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Microbial Biomass Is More Important than Runoff Export in Predicting Soil Inorganic Nitrogen Concentrations Following Forest Conversion in Subtropical China

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Abstract: Elevated runoff export and declines in soil microbial biomass and enzyme activity following forest conversion are known to reduce soil inorganic nitrogen (N) but their relative importance remains poorly understood. To explore their relative importance, we examined soil inorganic N (NH_4^+ and NO_3^-) concentrations in relation to microbial biomass, enzyme activity, and runoff export of inorganic N in a mature secondary forest, young (five years old) *Castanopsis carlessi* and *Cunninghamia lanceolate* (Chinese fir) plantations, and forests developing through assisted natural regeneration (ANR). The surface runoff export of inorganic N was greater, but fine root biomass, soil microbial biomass, enzyme activity, and inorganic N concentrations were smaller in the young plantations than the secondary forest and the young ANR forests. Microbial biomass, enzyme activity, and runoff inorganic N export explained 84% and 82% of the variation of soil NH_4^+ and NO_3^- concentrations, respectively. Soil microbial biomass contributed 61% and 94% of the explaining power for the variation of soil NH_4^+ and NO_3^- concentrations, respectively, among the forests. Positive relationships between microbial enzyme activity and soil inorganic N concentrations were likely mediated via microbial biomass as it was highly correlated with microbial enzyme activity. Although surface runoff export can reduce soil inorganic N, the effect attenuated a few years after forest conversion. By contrast, the differences in microbial biomass persisted for a long time, leading to its dominance in regulating soil inorganic N concentrations. Our results highlight that most of the variation in soil inorganic N concentration following forest conversion was related to soil microbial biomass and that assisted natural regeneration can effectively conserve soil N.

Keywords: assisted natural regeneration; fine root biomass; forest conversion; microbial biomass; soil inorganic nitrogen; surface runoff

Citation: Xu, C.; Lin, T.-C.; Huang, J.-C.; Yang, Z.; Liu, X.; Xiong, D.; Chen, S.; Wang, M.; Yang, L.; Yang, Y. Microbial Biomass Is More Important than Runoff Export in Predicting Soil Inorganic Nitrogen Concentrations Following Forest Conversion in Subtropical China. *Land* **2022**, *11*, 295. https://doi.org/10.3390/land11020295

Academic Editor: Krish Jayachandran

Received: 1 February 2022
Accepted: 12 February 2022
Published: 15 February 2022

1. Introduction

Large areas of natural forests have been replaced by forest plantations around the world. Globally the area of naturally regenerating forests decreased by 301 million ha while the area of forest plantations increased by 123 million ha between 1990 and 2020 [1]. China manages ~70 million ha monoculture forest plantations by 2013, the largest area in the world [2], with most of the forest plantations converted, directly or indirectly (i.e., converted to other land use types in the past), from natural forests [3]. Specifically, forest plantations increased 47% from 4.7 × 10^5 ha in 1998 to 6.9 × 10^5 ha in 2013 [4]. A large number of studies have examined the effects of forest conversion on important ecosystem services and processes [5–7]. The conversion of natural forests to forest plantations often causes soil degradation [8–10], especially the decline of nitrogen (N) availability [11–13]. Nitrogen is a common limiting nutrient element for ecosystem productivity [14] and is available to plants mainly in inorganic form (i.e., NH_4^+ and NO_3^-) in the soil. The depletion of soil inorganic N is of great ecological importance [15] and may constrain the fertilization effect associated with elevated atmosphere CO_2 concentration [16,17]. Thus, revealing key processes leading to the decline of soil inorganic N availability is critical to probe into the decline of net primary productivity and soil fertility following forest conversion [18–20].

Forest conversion can affect soil inorganic N availability [21] through altering soil microbial biomass, composition, and enzyme activity [22–24], as well as through increased N export via elevated surface runoff [25]. Because microorganisms participate in important N-cycling processes such as N fixation, nitrification, denitrification, and mineralization, changes in microbial abundance, composition, and activity have major influences on soil N availability. On the other hand, surface runoff is a major carrier of N export from ecosystems [26], so that changes in the quantity, intensity, and temporal patterns of runoff also have major effects on soil N availability [25,27].

Fine roots are the major link between plants and soil microorganisms [28,29]. Through exudation and turnover (and subsequent decay), fine roots add carbon into the soil. Fine root biomass has been shown to be positively related to soil microbial biomass N [30,31], and is a key factor affecting soil microbial composition in the subtropical region following forest conversion [32]. Rhizosphere N mineralization is a major source of soil inorganic N [33–35]. Root exudation may activate soil microorganisms to synthesize N-acquiring enzymes, thereby enhancing N mineralization [36–38]. Rhizosphere N transformation processes are also closely related with fine root biomass [39].

Many studies have reported changes in soil microbial biomass, community abundance, and inorganic N availability following forest conversion [12,31,40,41], but most of these focused on post-conversion mature forests. For example, a large number of studies in China have investigated microbial attributes and soil N availability in mature commercial plantations converted from natural forests [42–44], while the patterns in young and middle-age forest plantations, which account for 64% of the forest plantations by area in China [4], are largely unknown. Moreover, compared to mature forests, the role of soil N availability in ecosystem processes could be more important in young forests due to their high nutrient demands associated with rapid tree growth [45,46].

