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Plant nitrogen and phosphorus utilization under invasive pressure in a montane ecosystem of tropical China

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Abstract

1. Exotic plant invasion has been changing the vegetation composition and function of terrestrial ecosystems. Nitrogen (N) and phosphorus (P) are often the limiting nutrients for terrestrial plants. However, under invasive pressure, in situ plant N and P usage mechanisms remain poorly understood but are pivotal for a better understanding of plant invasion and coexistence in invaded ecosystems.
2. Nitrogen and P concentrations, natural ^{15}N abundance (δ^{15}N values) were investigated in leaves and soils under different invasive pressures (here expressed as the biomass percentages of invasive plants in each plot) for two invasive species (*Chromolaena odorata* and *Ageratina adenophora*) in Xishuangbanna in tropical China.
3. Soil N and P concentrations revealed the relatively N-rich but P-poor status of our study site. Under invasion, soil inorganic N (dominated by ammonium) and available P did not increase significantly. The leaf N and P of invasive plants increased, while leaf N increased but P decreased for native species. Natural δ^{15}N mass balance between leaves and soil inorganic N sources revealed that ammonium dominated N utilization in both natives and invaders. Invasive plants showed ammonium utilization with increasing leaf N levels, while native plants under no invasion showed nitrate utilization with increasing leaf N levels.
4. *Synthesis*. Increased soil ammonium availability contributed to preferential ammonium utilization by invasive plants and elevated ammonium utilization in natives, but the P competition of natives decreased in invaded ecosystems. These novel insights into nutrient dynamics in invaded ecosystems enhance our understanding of plant invasion and coexistence mechanisms.

KEYWORDS
ammonium preference, biodiversity, ecological stoichiometry, exotic plant invasion, phosphorus, plant coexistence, soil nitrogen availability, stable nitrogen isotope

1 | INTRODUCTION

Human-induced global change, such as elevated nitrogen (N) deposition, land use changes and global warming, promotes the invasion of exotic plants (Dukes & Mooney, 1999). Exotic plant invasion is also an important driving force for changes in the structure and function of terrestrial ecosystems such as biodiversity, nutrient cycling and the survival of native species (Ehrenfeld, 2003). In many regions, exotic plant invasion has resulted in irreversible biodiversity decline due to the disappearance of native species, and subsequent

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ecosystem instability through drastic changes in vegetation composition and productivity, depending on the invasive pressure (Hooper et al., 2005). Decreasing diversity of native species is often coupled with increasing productivities of invasive plants imposing invasive pressure on plant–soil systems (Ehrenfeld, 2003; Rout & Callaway, 2009).

Many previous studies have sought to understand why exotic plants can successfully invade new ecosystems and provoke a variable response among native species with some native plants disappearing while others coexist successfully with the invaders (Shea & Chesson, 2002). In general, a successful invasion of exotic plants is a function of both the invasiveness of exotic plants and invasibility of target environments (Milbau, Nijs, Lvan, Reheul, & Bde, 2003). Of the resources required for plant growth, it is critical to succeed in nutrient competition and assimilation to satisfy growth and biomass production, particularly for the invasive plants (Ehrenfeld, 2003; Vitousek, Porder, Houlton, & Chadwick, 2010). The failure to compete for limited or preferred nutrients is also an important reason for the disappearance of native species (Valliere, Irvine, Santiago, & Allen, 2017). Both invaders and co-occurring natives may adjust nutrient use strategies to maintain or improve their survival or adapt to limited resources in the invaded ecosystems (González et al., 2010). Therefore, the status/availability of soil nutrients and plant nutrient use are important to understand plant invasion and coexistence mechanisms.

