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Effect of the Moso Bamboo *Pyllostachys edulis* (Carrière) J.Houz. on Soil Phosphorus Bioavailability in a Broadleaf Forest (Jiangxi Province, China)

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Abstract: Moso bamboo (*Phyllostachys edulis* (Carrière) J.Houz.) is a fast-growing species that commonly invades neighboring broadleaf forests and has been widely reported in subtropical forest ecosystems. However, little is known about the effect on soil phosphorus (P) bioavailability and its potential influence factor during the *P. edulis* expansion. Here, the four soil P bioavailable fractions (i.e., $CaCl_2$-P, Citrate-P, Enzyme-P, and HCl-P), acid phosphatase activity, iron and aluminum oxides (Fe_d and Al_d), and soil total P pool at depths of 0–10 cm, 10–20 cm, and 20–40 cm were measured in three expanding interfaces (a broadleaf forest, a mixed bamboo–broadleaf forest, and a pure *P. edulis* forest) in subtropical forests of southern China. Regardless of soil depths, the $CaCl_2$-P content was significantly lower in the mixed bamboo–broadleaf forest than the other two forest types, with contents ranging from 0.09 to 0.16 mg/kg, whereas the HCl-P content was significantly lower in the broadleaf forest, with contents ranging from 3.42 to 14.33 mg/kg, and the Enzyme-P content and acid phosphatase activity were notably lower in *P. edulis* forest with contents of 0.17–0.52 mg/kg and 68.66–74.80 μmol MUF released g^{-1} min^{-1}, respectively. Moreover, the soil total P pool was enhanced in the mixed bamboo–broadleaf forest in 0–10 cm depth compared to broadleaf and *P. edulis* forests, with increases of 27.40% and 31.02%, respectively. The redundancy analysis showed that soil pH plays an important role in regulating soil P bioavailability during the *P. edulis* expansion ($p < 0.01$). From the above results, the invasion of *P. edulis* into broadleaf forests has resulted in soil P bioavailability and storage capacity. The results of this study suggest that when *P. edulis* invades broadleaf forests, it could affect the soil P bioavailability by elevating soil pH, which in turn drives and facilitates the completion of the expansion. This is important for understanding P cycling during the *P. edulis* forest expansion in subtropical regions.

Keywords: plant invasion; biological-based P extraction; subtropical forests

Citation: Yang, D.; Shi, F.; Fang, X.; Zhang, R.; Shi, J.; Zhang, Y. Effect of the Moso Bamboo *Pyllostachys edulis* (Carrière) J.Houz. on Soil Phosphorus Bioavailability in a Broadleaf Forest (Jiangxi Province, China). *Forests* **2024**, *15*, 328. https://doi.org/10.3390/f15020328

Academic Editor: Benjamin L. Turner

Received: 25 December 2023
Revised: 30 January 2024
Accepted: 31 January 2024
Published: 8 February 2024

1. Introduction

Phosphorus (P) is an important nutrient element in various ecosystems, and the cycling of P in soils is a basis for many key ecosystem functions [1]. In soil, P exists in a variety of forms that differ in their bioavailability to plants [2]. However, the form of P absorbed by plants is rather insoluble and shows slow diffusion in soil, becoming one of the macronutrients limiting the enhancement of forest primary productivity [3,4], especially in highly subtropical soils, since a large amount of P is occluded by iron and aluminum

oxides [5,6]. Studies have shown that the capacity and availability of soil P mainly depend on the changes in different P forms, which are closely related to biological processes [7,8]. Thus, with the desired better understanding of forest soil P status, assessing the soil P bioavailability has become an important research objective [9–11].

Moso bamboo (*Phyllostachys edulis* (Carrière) J.Houz.) is the most broadly distributed bamboo species in subtropical China. However, due to its rapid growth and reproduction ability, *P. edulis* has been expanding and occupying natural or secondary broadleaf forests in the past decades, forming a large area of bamboo forest. Broadleaf forests are widely known as an essential vegetation type that contributes to increased bio-diversity and environment conservation [12]. It is noted that the *P. edulis* expansion has been considered as one of the greatest contemporary threats to China's broadleaf forests [13,14]. Previous studies have shown that the *P. edulis* expansion had significantly affected the soil pH [15], enzyme activity [16], nitrogen mineralization rates [10], organic carbon chemistry composition [17], and microbial community structure and function [16]. Until now, no studies have ever examined the effects of the *P. edulis* expansion on soil P bioavailability. Therefore, understanding how the *P. edulis* expansion affects various P fractions will help to clarify the influence of the *P. edulis* expansion on soil P distribution patterns in adjacent forests and its potential mechanism.

Soil P bioavailability depends on both geochemical and biochemical processes [18–20]. These processes can influence the soil physiochemical and biological properties, such as soil pH, metal oxides (e.g., Fe oxides, Al oxides), inorganic nitrogen, organic carbon, total P, and activities of phosphatase enzymes [21–26]. Accordingly, the *P. edulis* expansion may alter soil P pool and P bioavailability and lead to the redistribution of soil P. Regrettably, these impacts have not yet been assessed in terms of direction and magnitude [27,28]. At present, the most commonly used method for assessing soil P fractions is the sequential leaching method by Hedley and its modified method [29,30]. However, this approach does not consider the contribution of biological processes and P bioavailability [31,32].

