, 1997).

Most studies reported soil P in a mass unit (mg P kg^{-1} soil). When unit of soil P was reported on a volume basis (e.g. kg P ha^{-1}, to a given depth), we converted it to the mass unit using soil bulk density. Where bulk density was not reported, we used soil organic matter content to approximate bulk density, following the methods of Berthrong *et al.* (2009). We adapted the procedure slightly by using 0.5, rather than 0.58, as the conversion factor between soil C content and soil organic matter content, following Pribyl (2010), who cautioned against the unwarranted specificity and potential C content overestimation associated with the traditional conversion factor. Where no bulk density, organic matter content, or C content was reported, we estimated bulk density at each depth increment using a linear relationship between bulk density and depth at the sites where bulk density was measured directly. This model was applied separately for control and afforested sites (Notes S1). Our calculated bulk density values were consistent with measured bulk densities. However, the calculations reflected either changes in organic matter content or average differences between control and afforested sites, and were not able to capture large changes in bulk density with afforestation, such as those resulting from physical compaction in site preparation, or reversal of compaction with cessation of plowing (Fig. S2).

To calculate P stocks for all measured stands, we used bulk density and the depth increment of each observation to express P content on an area basis, then summed the P contents to 20 cm depth. Where observations were taken to a maximum depth of < 20 cm, we extrapolated P concentration and bulk density to 20 cm by integrating linear depth functions of P concentration and bulk density, expressed as fractions of the concentration and bulk density in the shallowest depth increment, over the missing depth intervals. The linear functions were modeled using all profiles with at least two depth increments in the top 20 cm (based on the midpoint of each depth increment), and were calculated separately for control and afforested sites and for available and total P concentrations (Notes S2).

Because of the non-Gaussian distribution of the effect sizes, we used nonparametric approaches to test the hypothesis that the mean effect size is not equal to zero (that is, $\log_e(1/1)$). We bootstrapped 95% confidence intervals by sampling from the distribution of response ratios 10 000 times with replacement, using the number of stands per observation as weights for the sampling, and taking the 2.5th and 97.5th quantiles of the bootstrapped distribution (Efron, 1981). We considered changes in P content with afforestation to be significant at the $\alpha = 0.05$ level if this bootstrapped interval did not include zero. We used an unweighted analysis rather than weighting each stand by its reported sample size because of differences in the definition of samples between studies and possible dependence among samples within a stand. Variance-weighting methods were not appropriate for the composited 20-cm values used in this study. For numeric predictor variables, we fit linear relationships between each predictor and the response, using *t*-tests to evaluate their significance (Post & Kwon, 2000).

In analysis of total P, we removed one 'outlier' data point for which total P inexplicably increased by over 400% (Ahmed *et al.*, 2010).

To quantify the importance of different predictors in determining the response of P stocks and concentrations to afforestation, we used the machine learning technique 'random forests'. We generated 1000 regression 'trees', each recursively partitioning the P observations into groups, using the R package 'PARTY' (Strobl *et al.*, 2007). We grew regression trees without pruning (i.e. all partitions accepted), allowing three possible candidate variables at each node (three = square root of nine possible variables, following Hapfelmeier *et al.*, 2014). This nonparametric method allows us to consider all observations, including those with missing data, in assessing the relationship of predictors to the change in P concentration with afforestation. Predictor variable importance was assessed using the permutation variable importance (Hapfelmeier *et al.*, 2014). Briefly, this method randomly assigns observations at nodes where splits are based on the variable of interest, and compares the mean squared error of the resulting trees to that of the original trees with the observations correctly assigned at each split.

To assess the effects on changes in P of variables measured repeatedly within a site – stand age and soil depth – we used mixed linear models with site as a random effect. Each separately reported stand within a study (e.g. different species, or stands located in different watersheds) was considered to be an independent site. For relationships between stand age and P concentration, we considered all stand ages within a site to represent repeated measurements of the same site, although in most cases the 'repeated measures' were produced by measuring adjacent stands of different ages. To evaluate the long-term effects of afforestation, we used P concentration in afforested stands of different ages, rather than response ratio with control stands, as the dependent variable in assessing age relationships. This avoided the confounding effects of change in the control land use over time, independent of afforestation.

For relationships between depth and P concentration, as well as depth and change in total P, we also considered stands of different ages within a site to represent separate observations. Because of wide variation in available P between stands, we expressed P concentration at each depth as a fraction of the concentration in the shallowest depth increment in that stand. Concentration did not always decrease with increasing depth, so we log-transformed the ratios in order to weight increases and decreases equally.

All statistical analyses were performed in R v.3.2.1 (R Development Core Team, 2014). The NLME package (Pinheiro *et al.*, 2015) was used for mixed-effects regression, and the PARTY package (Hothorn *et al.*, 2006; Strobl *et al.*, 2007) for determining variable importance.