Nitrogen and P are the most common limiting nutrients for terrestrial plants (Elser et al., 2007; Vitousek et al., 2010). The ability of invasive plants to use N and P is important aspects for the invasiveness (González et al., 2010; Sardans et al., 2017). Many controlled experimental studies have characterized distinctly high photosynthetic and growth rates in invasive plants (Feng et al., 2011) benefitting from higher uptake and utilization efficiencies (Feng et al., 2009; Funk & Vitousek, 2007; Sardans et al., 2017), and longer residence time (Laungani & Knops, 2009) in the use of N and P. Intensified N or P competition from exotic plant invasion may have negative impacts on N or P availability for co-occurring plants (Eller & Oliveira, 2017; Valliere et al., 2017). Both experimental and empirical studies suggest that N enrichment in soils will promote plant growth (Baruch & Goldstein, 1999). This, in turn, could increase the vulnerability of plants to other limiting resources P, e.g. enhanced P limitation under soil N load, especially in P-poor soils (Eller & Oliveira, 2017; Elser et al., 2007). However, field evidence for interaction between plant N and P utilization is still lacking in invaded ecosystems (Strayer, 2012). Most previous studies of plant N and P use strategies are based on compared or disturbed methods in artificial experimental settings that are different from natural invaded ecosystems. More evidence from field sites is needed to verify the in situ N and P use strategies of native and invasive species. In particular, it is important to study plant N and P utilization under different invasive pressures which is difficult to simulate accurately in artificial experiments.

As the important aspects of invasibility, higher N and P availabilities potentially improve the invasion potential and productivity of invasive plants (Milbau et al., 2003), and invasion itself can alter soil N and P cycles (Ehrenfeld, 2003; Lee et al., 2017; Sardans et al., 2017). A positive feedback between exotic plant invasion and soil nutrient availabilities has been demonstrated by higher N and P concentrations and net production rates of N and available P in soils under invasion (Ehrenfeld, 2003; Lee, Flory, & Phillips, 2012), and attributed to (a) increased litter input and decomposition rates associated with invasion (Jo, Fridley, & Frank, 2017; Lee et al., 2017) and (b) modified microbial function and composition associated with soil N transformations (such as ammonia-oxidizing bacteria; Hawkes, Wren, Herman, & Firestone, 2005; McLeod et al., 2016). However, the effects of invasion on soil nutrient availabilities can differ between ammonium (NH_4^+), nitrate (NO_3^-) and P, thus the chemical compositions of available N form and the stoichiometry of available N and P would be altered. The resultant effects on N and P competition would then influence the co-occurrence of natives and invaders (Eller & Oliveira, 2017). Interestingly, Rossiter-Rachor, Setterfield, Douglas, Hutley, and Cook (2009) observed that the invasion of *Andropogon gayanus* in northern Australia stimulated ammonification but inhibited nitrification in soil. Increased NH_4^+ but decreased NO_3^- in soils was assumed to satisfy the NH_4^+ preference of the invaders (Rossiter-Rachor et al., 2009) but the responses in N use of natives and the effects on P competition remain unclear. Therefore, it is necessary to explore responses of species-specific N and P utilization to soil N and P availabilities under different invasive pressures.

Natural N isotopes (expressed as δ^{15}N values) in plants and soils have been suggested as an effective tool to understand plant–soil N dynamics (Craine et al., 2009; Evans, 2001), thus can provide unique insights into changes in N acquisition and utilization under different soil N status for plant species in invaded ecosystems (Evans & Belnap, 1999; Rascher, Hellmann, Maguas, & Werner, 2012). Under invasion, changes in plant diversity and productivity influence soil N dynamics (Rascher et al., 2012; Sperry, Belnap, & Evans, 2006), which often results in higher inorganic N and δ^{15}N signatures in soil (Evans & Belnap, 1999; Kleinebecker et al., 2014). Typically, elevated N availabilities in soil have been attributed to higher N-turnover rates and N loss, resulting in ^{15}N enrichments due to preferential removal of ^{14}N losses (Amundson et al., 2003; Craine et al., 2009, 2015). In soils, plant-available N sources mainly include NH_4^+ and NO_3^- (particularly in nonarctic and nonboreal ecosystems) (Chapin, Matson, & Vitousek, 2011; Craine et al., 2009, 2015). The δ^{15}N values of soil NH_4^+ are often distinctly higher than that of NO_3^- because nitrification causes substantial ^{15}N enrichment in residual NH_4^+ and ^{15}N depletion in newly produced NO_3^- (Denk et al., 2017; Koba et al., 2010). When plant-available N is dominated by NH_4^+, plants may prefer NH_4^+ over NO_3^- (McKane et al., 2002). Plant N uptake via mycorrhizal can make leaf δ^{15}N lower than source δ^{15}N (by −2.0‰, −3.2‰, −5.9‰ for plants associated with arbuscular mycorrhizae [AM], ectomycorrhizae, ericoid mycorrhizae, respectively; Craine et al., 2009), which should be considered when interpreting leaf δ^{15}N for plant N sources (Hobbie & Högberg, 2012). Thus, leaf δ^{15}N can be used to characterize plant-available N in soil and N preference among coexistence plants (Houlton, Sigman, Schuur, & Hedin, 2007; Rascher et al., 2012).

