Effects of Altitude, Soil, and Vegetation on Soil Nutrient and Enzyme Stoichiometric Ratios in the Lijiang River Basin: Postprint

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Abstract

The Lijiang River basin features diverse elevations, soil types, and vegetation types. To investigate the characteristics of soil nutrients and soil enzyme activities, this study examined surface soils (0–20 cm) under typical vegetation types (natural forest, bamboo forest, pine forest, orchard, paddy field) in calcareous and acidic soils of the Lijiang River basin, measuring soil nutrient contents and activities of carbon- and nitrogen-transformation-related extracellular enzymes (amylase, sucrase, urease, protease, catalase) and their stoichiometric characteristics. The results showed that: (1) Soils at high altitudes had relatively higher contents of total nitrogen (TN), total phosphorus (TP), and available phosphorus (AP), as well as activities of amylase, sucrase, urease, and protease, while catalase activity exhibited the opposite trend. (2) Compared with acidic soils, calcareous soils had higher TP and AP contents. In acidic soils, vegetation type significantly affected nitrogen and phosphorus nutrients, with artificial vegetation generally decreasing soil nitrogen but increasing phosphorus; whereas nutrient differences among vegetation types were relatively small in calcareous soils. (3) Compared with natural forests, artificial vegetation greatly reduced soil nitrogen-transforming enzyme activities, while soil carbon-transforming enzymes were less affected by anthropogenic activities. Stoichiometry of soil nitrogen and phosphorus enzyme activities revealed nitrogen limitation in natural forests but carbon limitation in artificial forests. (4) Canonical correspondence analysis (CCA) showed that soil physicochemical properties explained 86.56% of the variation in soil enzyme activities along the first and second axes, with the explanatory contribution ranking as: TN > pH > ammonium nitrogen (NH4+) > AP > TP > nitrate nitrogen (NO3-), among which the first three factors were the main drivers of differences in soil enzyme activities. In summary, the results indicate that acidic soils in the Lijiang River basin exhibit high ecological sensitivity to human disturbance, and vegetation changes can readily lead to nutrient

imbalances. Soil nutrient management should be emphasized to prevent loss of soil organic matter and enhance sustainable utilization of landscape resources in the Lijiang River basin. This study provides a theoretical basis for scientific conservation and development of local ecosystems.

Full Text

Effects of Altitude, Soil, and Vegetation on Soil Nutrient Contents and Enzyme Stoichiometry in the Lijiang River Basin

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Abstract: The Lijiang River Basin exhibits substantial variation in altitude, soil types, and vegetation. To investigate the characteristics of soil nutrients and extracellular enzyme activities, this study examined surface soils (0–20 cm) from typical vegetation types (natural forest, bamboo forest, *Pinus massoniana* forest, orchard, and rice paddy) on both calcareous and acidic soils in the Lijiang River Basin. We measured soil nutrient contents and activities of carbon- and nitrogen-transforming extracellular enzymes (amylase, sucrase, urease, protease, and catalase) and analyzed their stoichiometric ratios. The results showed that: (1) Soils at high altitudes had relatively higher contents of total nitrogen (TN), total phosphorus (TP), and available phosphorus (AP), as well as higher activities of amylase, sucrase, urease, and protease, whereas catalase activity showed the opposite trend. (2) Compared to acidic soils, calcareous soils had higher TP and AP contents. In acidic soils, vegetation type strongly influenced nitrogen and phosphorus nutrients, with anthropogenic vegetation generally decreasing soil nitrogen while increasing phosphorus; calcareous soils showed relatively small nutrient variation among vegetation types. (3) Compared to natural forests, anthropogenic vegetation greatly reduced nitrogen-transforming enzyme activities, while carbon-transforming enzymes were less affected by human disturbance. Enzyme stoichiometry revealed nitrogen limitation in natural forests but carbon limitation in artificial forests. (4) Canonical correspondence analysis (CCA) showed that soil physicochemical properties on the first and second axes explained 86.56% of the variation in soil enzyme activities, with the contribution order being TN > pH > ammonium nitrogen (NH), indicating these three factors were the main drivers of differences in soil enzyme activities. Overall, the results demonstrate that acidic soils in the Lijiang River Basin exhibit high eco-

logical sensitivity to anthropogenic disturbance, and vegetation changes readily lead to nutrient imbalance. Soil nutrient management should be prioritized to prevent soil organic matter loss and improve sustainable utilization of landscape resources. This study provides a theoretical basis for scientific conservation and development of local ecosystems.