The aim of this study was to explore the impact of the expansion of *P. edulis* into broadleaf forests on soil phosphorus pool and phosphorus components, as well as the main environmental factors contributing to this change. We used the substituting space-for-time approach to collect soil samples from a broadleaf forest, a mixed bamboo–broadleaf forest, and a pure *P. edulis* forest which represented non-invasive, mid-invasive, and serious invasive levels, respectively, in Jinggang Mountain Nature Reserve, Jiangxi Province, and compared the differences in soil P pool, acid phosphatase activity, and four P fractions ($CaCl_2$-P, Citrate-P, Enzyme-P, and HCl-P) in the 0–10 cm, 10–20 cm, and 20–40 cm depths. The principal objective of the study was to investigate the response of the soil phosphorus pool and phosphorus fractions to the expansion of *P. edulis* into broadleaved stands, and the main environmental factors causing this change. Specifically, hypotheses were tested for the following: (1) the *P. edulis* expansion would alter soil P bioavailability and acid phosphatase activity, thereby facilitating expansion, and (2) pH is the main influencing factor leading to changes in P fraction during the *P. edulis* expansion.

2. Materials and Methods

2.1. Study Sites

This study was conducted at the Dajing Forest Farm in the Jinggang Mountain National Nature Reserve (26°33′58″ N, 114°7′58″ E, Figure 1), Jiangxi Province, China, which has a humid subtropical monsoon climate with an average annual temperature of 14.2 °C and an average annual precipitation of 1856 mm. The soil types include red soil and red-yellow soil. This chosen site is located in the nature reserve and has not been exposed to direct anthropogenic disturbance. The regional vegetation is evergreen broadleaf forest and it is also a suitable area for *P. edulis*. Before the establishment of the reserve, owing to long-term harvesting by humans and natural disturbances, the original evergreen broadleaf forest was extensively degraded into a secondary forest. After the establishment of the nature reserve, the secondary evergreen broadleaf forest was in a positive stage of succession to the original

forest, but *P. edulis*, as a suitable species under subtropical climate conditions, has been invading and occupying adjacent forest stands at a rapid rate, resulting in the formation of a large area of mixed bamboo–broadleaf forest and pure *P. edulis* forest. The invasion of broadleaf forests by *P. edulis* has resulted in three different types of vegetation along the invasion path: pure *P. edulis* forest, mixed bamboo–broadleaf forest, and broadleaf forest.

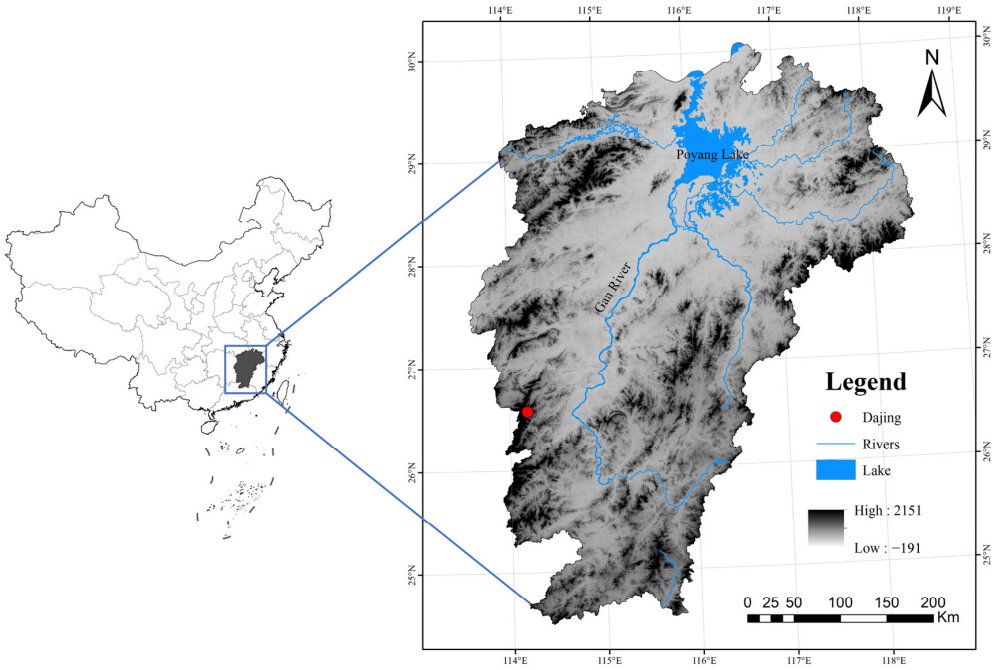

Figure 1. The geographical location of the study area.

2.2. Experimental Design and Soil Sampling

In June 2020, three typical sample strips were selected in the direction of the expansion of *P. edulis* into the broadleaf forest, containing pure *P. edulis*, mixed bamboo–broadleaf, and broadleaf forest, with each sample strip spaced at least 50 m. The sample site is at an elevation of 900 m. The broadleaf forest is a recovering secondary evergreen broadleaf forest, with the dominant species in the tree layer being *Machilus thunbergia*, and associated species including *Daphniphyllum macropodum*, *Alniphyllum fortunei*, etc. The tree layer is 17.0 m high, with an average diameter at breast height of 15.8 cm, a density of 1200 ind./ha, and a denseness of 0.85. The mixed bamboo–broadleaf forest was formed after *P. edulis* expanded into a broadleaf forest for 10 years. The ratio of *P. edulis* to wood is 8:1, in which *P. edulis* is about 15 m high and its density is about 4200 ind./ha. The *P. edulis* forest is a pure forest formed by natural expansion about 30 years ago, with a density of about 6200 ind./ha, an average diameter at breast height (DBH) of 8.5 cm, and an average height of 13.5 m.