Chromolaena odorata and *Ageratina adenophora* are perennial herbs native to Mexico but noxious invasive herbs in Asia, Oceania, Africa, Europe and the USA (Feng et al., 2009). In the 1940s, they first entered the mainland of China at Xishuangbanna, and have constituted a severe ecological problem since the 1950s (Feng et al., 2009). In common garden experiments, Feng et al. (2009) observed that *A. adenophora* allocated less N to cell walls (defence) and more N to photosynthesis (growth). This behaviour promotes increased light-saturated photosynthetic rates and growth. In addition, modification of the structure and function of soil microbial communities is an important part of the *A. adenophora* invasive strategy observed in both field and greenhouse experiments which, in turn leads to higher availability of N and P in soil (Niu, Liu, Wan, & Liu, 2007; Xiao, Feng, Schaefer, & Yang, 2014; Yu, Yu, Lu, & Ma, 2005). Currently, there are no explicit studies of plant diversity loss and productivity enhancement as a function of invasive pressure. Similarly, we lack in situ evidence of altered soil N dynamics, plant N and P availabilities and N preference in response to invasive pressure. Furthermore, both *C. odorata* and *A. adenophora* cause severe invasion in diverse habitats, but there are few studies, especially for *C. odorata*, of the N and P use in both species in the same location. To address this gap in knowledge, we investigated the species richness, above-ground biomass and leaf and soil N and P concentrations and δ^{15}N values in tropical ecosystems without invasion and with different invasive pressures of exotic Compositae plants (*C. odorata* and *A. adenophora*) in Xishuangbanna, SW China. The study is predicated on two testable hypotheses: (a) invasive plants have higher leaf N and P levels than natives through both their enhanced competitional abilities and the increasing of soil N and P availability under invasion (Ehrenfeld, 2003; Lee et al., 2012; Sardans et al., 2017); and (b) invasion affects native species beneficially in terms of N use while P use is compromised in the relatively N-rich but P-poor environment. Verification of these nutrient utilization responses has important implications for the understanding of invasion and coexistence.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted at Mt. Kongming (101.12°E, 22.14°N) in the Xishuangbanna, Yunnan province, SW China. Our study site is on the summit of the mountain at an altitude of 1,100 ± 10 m and has a gradual slope of <10°. The site is pristine with no agricultural or other human disturbance. The site has a subtropical monsoonal climate, with mean annual temperature and mean annual precipitation of 21°C and 1,600 mm, respectively. The soil and bedrock are yellow soil and limestone rock, respectively.

The native vegetation at the summit of Mt. Kongming was dominated by herbaceous and graminoid plant species, with few deciduous and evergreen shrubs and occasional conifer forest (mainly *Pinus massoniana* Lamb.). Most of the native species in our study site are widely distributed in tropical and subtropical China. The main reason for selecting this site was that *C. odorata* and *A. adenophora* have formed obvious different invasive pressures, respectively, this is uncommon in a place with uniform climatic and environmental conditions. Therefore, it is an ideal place to explore in situ nutrient dynamics of invasive and native plants related to invasive pressure and soil nutrient availability.

2.2 | Sample collection

We established three experimental blocks on three low hills at the Mt. Kongming research site, with areas of about 100 m × 100 m and altitudes of about 1,100–1,130 m for each block. The distance between the three blocks is about 50–80 m. In each block here are obvious patches of *C. odorata* invasion (about 20 m × 20 m), *A. adenophora* invasion (about 20 m × 20 m) and no invasion (about 10 m × 10 m). Plots of no invasion and plots with different invasive pressures were selected in corresponding patches. Native plants in noninvaded patches were dominated by family of Poaceae, Euphorbiaceae, Rubiaceae, Rosaceae, Malvaceae and Cyperaceae (Table S1). Native plants were noticeably less abundant in the invasion patches.