Results

Global changes in soil P with afforestation

Globally, afforested soil held less total P than nonafforested controls, whereas available P was unchanged with afforestation (Table 1; 20 cm depth). Total P concentrations (mg kg^{-1} soil) decreased by an average of 11.2%, with a bootstrapped 95% confidence interval (CI) of −16.9%, −5.4%. Available P concentrations did not change significantly, with a trend of increasing by 5.5% on average (95% CI −4.0%, +15.2%).

Changes in P stocks (kg ha^{-1}) in the top 20 cm of mineral soil were similar to changes in concentrations: −12.3% for total P (95% CI −17.8%, −6.5%) and a nonsignificant change of +3.33% for available P (95% CI −5.9%, +12.8%). The trend toward larger decrease in stocks compared with concentrations can be attributed to an average decrease in bulk density with afforestation (Fig. S2). For 93 independent stands in which bulk density was measured directly, the bulk density in the top 20 cm was 5.5% lower at the afforested site than at the control site (95% CI −7.8%, −3.2%). The mean bulk density of the top 20 cm in nonafforested stands was 1.25 g cm^{-3}, with a minimum of 0.44 g cm^{-3} for a volcanic ash soil (Scowcroft *et al.*, 2004) and a maximum of 1.85 g cm^{-3} for a compacted sodic soil (Tripathi & Singh, 2005).

Factors affecting change in soil P

Land-use history variables and climate were most important for determining changes in total and available P (Table 2). These predictors captured important trends in P responses to afforestation, if not the substantial variability among observations (Fig. S3). In addition, P extraction method was an important predictor of change in P with afforestation (Table 2).

Land cover/use Prior land cover was the most important predictor of change in both total and available P with afforestation (Table 2). Available P tended to decrease with afforestation on former agricultural land (crop and pasture; significant decrease of

Table 1 Global characteristics (mean, median, minimum, and maximum values and sampling sizes) and changes in soil total and available phosphorus (P) with afforestation, to a depth of 20 cm

	Total P					Available P				
	Mean	Med	Min	Max	*n*	Mean	Med	Min	Max	*n*
P concentration, nonafforested (mg kg^{-1})	502.4	479.4	13.0	1341.0	84*	30.45	11.0	0.25	274.6	122
P stock, nonafforested (kg ha^{-1})	1189	1103	34.6	3108	84	69.8	24.3	0.70	670.6	122
Change in P concentration (% change)	−11.22	−5.5	−73.9	+143.0	116	+5.45	+8.4	−94.0	+410.4	180
Change in P stock (% change)	−12.34	−6.1	−71.4	+115.6	116	+3.33	+6.3	−93.5	+390.9	180

*Within a study, multiple afforested stands may share a control; only unique controls were used to calculate mean nonafforested stocks and concentrations.

Table 2 Relative importance scores (RIS) of variables contributing to the change in phosphorus (P) concentration with afforestation. Numbers are predictor variable importance estimated by permutation at nodes based on the given variable, using the machine learning technique (see the Materials and Methods section)

	Total P		Available P	
Rank	Variables	RIS	Variables	RIS
1	Prior land cover	0.0141	Prior land cover	0.0383
2	Extraction method	0.0121	Climate zone	0.0334
3	Climate zone	0.0100	Extraction method	0.0259
4	Soil texture	0.0057	Prior degradation status	0.0213
5	Average stand age	0.0048	Mean annual temperature	0.0190
6	Prior degradation status	0.0034	Soil pH value	0.0157
7	Mean annual temperature	0.0020	Average stand age	0.0087
8	Mean annual precipitation	0.0013	Mean annual precipitation	0.0069
9	Soil pH value	0.0013	Soil texture	0.0034
10	Species class	0.0009	Species class	0.0008

19.6% on former cropland) and to increase where afforestation replaced native vegetation (grassland, shrubland and savanna; significant increase of 24.8% on former grassland) (Fig. 2b). Available P also increased significantly by 51.7% on lands where no prior land use was specified other than 'degraded' land (Fig. 2b). By contrast, total P decreased significantly on both former agricultural and native land covers: by 23.1% on former grassland, 10.5% on cropland, 11.5% on savanna, and 7.1% on pasture (Fig. 2a).

When prior land use was simplified as degraded or nondegraded, available P concentration increased significantly by 21.7% at previously degraded sites, where total P did not change significantly (Fig. 3b). At nondegraded sites, total P decreased significantly by 15.3% and available P did not change significantly (Fig. 3a).

Current land cover – the type of tree used for afforestation – particularly affected the change in total P (Table 2). *Pinus*, the most common single genus, was associated with larger decreases in total P (18.0%) than were other genera (Fig. 4a). Total P also decreased significantly for noneucalyptus broadleaves (11.6%) and mixed genera (10.4%). Species class was not important for available P, which did not change significantly in any individual species category (Fig. 4b).