Replacing natural forests with forest plantations is often accompanied by elevated surface runoff due to decreased vegetation cover and soil infiltration capacity [47–49]. Surface runoff N export is a major pathway of ecosystem N loss [50], especially in humid montane ecosystems characterized by high surface runoff [51]. However, a recent study spanning tropical, subtropical, and temperate forests indicated that soil NO_3^- export via denitrification was six-fold the amount exported via leaching to runoff [52], suggesting that microbial processes played an important role in regulating soil inorganic N availability. Although studies have examined the effects of forest conversion on N availability [53–55], few studies have explicitly quantified the relative importance of changes in soil microbial properties and runoff N export on soil N availability.

In this study, we quantitatively examined the importance of surface runoff, soil microbial biomass, and enzyme activity in explaining differences in soil inorganic N concentration in a mature secondary forest and three types of young forest in southeastern China. Specifically, we addressed the following questions. First, is the response of soil inorganic N concentration to forest conversion similar among different types of young forests? Second, which is a more important predicting factor of differences in post-conversion soil inorganic N concentrations among young forests, microbial biomass, enzyme activity or N export via surface runoff?

2. Materials and Methods

2.1. Site Description

The study was carried out in the Fujian Sanming Forest Ecosystem National Observation and Research Station in southeastern China. This region has a maritime subtropical monsoon climate, with a mean annual rainfall of 1550 mm (approximately 80% occurring in March–August) and an annual mean temperature of 20.1 °C (10 °C in January and 30 °C in July) from 2011 to 2015 [56]. The landscape is characterized by low-elevation mountains and hills with a mean slope of ~30°. The soil developed from biotite granite can be classified as sandy clay Ferric Acrisol. The main natural vegetation is subtropical evergreen broadleaf forests dominated by species of Fagaceae.

2.2. Experimental Design

Details of the experimental design and the treatments can be found in the study by Yang et al. [57]. Briefly, four types of forest, including a mature secondary natural forest and three types of young forest, were used to explore the relationships among soil inorganic N concentrations and fine root biomass, microbial biomass, microbial enzyme activity, and the surface runoff export of inorganic N (NH_4^+ and NO_3^-). The three types of young forest are assisted natural regeneration (ANR) forests, *Castanopsis carlessi* (Hemsl.) Hayata plantations, and Chinese-fir (*Cunninghamia lanceolata* (Lamb.) Hook) plantations. The forests are in close proximity, with similar edaphic and topographical (slope angle and aspect) characteristics [56]. The secondary forest was naturally regenerated from a selectively logged natural forest in 1976. In December 2011, part of the secondary forest was cleared to establish the young forests. For each of the three types of young forest, three 30 m by 40 m plots were randomly established in the up, middle, and down slope with a randomized block design. Within the remaining uncut mature secondary forest, three plots were also established in the up, middle, and down slopes.

In the young ANR forests, the boles were removed and branches, twigs, and leaves were retained. Seedlings germinated from seed bank or sprouted from tree stumps and soil were conserved in the first 3 years and then left for development through secondary succession. The growth of seedlings in the ANR forests was facilitated by slashing some shade-intolerant and densely clustered plants in 2015. The young Chinese-fir and young *Castanopsis* plantations were established by planting seedlings at a density of 2860 and 2400 plants per hectare, respectively, following residue burning three months after the logging in March 2012 to mimic the common practices of forest plantations in the region. In the Chinese-fir and *Castanopsis* plantations, weeding was carried out twice a year in the first 3–5 years until canopy closure. No fertilizers were used in any of the forests.

2.3. Soil and Fine Root Sampling, and Fine Root Biomass Estimation

Six soil cores were randomly collected from the surface layer (0–10 cm) in each plot in April 2017 when the young forests were five years old. Before sample collection, litter and fermented materials were carefully removed. Samples were immediately brought to the laboratory at the site and refrigerated at 4 °C. Fine roots (diameter < 2 mm) were carefully selected, and then the soil samples were sieved through 2 mm mesh to remove gravel and plant debris within 24 h of sampling. Sieved soil samples from the same plot were combined to form one composite sample and refrigerated at -20 °C prior to further analyses, which took place within a week. Fine roots were washed with deionized water and then oven-dried at 65 °C until the weight remained constant. Fine root biomass of each plot was estimated from fine root dry weight per unit area of each sampling core, following Ostonen et al. [58].

2.4. Soil Physical and Chemical Property Analysis

Soil bulk density was determined using a known volume stainless steel cylinder. Soil NH_4^+ and NO_3^- were extracted with 2 mol L^{-1} KCl solution with a soil-to-solution ratio of 1:5 (*v*/*v*) and determined with a continuous flow injection analyzer (Skalar San++, Breda, The Netherlands).

2.5. Soil Microbial Properties Assay

Analysis of phospholipid fatty acids (PLFAs) was employed to evaluate soil microbial biomass and community composition following Huang et al. [59]. The extracted fatty acid methyl esters (FAMEs) were quantified and identified by using Gas Chromatography (Hewlett Packard 5890 GC, Agilent, Palo Alto, California, USA) equipped with the MIDI Sherlock Microbial Identification System (MIDI Inc., Newark, DE, USA). Each fatty acid group was quantified by comparing individual peak areas with that of the internal standard 19:0 (Matreya Inc., State College, PA, USA), and its quantity was expressed in nmol PLFA per gram of dry soil. Microbial communities were classified into the following groups: Gram-positive (GP) bacteria (i15:0, a15:0, i16:0, i17:0 and a17:0), Gram-negative (GN) bacteria (16:1ω7c, 18:1ω7c, cy17:0 and cy19:0), actinomycetes (ACT) (10Me16:0, 10Me17:0 and 10Me18:0), arbuscular mycorrhizal fungi (AMF) (16:1ω5), and total fungi (the sum of 18:2ω6,9c and 18:1ω9c), following previous studies [60–63].