Five replicated plots of 10 m × 40 m each were set up in each forest type, with a total of 15 plots established. Soil samples were collected from these plots at depths of 0–10 cm, 10–20 cm, and 20–40 cm. Each soil sample was formed by homogenizing the soil after removing the litter layer at low, medium, and high elevations along the hillside. Therefore, this study included a total of 45 subsamples (3 forest types × 5 replicates × 3 soil depths). All soil samples were placed in sterile self-sealing bags and maintained at low temperatures for transportation to the laboratory. The composite samples were passed through a 2.0 mm sieve to remove large rocks, visible roots, and debris. Finally, fresh samples were divided into two subsamples: one subsample was stored at 4 °C for the determination of P fractions and enzyme activity, and another subsample was airdried for soil chemical analysis.

2.3. Soil Chemical Properties

Soil pH was measured from a soil suspension (1:2.5, w/v) using a pH meter (PHS-3E; REX, Suzhou, China). Soil moisture (SWC) was measured by mass loss after drying at 105 °C to a constant weight. Soil organic carbon (SOC) was determined using the H_2SO_4-$K_2Cr_2O_7$ oxidation method. Soil total nitrogen (TN) and P (TP) concentrations were determined using a continuous-flow autoanalyzer (Auto Analyzer III, Bran + Luebbe GmbH, Norderstedt, Germany) after digestion in 5 mL of H_2SO_4 with a catalyst. Concentrations of soil NH_4^+-N, NO_3^--N, and available P (Olsen-P) were analyzed colorimetrically with a SmartChem140 Discrete Analyzer (Westco Scientific, Danbury, CT, USA) [33]. Among them, NH_4^+-N and NO_3^--N were measured using 90 mL 2 mol/L KCl with 20 g fresh soil leaching, and Olsen-P was measured using 5 g airdried soil and 50 mL ammonium fluoride-hydrochloric acid leaching. Al and Fe oxides were extracted with dithionite-citrate-bicarbonate (DCB) solutions [34] for free Al (Al_d) and Fe (Fe_d), diluted, and tested using an iron-aluminum combined colorimetric method with a spectrophotometer (Metash UV/u20125200, Nanjing, China).

2.4. Soil P Fractions

P fractions were determined using the biological-based P extraction approach that quantifies the inorganic P supply pathways of organic acid complexation/dissolution, enzyme hydrolysis, and proton excretion-induced acidification mechanisms, as well as the amount of dissolved inorganic P in the soil solution, which can highly improve the mechanistic understanding of soil P biogeochemical cycles and P bioavailability [31]. The procedure is as follows. Four 0.5 g fresh soil samples were added in parallel to 10 mL of the following extracts: (1) 10 mM $CaCl_2$ solution ($CaCl_2$-P); (2) 10 mM citric acid solution (Citrate-P); (3) 0.02 units/mL of acid phosphatase solution (Sigma P3627; Enzyme Commission Number 232-630-9; Sigma-Aldrich, Shanghai, China) (Enzyme-P); and (4) 1 M HCl solution (HCl-P). The mixture was shaken at 200 rpm for 3 h. It was then centrifuged at 3220× g for 30 min to collect the supernatant. After appropriate dilution of the supernatant, the soil P content was determined using the malachite green method [35] to represent soluble and weakly adsorbed inorganic P, active inorganic P sorbed to clay particles or weakly bound in inorganic precipitates, organic P readily mineralized by acid phosphatase enzymes, and recalcitrant inorganic P, respectively [31].

2.5. Soil Acid Phosphatase Activity

The 96-well microplates were used to determine soil acid phosphatase activity (AP) [36]. A total of 1.5 g of fresh soil was added to 125 mL of 50 mM sodium acetate buffer (pH = 5.3) and stirred well to obtain a soil suspension. A total of 200 µL of soil suspension and 50 µL of 4-Methyumbelliferyl phosphate were added to the microtiter plate, and control was made with 200 µL of soil suspension and 50 µL of sodium acetate buffer. After the dark incubation of the assay plates at 20 °C for 4 h, fluorescence values were detected using a microplate fluorometer (SpectraMax M2, Molecular Devices, Sunnyvale, CA, USA) at an excitation wavelength of 365 nm and an emission cutoff of 450 nm, respectively.

2.6. Calculation and Statistical Analyses

Soil total P pool (g m^{-2}) was calculated with the fixed depth method:

$$\text{Soil total P pool} = \sum_{i=1}^{n} D_i \times B_i \times P_i \times 0.1$$

where D_i, B_i, and P_i are the thickness (cm), bulk density (g cm^{-3}), and soil total P concentration (g kg^{-1}) of the ith soil layer, respectively, and 0.1 is a conversion factor.

All data were assessed using the Shapiro–Wilk normality test. One-way analysis of variance (ANOVA) and Duncan's test was used to assess differences among three types of vegetation in the same soil depth and among different soil depths in the same type of vegetation. Two-way analysis of variance (ANOVA) tests were used to identify the

interaction effects of vegetation and soil depths on soil properties, AP, P fractions, and total P pool. The statistical significance level was set at 0.05. This part of the data analysis was carried out using SPSS 19.0 for Windows (SPSS Inc., Chicago, IL, USA), and the Origin 2018 software package (Origin Lab., Hampton, VA, USA) was used to produce figures. Redundancy analysis (RDA) was performed between soil phosphorus-related indicators and soil variables in each soil layer using the vegan package [37,38] in R (version 4.0.2), and the data were log-transformed when necessary.