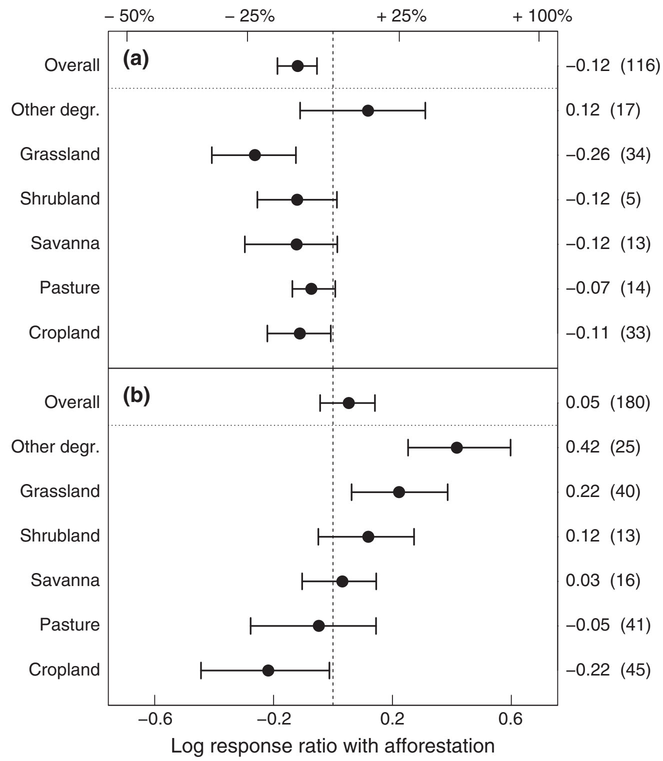

Fig. 2 Responses of (a) total and (b) available soil phosphorus concentrations to afforestation on different prior land cover types. Error bars represent 95% bootstrap confidence intervals. The upper axis shows log response ratios in units of per cent change. Right side labels show category means (number of observations). 'Other degr.' indicates observations for which no prior land cover was specified other than 'degraded', as well as former mine spoil sites (three sites).

Climate Total P decreased most significantly at tropical sites, by 29.8% (Fig. 5a), while available P increased significantly only at subtropical sites, by 36.4% (Fig. 5b). Otherwise, the five climate zones identified in this study generally did not differ in their average responses of P to afforestation (Fig. 5). Total P also decreased significantly at temperate maritime sites (9.8%) and temperate continental sites (13.5%), and available P decreased significantly at the three sampled boreal sites, by 19.5%.

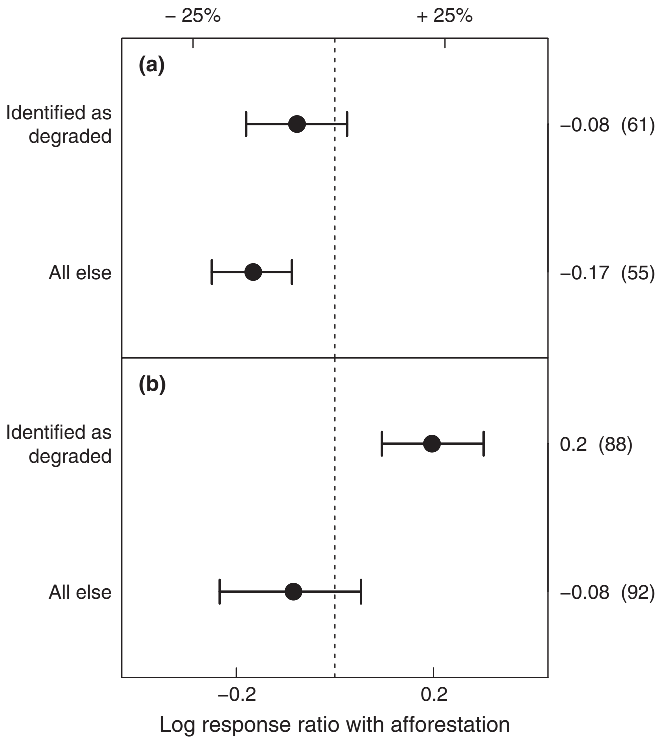

Fig. 3 Responses of (a) total and (b) available soil phosphorus concentrations to afforestation on previously degraded and nondegraded soils. Error bars represent 95% bootstrap confidence intervals. The upper axis shows log response ratios in units of per cent change. Right side labels show category means (number of observations).