2.6. Potential Soil Enzyme Activity Measurement

Enzyme activities of acid phosphatase (AP), β-1, 4-glucosidase (BG), Nacetyl-β-d-glucosaminidase (NAG), Cellobiohydrolase (CBH), and peroxidase (PER) were measured using fluorometric method modified from Saiya-Cork et al. [64]. The pre-measurement treatment was based on Liu et al. [65]. Fluorescence was measured using a Spectra Max M5 Molecular Devices (US) multiplate reader with an excitation of 365 nm and an emission of 450 nm, at 20 and 100 flashes.

2.7. NH_4^+ and NO_3^- Export via Runoff

One 20 m (along the slope) × 5 m (along the contour line) runoff plot was installed in each replicated plot of the young forests following the Water and Soil Conservation Experiment Specification (SL 419—2007) published by the Ministry of Water Resources of the People's Republic of China. A stainless-steel tank of 2 m (length) × 1 m (width) × 1 m (height) was installed at the bottom of each runoff plot to collect surface runoff. Because the mature forest yielded less runoff than young forests [66], a 1 m × 1 m × 1 m runoff tank was installed at the bottom of each runoff plot of the mature secondary forest. Runoff was recorded and sampled after each rainfall event (with measurable runoff in the steel tank) between 2012 and 2015. A sub-sample of 100 mL was passed through a 0.45 μm syringe filter. NH_4^+ and NO_3^- concentrations of filtered samples were analyzed using a Continuous Flow Injection Analyzer (Skalar San++, Breda, The Netherlands). Runoff NH_4^+ and NO_3^- exports of each runoff event were calculated by multiplying NH_4^+ and NO_3^- concentrations by runoff volume. More detail can be found in the study by Yang et al. [57].

2.8. Data Analysis

Differences in soil mineral N concentration, microbial attributes, and annual runoff NH_4^+ and NO_3^- export among the four forest types were examined using one-way ANOVA after Levene Homogeneity test followed by least significant difference tests at $p < 0.05$. Pearson correlation analysis was used to investigate the relations between microbial attributes, fine root biomass and soil NH_4^+ and NO_3^- concentrations. The above analyses were performed using SPSS 22.0 (SPSS Inc., Chicago, IL, USA).

The roles of total microbial biomass, enzyme activity, and runoff inorganic N export in explaining variation in soil inorganic N concentrations among the forests were examined using multiple regression models. Following Bååth and Anderson [60], total PLFAs was used to represent microbial biomass. Total activity of the five enzymes was used to represent microbial enzyme activity. All predictors and response variables were standardized using Z-score and predictors were log-transformed when necessary. To partition the relative importance of the three predictors of soil NH_4^+ and NO_3^- concentrations, we calculated the predicting power of each predictor and compared it with the predicting power of all predictors combined using R version 3.3.1 (R core team, 2016).

3. Results

3.1. Soil Inorganic N Concentrations, Microbial Properties, and Physicochemical Properties

The conversion of the mature secondary forest into young Chinese-fir and *Castanopsis* plantations significantly reduced soil NH_4^+ and NO_3^- concentrations (Figure 1). The soil NH_4^+ and NO_3^- concentrations in the plantations were only 24%~38% of those in the mature secondary forest (Figure 1). However, forest conversion did not significantly reduce NH_4^+ and NO_3^- concentrations in the young ANR forests, which had a significantly higher mean NH_4^+ concentration relative to that of the young Chinese-fir and *Castanopsis* plantations and a higher mean NO_3^- than that of the young Chinese-fir plantations (Figure 1).

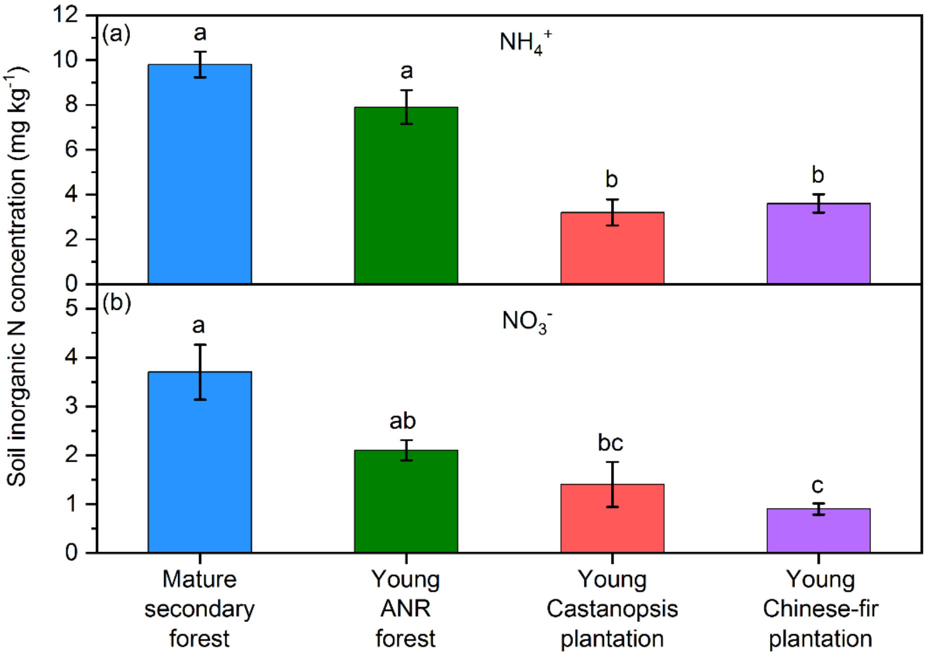

Figure 1. Soil NH_4^+ (**a**) and NO_3^- (**b**) concentrations (mean ± standard error) in different types of forest. ANR: assisted natural regeneration. Forests sharing no common letters are significantly different at $\alpha = 0.05$.