Before sampling, we conducted the measurements of above-ground biomass and species compositions based on a subjective judgement of no invasion, light invasion and severe invasion, with seven plots for each. The above-ground biomass and species composition of plants were investigated in July of 2011 for all seven plots (1 m × 1 m for each) in no invasion patches of three blocks (3, 2, 2 plots for each), fourteen plots (1 m × 1 m for each) in *C. odorata* invasion patches of three blocks (5, 5, 4 plots for each) and fourteen plots (1 m × 1 m for each) in *A. adenophora* invasion patches of three blocks (5, 5, 4 plots for each). The biomass materials harvested from above-ground were separated by plot and plant species and dried at 105°C for 30 min until a constant weight was reached at 75°C. The plot-based biomass and presence of each species were used to calculate those of no invasion and invasion, thus replicate number of species-specific values is at most equal to plot number. After getting the data for biomass and species compositions, however, we found that the biomass percentages of invasive plants in invaded plots can more accurately express the invasive pressure than the simple comparison between light and severe invasion. Therefore, the total number of invasion plots were 14 for each invasive species, which is more than that (seven) no invasion plots.

Our drying protocol for the biomass measurements involved drying at temperatures much higher than that recommended for leaf δ^{15}N analyses, e.g. Brearley (2009) found that drying plant materials >60°C can affect the δ^{15}N signatures to a significant degree. Also, soil samples were not collected simultaneously to those used for the biomass measurements. Consequently, the plant samples used for biomass measurements were not used for N analyses in our study. Instead, on the basis of the plant biomass and species composition results, a new set of leaf and soil samples (for 0–20 cm of mineral layer) for chemical and isotopic analyses were collected in new plots adjacent to corresponding types of no invasion, light invasion and severe invasion patches. Such specific sampling regime for

δ^{15}N analyses was also adopted in Kleinebecker et al. (2014). In our study, mature and green leaves of dominant species were sampled for totally three plots (2 m × 2 m for each) in no invasion patches of three blocks (one plot for each), six plots (2 m × 2 m for each) in *C. odorata* invasion patches of three blocks (two plots for each) and six plots (2 m × 2 m for each) in *A. adenophora* invasion patches of three blocks (two plots for each). To obtain adequate sample amount for analyses in this study, leaf samples of each species were aggregated from multiple individuals to generate into one sample per species for each plot. Thus, the number of species-specific leaf samples is at most equal to the plot number (≤3 under no invasion, ≤6 under invasion), depending on their presence. For soils, four replicate samples were sampled for each plot. The main reason that fewer plots were sampled for chemical analyses (totally 15 plots) than for biomass measurements (totally 35 plots) was to minimize destruction of the field site (especially soil sampling). The 15 plots adjacent to plots sampled for chemical analyses have consistent variations of biomass and species number for all 35 plots (Figure 1). Accordingly, the invasive pressure of those 15 plots was used for interpreting chemical parameters.

2.3 | Chemical analyses

Within 8 hr after sampling, sample pretreatments were conducted in the laboratory at the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, China. After strictly washing, leaf samples were oven-dried at 60°C until a constant weight was achieved and then ground to fine powder using a ball mill (MM200; Retsch, Haan, Germany) in preparation for analysis of N and P concentrations and δ^{15}N. Fresh soil samples were passed through a 2-mm mesh sieve to remove impurities and coarse fragments (e.g. roots, sands and rocks). Part of the sieved soil was dried at 105°C to constant weights for measuring water contents. Part of the sieved soil was immediately extracted using 2 M KCl solution for measuring concentrations and δ^{15}N values of dissolved inorganic N (DIN; NH_4^+ plus NO_3^-). Part of the sieved soil was air-dried for analysing available P. The remaining sieved soil was oven-dried and then ground to fine powder using a ball mill (MM200; Retsch) for analysing total N (TN) and δ^{15}N values, available P and total P (TP) concentrations.

Briefly, 8 g soil in 40 ml KCl solution was shaken for 1.5 hr and then centrifuged. The supernatant was filtered using a glass filter (GF/F; Whatman Int. Ltd., Maidstone, UK) and frozen at −20°C until analyses. The KCl salts and filters were heated to 450°C for 4 hr to reduce the N blank before use. The NH_4^+ concentrations in soil extracts were determined by the indophenol blue method followed by colorimetry, and the NO_3^- concentrations was colorimetrically determined using an autoanalyser (SKALAR San plus; Skalar, Breda, the Netherlands).