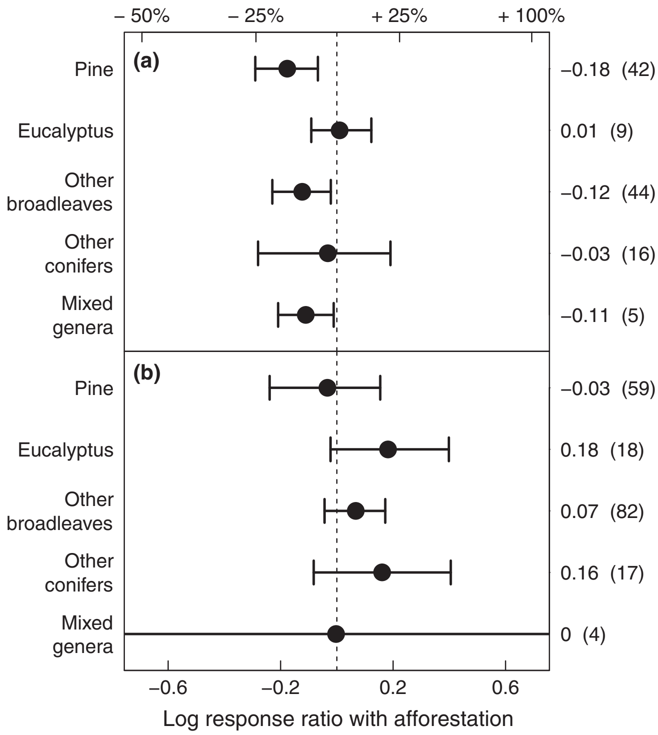

Fig. 4 Responses of (a) total and (b) available soil phosphorus concentrations to afforestation with different plantation types. Error bars represent 95% bootstrap confidence intervals. The upper axis shows log response ratios in units of per cent change. Right side labels show category means (number of observations).

Increasing mean annual temperature was associated with increases in available P with afforestation, but not with change in total P (Fig. 6b). Mean annual precipitation was not an important predictor of change in P (Table 2). The observations were unevenly distributed along the range of precipitations; only six observations of total P (one outlier was removed from the data analysis) came from sites with > 2000 mm of precipitation yr^{-1}, but the maximum precipitation was nearly 5000 mm yr^{-1}.

Soil properties Changes in soil pH with afforestation affected available P, which increased in acidic and alkaline soils but decreased in neutral soils (based on control pH values; Fig. 7b). In alkaline soils, available P increased as pH decreased (slope = −0.31; $P = 0.028$; $r^2 = 0.15$; $n = 27$; Fig. S4). Control values and changes in soil pH were less important for total P (Table 2). Neutral soils experienced larger decreases in total P than did alkaline soils (Fig. 7a), and change in total P was positively correlated with change in pH in neutral soils (slope = 1.22; $r^2 = 0.61$; $P < 0.001$; $n = 29$; Fig. S4).

Total P tended to undergo larger changes in coarser textured soils, significantly decreasing in sand (by 22.2%) and loam (8.6%) but not in clay (Fig. 8a). Mean change in available P was nearly identical among soil textures (Fig. 8b). Change in available P exhibited a weak negative relationship with clay content at previously degraded sites (slope = −0.009; $r^2 = 0.06$; $P = 0.039$; $n = 58$), but clay content had no overall effect on total or available P response.

Extraction method When included alongside the site-specific predictors, P extraction method was ranked as the second most important predictor of change in total P, and the third most important predictor of change in available P (Table 2). Total P concentration decreased significantly in studies using mild acid extraction of combusted soil, sulfuric acid (generally in conjunction with perchloric acid or other strong acids), and sequential extractions such as the Hedley procedure, and decreased significantly with afforestation in the studies using less common methods such as sodium hydroxide fusion (Fig. 9a). Available P concentration increased significantly with the most common extraction technique, bicarbonate extraction, but decreased in the few replicates using anion exchange resins, which on average were associated with much higher available P concentrations than were the other methods (Fig. 9b).

Stand age Total P in the top 20 cm of soil was unchanged with stand age, when sampled either at multiple time-points or along a chronosequence (Table 3; Fig. S5). By contrast, the concentration of available P increased with age within stands (Table 3; Fig. S6).

Sampling depth Within stands where soil P was sampled at multiple depths, total P tended to decrease more with afforestation at greater depths (Table S3). Changes in available P concentrations did not vary significantly with depth, although the

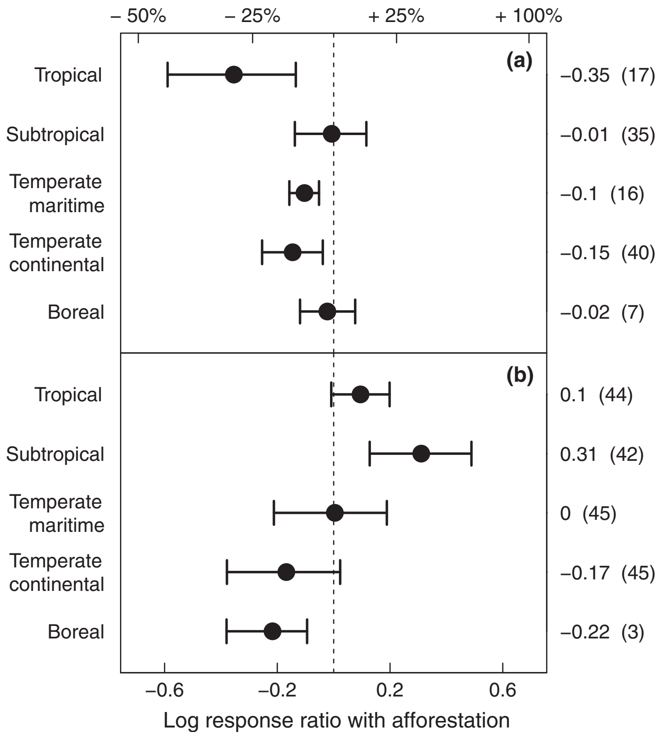

Fig. 5 Responses of (a) total and (b) available soil phosphorus concentrations to afforestation on different climate zones. Error bars represent 95% bootstrap confidence intervals. The upper axis shows log response ratios in units of per cent change. Right side labels show category means (number of observations). The polar climate zone is represented by only a single site and is excluded from this analysis.