The concentrations of GP, GN, AMF, actinomycetes, fungi, and total PLFAs were all higher in the mature secondary forest and the young ANR forests than in the young plantations, whereas no significant differences were found between the mature secondary forest and the young ANR forests (Figure 2). The total PLFAs in the mature secondary forest was 45% higher than in the young plantations (Figure 2).

The activity of the enzymes was lower in the young plantations than in the mature secondary forest and young ANR forests except that there was no significant difference in BG activity among different forest types and no significant differences in AP activity between the Chinese-fir plantations, the mature secondary forest and the young ANR forests (Figure 3). No significant differences were found between the mature secondary forest and the young ANR forests and no significant differences were found between the two types of young forest plantation in the activity of any of the five enzymes (Figure 3).

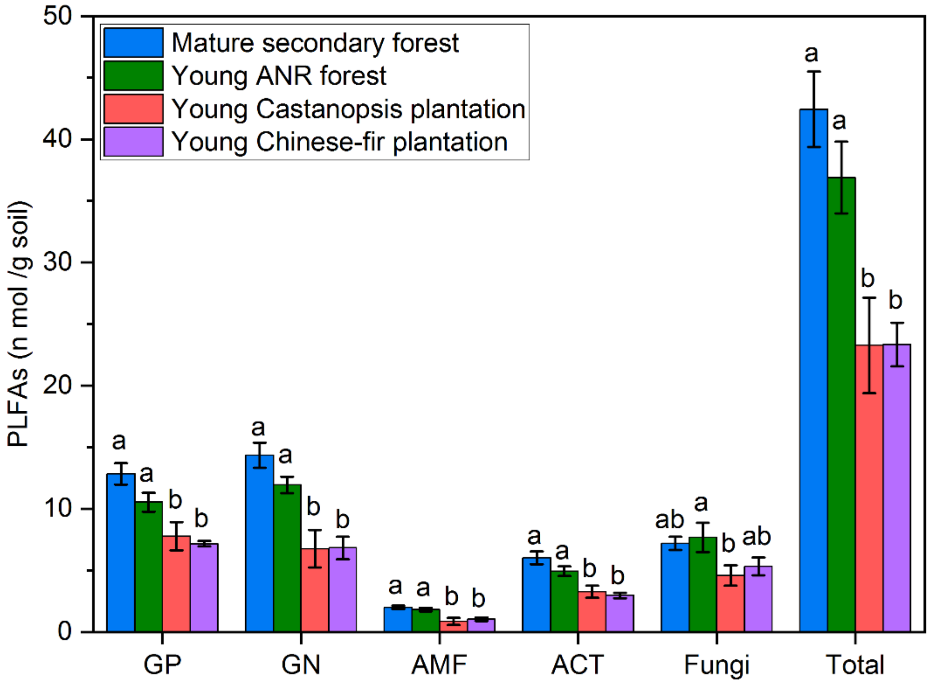

Figure 2. PLFA concentration (mean ± standard error) of Gram-positive (GP), Gram-negative (GN), arbuscular mycorrhizal fungi (AMF), actinomycetes (ACT), fungi, and all microbes (Total) in in different types of forests. ANR: assisted natural regeneration. For each group and the total, forests sharing no common letters are significantly different at α = 0.05.

