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ORIGINAL PAPER

Impacts of bamboo invasion on soil macro- and micronutrients in temperate red pine stands

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Abstract
This study was performed to determine the effects of bamboo invasion on the soil properties of different bamboo stands. The study sites included pure bamboo stands (BF), mixed stands of bamboo and pine trees (MF), and pure pine stands without bamboo (PF). These stands comprised three different bamboo species, namely, *Phyllostachys bambusoides* Sieb. et Zucc, *P. nigra* var. *henonis* Stapf ex. Rendle, and *P. pubescens* (Mazel Ohwi), South Korea. Soil samples were collected from a depth of 0–10 cm to measure their physical and chemical properties. The BF stands had higher soil pH and water content, but lower light availability and soil bulk density than the PF stands. The MF stands generally showed an intermediate value between those of the BF and PF stands. While concentrations of macronutrients such as N, P, K^+, and Ca^{2+} were generally higher in the BF stands, micronutrients exhibited inconsistent patterns. The BF stands had the lowest Fe concentration but the highest Mn and Si concentrations. These changes in macro- and micronutrients corresponded to the increase in soil pH and water content caused by bamboo invasion ($R^2 = 0.32 - 0.77$, $P < 0.05$). However, there was no significant interaction effect between the bamboo invasion and invading bamboo species. Overall, the results suggest that the extent of change in soil nutrients after *Phyllostachys* bamboo invasion could be related to the shifts in soil properties with invasion intensity instead of the invading bamboo species.

Keywords Biological invasion · Forest soil · Nutrient availability · *Phyllostachys* species · Soil properties

Introduction

Bamboo species are widespread in forest ecosystems worldwide and are used for diverse purposes in human society. Traditionally, bamboo provides a principal material for daily use products and construction, especially in rural areas, and its new growing shoots are used as a low-fat food source (Gupta and Kumar 2008). Culms and fibers from bamboo also constitute a considerable proportion of substitutes for wood materials in the pulp, charcoal, and renewable energy industries (Sawarkar et al. 2020). As a result, research efforts have been focused on developing management strategies and evaluating the socioeconomic sustainability of bamboo plantations (Bonilla et al. 2010; Kim et al. 2018; Wu et al. 2015).

Despite its importance, uncontrolled invasion and expansion of bamboo may harm neighboring forest ecosystems (Canavan et al. 2017; Buziquia et al. 2019; Xu et al. 2020). The invasion of bamboo strongly affects nutrient cycles in invaded forest ecosystems because the structure and diversity of the invaded forests are altered through increased competition and tree mortality under dense bamboo canopy and rhizome systems (Buziquia et al. 2019). Umemura and Takenaka (2015) found that the invasion of *Chamaecyparis obtusa* forests in Japan changed nutrient availability with an increase in soil pH. The soil quality of a cedar plantation (*Cryptomeria japonica*) in Taiwan was degraded by the invasion of Moso bamboo (*Phyllostachys edulis*), with a reduction in the carbon and nitrogen pools (Shiau and Chiu 2017). Tian et al. (2020) suggested that bamboo invasion in subtropical forests decreases soil nutrient concentrations. Shifts in nematode abundance and bacterial taxonomic diversity during bamboo invasion have been detected, through which

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soil biogeochemical processes can change accordingly (Xiao et al. 2023; Xu et al. 2015). Such effects are often detectable in transitional forests between bamboo and other woody species and not only in areas dominated by bamboo (Xu et al. 2020).

Three bamboo species (*Phyllostachys bambusoides* Sieb. et Zucc, *P. nigra* var. *henonis* Stapf ex. Rendle, and *P. pubescens* (Mazel) Ohwi) are extensively distributed throughout southern Korea (Yoo et al. 2017; Kwak et al. 2021). They were intensively planted for edible shoots and for use in making furniture, agricultural tools, and handcrafts. However, bamboo stands have remained unmanaged and abandoned because of their low commercial value and the reduction in demand for bamboo after the 1970s. Therefore, expansion of bamboo species has occurred in abandoned bamboo stands. Bamboo stands have expanded from 6125 to 22,000 ha over the last 30 years, which has resulted in bamboo species becoming invasive in neighboring forest areas (Yoo et al. 2017). However, few studies have reported changes in soil properties induced by the invasion of bamboo into neighboring forests (Kwak et al. 2021).

The objective of this study was to determine the effects of *Phyllostachys* bamboo invasion on nutrient responses of soil properties in different bamboo stands. Here, bamboo invasion sites near Korean red pine (*Pinus densiflora* Sieb. & Zucc.) stands were investigated, because this is one of the most dominant forest types in the country (Korea Forest Service 2022). The research hypotheses are as follows: (1) Bamboo invasion may increase soil nutrient pools by altering the soil pH and other soil properties (Shiau and Chiu 2017; Tian et al. 2020). (2) Such changes in the soils may differ with invading bamboo species (bamboo invasion × species interaction), given that the nutrient contents in bamboo leaves and roots could be species-specific (Baek et al. 2022; Park et al. 2017).