3. Results

3.1. Soil Chemical Properties

The vegetation type significantly affected soil pH, SWC, the contents of NH_4^+-N, NO_3^--N, SOC, TN, TP, Olsen-P, Fe_d, and Al_d ($p < 0.05$). The soil depth affected the contents of NH_4^+-N, NO_3^--N, SOC, TN, TP, and Fe_d, besides SWC. The interaction between vegetation and soil depth significantly affected the content of NO_3^--N (Table 1). Specifically, compared to a broadleaf forest, soil pH significantly increased in the *P. edulis* forest and the mixed bamboo–broadleaf forest, by 7.93%–9.50% and 5.57%–10.79%, respectively; as well as soil SWC, the content of NO_3^--N, SOC, TN, and Al_d was decreased in the 0–40 cm depths of the *P. edulis* forest, and the content of NH_4^+-N was only significantly increased in the 0–10 cm depth, by 15.19% and 14.08%, respectively. In addition, the contents of TP and Fe_d were not significantly discrepant among the three forests. The soil Olsen-P concentration was significantly lower by 27.79%–38.39% in the mixed bamboo–broadleaf forest compared to the other two forest types, whereas the differences in soil Olsen-P content between the broadleaf forest and the *P. edulis* forest were not significant (Table 1).

3.2. Soil P Pool, P Fractions, and Acid Phosphatase Activity

The *P. edulis* expansion process significantly affected the total soil P pool content in the 0–10 cm soil layer, which was higher in the mixed bamboo–broadleaf forest than in the other two forest types (Figure 2). While the vegetation type highly significantly affected the $CaCl_2$-P, Enzyme-P, and HCl-P content, the soil depth significantly affected all four phosphorus fractions, but the interaction effect only significantly affected the $CaCl_2$-P content (Figure 3). Across all soil depths, the contents of all P fractions showed the same trend among the three types of vegetation. Specifically, the soil $CaCl_2$-P content was significantly lower in the mixed bamboo–broadleaf forest than in the other two forest types. The soil Enzyme-P content was lowest in the *P. edulis* forest, 0.17–0.52 mg/kg, the HCl-P content was lowest in the broadleaf forest, 3.42–14.33 mg/kg, whereas the Citrate-P content was not significantly different among the three types of vegetation (Figure 3). Furthermore, the acid phosphatase activity was significantly lower in the *P. edulis* forest than the other forest types (Figure 2).

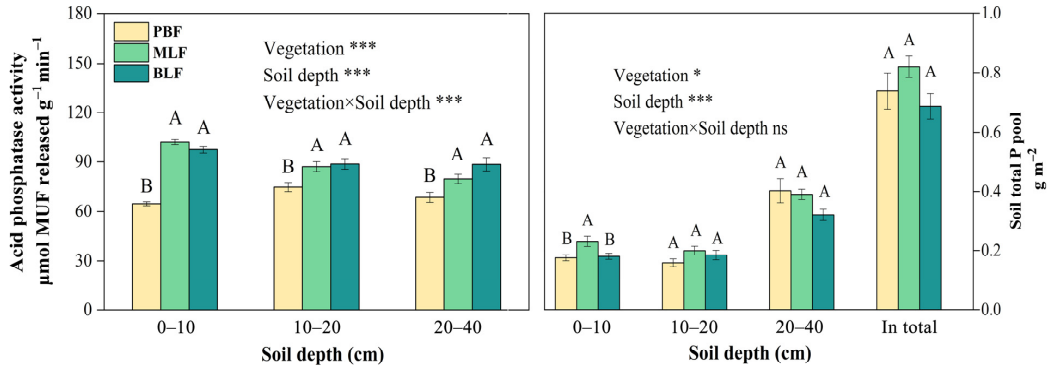

Figure 2. Effect of the *P. edulis* expansion into broadleaf forest on soil acid phosphatase activity (**left**) and total phosphorus pool (**right**). The data are the average values and the error bars are the standard deviation ($n = 5$). Different uppercase letters indicate significant differences among the three stands in the same soil depth ($p < 0.05$). ns, $p > 0.05$; * $p < 0.05$, *** $p < 0.001$.

Table 1. Characteristics of soil physicochemical properties among the three typical vegetation forests during the expansion of *P. edulis* into broadleaf forest under different soil layers.