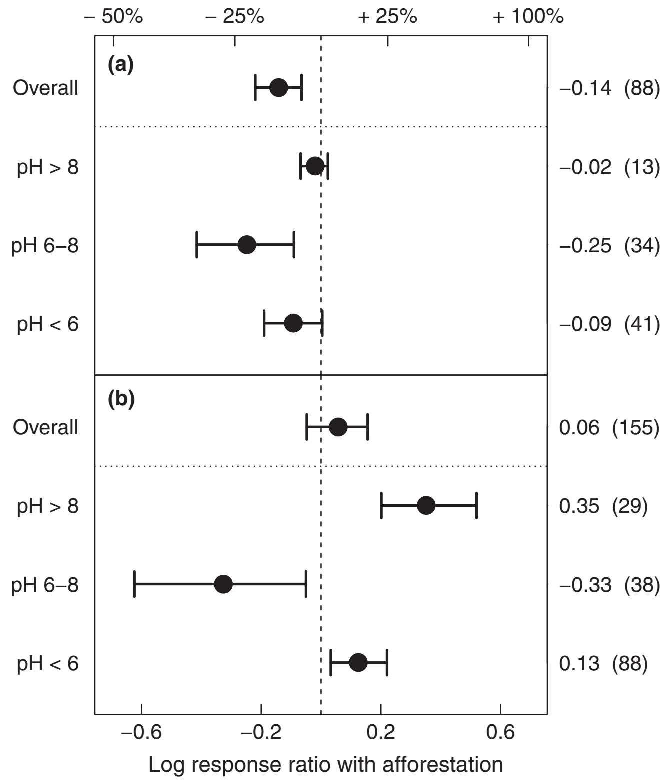

Fig. 7 Responses of (a) total and (b) available soil phosphorus concentrations to afforestation on alkaline, neutral, and acidic soils. Error bars represent 95% bootstrap confidence intervals. The upper axis shows log response ratios in units of per cent change. Right side labels show category means (number of observations).

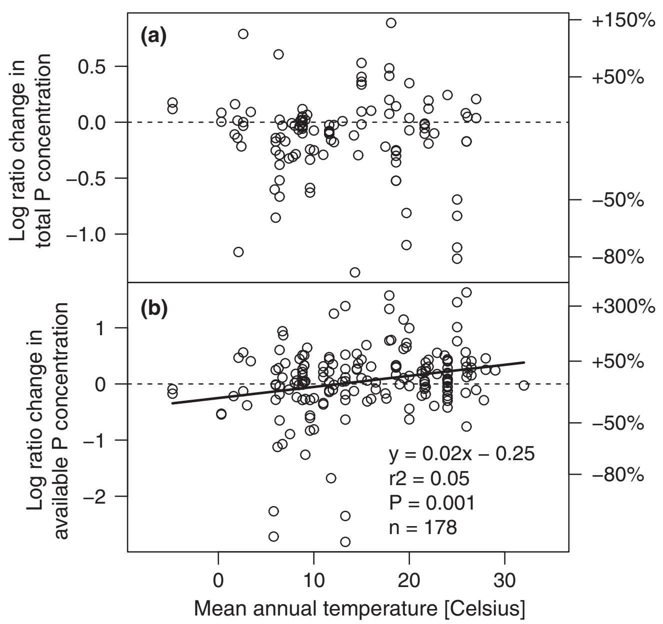

Fig. 6 Responses of (a) total and (b) available soil phosphorus (P) concentrations to afforestation as a function of mean annual temperature. Model specifics are given for significant linear models fit by the least squares method. The right side axis shows the log response ratio as per cent change in phosphorus concentration between control and afforested sites.

absolute value of change in available P tended to increase with depth (Table S3).

In terms of P concentration, total P decreased with increasing depth, a trend that was generally consistent across sites. Available P also generally decreased with increasing depth, but increased substantially at some sites. Decreasing P concentrations with depth were observed at both control and afforested sites. For total P, the decrease in concentration with depth was more rapid at afforested sites than at control sites, while the opposite was true for available P (Table S3).

Discussion

Our global meta-analysis showed an overall depletion of total soil P in the top 20 cm of mineral soil after afforestation (Table 1). Uptake of P and sequestration in biomass and litter likely drives the decreases in total P (Vitousek *et al.*, 2010), as the aboveground biomass of trees generally exceeds that of the prior vegetation and leaching losses of P from forest systems are generally low (Attiwill & Adams, 1993; Smil, 2000). Cessation of P fertilizer input with afforestation might also result in lower soil P in planted forests than in agricultural soils (MacDonald *et al.*, 2012).