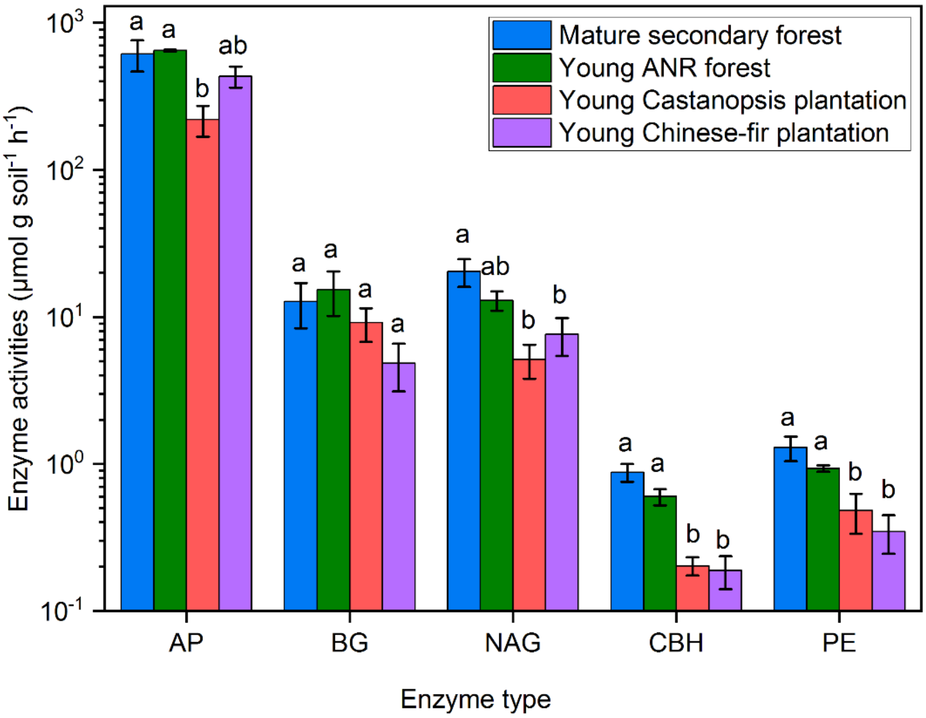

Figure 3. Potential extracellular enzyme activity (mean ± standard error) of acid phosphatase (AP), β-1,4-glucosidase (BG), Nacetyl-β-d-glucosaminidase (NAG), Cellobiohydrolase (CBH), and peroxidase (PER) in different types of forests ANR: assisted natural regeneration. For each enzyme, forests sharing no common letters are significantly different at α = 0.05.

The fine root biomass in the young ANR forests was significantly higher than that in the young plantations, but it was significantly lower than in the mature secondary forest (Table 1).

Table 1. Soil bulk density and fine root biomass of mature secondary forests, forests developing from assisted natural regeneration (ANR), young *Castanopsis carlesii* plantations, and young Chinese-fir plantations. For each raw, forests sharing no common letters are significantly different at α = 0.05.

	Mature Secondary Forest	**Young ANR Forest**	**Young Castanopsis Plantation**	**Young Chinese-Fir Plantation**
Bulk density (g cm^{-3})	1.1 (0.03) ^{b}	1.1 (0.03) ^{b}	1.1 (0.06) ^{ab}	1.2 (0.05) ^{a}
Fine root biomass (g m^{-2})	436.4 (56.4) ^{a}	334.0 (26.9) ^{b}	186.7 (38.5) ^{c}	244.2 (21.3) ^{c}

3.2. *Surface Runoff* NH_4^+ *and* NO_3^- *Export*

Surface runoff NH_4^+ and NO_3^- exports were much higher in the young Chinese-fir and *Castanopsis* plantations relative to those in the mature secondary forest and the young ANR forests in the first year, but the differences declined sustainably in the second and third years (Figures 4 and 5). Over the three-year period (2012–2015), runoff NH_4^+ and NO_3^- exports were similar between the mature secondary forest and the young ANR forests. The total runoff NH_4^+ export in the young Chinese-fir and *Castanopsis* plantations was 3.5~6.7 times that in the mature secondary forest, and the total runoff NO_3^- export in the young Chinese-fir and *Castanopsis* plantations was 9.9~17.8 times of that in the mature secondary forest over the three years (Figure 5). However, no significant differences in NH_4^+ and NO_3^- exports were detected between the young ANR forests and the mature secondary forest in the same period (Figure 5).

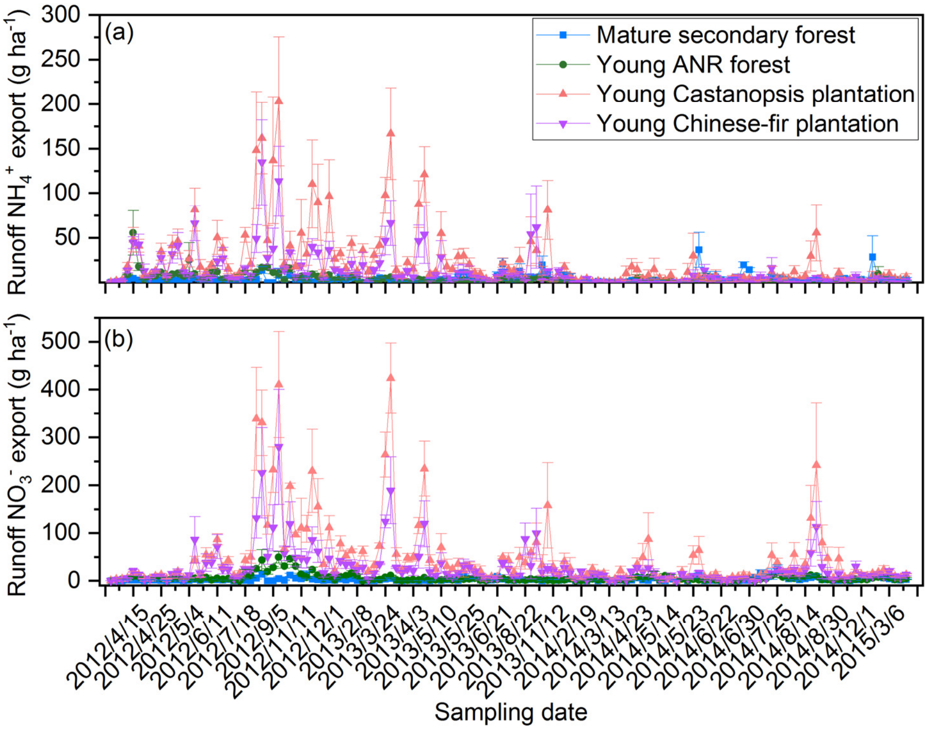

Figure 4. Runoff NH_4^+ (**a**) and NO_3^- (**b**) exports (mean ± standard error) of individual rainfall events in different types of forests. ANR: assisted natural regeneration.