Materials and methods

Study site and experimental design

The sites in this study were located in three regions, namely Jinju-si, Damyang-gun, and Sacheon-si with *P. nigra* var. *henonis* stands, five regions with *Phyllostachys bambusoides* stands, that is, Jinju-si, Goseong-gun, Damyang-gun, Sacheon-si, and Hadong-gun, and three regions with *P. pubescens* stands, namely Sacheon-si, Geoje-si, and Jinju-si in southern Korea (Fig. 1). The mean annual precipitation and temperature in the study areas over 30 years were 1470 mm year^{-1} and 14.2 °C for Goseong-gun, 1518 mm year^{-1} and 13.4 °C for Jinju-si, 1675 mm year^{-1} and 14.5 °C for Hadong-gun, 1446 mm year^{-1} and 14.7 °C for Sacheon-si, 1930 mm year^{-1} and 14.4 °C for Geoje-si, and 1344 mm year^{-1} and 13.2 °C for Damyang-gun, respectively (Korea Meteorological Administration 2017).

A preliminary investigation was performed to clarify the distribution of bamboo invasion and the neighboring vegetation using a high-resolution aerial map (e.g., map.kakao.com). Bamboo invasion and abandoned status were confirmed during field surveys. Most bamboo stands in

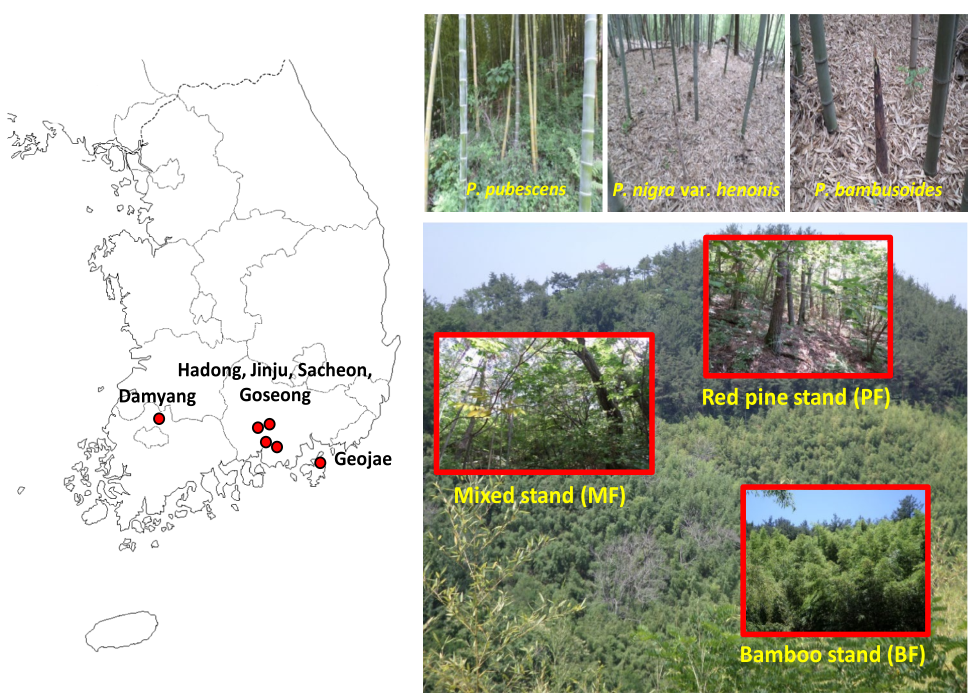

Fig. 1 Location of study site and bamboo stands (BF), mixed stands (MF) with bamboos and red pine, and red pine stands (PF)

the study sites have been unmanaged and abandoned. The nutrient information of bamboo tissue in the study site was described elsewhere (Baek et al. 2022). The soils in the study site were well drained and moist or dry. In Hadong-gun, Damyang-gun, and Geoje-si, there were brown forest soils (inceptisols of the USDA soil taxonomy) with a loamy texture originating from granite or granite gneiss. In contrast, the soils in Goseong-gun, Jinju-si, and Sacheon-si were slightly dry dark reddish-brown forest soils (inceptisols of the USDA soil taxonomy) originating from sandstone or shale. The altitude of the bamboo stands was 12–158 m in the *P. nigra* var. *henonis*, 17–212 m for *P. bambusoides,* and 17–103 m for *P. pubescens* (Table 1). This study was conducted at three successive quadrats (approximately) along bamboo stands established in each three treatment plot where bamboo had invaded into the adjacent red pine (*Pinus densiflora* S. et Z.) stands. The direction of bamboo expansion into the red pine was generally from the foot of the slope to the upper slope. Three quadrats (5 × 5 m) at each site included a pure bamboo stand (BF), a mixed stand comprising living bamboo and pine trees (MF), and a pure pine stand without bamboo (PF). The experimental design comprised a completely randomized design, including three plots of 5 × 5 m in each bamboo stand. The plots were set up in the middle of the stands to reduce edge effects. The diameter at breast height (DBH) of all the bamboo and trees in each plot was measured in June and July 2017 at 1.2 m in height. Photosynthetically active radiation (PAR) during the sampling was once measured using an EGM-4 environmental gas monitor (PP Systems, Hitching, UK) connected to an external PAR sensor (PP Systems).