Keywords: calcareous soil, acidic soil, vegetation type, enzyme activity, stoichiometry, Lijiang River Basin

Classification Code: Q948

Introduction

Soil enzymes are among the most active components in soils, primarily derived from secretions and residues of plants, animals, and microorganisms. They catalyze a series of biochemical processes including mineralization and hydrolysis of complex carbon-, nitrogen-, and phosphorus-containing organic compounds, thereby promoting decomposition of soil organic matter (Burns et al., 2013). Enzyme activities sensitively reflect the direction and intensity of soil biochemical processes (Cao et al., 2003; Yang et al., 2020). Changes in vegetation type alter ecosystem characteristics such as vegetation community composition and developmental stage (Feng et al., 2019; Wang et al., 2019), soil microbial community composition (Lauber et al., 2013), and soil hydrothermal conditions (Yang et al., 2009), which collectively affect soil physicochemical properties including pH, nutrient contents, and stoichiometric characteristics (Zhao et al., 2018; Tian et al., 2019; Lin et al., 2021), as well as soil temperature and moisture (Jiang et al., 2018), thereby directly or indirectly influencing soil enzyme activities (Shao et al., 2021; Duan et al., 2020).

Differences in temperature and humidity along altitudinal gradients strongly affect soil biochemical processes, influencing the distribution of soil nutrients and vegetation types (Fierer et al., 2013; Gaston, 2000) and causing substantial variation in soil enzyme activities. Margesin et al. (2014) found that soil enzyme activities decreased with increasing altitude in the Alps, whereas Zuo et al. (2018) reported opposite results for mountains in Xinjiang. Li et al. (2020) observed that activities of catalase, urease, and sucrase increased with altitude in typical evergreen broadleaf forests of southeastern Yunnan, while acid phosphatase activity first decreased then increased. These contrasting results indicate that the key factors influencing soil enzyme activities along altitudinal gradients vary significantly among regions and climate zones, necessitating targeted research for different areas.

Soil enzyme stoichiometry reflects the biogeochemical equilibrium between microbial nutrient demand and soil nutrient limitation (Hill et al., 2012; Zhang et al., 2018). At the global scale, the soil enzyme stoichiometric ratio is approximately 1:1:1, but at regional scales, actual values deviate due to soil nutrient constraints on microbial activity (Zhang et al., 2019; Zhao et al., 2018). Different vegetation types exhibit variations in nutrient sources, cycling, contents, and availability, indirectly affecting the processes by which plants and microorganisms acquire nutrients through extracellular enzyme secretion (Tian et al., 2019; Gong and Cai, 2018; Long et al., 2004). Xu et al. (2020) found that sucrase activity was independent of vegetation type in adjacent cropland and forest soils in Hailun City, Heilongjiang, while urease activity was strongly affected by vegetation type and catalase activity was primarily influenced by soil organic carbon. Zhou et al. (2020) reported that sucrase and catalase activities in upland red soils were less affected by vegetation type, whereas urease activity showed greater vegetation-type dependence. Zhong et al. (2021) found that soil physicochemical properties and vegetation diversity were the main factors regulating soil enzyme activities and stoichiometry. Cui et al. (2018) demonstrated that vegetation type had a greater influence on enzyme stoichiometry than soil type. Therefore, further research is needed on the variation in soil enzyme stoichiometry and its influencing factors in the Lijiang River Basin.