Soil available P was extracted with 0.5 M $NaHCO_3$ (extractant/soil ratio was 20:1) after shaking for 30 min. Samples were filtered through a 0.45-μm nonphosphorus filter papers. For TP, 0.25 g of pulverized dried soil samples was diluted with the acid mixture HNO_3 (60%) and H_2O_2 (30% w/w) and digested in a MARSXpress microwave system (CEM, Matthews, NC, USA). The digested solutions were brought to a final volume of 50 ml with ultrapure water and at 1.0% HNO_3. Both TP and available P in the filtrate were determined by the Molybdenum-blue method (Murphy & Riley, 1962). For leaf P, 10 ml of 36 N H_2SO_4 and 1 ml of $HClO_4$ were added to a 0.8 mg leaf sample and heated at 360°C for 4 hr. After this mineralization step, P concentrations were measured on a spectrophotometer using the Molybdenum-blue method (Murphy & Riley, 1962).

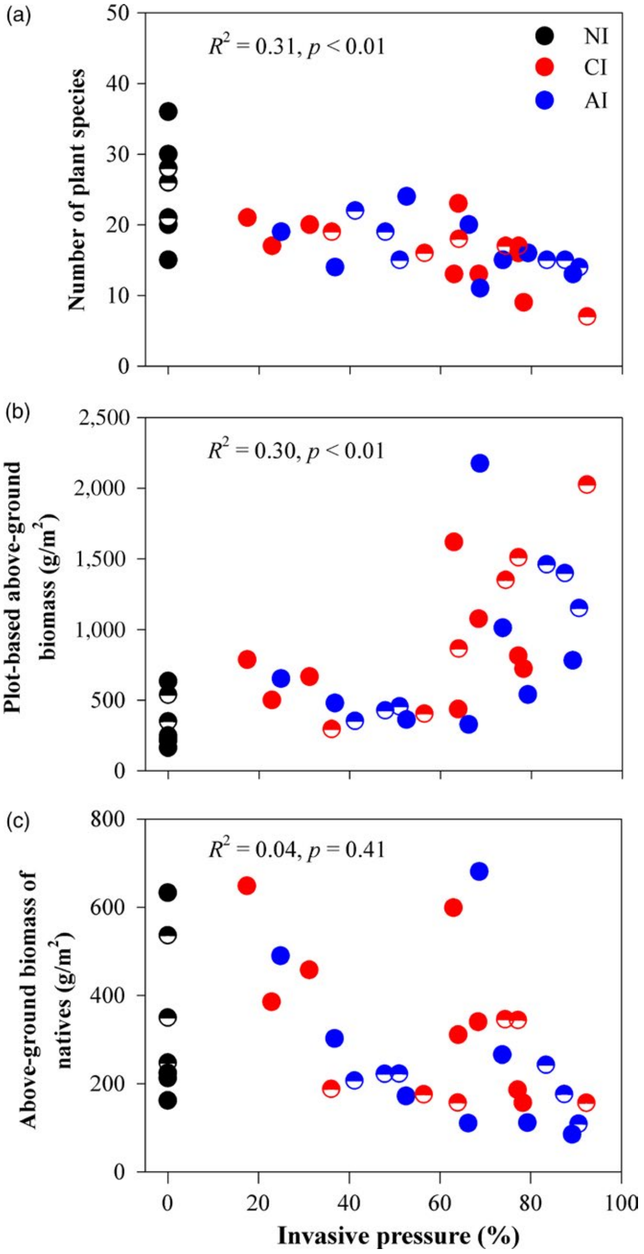

FIGURE 1 Variations of (a) plant species number, (b) total above-ground biomass of all plants and (c) total above-ground biomass of native plants with the invasive pressure. Semifilled cycles showed plots adjacent to those sampled for nutrients analyses. NI, no invasion; AI, *Ageratina adenophora* invasion; CI, *Chromolaena odorata* invasion [Colour figure can be viewed at wileyonlinelibrary.com]

Total N concentrations (%, dry weight) in leaves and soil samples were determined using an elemental analyser (Elementar Analysensysteme GmbH, Germany). Based on N contents, total $\delta^{15}N$ values of about 50 μg N in each leaf and soil sample were determined by a Thermo MAT 253 isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany) coupled with an elemental analyser (Flash EA 2000). IAEA-N-1 (Ammonium sulphate; $\delta^{15}N = 0.4‰$), USGS25 (Ammonium sulphate, $\delta^{15}N = -30.4‰$) and IAEA-NO-3 (Potassium nitrate; $\delta^{15}N = +4.7‰$) were used as standards for the calibration of $\delta^{15}N$ values. The average standard deviation of triplicate analyses of an individual sample for total $\delta^{15}N$ of leaf and soil was ±0.1‰.