Analysis of soil properties

Two soil samples were collected per each plot in June and July 2017 at three locations at a soil depth at 0–10 cm, with 405 cm^3 soil sampling cores (7.04 cm inner diameter and 10.4 cm height) using a core sampling technique (Xu et al. 2016) after removing the organic horizons. The soil samples were then transported to a laboratory and sieved through a

Table 1 Culm density and mean diameter at breast height in bamboo stands, mixed stands, and red pine stands in three bamboo species

Stand	Region	Location	Altitude (m)	Aspect	Forest type	DBH (cm)	Culm density (Culm ha^{-1})
Phyllostachys nigra var. *henonis*	Damyang, Jinju, Sacheon	– 35°12′26"N, 128°10′22"E	158	S	BF (*n* = 10)	Bamboo: 5.34 ± 0.27*	Bamboo: 8000 ± 1336
		– 35°19′43"N, 126°57′23"E	137	SE			
		–35°19′42"N, 126°57′25"E	130	W	MF (n = 10)	Bamboo: 5.46 ± 0.28 Tree: 21.40 ± 1.92	Bamboo: 4355 ± 308 Tree: 1200 ± 94
		–35°19′40"N, 126°57′29"E	113	E			
		–35°19′35"N, 126°57′41"E	134	SE	PF (*n* = 10)	Tree: 24.74 ± 2.94	Tree: 1688 ± 344
		–35°19′35"N, 126°57′40"E	115	W			
		–35°06′24"N, 128°04′11"E	97	SW			
		–35°06′13"N, 128°03′56"E	27	NW			
		–35°04′13"N, 128°02′01"E	21	NW			
		–35°04′10"N, 128°02′04"E	12	NE			
P. bambusoides	Damyang, Jinju, Sacheon, Hadong, Goseong	–35°12′23"N, 128°10′06"E	115	NE	BF (*n* = 10)	Bamboo: 4.44 ± 0.42	Bamboo: 6800 ± 1,347
		–34°59′19"N, 128°09′02"E	212	NE			
		–35°19′36"N, 126°57′29"E	109	NE	MF (*n* = 10)	Bamboo: 5.07 ± 0.51 Tree: 26.54 ± 2.63	Bamboo: 3155 ± 526 Tree: 888 ± 88
		–35°20′10"N, 127°02′34"E	81	N			
		–35°20′14"N, 127°02′40"E	146	SW	PF (*n* = 10)	Tree: 22.12 ± 2.29	Tree: 1650 ± 219
		–35°05′13"N, 128°01′23"E	105	NE			
		–35°03′29"N, 127°57′27"E	83	SE			
		–35°04′03"N, 127°57′14"E	17	NW			
		–35°12′09"N, 127°53′17"E	103	S			
		–35°12′30"N, 128°10′16"E	101	E			
P. pubescens	Jinju, Sacheon Geoje	–35°00′30"N, 128°08′01"E	99	E	BF (*n* = 10)	Bamboo: 8.45 ± 0.59	Bamboo: 5680 ± 790
		–34°57′38"N, 128°40′03"E	47	W			
		–34°57′58"N, 128°39′14"E	58	S	MF (*n* = 10)	Bamboo: 7.85 ± 0.69 Tree: 19.86 ± 2.26	Bamboo: 2160 ± 305 Tree:1080 ± 134
		–34°58′32"N, 128°39′26"E	16	NW			
		–34°58′52"N, 128°38′29"E	75	NE	PF (*n* = 10)	Tree: 20.97 ± 2.11	Tree: 1600 ± 84
		–34°58′42"N, 128°38′19"E	52	E			
		–35°05′12"N, 128°01′27"E	88	NE			
		–35°03′17"N, 128°57′23"E	103	NW			
		–35°09′41"N, 128°05′55"E	85	NE			
		–35°09′34"N, 128°06′09"E	83	SE			
Mean	–	–	–	–	BF	Bamboo: 6.10 ± 0.42	Bamboo: 6786 ± 678
					MF	Bamboo: 6.19 ± 0.38 Tree: 22.5 ± 1.38	Bamboo: 3185 ± 277 Tree: 1057 ± 65
					PF	Tree: 22.57 ± 1.40	Tree: 1644 ± 130

BF bamboo stands; *MF* mixed stands with bamboos and trees; and *PF* pine stands

*Mean ± Standard errors

2-mm mesh sieve to measure coarse fragment of > 2 mm. One soil sample was used to measure the bulk density and soil water content after drying at 105 °C. The other soil core samples were used to measure the soil nutrients from air-dried samples.

Soil pH (1:5 soil: water suspension) and electrical conductivity (EC) were measured using an ion-selective glass electrode (ISTEC Model pH-220L, Seoul, Korea) and EC meter (Thermo Fisher Scientific Orion 3-star, Singapore), respectively. An elemental analyzer (Vario MACRO cube, Langenselbold, Germany) was used to determine the soil C and N concentrations. The available soil P concentrations extracted using NH_4F and HCl solutions (Kalra and Maynard 1991) were determined using a UV spectrophotometer (Jenway 6505, Staffordshire, UK). Following extraction using NH_4Cl solution (Kalra and Maynard 1991) with a mechanical vacuum extractor (Model 24VE, SampleTeck, Science Hill, KY, USA), exchangeable cation (K^+, Ca^{2+}, and Mg^{2+}) and micronutrient (Cu, Fe, Mn, Ni, Si, and Zn) concentrations were determined using ICP-OES (PerkinElmer Optima 5300DV, Shelton, CT, USA).