Calcareous soils are characterized by high pH values and calcium and magnesium contents, with generally high soil organic carbon contents, making them important organic carbon pools (Cao et al., 2003). Fan et al. (2018) found that activities of carbonic anhydrase, catalase, urease, and acid phosphatase were higher in karst areas than in non-karst areas. Wei et al. (2008) reported that catalase, sucrase, urease, and cellulase activities were higher in karst areas, while protease activity showed the opposite pattern. Chen et al. (2018) showed that -1,4-glucosidase, leucine aminopeptidase, and polyphenol oxidase activities were significantly higher in karst forests than in non-karst forests, but -N-acetylglucosaminidase and acid phosphatase activities were significantly lower. The ratios of -1,4-glucosidase:acid phosphatase, -1,4-glucosidase:(-N-acetylglucosaminidase+leucine aminopeptidase), and (-N-acetylglucosaminidase+leucine aminopeptidase):acid phosphatase were higher in karst forests. These findings indicate that different soils exhibit distinct enzyme activities due to nutrient content differences, highlighting the need to further elucidate the relationship between nutrient limitation and enzyme activity.

Karst landforms are widely distributed in southwestern China. Karst regions are characterized by thin soil development, strong soil leakage, relatively fragile ecological environments, and rocky desertification as the primary form of land degradation (Cao et al., 2015). Unreasonable human development has accelerated soil erosion, reduced land productivity, and exacerbated rocky desertification (Zhang et al., 2010). The Lijiang River originates from Mao' er Mountain in northeastern Guangxi with granite bedrock, flows through the karst limestone area of Guilin, and serves as a lifeline for the region with important ecological and economic significance. Due to economic development and urbanization, the Lijiang River Basin has experienced increasing impacts from grain cultivation and fruit forestry over the past two decades (Luo et al., 2021), resulting in dramatic vegetation type changes. To maintain ecosystem stability in the basin, systematic analysis and assessment of how different anthropogenic vegetation types affect nutrient cycling characteristics and influencing factors in both karst and non-karst soil ecosystems are urgently needed. Current research on karst calcareous soils has primarily focused on rocky desertification and ecological restoration, showing that soil nutrients change significantly across different restoration stages due to variations in soil texture and vegetation composition (Yu et al., 2019; Wang et al., 2018), and that extracellular enzyme activities differ markedly (Chen et al., 2017; Zhao et al., 2021; Guan et al., 2022). Studies have shown significant correlations between carbon-nitrogen-phosphorus transforming enzymes and soil nutrients, indicating that enzyme activities control soil nutrient cycling (Xu et al., 2014), and that vegetation type changes alter soil nutrient balance (Sun et al., 2021). However, few studies have examined the effects of different vegetation types on soil nutrients and enzyme activities across different parent material-developed soil types from a watershed perspective, limiting comprehensive management strategies tailored to specific vegetation and soil conditions.

Therefore, this study selected the Lijiang River Basin (from Mao' er Mountain at the source to the downstream Yangshuo section) as the research area. By comparing surface soils (0–20 cm) from ten plots across different vegetation types on acidic and calcareous soils, we employed extracellular enzyme activity and soil physicochemical property analyses to investigate soil nutrient contents and extracellular enzyme activity characteristics, revealing nutrient limitation patterns in microbial growth and metabolism. We addressed the following questions: (1) How do soil nutrient contents and enzyme activities vary under different vegetation types? (2) What are the dominant environmental factors influencing soil enzyme activities under different natural conditions (altitude and soil type)? (3) How do anthropogenic vegetation types affect soil nutrient contents and enzyme activities, and do these changes cause shifts in soil nutrient limitation?

1.1 Study Area

The study area extended from Mao' er Mountain in Xing' an County in northern Guilin to Yangshuo County in the south, spanning latitudes from 24°50 12.4 to 25°53 01.5 and altitudes from 135 to 1,120 m. The region has a subtropical monsoon climate with abundant sunlight, distinct seasons, an average annual temperature of 17–20 °C, annual precipitation of 1,400–2,600 mm (decreasing from north to south), and annual evaporation of 137–1,857 mm. Rainfall and temperature are generally synchronized seasonally. The Lijiang River source lies within Mao' er Mountain Forest Park, where soils are developed from granite parent material as alpine yellow soils with acidic pH and high forest coverage. Downstream from Mao' er Mountain, from Lingchuan County in the middle reaches, soil types gradually transition to calcareous soils developed from limestone and dolomite with neutral or weakly acidic pH, though acidic red soils are also distributed. Dominant vegetation types include artificial economic forests such as *Pinus massoniana* and bamboo (*Phyllostachys pubescens*) forests, as well as cropland. In downstream Yangshuo County, the main artificial vegetation types are kumquat and honey orange orchards.