Despite the substantial depletion of total soil P, our meta-analysis showed that afforestation did not significantly change the

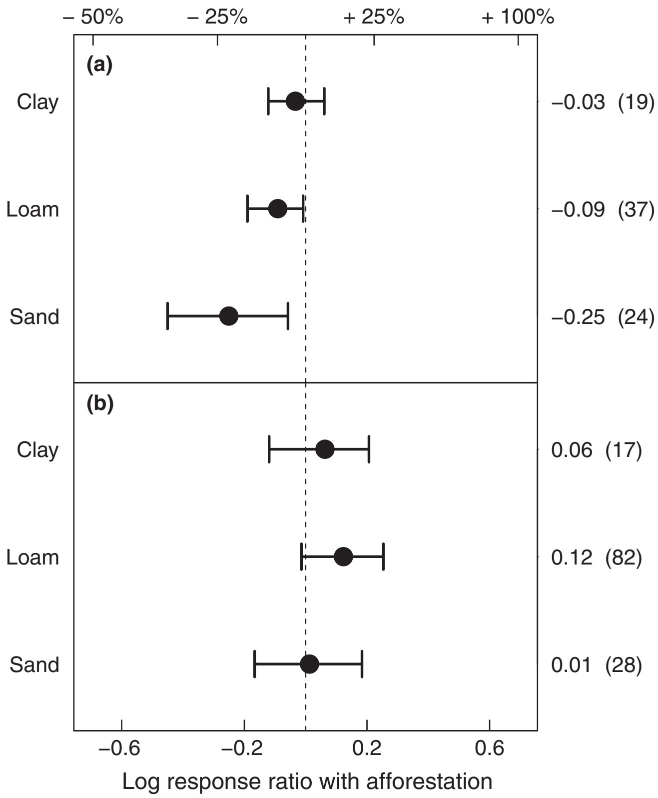

Fig. 8 Responses of (a) total and (b) available soil phosphorus concentrations to afforestation stratified by soil texture. Error bars represent 95% bootstrap confidence intervals. The upper axis shows log response ratios in units of per cent change. Right side labels show category means (number of observations).

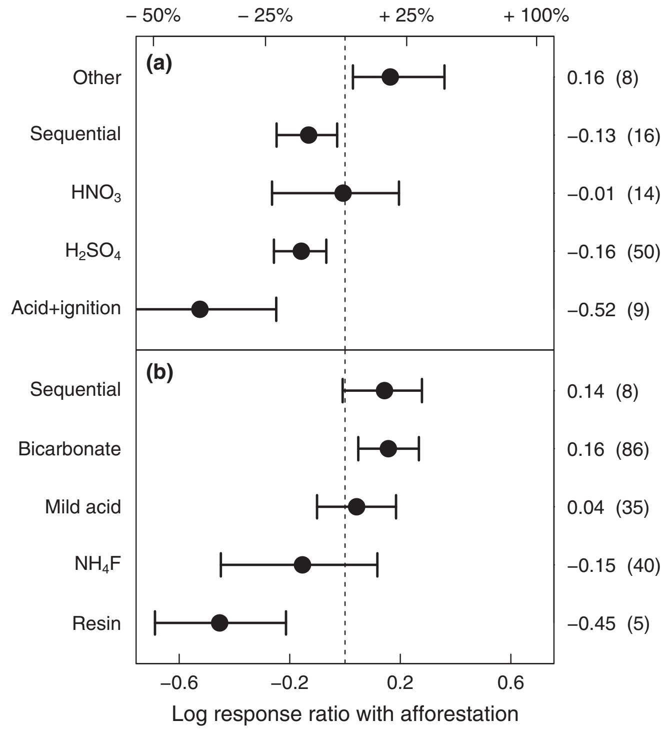

Fig. 9 Responses of (a) total and (b) available soil phosphorus concentrations to afforestation with different methods of phosphorus extraction from soil. Error bars represent 95% bootstrap confidence intervals. The upper axis shows log response ratios in units of per cent change. Right side labels show category means (number of observations). Mild acids are primarily dilute H_2SO_4 and HCl; 'other' methods for total phosphorus include NaOH fusion, 'NP elemental analyzer', and unspecified acid extraction.

concentration of available P (Table 1). Considering the limited P inputs in plantation forests (Condron & Tiessen, 2005; Laclau *et al.*, 2005), this finding suggests that afforestation promoted P mobilization. To meet greater P demands, trees may invest more C and other resources in root exudates and microbial symbioses that degrade clay minerals or organic P compounds (Chen *et al.*, 2008).

Contrary to our expectation, time since afforestation had no consistent impact on total P (Table 3, Fig. S5). The lack of change in soil total P with time since afforestation indicates that the decreases in total P tend to occur shortly following afforestation. This may be attributable to one-time management effects, such as cessation of fertilization or leaching or erosion losses in site preparation. Alternatively, P may be rapidly taken up by growing saplings, then recycled internally through reabsorption and litter decomposition following canopy closure (Miller, 1979; Chen *et al.*, 2000). Accumulation and recycling of relatively P-rich litter may also account for the observed increase in available P with time in the top 20 cm (Table 3; Fig. S6). However, the dearth of long-term observations of afforested soils (only 30 studies measured available P at more than one stand age, and only 19 did so for total P) may limit the conclusions that can be drawn from these trends. In addition, P may be brought up from depths below 20 cm, concentrating total and available P near the surface while depleting total P at greater depths (Jobbágy & Jackson, 2001). More data on changes in P through time at greater depth would allow us to further test these hypotheses.