Data analysis

A generalized linear mixed model approach was used to test the main effects (three forest types (BF, MF, and PF) of stands [F] and bamboo species [B]) and their interactions (F × B) on PAR, soil properties, namely bulk density, coarse fragments, water content, pH, and EC, macronutrients including C, N, P, K^+, Ca^{2+}, and Mg^{2+}, and micronutrients including Cu, Fe, Mn, Ni, Si, and Zn. This analysis included a random effect of region and post hoc Tukey's multiple comparison test ($P < 0.05$). Using the Shapiro–Wilk test, all variables except for soil bulk density and pH were square-root transformed for normalization. Multivariate differences in macronutrients and micronutrients were also assessed using permutational multivariate analysis of variance (PERMANOVA) with 9999 permutations and post hoc Bonferroni test ($P < 0.05$). Pairwise relationships were described using a generalized linear mixed model with a random effect of region ($P < 0.05$). Statistical analyses were conducted using the lme4, vegan, and pairwise Adonis packages in R 4.2.1.

Results

The densities of the culms were lower for MF (*P. pubescens*: 2160 culms ha^{-1}; *P. bambusoides*: 3155 culms ha^{-1}; *P. nigra* var. *henonis*: 4335 culms ha^{-1}) than in BF (*P. pubescens*: 5680 culms ha^{-1}; *P. bambusoides*: 6800 culms ha^{-1}; *P. nigra* var. *henonis*: 8000 culms ha^{-1}) stands. However, tree densities were higher in the PF stands than in the MF stands (Table 1). The low tree density in the MF stands could be due to the dieback of red pine trees following bamboo invasion. The DBH of the three bamboo species was generally higher in the MF stands than in the BF stands, except for in the *P. pubescens* stands.

No significant two-factor interactions between bamboo invasion and bamboo species were detected for PAR, soil properties, macronutrients, or micronutrients (Figs. 2, 3, 4). The effect of bamboo invasion was significant for PAR, soil bulk density, water content, pH, and N, P, K^+, Ca^{2+}, Fe, Mn, and Si concentrations, whereas the effect of bamboo species was significant only for coarse fragments and soil Fe concentrations. PAR and soil bulk density were higher in the PF stands than in the BF stands (Fig. 2a, b). Conversely, soil water content and pH were higher in the BF stands than in the PF stands (Fig. 2d, e).

There was a significant multivariate effect of bamboo invasion on macronutrients rather than micronutrients (Table 2). This indicated that only macronutrients shared similar, consistent patterns in relation to the bamboo invasion. Post hoc Bonferroni tests showed significant multivariate differences in macronutrients between the BF and PF. Univariate comparisons showed that soil N, P, K^+, and Ca^{2+} concentrations were higher in BF than in PF (Fig. 3). Soil C and Mg^{2+} concentrations did not differ significantly, despite showing a similar pattern to the other macronutrients. Among the micronutrients, soil Fe concentration was higher in PF than in BF, whereas soil Mn and Si concentrations were higher in BF than in PF (Fig. 4). The soil Cu, Ni, and Zn concentrations were not significantly different between PF and BF. Differences between MF and either BF or PF were only significant for soil N, Fe, and Si concentrations (Figs. 3b, 4b, f).

Pairwise relationship tests showed that the soil bulk density decreased with bamboo culm density (Fig. 5a). Soil K^+ and Ca^{2+} concentrations increased with soil pH (Fig. 5b, c), whereas the soil Fe concentration decreased (Fig. 5d). Soil N and Si concentrations increased with increasing soil water content (Fig. 5e–f).

Discussion

The results have highlighted the distinct environments of the bamboo invasion sites compared to those of the pine sites. The BF stands contained decreased PAR and soil bulk