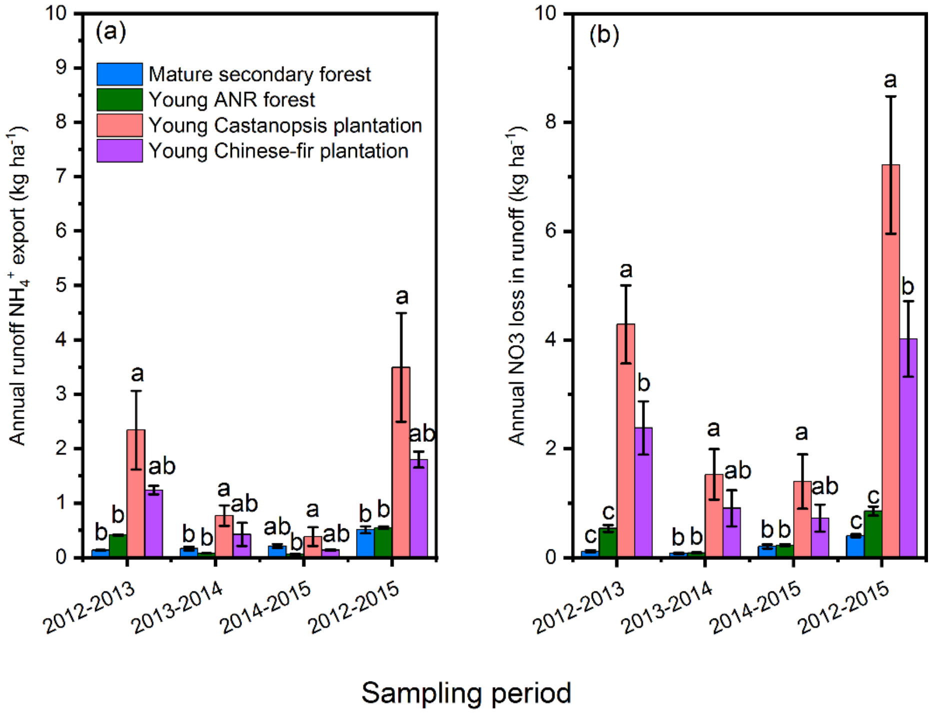

Figure 5. Annual runoff NH_4^+ (**a**) and NO_3^- (**b**) exports (mean ± standard error) in different types of forests. ANR: assisted natural regeneration. For annual runoff export, forests sharing no common letters are significantly different at $\alpha = 0.05$.

3.3. Soil Inorganic N Concentration in Relation to Soil Microbial Attributes and Surface Runoff

Soil NH_4^+ concentration was positively correlated with AP, NAG, CBH, and PER activity, microbial PLFAs of GP, GN, AMF, ACT, and fungi, and fine root biomass (Figure 6). Similarly, except for AP, BG, and NAG, soil NO_3^- concentration was positively correlated with the measured microbial variables and fine root biomass (Figure 5). Both soil NH_4^+ and NO_3^- concentrations were significantly and negatively correlated with runoff NH_4^+ and NO_3^- export (Figure 6).

The soil microbial biomass, as indicated by total PLFAs, was the only significant variable predicting soil NH_4^+ and NO_3^- concentrations based on the regression models. The total PLFAs contributed 61% of the explaining power of the regression model for soil NH_4^+ concentration while it contributed 94% of the explaining power of the model for soil NO_3^- concentration (Figure 7).

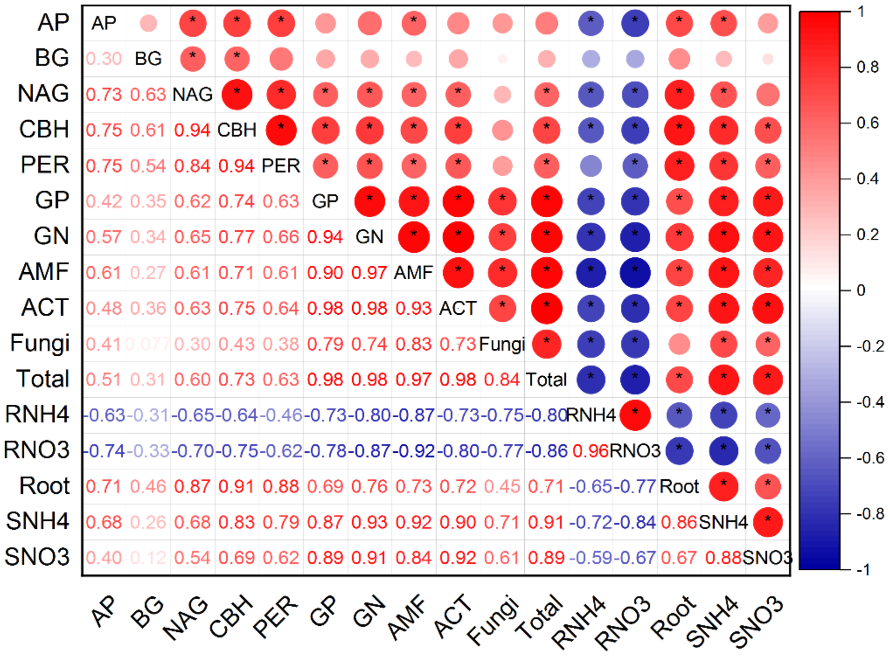

Figure 6. Pearson correlations among microbial PLFAs of Gram-positive (GP), Gram-negative (GN), arbuscular mycorrhizal fungi (AMF), actinomycetes (ACT), fungi, and total PLFAs, activity of acid phosphatase (AP), β-1,4-glucosidase (BG), Nacetyl-β-d-glucosaminidase (NAG), Cellobiohydrolase (CBH), and peroxidase (PER), cumulative runoff NH_4^+ (RNH4), cumulative runoff NO_3^- (RNO3), fine root biomass (Root), soil NH_4^+ (SNH4), and soil NO_3^- (SNO3). The numbers in the lower triangular matrix show the correlation coefficient between each pair of variables. Circle sizes in the upper triangular matrix reflect the values of the correlation coefficients, with red and blue color representing positive and negative values. The asterisk in the circle denotes p value < 0.05.