Table 3 Fixed-effects components of model fits for relationships between phosphorus (P, top 20 cm) and stand age within sites

Model	Parameter	Estimate	SE	*t*-value	*P*-value
TP ~ age	Intercept	403.9	73.21	5.512	< 0.001
	Age	0.039	1.10	0.036	0.972
$\log_e$(AP) ~ age	Intercept	2.334	0.156	14.922	< 0.001
	Age	0.011	0.003	3.458	< 0.001

TP, total P; AP, available P.

The observed increase in available P with time (Table 3; Fig. S6) contradicts the hypothesis that P availability would decrease as P uptake and possible removal in biomass harvest depleted the total P pool. Increased P availability suggests that P is mobilized more rapidly than it is taken up by plants, and therefore afforestation did not appear to directly induce P limitation. Turner & Lambert (1986) estimated that in Australia, it would take at least 320 yr (four plantation rotations) before depletion of phosphorus and calcium would impair *Eucalyptus* productivity, based on the nutrients in total biomass and total soil pools. As shown in their calculation, the available P pool is usually small relative to the total P pool from which it is replenished, and biomass harvest is an important mechanism by which total P pools might be depleted to the point at which they can no longer buffer the available P concentration. However, most of the studies we reviewed, and particularly those with stand ages of multiple decades, were in their first rotation or were never intended for harvest. The number of harvests needed to observe P limitation after afforestation merits further study.

The history of land cover was found to be the most important factor determining the dynamics of soil P after afforestation (Table 2). Soil available P typically increased after afforestation replaced native vegetation, but decreased on prior agriculture lands (pasture and especially cropland; Fig. 2b). However, reduced P availability does not necessarily indicate P limitation; rather, it may simply reflect the loss of P inputs in excess of plant demands as part of agricultural management (MacDonald *et al.*, 2012). Agricultural lands are commonly fertilized with phosphate and other nutrients to maintain high crop yield or forage productivity, which may contribute to pulses of available P in soils (McLauchlan, 2006). Tillage and grazing disturbance may also enhance P availability by stimulating microbial decomposition of soil organic matter (Laganière *et al.*, 2010) and hence the release of nutrient including P (Daroub *et al.*, 2001; McLauchlan, 2006). Accordingly, transitions between agriculture and other land uses are commonly associated with decreases in labile P, particularly in the case of former croplands. However, these decreases may be smaller in the case of afforestation than for other post-agricultural vegetation types, suggesting a balance between afforestation-mediated increases in P availability and the decreases associated with cessation of agriculture (MacDonald *et al.*, 2012).

Despite the overall decrease in total soil P with afforestation, total P tended to increase on wastelands, mine spoils, bare and degraded lands (Fig. 2a) which usually have relatively low vegetation cover and may lose P by soil erosion. Afforestation in these lands may limit P leaching and erosion losses as a result of root growth and canopy development. In some cases, the increase in P resulting from reduced soil erosion may offset or even exceed the uptake by tree growth (Zheng *et al.*, 2005). Accordingly, available P increased significantly on formerly degraded lands (Fig. 3b). The degraded/nondegraded dichotomy may also be interpreted as an important distinction, with respect to P, between afforestation intended to restore or protect ecosystems and afforestation for production of wood (FAO Global Forest Resources Assessment, 2015).

Compared with prior land cover, the current land cover (tree species planted) had a smaller effect on soil P dynamics after afforestation (Table 2). We expected *Pinus* and *Eucalyptus*, fast-growing genera often used in production forestry, to decrease total P more than other genera, as a result of rapid P uptake and possible removal of biomass in harvest. This was true for *Pinus* in our study, but not for *Eucalyptus* (Fig. 4a). It seems that genus did not provide a good proxy for production forestry in our data set: in some cases, eucalyptus was planted expressly for soil restoration (Mishra *et al.*, 2003; Jeddi *et al.*, 2009). In restoration projects, we would expect lower biomass per hectare, less management for rapid growth, and much lower harvest losses than in a production forestry system, resulting in less P depletion than in production-oriented systems. Differences in P use efficiency or rooting depth between the two tree genera may also be responsible for these contrasting results (Gotore *et al.*, 2014). Previous work found stronger afforestation effects on soil C, N, and K for pine than for other genera, possibly related to the soil acidification and organic layer accumulation associated with pines (removing nutrients from the mineral soil), as well as to larger sample sizes for *Pinus* than other genera (Berthrong *et al.*, 2009; Laganière *et al.*, 2010).