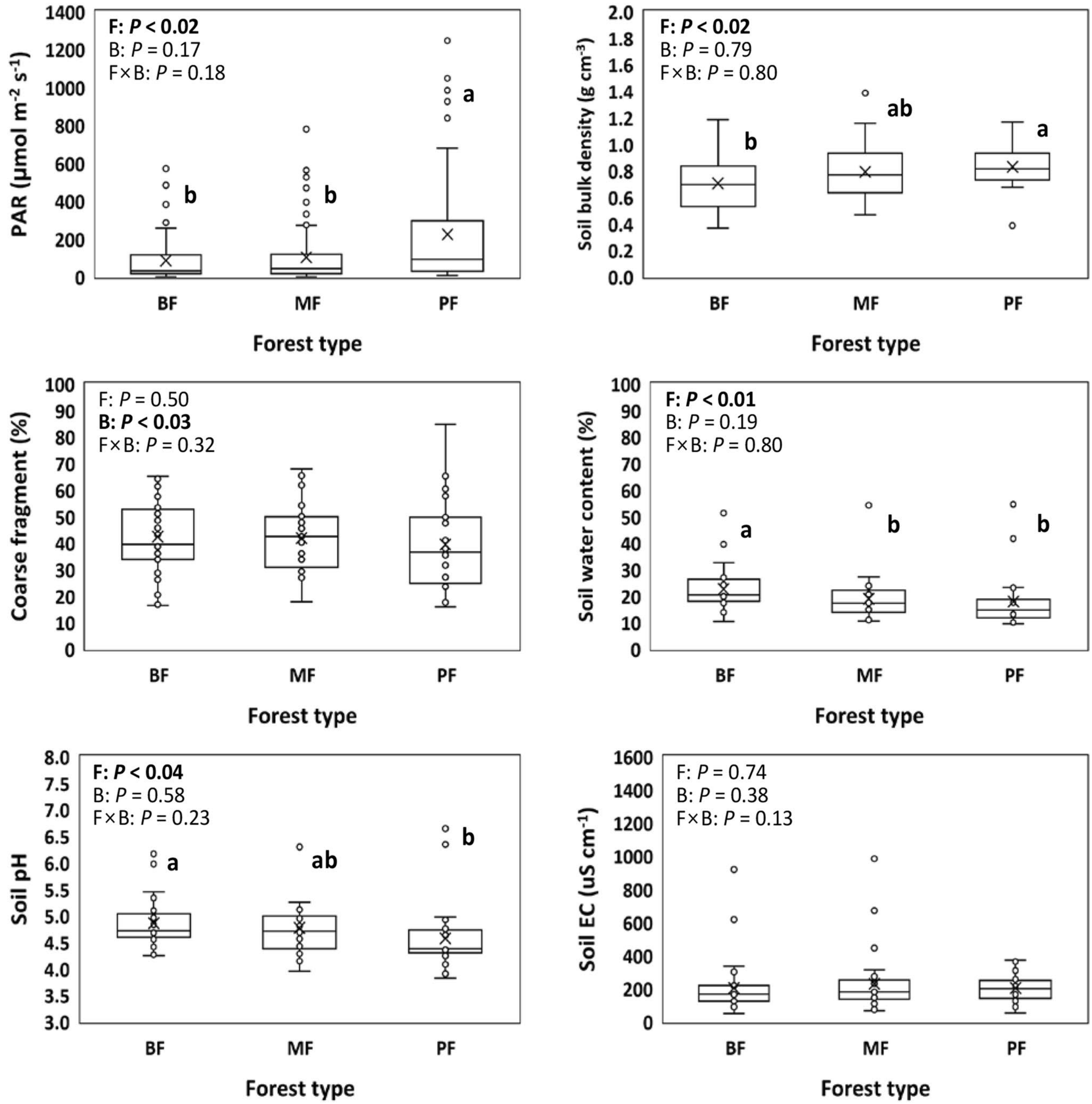

Fig. 2 Photosynthetically active radiation (PAR), soil bulk density, coarse fragments, soil water content, soil pH, and soil EC in three different bamboo stands (*F* forest type; *B* bamboo species; *F*×*B* interactions; *BF* bamboo stands; *MF* mixed stands with bamboos and red pine; and *PF* red pine stands). The box represents the median and the 25th and 75th percentiles, × represents the arithmetic mean, the solid lines extend to 1.5 of the interquartile range, and the values outside this range are indicated by circles. Different letters on the bar represent a significant difference at $P < 0.05$

density and increased soil water content and pH. These changes in PAR and soil properties may be attributed to overcrowding of the canopy and rhizome system of the invading bamboo. Bamboo species generally establish a complex root–rhizome system that can loosen the soil physical structure and bulk density (Kaushal et al. 2020). Our