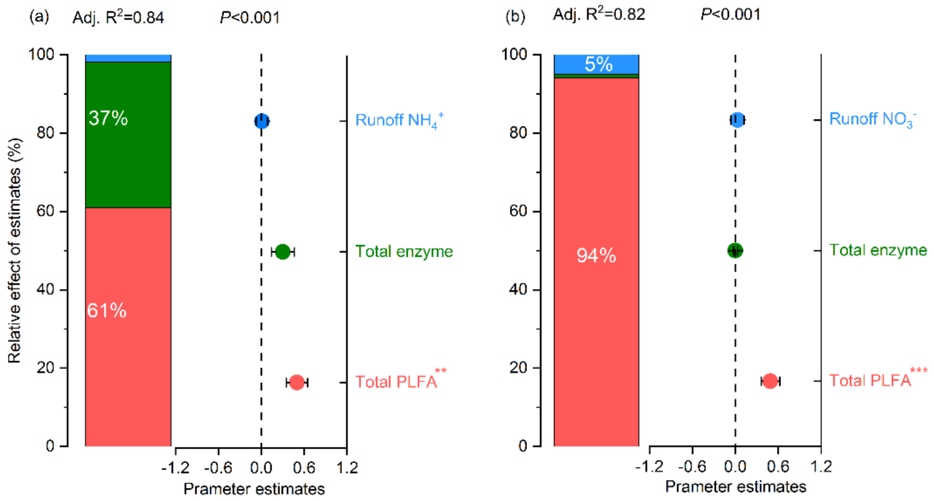

Figure 7. Relative importance of microbial PLFAs (total PLFAs of Gram-positive (GP), Gram-negative (GN), arbuscular mycorrhizal fungi (AMF), actinomycetes (ACT), fungi), soil microbial enzyme activity (total of acid phosphatase (AP), β-1,4-glucosidase (BG), Nacetyl-β-d-glucosaminidase (NAG), Cellobiohydrolase (CBH), peroxidase (PER)), and runoff inorganic N export on predicting soil NH_4^+ (**a**) and NO_3^- (**b**) concentrations. ** $p < 0.01$, *** $p < 0.001$.

4. Discussion

4.1. Soil Inorganic N in Relation to Soil Microbial Attributes and Surface Runoff Inorganic N Export

The differences in soil and runoff inorganic N concentrations among the four types of forests suggest that different types of forest conversion have different effects on inorganic N availability. Although the young forests were of the same age, unlike the reduced soil inorganic N concentrations in the young plantations, the young ANR forests had soil inorganic N concentrations similar to that of the mature secondary forest (Figure 1), in accordance with variation in soil total N concentration among the forests [67]. In addition, runoff inorganic N export from the young ANR forests was also similar to that from the mature secondary forest, and was only 12%~30% of that from the young plantations (Figure 5a,b). These results suggest that assisted natural regeneration following clear-cut can effectively conserve soil inorganic N and support that forests developed through assisted natural regeneration have the potential to retain ecosystem services similar to those of mature secondary forests [57,68,69].

Variation in soil inorganic N concentrations among the young forests was associated with their differences in microbial biomass and enzyme activity (Figure 6). In our study, the young ANR forests had levels of microbial PLFAs and enzyme activity similar to the mature secondary forest and higher than those of the young forest plantations. High microbial biomass and activity help to enhance N mineralization and, therefore, contributed to the higher soil inorganic N concentrations in the young ANR forests than the young forest plantations (Figure 1). Because root-derived C is an important C source for soil microorganisms [70–73], the higher microbial biomass and enzyme activity in the young ANR forests than the young forest plantations may be ascribed to its higher fine root biomass.

Different forms of nitrogen transformation, including ammonification, nitrification, denitrification, and microbial immobilization, all involve microorganisms [74]. These processes largely determine the proportions of different forms of N in and leaving the soil [75]. For example, high rates of nitrification may cause large leaching loss of NO_3^- via surface runoff [76]. Denitrification that reduced soil NO_3^- availability was unlikely the dominant process affecting soil inorganic N concentration in the present study as the positive relationship between soil NO_3^- concentration and microbial PLFAs suggests that enhanced microbial biomass positively, instead of negatively, affected soil NO_3^-. The positive relationships between microbial PLFAs and soil NH_4^+ and NO_3^- concentrations point to the importance of ammonification and nitrification in regulating soil inorganic N availability in the studied forests.

The more rapid plant growth in the ANR forests than the young plantations [57] likely contributed to the higher root biomass, which provided soil microbes with more carbon via root exudation, thereby contributing to greater N mineralization in the ANR forests than in the forest plantations. In addition, the more rapid plant growth also provided greater shading and had greater canopy interception and evapotranspiration [56] in the ANR forests than in the young forest plantations, all of which reduced surface runoff and rain splash, leading to minimized runoff inorganic N export in the ANR forests [25].