We confirmed that climate influenced soil P dynamics after afforestation, as climate zone was identified as an important predictor for the change in both total P and available P (Table 2). This was supported by the significant positive relationship between temperature and change in soil available P (Fig. 6b). Warmer climates could facilitate tree growth and microbial P mineralization with afforestation. Accordingly, P availability tended to increase after afforestation in tropical and subtropical zones, while total P decreased more in these zones (Fig. 5a,b). Considering that declines in total P will decrease the capacity to replenish the available P pool, P limitation could be a major issue in tropical plantations as a result of commonly low-P soils (Vitousek *et al.*, 2010). By contrast, the ability of root exudates and microbial symbioses to degrade rock or organic P compounds may be limited by the low temperature in the boreal zone, so trees may depend more heavily on existing labile forms of P than on newly mineralized P, ultimately decreasing the available P pool (Fig. 5b).

While the availability of plant nutrients, including P, is largely controlled by soil properties such as pH and texture (Williston & LaFayette, 1978; Duong *et al.*, 2012), our results indicated a secondary role of soil properties in determining changes in P with afforestation. Available P was more sensitive to soil pH than to soil texture (Table 2), and increasing P availability was associated with decreasing pH on alkaline soils (Fig. S4). On these soils, acidification associated with afforestation could dissolve solid Ca and Mg phosphates, releasing P (Giesler *et al.*, 2002; Devau *et al.*, 2009). By contrast, changes in total P were more affected by soil texture than by pH. Both texture and pH may mediate P sorption chemistry, as clay offers more binding sites for P than does sand (Hansen *et al.*, 2002). Accordingly, we observed significant decreases in total P on sand and loam soils (Fig. 8a), but not on clay soils, where stronger P sorption may limit P uptake by trees.

As with any meta-analysis, our results reflect uncertainty and assumptions in the component studies. Chief sources of this uncertainty include variation in the methods used to determine total and available P among studies, inconsistent reporting of prior and current land use at control and afforested sites, and the limited number of studies reporting from multiple depths and ages within individual stands.

Our analysis suggests a significant effect of P extraction methods on the response to afforestation (Table 2). This effect may be attributable to the use of different methods for different soil types. Bicarbonate extractions were commonly used in soils with higher pH, which were also more likely to experience increases in

P availability with afforestation, and resin extractions were primarily used in soils with particularly high quantities of available P in the control sites. Methods may also vary in their ability to detect small changes in P concentration, altering the magnitude of the observed changes. Thus, the importance of the extraction method is probably a result of a combination of methodological artifacts and covariance with physically significant soil properties. The variable importance ranking method we used does not eliminate correlated variables, but does decrease their importance and leverages the correlation to make reasonable substitutions for missing data, an advantage over standard regression techniques that could not be used to rank the importance of the variables without excluding large numbers of samples.

Land-use comparison studies, as well as chronosequence designs, are predicated on the comparability of control and treatment (afforested) sites with respect to edaphoclimatic properties, an assumption which will be appropriate to different degrees for the individual studies analyzed in this work. To facilitate synthesis and explanatory power, studies should report bulk density data for all depth increments assessed, and we encourage collection of data from greater soil depths. Studies making comparisons between land uses should also quantify the comparability of the control and treatment sites, and, where possible, provide complete land-use history data in the site description.

Conclusions

To the best of our knowledge, this is the first comprehensive evaluation of global patterns and controls for soil P change after afforestation. Our meta-analysis showed substantial depletion in soil total P after afforestation across a broad range of locations, but no overall change in soil available P. The effects of afforestation on soil P stocks and availability depended on historic land management and climate more than soil properties and tree species planted. On some previously degraded lands, afforestation may increase soil nutrient availability without significantly reducing total P, and hence restore ecosystem productivity. However, the large declines in total P together with increased available P in the tropics after afforestation may deepen the risk of P limitation over the long term, as the capacity to replenish the available P pool decreases. Afforestation policies must account for land use history, climate, and soil properties, as well as the potential to deplete nutrient stocks and other resources, if the goal of afforestation is to create sustainable forest ecosystems.

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Author contributions

Q.D., D.E.M., D.H. and R.B.J. designed the research, Y.X., D.E.M., Q.D., and C-L.Y. collected the data, D.E.M. and Q.D. performed the analysis, Q.D. and D.E.M. wrote the manuscript, and all co-authors edited the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Histogram of maximum sampling depth among independent study sites.

Fig. S2 Measured and calculated average bulk densities in top 20 cm of paired control and afforested sites.

Fig. S3 Predicted and observed responses of total and available phosphorus to afforestation, based on random forest regression with nine predictors.

Fig. S4 Relationship between change in available phosphorus and change in pH differs with control pH category.

Fig. S5 Relationship between total phosphorus concentration and stand age within sites.

Fig. S6 Relationship between available phosphorus concentration and stand age within sites.

Table S1 Studies included in the meta-analysis

Table S2 Sources for the global database of soil total and available phosphorus with afforestation, to a depth of 20 cm

Table S3 Model fits for relationships between phosphorus concentrations and depth

Notes S1 Unknown bulk density for unit conversion.

Notes S2 Bulk density and P content extrapolation to 20 cm.

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