Soil Depth	Vegetation	pH	Moisture (%)	NH_4^+-N (mg kg^{-1})	NO_3^--N (mg kg^{-1})	SOC (g kg^{-1})	TN (g kg^{-1})	TP (g kg^{-1})	Olsen-P (mg kg^{-1})	Fe_d (g kg^{-1})	Al_d (g kg^{-1})
0–10 cm	PBF	5.04 ± 0.04A	57.98 ± 2.93B	19.08 ± 0.55A	2.70 ± 0.52C	54.95 ± 2.47B	3.47 ± 0.05B	0.53 ± 0.04A	3.21 ± 0.12A	16.62 ± 0.46A	6.48 ± 0.08C
	MLF	5.03 ± 0.06A	69.01 ± 3.42A	18.90 ± 0.58A	4.60 ± 1.73B	77.12 ± 5.51A	3.70 ± 0.12B	0.48 ± 0.02A	2.43 ± 0.30B	17.51 ± 0.24A	6.74 ± 0.05B
	BLF	4.67 ± 0.11B	69.99 ± 2.76A	16.56 ± 0.56B	6.78 ± 0.23A	76.93 ± 4.25A	3.98 ± 0.07A	0.48 ± 0.03A	3.37 ± 0.24A	17.51 ± 0.23A	7.03 ± 0.10A
10–20 cm	PBF	5.07 ± 0.02A	42.11 ± 2.17B	9.83 ± 1.01A	1.19 ± 0.61B	33.13 ± 2.56B	1.80 ± 0.08B	0.47 ± 0.03A	2.99 ± 0.17A	17.73 ± 0.48A	6.65 ± 0.13B
	MLF	5.13 ± 0.03A	55.06 ± 2.16A	8.93 ± 0.74A	2.25 ± 0.85A	43.97 ± 2.24A	2.43 ± 0.10A	0.41 ± 0.01A	2.09 ± 0.31B	17.96 ± 0.16A	6.79 ± 0.12B
	BLF	4.63 ± 0.04B	52.26 ± 1.33A	7.98 ± 0.81A	2.48 ± 0.30A	42.33 ± 2.56A	2.36 ± 0.12A	0.41 ± 0.03A	3.07 ± 0.18A	18.22 ± 0.11A	7.21 ± 0.12A
20–40 cm	PBF	5.18 ± 0.03A	42.47 ± 3.13B	7.05 ± 0.67A	1.58 ± 0.35B	23.96 ± 1.64B	1.36 ± 0.03C	0.43 ± 0.04A	3.43 ± 0.11A	17.60 ± 0.58A	6.60 ± 0.12B
	MLF	5.04 ± 0.06A	53.26 ± 2.43A	5.77 ± 0.35A	1.48 ± 0.47B	33.37 ± 2.02A	1.74 ± 0.06B	0.39 ± 0.02A	1.93 ± 0.39B	18.05 ± 0.17A	6.75 ± 0.11B
	BLF	4.78 ± 0.06B	48.09 ± 0.84AB	6.14 ± 0.37A	2.51 ± 0.40A	33.19 ± 3.04A	1.96 ± 0.06A	0.36 ± 0.03A	3.14 ± 0.12A	18.27 ± 0.04A	7.24 ± 0.06A
Variance analysis of *F*-statistics											
Vegetation		48.54 ***	18.32 ***	5.38 **	63.62 ***	19.37 ***	37.08 ***	3.54 *	19.60 ***	3.60 *	25.73 ***
Soil depth		1.90 ^{ns}	46.18 ***	269.53 ***	148.88 ***	129.09 ***	495.00 ***	10.27 ***	1.10 ^{ns}	5.44 **	1.46 ^{ns}
Soil depth × Vegetation		1.32 ^{ns}	0.59 ^{ns}	1.07 ^{ns}	15.81 ***	1.76 ^{ns}	1.92 ^{ns}	0.09 ^{ns}	0.66 ^{ns}	0.28 ^{ns}	0.26 ^{ns}

Note: PBF, pure *P. edulis* forest; MLF, mixed bamboo–broadleaf forest; BLF, broadleaf forest; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; Olsen-P, available P; Fe_d, free Fe oxides; Al_d, free Al oxides. Data are means ± S.E., $n = 5$. Different uppercase letters indicate significant differences among the three stands in the same soil depth ($p < 0.05$). Significance level of F values: ^{ns} not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

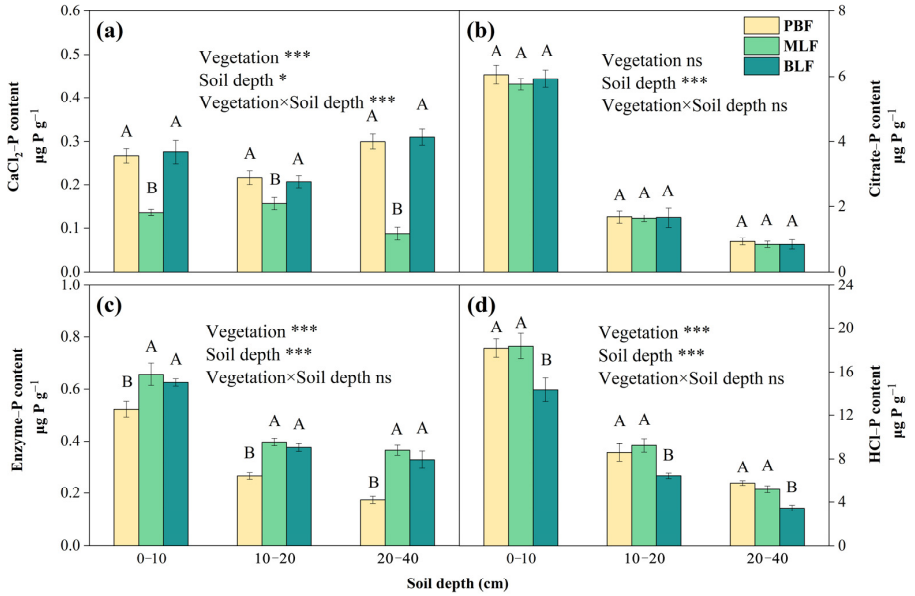

Figure 3. Effects of the *P. edulis* expansion on $CaCl_2$-P (**a**), Citrate-P (**b**), Enzyme-P (**c**) and HCl-P (**d**) content in broadleaf forest. The data are the average values and the error bars are the standard deviation (n = 5). Different uppercase letters indicate significant differences among the three stands in the same soil depth ($p < 0.05$). ns, $p > 0.05$; * $p < 0.05$, *** $p < 0.001$.