1.2 Soil Sampling and Analysis

In July 2016, we selected five widely distributed vegetation types—natural forest, bamboo forest, *Pinus massoniana* forest, orchard, and rice paddy—based on the distribution characteristics of major soils, vegetation, and economic crops from high altitude (1,120 m) to low altitude (135 m) areas in the Lijiang River Basin, collecting soil samples from ten plots (Table 1). Natural forests were all evergreen broadleaf forests. Dominant tree species in the Mao' er Mountain plot included *Osmanthus fragrans*, *Rhododendron pachyphyllum*, and *Cyclobalanopsis glauca*. In low-altitude calcareous soil natural forests, *Cyclobalanopsis glauca* formed a single dominant species, while in acidic soil natural forests, dominant species were *Cyclobalanopsis glauca* and *Cinnamomum camphora* with lush ground vegetation and no obvious human disturbance. Bamboo (*Phyllostachys pubescens*) and *Pinus massoniana* forests were artificially planted with some ground vegetation manually cleared. At each plot, we established a 20 m × 20 m area and collected five surface soil samples (0–20 cm) using a five-point sampling method after removing surface litter, then mixed them to obtain ten composite soil samples. Samples were transported to the laboratory, where roots and stones were manually removed and soils were passed through a 2 mm sieve. Soil samples were divided into two portions: one stored at 4 °C for determination of ammonium nitrogen (NH), nitrate nitrogen (NO), and five extracellular enzyme activities (sucrase and amylase for carbon transformation, urease and protease for nitrogen transformation, and catalase for redox processes); the other oven-dried at 60 °C to constant weight for determination of total nitrogen (TN), total phosphorus (TP), available phosphorus (AP), and pH. All measurements except TN were performed in triplicate.

Soil pH was measured potentiometrically (soil:water ratio of 2.5:1). NH and NO were extracted with potassium chloride solution and measured spectrophotometrically. TN and TP were determined by H SO -HClO -H O digestion. AP was extracted with sodium bicarbonate and measured using the molybdenum-antimony anti-color method. Extracellular enzyme activities were measured as follows (Guan, 1986): urease by phenol-sodium hypochlorite colorimetry, sucrase by 3,5-dinitrosalicylic acid colorimetry, catalase by potassium permanganate titration, protease by ninhydrin colorimetry, and amylase by dinitrosalicylic acid colorimetry.

1.3 Data Processing and Analysis

We used the relative enzymatic stoichiometric ratio (sucrase + amylase)/(urease + protease) to characterize the utilization intensity of extracellular enzymes for organic carbon versus organic nitrogen. All statistical analyses were performed in SPSS 22.0. Two-way ANOVA was conducted with altitude and vegetation type, and soil type and vegetation type as controlling factors for soil enzyme activities. One-way ANOVA followed by Duncan' s multiple comparison test (= 0.05) was used to assess significant differences in soil nitrogen and phosphorus contents and enzyme activities. Canonical correspondence analysis (CCA) between soil physicochemical properties and enzyme activities was performed using Canoco 5 for Windows.