The $\delta^{15}N$ values of NO_3^- and NH_4^+ were measured for soil extract samples with adequate amounts and N concentrations (Table 1). The $\delta^{15}N$ of NO_3^- was measured using the denitrifier method (Casciotti, Sigman, Hastings, Böhlke, & Hilkert, 2002; Koba et al., 2010; Sigman et al., 2001). The denitrifying bacteria (*Pseudomonas aureofaciens*; ATCC 13985) were used to convert NO_3^- in soil extracts into gaseous N_2O in 20 ml vials prior to isotopic analyses. Then, $\delta^{15}N$ values of the bacterial-converted N_2O were measured on a Delta V Advantage isotope ratio mass spectrometer coupled with GasBench II (Thermo Fisher Scientific) equipped with a Poraplot column (25 m × 0.32 mm × 10 μm), Precon (Thermo Fisher Scientific K.K.). We ran several standards (USGS-34, USGS-35 and IAEA-NO_3^-) to get the calibration curve for measured $\delta^{15}N$ values of our samples. We also analysed several samples of the KCl solution to correct for the $\delta^{15}N$ effect of the NO_3^- blank. The average standard deviations for replicate analyses of an individual sample were ±0.5‰ (*SD*) for $\delta^{15}N$ in NO_3^-.

The diffusion method was used to recover NH_4^+ from the soil extracts (Koba et al., 2010). Soil extracts were pipetted into a 10 ml glass vial (Chromacol, 125 × 20-CV-P210). A glass fibre filter (GF/D, 1 cm diameter, treated at 450°C for 4 hr; Whatman Int. Ltd.) acidified with 20 μl of 2 M H_2SO_4 and wrapped with Teflon tape was added to the vial. After the addition of 0.02 g of MgO (treated at 450°C for 4 hr), the vial was quickly closed with an aluminium crimp cap and a butyl rubber stopper. We used a constant volume (5 ml) for samples and standards to correct the $\delta^{15}N$ affected by the N blank from KCl and the reagents in this diffusion procedure. Several international standards (USGS-25, USGS-26 and IAEA-N-1) dissolved in the same KCl solution were diffused as samples to obtain the calibration curve. Several blank samples (5 ml of KCl solution) were also run in parallel for the blank correction. The vials were incubated at 40°C for 7 days using an oven-shaker with a horizontal shaking speed of 180 rpm. The concentrated NH_4^+ on the glass fibre filter was digested to NO_3^- using the method of persulfate oxidation, then the NO_3^- was converted to N_2O using the chemical methods as described by Lachouani, Frank, and Wanek (2010) and Liu, Fang, Tu, and Pan (2014). Briefly, the NO_3^- was reduced to nitrite (NO_2^-) by vanadium trichloride then to N_2O by sodium azide in a coupled reaction. The $\delta^{15}N$ of the produced N_2O was determined by an isotope ratio mass spectrometer (IsoPrime100; IsoPrime Limited, Stockport, UK) interfaced with TraceGas precon (IsoPrime Limited). The average standard deviation for triplicate analyses of an individual sample for the $\delta^{15}N$ of NH_4^+ was ±0.5‰.

The $\delta^{15}N$ values in leaves and soils were expressed in parts per thousand (per mille): $\delta^{15}N = (R_{sample}/R_{standard} - 1) \times 1{,}000$, where $R = {}^{15}N/{}^{14}N$ in samples and the standard (atmospheric N_2 and $R_{standard} = 0.0036765$).