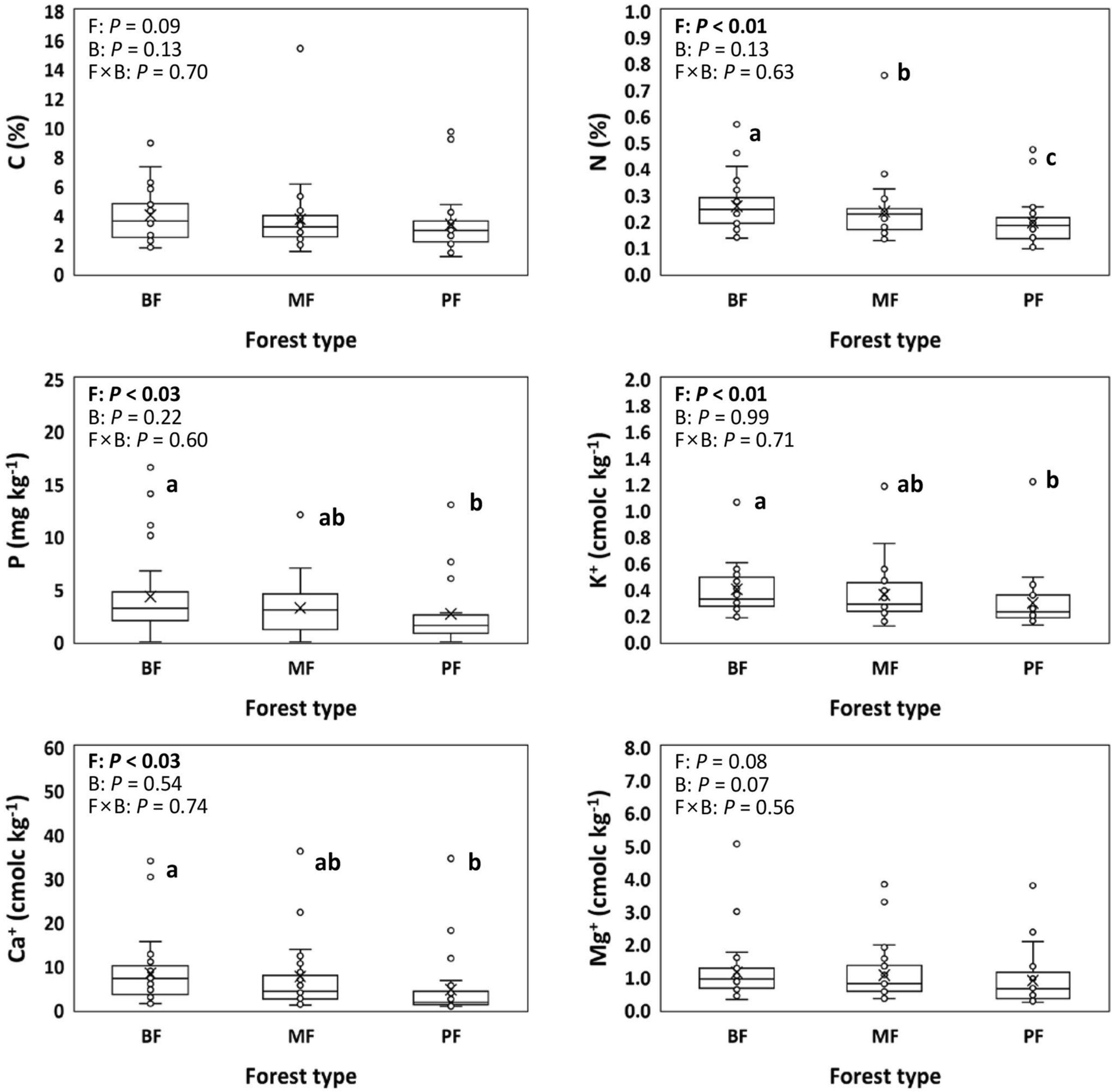

Fig. 3 Macronutrients at 10 cm soil depth in three bamboo stands (*F* forest type; *B* bamboo species; *F*×*B* interactions; *BF* bamboo stands; *MF* mixed stands with bamboos and red pine; and *PF* red pine stands). The box represents the median and the 25th and 75th percentiles, × represents the arithmetic mean, the solid lines extend to 1.5 of the interquartile range, and the values outside this range are indicated by circles. Different letters on the bar represent a significant difference at $P < 0.05$

results have supported this explanation given the negative relationship between soil bulk density and bamboo culm density. Fujihara et al. (2016) also found that bamboo forests have much greater root mass and lower bulk density than bamboo expansion and deciduous forests. The shifts detected in microclimate were expected because closed bamboo canopies may shade out the soil surface, and the loose soil structure can enlarge soil aggregates to contain water