2.1 Soil Nitrogen and Phosphorus Contents

Calcareous soils had significantly higher mean pH values than acidic soils ($P < 0.05$) (Table 1). In acidic soils, high-altitude natural forests had higher TN, TP, and AP contents than low-altitude natural forests, with inorganic nitrogen dominated by NO and relatively low NH , reflecting high organic matter accumulation at high altitudes. High-altitude bamboo forests also had relatively high TN and NO contents. Human land use altered soil nutrient composition to varying degrees, with substantial differences between soil and vegetation types. In low-altitude acidic soils, compared to natural forests, all vegetation types showed significantly reduced soil TN and NO contents ($P < 0.05$). Orchards exhibited significantly increased TP and AP accumulation ($P < 0.05$), while other vegetation types (bamboo and *Pinus massoniana* forests) mainly showed decreased readily available nutrients (average NO and AP contents). The decline in soil TN and NO reflected increased mineralization, plant uptake, and leaching losses, leading to reduced soil fertility. In contrast, phosphorus nutrients showed increasing trends under anthropogenic disturbance. In calcareous soils, all vegetation types showed varying degrees of increase in nutrient contents compared to natural forests, with the most significant increases in rice paddies. Low-altitude calcareous soils had relatively higher TP contents than their acidic counterparts. The two artificial forests on calcareous soils did not show obvious nutrient loss compared to natural forests, indicating lower sensitivity of calcareous soil nutrients to anthropogenic disturbance.

Table 1 Soil pH values and nitrogen and phosphorus contents under different vegetation covers (n = 3)

Note: H-G-NF = high altitude, acid soil, natural forest; H-G-BP = high altitude, acid soil, bamboo forest; L-G-NF = low altitude, acid soil, natural forest; L-G-BP = low altitude, acid soil, bamboo forest; L-G-OG = low altitude, acid soil, orchard; L-G-PP = low altitude, acid soil, Pinus massoniana*; L-G-RP = low altitude, acid soil, rice paddy; L-K-NF = low altitude, limestone soil, natural forest; L-K-OG = low altitude, limestone soil, orchard; L-K-RP = low altitude, limestone soil, rice paddy. Different uppercase letters indicate significant differences among vegetation types within the same soil type ($P < 0.05$); different lowercase letters indicate significant differences between soil types for the same vegetation type ($P < 0.05$) based on one-way ANOVA.*

2.2 Soil Enzyme Activities and Their Stoichiometric Ratios

Altitude, vegetation type, and soil type significantly affected soil enzyme activities (Table 2). In acidic soils, nitrogen-transforming enzyme activities (urease and protease) in high-altitude natural forests were significantly higher than in low-altitude vegetation types ($P < 0.05$). Protease activity in high-altitude bamboo forests was also significantly higher than in other vegetation types (Fig. 1C, D). Carbon-transforming enzyme activities (sucrase and amylase) were relatively higher in high-altitude soils (Fig. 1A, B), while catalase showed the opposite trend (Fig. 1E). In low-altitude acidic soils, amylase activities in bamboo forests and orchards were significantly lower than in natural forests, *Pinus massoniana* forests, and rice paddies ($P < 0.05$), while urease activities in orchards and *Pinus massoniana* forests were nearly zero. In calcareous soils, sucrase activity in rice paddies was significantly lower than in natural forests ($P < 0.05$), while urease activity was significantly higher ($P < 0.05$). Vegetation type had little effect on amylase and protease activities in calcareous soils. Carbon-cycling enzymes (sucrase and amylase) and catalase activities in calcareous soils were significantly higher than in corresponding vegetation types on acidic soils ($P < 0.05$). Natural forests on calcareous soils had relatively higher carbon-transforming enzyme activities than artificial vegetation types, while nitrogen-transforming enzyme activities were very low in artificial vegetation soils. Overall, vegetation type had relatively minor effects on carbon-cycling enzymes (especially amylase), whereas nitrogen-cycling enzymes (especially urease) showed greater variation by vegetation type than by soil type (Table 2).

Due to low urease activities in low-altitude acidic soil orchards and *Pinus massoniana* forests and in calcareous soil orchards (Fig. 1), their enzyme stoichiometric ratios (sucrase + amylase)/(urease + protease) were significantly higher than in other soils ($P < 0.05$) (Fig. 2). High-altitude areas and low-altitude natural forests had lower ratios, indicating relatively higher nitrogen-transforming enzyme activities and reflecting nitrogen limitation. Ratios in acidic soil natural forests were lower than in all artificial forests and rice paddies. In calcareous soils, orchard ratios were significantly higher than in natural forests and rice paddies ($P < 0.05$). No consistent pattern emerged between the two soil types for the same vegetation type. Except for calcareous soil rice paddies, all vegetation types showed substantially increased enzymatic stoichiometric ratios, indicating relatively higher carbon-transforming enzyme activities and reflecting a shift from nitrogen to carbon limitation following conversion from natural to artificial forests.