Studies in subtropical China have reported declines in soil fertility and N mineralization and nitrification following the conversion of natural broadleaved forests to forest plantations [10,12]. Our study indicates that with minimal human intervention, naturally regenerated forests can retain levels of soil inorganic N similar to that of mature secondary forests (Figure 1). Due to the close link between soil N availability and net primary productivity and carbon sequestration [77–79], searching for forest management practices that maximize soil N availability is of major importance in carbon and N cycling [80,81]. Our study illustrates that assisted natural regeneration could be an effective forest management practice for maintaining net primary productivity and carbon sequestration capacity. Assisted natural regeneration has also been shown to be effective in conserving biodiversity and soil and water conservation [57,82]. Future studies examining the effectiveness of ANR on maintaining soil N and net primary productivity in other regions would help to evaluate the applicability of our results on a global scale.

4.2. The Dominant Factors Influencing Post-Conversion Soil Inorganic N Concentrations

Although soil inorganic N concentrations were significantly correlated with enzyme activity and runoff export of NH_4^+ and NO_3^-, through partitioning the variance (Figure 7), we found that microbial biomass was more important than microbial enzyme activity and surface runoff export in explaining the variation in the soil inorganic N concentrations among the forests (Figure 7). Because the young forests were all converted from the same secondary forest at the same time, the soil inorganic N concentrations of the forests should be similar prior to the experimental treatment. Thus, the variation in soil inorganic N among the forests occurred after forest conversion, either through differences in inorganic N loss and/or via mineralization among the forests. The greater explaining power of microbial biomass than runoff export suggests that post-conversion soil N availability is more closely related to its formation than its loss via runoff.

Soil microbial enzyme activity is certainly related to microbial biomass, so it is not surprising that both were positively correlated with soil inorganic N concentrations (Figure 6). However, the greater predictive power of microbial biomass than enzyme activity on the variation in soil mineral N concentrations suggests that although they both affect N mineralization [83,84], much of the variation in enzyme activity among the forests might be attributable to their differences in microbial biomass. In other words, N mineralization was likely more limited by microbial biomass than enzyme activity in the studied forests. Many studies have examined the effects of land use change, including forest conversion, on soil microbial enzyme activity [42,43,85–87]; based on our results, much of the effect could be mediated by changes in microbial biomass.

Although surface runoff can export a large quantity of N, it only takes place during rainfall events, unlike microbial N transformation, which takes place continuously. Thus, although immediately following the forest conversion large amounts of inorganic N, especially the highly mobile NO_3^-, were exported by surface runoff (Figure 4a,b), the runoff export effect attenuated substantially when the young forests began to grow rapidly (Figure 4a,b). For example, maximum NO_3^- export via surface runoff from the young Chinese-fir plantations was 280 g ha^{-1} for a single runoff event in the first year, but it dropped to 113 g ha^{-1} in the third year (Figure 4b). By the third year, annual NH_4^+ loss in the young Chinese-fir plantations was not significantly different from the loss in the mature secondary forest (Figure 5a). The quick decreases in the severity of the runoff events undermined its role in affecting soil N availability.

While the clearing-induced enhancement of surface runoff decreases with time as trees grow, fine root biomass typically increases with time before forests mature [88]. Thus, the importance of the effect of the loss of inorganic N via surface runoff export on soil inorganic N concentrations decreased substantially in a few years following the conversion of mature secondary forests to forest plantations. By contrast, the role of microbial biomass, which is positively related to fine root biomass, on N mineralization tends to increase and persist for a much longer period of time. The temporal contrast in their importance in affecting soil inorganic N availability led to the greater predictive power of microbial biomass than surface runoff inorganic N export on variation of soil inorganic N concentrations among the forests.

5. Conclusions

Compared to the mature secondary forest, soil inorganic N concentrations were lower in the young Chinese-fir plantations and *Catasnopsis* plantations, but not the young forests established through assisted natural regeneration (ANR) five years following the conversion. This result highlights that natural regeneration with minimal human intervention can effectively maintain soil N availability. The more rapid plant growth in the young ANR forests than in the two young plantations likely provided soil microbes with more carbon via roots, which contributed to greater N mineralization and, thus, higher mineral N concentrations in the ANR forests than in the young plantations. More rapid plant growth also reduced N export via runoff due to greater canopy interception and evapotranspiration. The results of the variation partition indicate that microbial biomass is the dominant factor in predicting soil inorganic N concentrations, suggesting that N mineralization, rather than its loss via runoff, is the key to post-conversion soil inorganic N availability. The effects of forest conversion on elevating surface runoff diminished a few years later as the trees grew, while the differences in microbial biomass among the different forest types increased with time, leading to the greater predictive power of microbial biomass than surface runoff on soil inorganic N concentrations.

Author Contributions: Conceptualization, C.X., T.-C.L. and Y.Y.; methodology, C.X., M.W. and L.Y.; software, C.X.; validation, C.X. and T.-C.L.; formal analysis, J.-C.H.; investigation, C.X., X.L., D.X. and S.C.; resources, Y.Y.; data curation, C.X. and T.-C.L.; writing—original draft preparation, C.X. and T.-C.L.; writing—review and editing, C.X. and T.-C.L.; visualization, C.X. and Z.Y.; supervision, Y.Y.; project administration, Y.Y.; funding acquisition, Y.Y. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the National Nature Science Foundation of China (grant numbers: 32101495 and 31930071) and Special Projects for Public Welfare Research Institutes in Fujian Province (grant number: 2020R1002004).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

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

Acknowledgments: We gratefully acknowledge our colleagues for their efforts on this long-term experiment. Special thanks to Chengfang Lin, Guangshui Chen, and Jinsheng Xie for their efforts in the plot design and establishment.

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

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