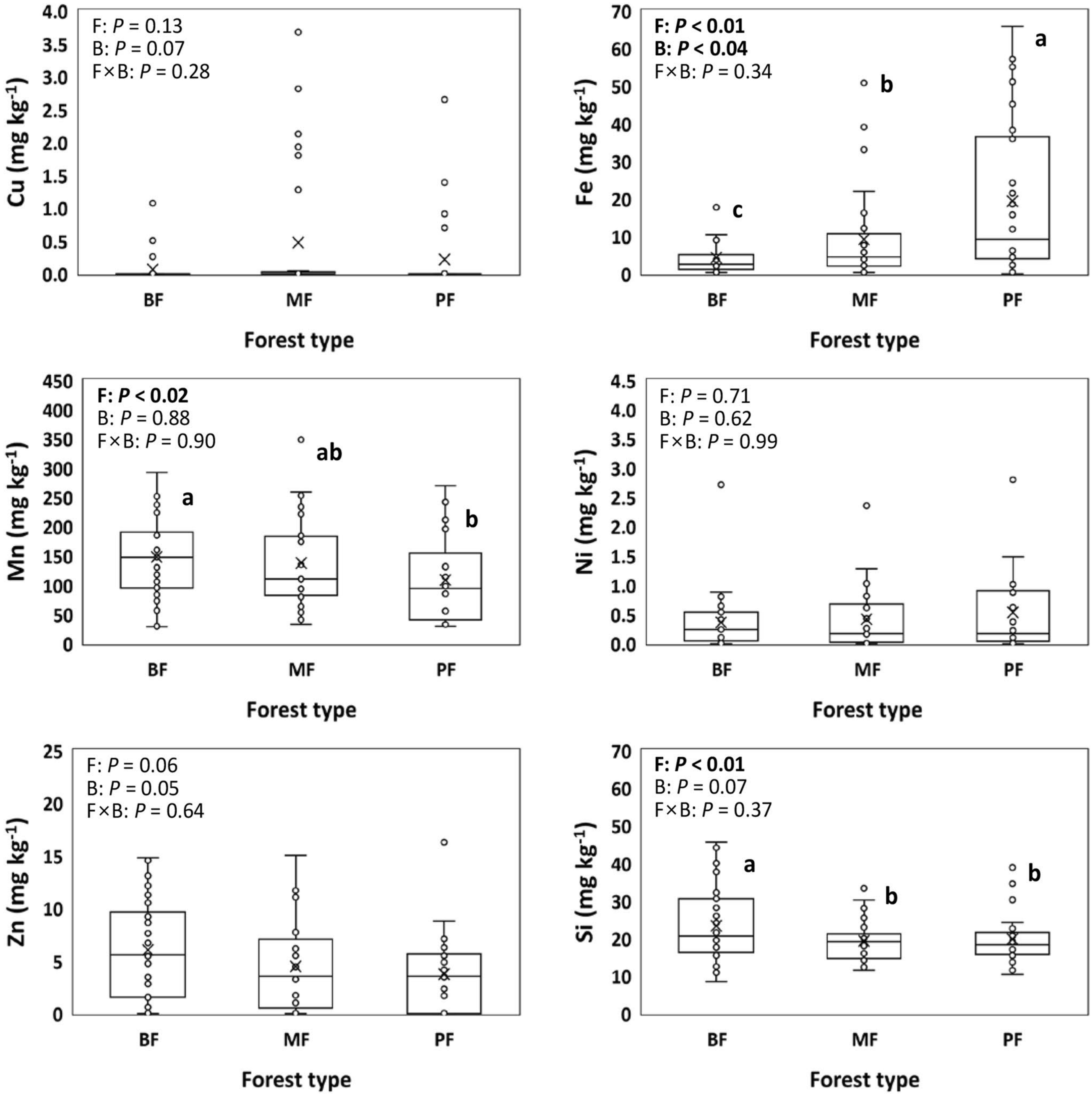

Fig. 4 Micronutrients at 10 cm soil depth in three bamboo stands (*F* forest type; *B* bamboo species; *F*×*B* interactions; *BF* bamboo stands; *MF* mixed stands with bamboos and red pine; and *PF* red pine stands). The box represents the median and the 25th and 75th percentiles, × represents the arithmetic mean, the solid lines extend to 1.5 of the interquartile range and the values outside this range are indicated by circles. Different letters on the bar represent a significant difference at $P < 0.05$

(Kaushal et al. 2020). Although compacted soil surfaces and reduced soil water availability and pH have been recorded under bamboo canopies (Bai et al. 2016; Lin et al. 2018), such patterns were not prevalent in our study.

Regarding the first hypothesis, bamboo invasion tends to elevate soil macronutrient concentrations, especially soil N, P, K^+, and Ca^{2+}. Macronutrient concentrations in the MF stands generally showed intermediate values between those

Table 2 Results of permutational multivariate analysis of variance on macronutrients (C, N, P, K^+, Ca^{2+}, and Mg^{2+}) and micronutrients (Cu, Fe, Mn, Ni, Zn, and Si)

Main effect	Macronutrients		Micronutrients	
	P-value	Post hoc tests	*P*-value	Post hoc tests
F	< 0.01	BF vs PF: $P < 0.01$	0.44	BF vs PF: $P = 0.06$
B	0.62	BF vs MF: $P = 0.37$	0.16	BF vs MF: $P = 0.50$
F × B	0.66	PF vs MF: $P = 0.12$	0.69	PF vs MF: $P = 0.20$

Post hoc tests are adjusted by Bonferroni correction

BF bamboo stands; *MF* mixed stands with bamboos and trees; and *PF* pine stands

in the BF and PF stands. Similar patterns were detected for some micronutrients (Mn and Si), whereas the Fe concentration was lowest in the BF stands. Fujihara et al. (2016) suggested that the nutrient concentration in bamboo expansion sites could be attributed to an increase in the bamboo root mass. While soil C and N pools in Moso bamboo stands of China decrease with the expansion of broadleaved evergreen forests due to accelerated organic matter decomposition (Bai et al. 2016), such a reduction in soil nutrients was not recorded across our study sites.

The changes detected in soil nutrients under bamboo invasion may be attributed to differences in soil properties such as pH and water content. There was an increase in the exchangeable cations, Ca^{2+} and K^+ along soil pH gradients, whereas the Fe concentration had a continuously decreasing pattern. This may be because an increase in soil pH after bamboo invasion is closely related to the displacement of protons by exchangeable cations on the surface soil and different cation uptakes according to bamboo species (Umemura and Takenaka 2015). However, some micronutrient ions become less soluble under increased soil pH conditions (Chuan et al. 1996), which may lead to lowered soil Fe availability in BF and MF stands. Meanwhile, soil N and Si concentrations had a positive relationship with soil water content, which was highest in the BF stands and lowest in the PF stands. This is consistent with previous findings, demonstrating that the development of belowground rhizome systems can reduce the potential loss of soil nutrients by creating water-stable aggregates, increasing water-holding capacity, and decelerating soil erosion in bamboo stands (Kaushal et al. 2020). Wakimoto and Tazaki (2001) found that soil Si concentration in mineral soils increased because of litter input from invading bamboo.

Our results have shown no interaction effect between bamboo invasion and bamboo species. This was in contrast with our second hypothesis on species-specific effects because the nutrient composition and decomposition rate of bamboo tissues are known to differ based on bamboo species (Baek et al. 2022; Nath and Das 2011). Kaushal et al. (2020) also found that the direction of change in soil nutrient concentrations after bamboo planting was similar to that of bamboo species, although the magnitude of these changes slightly differed. This trend may have occurred because soil nutrient conditions generally depend on other environmental factors, including stand age, parent material, microtopography, and microbial community composition. On the other hand, soil properties in the three forest types may simply reflect topographic variations on a small spatial scale because the BF stands were generally located on a slightly lower slope than the PF or MF stands. From this perspective, the lack of the interaction between bamboo invasion and species suggests that the patterns in soil nutrients under bamboo invasion might be associated with the varying soil chemistry along the topographic variations rather than the bamboo species-specific differences (Baek et al. 2022).