Table 2 Results of two-way ANOVA of different factors on soil enzyme activities (P values)

Note: $P < 0.05$. The first three rows show results for altitude, vegetation type, and their interaction; the latter three rows show results for soil type, vegetation type, and their interaction.

Fig. 1 Enzyme activities of sucrase (A), amylase (B), urease (C), protease (D), and catalase (E) in different soil and vegetation types.

Fig. 2 Stoichiometric ratio of soil C/N enzyme activity under different vegetation types.

2.3 Relationships Between Soil Enzyme Activities and Physicochemical Properties

Canonical correspondence analysis (CCA) was used to explore the effects of soil physicochemical properties on enzyme activities (Fig. 3). Table 3 shows the explanatory power of soil pH and nutrient contents for differences in the five enzyme activities and their stoichiometric ratios. The selected soil properties explained 80.91% and 5.65% of the variation on the first and second axes, respectively, with a cumulative explanation of 86.56%, indicating that the first two axes captured most information on enzyme activity variation driven by soil pH and nutrient contents. Soil TN, pH, and NH explained 71.0%, 14.3%, and 10.4% of the variation, respectively, confirming that these three factors were the main drivers of differences in soil enzyme activities.

Fig. 3 Biplot of the first two axes of CCA for soil physicochemical properties and enzyme activities (n = 10).

Table 3 Importance and significance of soil physicochemical properties

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3.1 Effects of Natural Factors and Vegetation Types on Nutrient Distribution

Soil serves as a critical carrier of terrestrial ecosystems, and its nutrient status is influenced by climate, altitude, topography, vegetation type, soil type, and anthropogenic disturbance, exhibiting high spatial heterogeneity (Wang et al., 2018). Investigating soil nutrient contents and cycling characteristics across different vegetation types at the watershed scale provides the foundation for assessing ecosystem function status, anthropogenic disturbance levels, and nutrient cycling sensitivity of different vegetation units. Changes in artificial vegetation types regulate both soil resource inputs and microclimatic conditions, significantly affecting soil organic carbon and nitrogen pools and nutrient cycling pathways (Jiang et al., 2011). This study compared two typical soil types in the Lijiang River Basin: acidic red soils mainly distributed in the upper and middle reaches, and calcareous soils concentrated in the middle and lower reaches. The results showed that altitude, vegetation type, and soil type significantly affected soil nutrients. Soil parent material is a major factor causing variation in soil nutrients, particularly phosphorus content, which can explain 42% of TP variation, with calcareous soils typically having higher phosphorus contents than acidic soils (Porder and Ramachandran, 2013; Xiao et al., 2021). Additionally, pH differences between the two soil types affect phosphorus forms and stability, influencing its accumulation (Condron and Newman, 2011). The altitude factor reflects integrated changes in hydrothermal conditions, plant community composition, litter properties, microclimate, and soil physicochemical properties along altitudinal gradients. High nutrient accumulation in high-altitude acidic soils of the Lijiang River Basin is consistent with findings by Li et al. (2016) and Lin et al. (2019). In subtropical forest soils, organic matter and nutrient contents vary with altitude, influenced by both climatic factors and vegetation types, while organic matter decomposition rates are also constrained by nutrient limitation due to higher carbon:nitrogen and carbon:phosphorus ratios (He et al., 2016). Furthermore, well-preserved primary forests at high altitudes in the Lijiang River Basin have large vegetation biomass, and substantial inputs of plant and animal residues facilitate nutrient accumulation (Song et al., 2016).