The vegetation type and soil depth significantly affected all phosphorus fraction ratios, while the interaction only significantly affected Citrate-P/$CaCl_2$-P, Enzyme-P/$CaCl_2$-P, HCl-P/$CaCl_2$-P, and Enzyme-P/HCl-P (Table 2). Similar trends were observed for all fraction ratios among the three forest types across all soil depths. In particular, the ratios of soil Citrate-P/$CaCl_2$-P, Enzyme-P/$CaCl_2$-P, and HCl-P/$CaCl_2$-P in the mixed bamboo–broadleaf forest, with ranges of 10.55–43.06, 2.64–4.91, and 59.97–136.07, respectively, were significantly higher than those in the *P. edulis* and broadleaf forests. The soil Citrate-P/Enzyme-P ratios were highest in the *P. edulis* forest, in the range of 5.39–11.78, and both the Citrate-P/HCl-P and Enzyme-P/HCl-P ratios were highest in the broadleaf forest, the range of 0.24–0.42 and 0.05–0.10, respectively.

Table 2. Soil biologically based phosphorus fraction ratios among the three typical vegetation forests during the expansion of *P. edulis* into broadleaf forest under different soil layers.

Soil Depth	Vegetation	Citrate-P/$CaCl_2$-P	Enzyme-P/$CaCl_2$-P	HCl-P/$CaCl_2$-P	Citrate-P/Enzyme-P	Citrate-P/HCl-P	Enzyme-P/HCl-P
0–10 cm	PBF	22.92 ± 1.46B	1.98 ± 0.17B	68.92 ± 4.46B	11.78 ± 0.95A	0.34 ± 0.03AB	0.03 ± 0.00B
	MLF	43.06 ± 3.16A	4.91 ± 0.43A	136.07 ± 8.66A	8.96 ± 0.78B	0.32 ± 0.03B	0.04 ± 0.00AB
	BLF	22.07 ± 1.67B	2.35 ± 0.21B	53.77 ± 6.80B	9.49 ± 0.41AB	0.42 ± 0.04A	0.05 ± 0.00A
10–20 cm	PBF	7.65 ± 0.52B	1.24 ± 0.03B	39.72 ± 2.29B	6.21 ± 0.52A	0.19 ± 0.01AB	0.03 ± 0.00C
	MLF	10.60 ± 0.67A	2.64 ± 0.31A	59.97 ± 3.73A	4.13 ± 0.30B	0.18 ± 0.01B	0.04 ± 0.00B
	BLF	7.93 ± 1.10B	1.86 ± 0.17B	31.65 ± 2.42B	4.38 ± 0.75B	0.25 ± 0.04A	0.06 ± 0.00A
20–40 cm	PBF	3.22 ± 0.56B	0.59 ± 0.07B	19.46 ± 1.68B	5.39 ± 0.50A	0.16 ± 0.01B	0.03 ± 0.00B
	MLF	10.55 ± 1.68A	4.87 ± 1.12A	65.78 ± 10.91A	2.30 ± 0.23B	0.16 ± 0.01B	0.07 ± 0.01A
	BLF	2.81 ± 0.55B	1.07 ± 0.10B	11.28 ± 1.29B	2.69 ± 0.58B	0.24 ± 0.03A	0.10 ± 0.02A
Variance analysis of *F*-statistics							
Vegetation		47.14 ***	38.45 ***	79.66 ***	17.22 ***	11.30 ***	23.62 ***
Soil depth		222.46 ***	6.10 **	75.60 ***	100.66 ***	45.34 ***	17.08 ***
Soil depth × Vegetation		12.54 ***	3.97 **	6.72 ***	0.23 ^{ns}	0.15 ^{ns}	4.67 **

Note: PBF, pure *P. edulis* forest; MLF, mixed bamboo–broadleaf forest; BLF, broadleaf forest. Data are means ± S.E., n = 5. Different uppercase letters indicate significant differences among the three stands in the same soil depth ($p < 0.05$). Significance level of F values: ^{ns} not significant, ** $p < 0.01$, *** $p < 0.001$.

3.3. Linkages between Soil Chemical Properties and P-Related Indicators

The RDA results showed that the distribution of soil P-related indicators in different soil layers showed significant segregation during the expansion of *P. edulis* (Figure 4). The environmental factors examined explained 55.33%, 29.90%, and 51.16% of the variation in soil P-related indicators at depths of 0–10 cm, 10–20 cm, and 20–40 cm, respectively. Interestingly, we found that the soil P-related indicators mainly diverged along the RDA1 in each soil depth. The first axis has the highest interpretation rate, explaining 53.15%, 18.79%, and 31.14% of the total variation (Figure 4). The soil pH significantly influenced the variation of the distribution of soil P ($p < 0.01$), and was positively correlated with HCl-P in each depth. In addition, the distribution of soil P was significantly influenced by SWC and NO_3^--N in the 0–10 cm depth and NH_4^+-N in the 20–40 cm depth.