In this context, the interaction effects of invading bamboo species may become non-significant and confounding. Overall, our findings have indicated that the level of changes in soil nutrients after *Phyllostachys* bamboo invasion could be related to shifts in soil properties, rather than the invading bamboo species.

Conclusions

Invasion of bamboo species is an important issue in forest management. In our study, bamboo invasion increased soil pH, water content, macronutrients (N, P, K^+, and Ca^{2+}), and Mn and Si concentrations. However, there was a decrease in PAR, soil bulk density, and Fe concentration. The impact of bamboo invasion on soil nutrients is related to changes in soil properties such as pH and water content. However, soil nutrient availability following bamboo invasion showed little influence from extrinsic factors such as different bamboo species. There were no interactive effects between bamboo invasion and bamboo species. These results suggest that soil nutrient availability in bamboo-invaded forests may be controlled by changes in soil properties according to bamboo invasion intensity rather than by the invading species themselves.

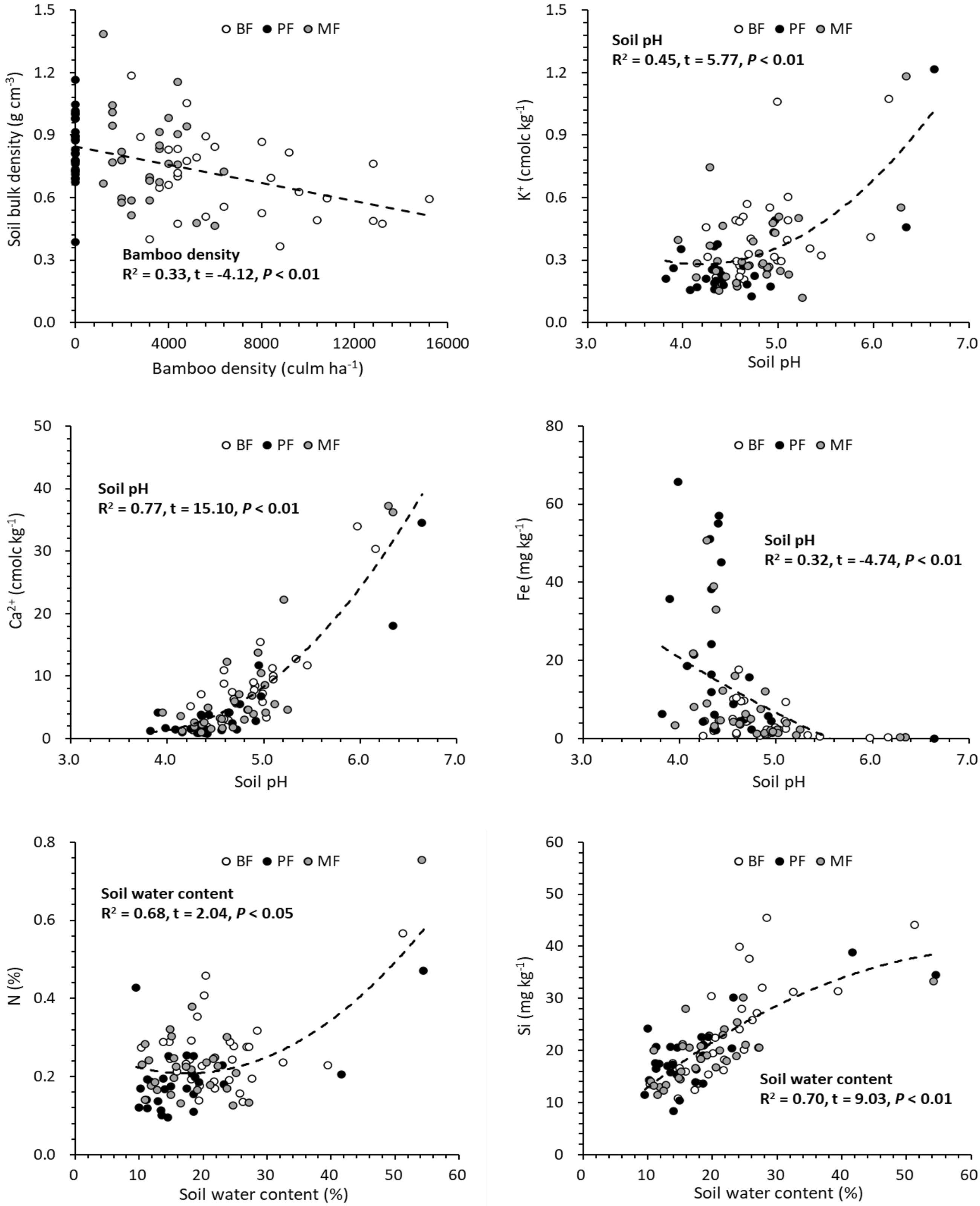

Fig. 5 Pairwise relationships of soil bulk density, macronutrients, and micronutrients with bamboo density, soil pH, and soil water content across three bamboo stands (*BF* bamboo stands; *MF* mixed stands with bamboos and red pine; and *PF* red pine stands). R^2, t, and P values in the panels are estimated by the generalized linear mixed model using region as a random effect factor

Author contributions CK and GB designed and conducted field trial with funding acquisition. GB and SK processed the data and wrote the paper. All authors discussed the results and commented on the manuscript.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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