Compared to natural ecosystems, anthropogenic land use altered soil nutrients to varying degrees, with substantial differences related to soil and vegetation types. This study found that acidic soils in the Lijiang River Basin responded more significantly to vegetation type changes, while calcareous soils showed lower nutrient sensitivity. This may be attributed to the higher acid buffering capacity of calcareous soils and the high stability of abundant organic matter-calcium complexes, which facilitate organic carbon accumulation and formation of water-stable aggregates (Wu et al., 2018). Similarly, Tian et al. (2019) found that soil organic matter and total phosphorus varied little among different vegetation types in karst areas of Huajiang, Guizhou, while natural forests had higher total nitrogen than other vegetation types, indicating that karst natural forests have advantages in promoting soil nutrient accumulation. On the other hand, anthropogenic management increased readily available nutrient contents through fertilization, most evident in rice paddies with the strongest human intervention (Liao et al., 2016). Meanwhile, tillage improved aeration and promoted organic matter mineralization (Tao et al., 2017), thereby increasing NH and AP contents.

3.2 Effects of Natural Factors and Vegetation Type Changes on Soil Extracellular Enzyme Activities and Stoichiometry

Differences in soil nutrient contents and transformation across soil and vegetation types are controlled by extracellular enzymes secreted by plant roots and soil microorganisms (Zhou and Wang, 2016; Sun et al., 2021). This study found that enzyme activities were higher in high-altitude soils and positively correlated with soil TN and TP, consistent with results from Nie et al. (2018) and Zhou et al. (2019), indicating that abundant nutrients at high altitudes drive high enzyme activities. Conversely, catalase activity was significantly higher in low-altitude soils, inconsistent with findings by Yuan et al. (2013) and Yao et al. (2019). Since catalase is an important oxidoreductase that alleviates hydrogen peroxide stress from pollution (Shi et al., 2012; Zhou et al., 2020), this pattern reflects microbial responses to pollution stress in low-altitude soils. Nitrogen-transforming enzyme activities decreased sharply with decreasing altitude, indicating nitrogen limitation in high-altitude soils and carbon limitation in low-altitude soils with reduced organic matter content. Soil pH influences enzyme activities by altering nutrient bioavailability (Sun et al., 2021). This study found that near-neutral pH in calcareous soils resulted in higher nutrient bioavailability and stronger enzyme activities, reflecting greater mineralization potential (Curtin et al., 1998), as confirmed by CCA showing pH positively correlated with enzyme activity as the second most important factor explaining variation. Comparison between natural and artificial forests revealed a shift from nitrogen to carbon limitation, with enzyme stoichiometry more affected by vegetation type than soil type, indicating that anthropogenic activity is a key factor driving shifts in nutrient limitation. Under human disturbance, vegetation type changes cause soil organic carbon loss (Yang et al., 2003; Lai et al., 2016). Litter quantity and quality are major factors affecting soil enzyme stoichiometry (Luan et al., 2020), and changes in litter inputs alter soil organic matter input-accumulation and nutrient status, thereby affecting mineralization rates (Gillis and Price, 2016). Additionally, anthropogenic activities directly increase nutrients such as nitrogen and phosphorus, reducing microbial demand for nutrient acquisition through enzyme secretion, so human land use has greater impacts on nitrogen-cycling enzyme activities (Zheng et al., 2020).

This study addressed the high spatial heterogeneity of altitude, vegetation, and soil types in the Lijiang River Basin by comparing acidic and calcareous soils from high to low altitudes under natural and artificial forest conditions. The findings reveal that: (1) Altitude, soil type, and vegetation type are the main factors affecting soil nutrient contents and enzyme activities in the Lijiang River Basin. (2) High-altitude forest soils have high nutrient contents and extracellular enzyme activities, showing ecosystem nitrogen limitation characteristics. (3) Acidic soil nutrients are more susceptible to anthropogenic disturbance, while calcareous soils have higher TP and AP contents and stronger resistance to human interference. (4) In low-altitude areas, conversion to artificial vegetation types drives a shift from nitrogen to carbon limitation in soil enzyme activities, with TN, pH, and NH being the main factors influencing enzyme activities. This demonstrates that anthropogenic use both increases exogenous nitrogen supply and causes soil fertility loss. The study reveals high ecological sensitivity of acidic soils in the Lijiang River Basin, suggesting that conservation measures should focus on maintaining soil fertility to enhance sustainable conservation and utilization of natural landscape resources.

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Note: Figure translations are in progress. See original paper for figures.