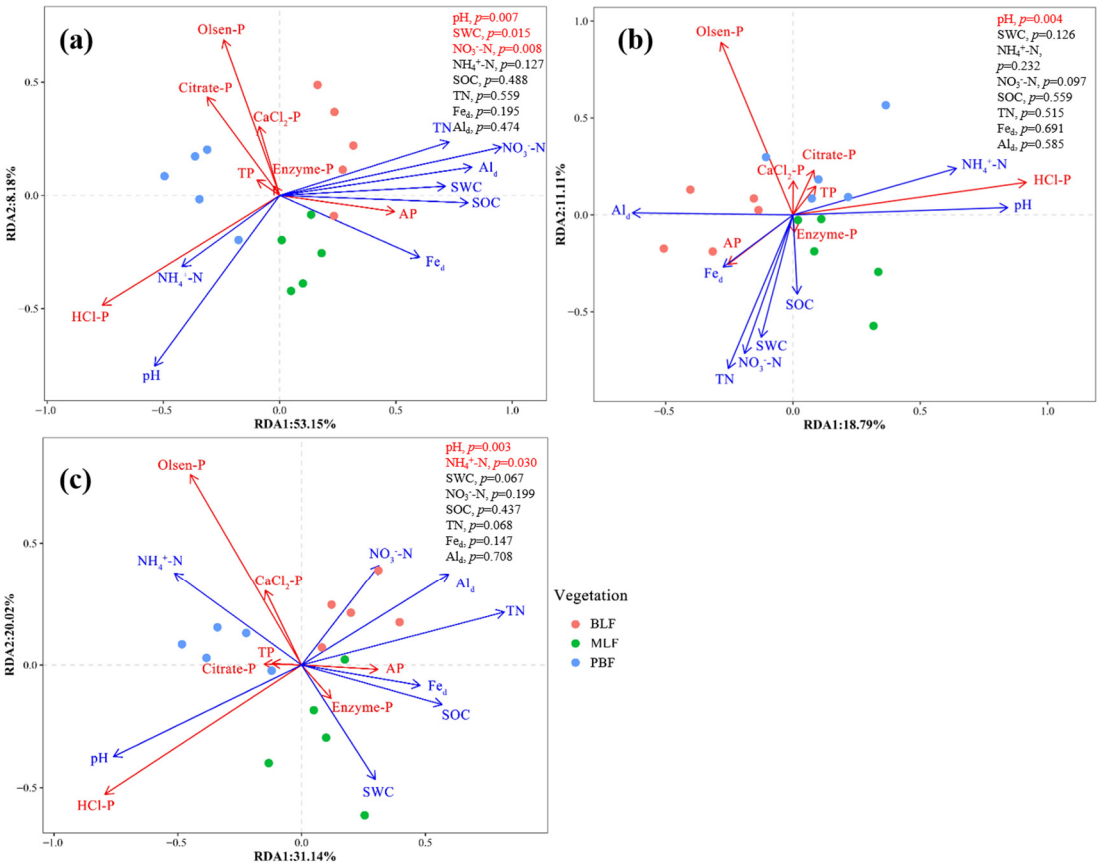

Figure 4. Redundancy analysis (RDA) diagrams, showing the relationships between the soil variables and soil phosphorus-related indicators at depths of 0–10 cm (**a**), 10–20 cm (**b**), and 20–40 cm (**c**), respectively. The explained variations of the first and second axes are given in brackets. Vectors represent soil phosphorus-related indicators with red arrows; the blue arrows indicate the soil variables; the types of vegetation are represented by solid circles of different colors.

4. Discussion

4.1. P. edulis Expansion Significantly Altered Soil P Status

The expansion of *P. edulis* into adjacent forests is one of the most serious environmental problems in subtropical China [12,39,40]. Evidence from previous studies suggests that the *P. edulis* expansion has distinct effects on C and N cycling at the ecosystem level [41,42]. Our study provides evidence that this process also leads to affected P effectiveness and P bioavailability in the soil. To be specific, the soil total P pool content during the *P. edulis* expansion into broadleaf forests varied significantly only in the 0–10 cm depth, whereas there was no significant change in soil total P and all the total P pools in the depth of 0–40 cm (Table 1 and Figure 4). This is slightly different from the findings of Wu et al. [27],

who reported that the soil total P decreased significantly after the *P. edulis* invaded the adjacent coniferous forests in Lushan Mountain, and the reason for this discrepancy may be a result of different litter quality and stand/site conditions between coniferous forests and broadleaf forests [43]. It is noteworthy that the Olsen-P content in the soil profile was redistributed by the expansion of *P. edulis*, as evidenced by the significantly lower levels of the mixed bamboo–broadleaf forest compared to the other two forest types in all soil layers (Table 1). This phenomenon would be caused by the following reasons. First, when the mixed bamboo–broadleaf forest was formed, the increase in species richness was accompanied by an increase in nutrient demand from the stand [32], which may have led to a greater demand from the species than the supply from the soil. Meanwhile, the change in soil pH and Al_d content had an opposite relationship to the response of the Olsen-P content in the mixed bamboo–broadleaf forest which also verified the phenomenon. Second, the nutrient turnover and fine root biomass of *P. edulis* significantly increased the nutrient uptake and turnover capacity after the formation of the pure *P. edulis* forest [27,44], which in turn increased the soil Olsen-P content.

In P-limited habitats, plants and soil microorganisms release excretions to destabilize organic–mineral associations and aggregates to obtain P [45]. The ratios of Citrate-P/$CaCl_2$-P, Enzyme-P/$CaCl_2$-P, and HCl-P/$CaCl_2$-P were all greater than 1 in all soil depths of each stand, showing that, in addition to the uptake of $CaCl_2$-P from soil pore water, the excretion of both acid and phosphatase into the soil may be an effective strategy for P acquisition by the plants during the invasion of *P. edulis* (Table 2). We found that the expansion of *P. edulis* to form a mixed bamboo–broadleaf forest significantly decreased the soil $CaCl_2$-P and increased the HCl-P content. The possible explanation for this outcome may be that the dominant tree species after mixing were all arbuscular mycorrhizal (AM) species [46], and AM fungi acquired P mainly based on their high-affinity uptake system and rapid translocation to the plant [6,47], which then led to a reduction in soil soluble P levels after hybridization. Meanwhile, HCl-P represents the moderately active stable inorganic P in soil, which can be obtained through proton extrusion by biota [31], and aluminum oxides as the primary metal minerals for adsorbed soluble P in southern red soils [48]. The Al_d content significantly decreased during expansion (Table 1), suggesting an increase in adsorbed and precipitated P [23]. In addition, the ratio of HCl-P/$CaCl_2$-P increased 1.97-fold when forming mixed forests, suggesting that the excretion of protons by plants may be an important strategy for their P acquisition. Compared to the mixed bamboo–broadleaf forest, *P. edulis* forest soils after expansion had an increased $CaCl_2$-P content and a decreased phosphatase activity and Enzyme-P content (Figures 2 and 3). This result is closely related to changes in the composition of plant root systems and soil microbial communities during expansion [49–51]. Firstly, lower tree species lead to less competitive pressure and increased resource availability [52]. Secondly, *P. edulis* has a denser fine root biomass for absorbing soluble phosphorus in the pore space compared to broadleaf species [53], and thirdly, microorganisms are very sensitive to changes in the environment, but the chemical composition and the secretion types released are significantly diverse among trees, which can dramatically affect microbial communities as well as soil enzyme activities [32]. We also found no significant differences in the soil Citrate-P content among the three stands throughout the expansion, suggesting that the change in vegetation types significantly impacts the hydrogen proton concentration ($H^+/OH^-/HCO_3^-$) and phosphatase activity, not organic acids types [32,54].

4.2. Soil pH Drives Changes in P Fraction in the Soil Layer during Expansion

The redundancy analysis results showed that soil pH was the most significant driver of variation in bioavailable P fractions in the soil layer (Figure 4), which is consistent with most studies [21,32,55,56] and supports our hypothesis. In this study, the soil pH increased significantly during the *P. edulis* expansion, and this change may have affected the soil P bioavailability in several ways. First, the *P. edulis* expansion process affects pH by altering the balance between hydrogen ion production and consumption [57], and

as pH increases, Al and Fe phosphates, which are presumably the dominant forms of P minerals in acid soils, gradually lose their positive surface charge and their P adsorption capacity, thus expelling phosphate [58]. Our finding of a significantly lower Al_d content in the *P. edulis* forest could partly support this explanation (Table 1). Second, soil bacteria and fungi prefer neutral pH environments; the expansion of *P. edulis* improves the soil pH and thus increases microbial diversity and supports soil ecosystem multifunctionality, including P cycling [59,60]. Previous studies have found that the soil pH can influence P-related microorganisms by directly affecting their growth and their interactions with each other [21,61]. In addition, different vegetation types secrete different organic acids, which in turn recruit microbial communities with different functional activities [62], and changes in vegetation taxa as a direct result of the *P. edulis* expansion process have been shown to significantly alter microbial community structure [39,41]. Third, *P. edulis* is a typical silica-accumulating plant [63], while silicon and P have similar chemical properties and structures, and silicon is in direct competition with P for sorption sites on iron oxides and other soil minerals increasing nutrient mobilization. Concretely, increasing silicon availability in soils leads to a mobilization of Fe(II)-P phases from mineral surfaces, increasing P availability/mobility in soils [64,65].

5. Conclusions

The impact of *P. edulis* invasion on the ecosystem structure and function of native plant habitats has attracted much attention, but the effect of this process on soil bioavailable P remains an enigma. In this study, we measured the bioavailable P fractions at three soil depths in three stands formed by the *P. edulis* expansion into broadleaf forests. Several conclusions are presented below:

(1) The *P. edulis* expansion altered the soil P pool and bioavailability in the subtropical region of China. The Olsen-P content and $CaCl_2$-P were significantly lower in the mixed bamboo–broadleaf forest than in the broadleaf forest and the pure *P. edulis* forest, whereas the soil total P pool content in the 0–10 cm depths was increased. The HCl-P and Enzyme-P content were higher in the mixed bamboo–broadleaf forest than in the other two forest types.

(2) The acid phosphatase activity was significantly higher in the mixed bamboo–broadleaf forest compared to the *P. edulis* forest.

(3) The positive relationship between the soil pH and HCl-P fraction indicated that the soil pH was an important factor in altering the P bioavailability during the *P. edulis* expansion.

Overall, the *P. edulis* expansion has altered soil P bioavailability to fulfill plant P requirements. We predicted that the effect on the soil bioavailability P content may be increasing with the gradual intensity of the *P. edulis* expansion. However, further in-depth studies are needed.

Author Contributions: D.Y.: data curation, conceptualization, writing—original draft, and writing—review and editing. Y.Z.: writing—review and editing. F.S.: supervision. X.F.: supervision. R.Z.: investigation. J.S.: supervision. All authors have read and agreed to the published version of the manuscript.

Funding: This study was financed by the National Natural Science Foundation of China (32160357 & 31660190 & 42067049); Jiangxi Provincial Department of Science and Technology Project (20232BBF60022 & 20232BAB205046); and Jiangxi "Double Thousand Plan" (jxsq2023102214 & jxsq2019201080).

Data Availability Statement: The data that support the findings of this study are available from the corresponding author upon reasonable request.

Conflicts of Interest: The authors declare no conflicts of interest.

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