2.4 | Isotope mass balance calculations of soil N contributions to plant N

Tropical and subtropical ecosystems usually have higher N cycling rates compared with high-latitude and high-altitude ecosystems where N mineralization and nitrification are generally lower and plants rely more on organic N sources (Elser et al., 2007; Liu et al., 2018; Vitousek et al., 2010; von Felten et al., 2009). Until now, most

TABLE 1 Concentrations (expressed as dry weight) of TN, TP, NO_3^--N, NH_4^+-N and available P, and $\delta^{15}N$ values of TN, NO_3^- and NH_4^+ in soils under no invasion, *Chromolaena odorata* invasion and *Ageratina adenophora* invasion. Values of Mean ± *SD* are shown. DIN: dissolved inorganic N. *n* (the number of replicate samples) were 3, 6 and 6 for no invasion, *C. odorata* invasion and *A. adenophora* invasion plots, respectively unless specified in the parenthesis

Soil N and P	No invasion	*C. odorata* invasion	*A. adenophora* invasion	*df*	*F*	*p*
TN (%)	0.3 ± 0.0	0.3 ± 0.1	0.3 ± 0.1	14	0.124	0.884
TP (mg/g)	0.44 ± 0.06	0.50 ± 0.09	0.89 ± 0.45	14	3.477	0.064
NO_3^- (mg-N/kg)	17.1 ± 2.1	16.9 ± 4.2	16.7 ± 2.4	14	0.016	0.984
NH_4^+ (mg-N/kg)	21.4 ± 7.1	29.4 ± 14.9	33.5 ± 13.8	14	0.811	0.467
NH_4^+-N/DIN (%)	54.5 ± 10.3	61.5 ± 5.8	64.1 ± 7.8	14	1.645	0.234
Available P (mg/kg)	3.6 ± 0.8	3.4 ± 1.7	5.4 ± 3.8	13	0.867	0.447
$\delta^{15}N$-TN (‰)	4.9 ± 0.1	5.8 ± 0.4	5.6 ± 0.7	13	2.646	0.115
$\delta^{15}N$-NO_3^- (‰)	−8.1 (1)	−8.0 ± 1.1 (3)	−7.4 ± 2.0 (4)	6	0.379	0.553
$\delta^{15}N$-NH_4^+ (‰)	10.8 ± 0.9 (2)	9.6 ± 1.1 (6)	9.9 ± 2.0 (5)	10	0.516	0.830

studies on plant N uptake in tropical ecosystems have stressed inorganic N due to its much higher availability than organic N (Andersen, Mayor, & Turner, 2017; Craine et al., 2009, 2015; Houlton et al., 2007). Moreover, plant dissolved organic nitrogen (DON) use was often demonstrated experimentally by the uptake of one or a few ^{15}N-labelled amino acids, which cannot elucidate the real availability of the whole soil DON pool to plants (Kahmen, Livesley, & Arndt, 2009), so that substantial uncertainties existed in the source contributions estimated by using the δ^{15}N of the whole DON pool (e.g. Liu et al., 2013). Consequently, we assume NH_4^+ and NO_3^- to be the dominant N sources for plants in tropical ecosystems (e.g. Andersen et al., 2017; Houlton et al., 2007), and use a δ^{15}N mass balance between leaf N and source N (referred to Houlton et al., 2007; Equation 1) to evaluate the fractional contributions of soil NH_4^+ (f_{NH4+}) and NO_3^- (f_{NO3-}) to plant N by considering isotope effects during plant N uptake and assimilation (ε).

$$\delta^{15}N_{leaf} = (\delta^{15}N_{NH4+} \times f_{NH4+} + \delta^{15}N_{NO3-} \times f_{NO3-}) - \varepsilon \qquad (1)$$

where $1 = f_{NH4+} + f_{NO3-}$ and $\varepsilon = \varepsilon_u + \varepsilon_i \times [L_{below}/(L_{above} + L_{below})]$. The ε_u denotes the isotope effects during root N uptake, ε_i denotes the isotope effects between N sources of the whole plant and leaves due to differing N allocation/assimilation between above- and below-ground tissues (Houlton et al., 2007). In our study, plant species were associated with AM that can make plant-assimilated N lower in δ^{15}N than soil N sources (ε_u = *c.* 2.0‰; Craine et al., 2009) or with no mycorrhizae that makes no isotope effect during N uptake (ε_u = 0.0‰; Craine et al., 2009). L_{above} and L_{below} represent above- and below-ground N losses, respectively, which are often assumed to be equal (Houlton et al., 2007). Because it is difficult to measure the whole-plant δ^{15}N values for many plants due to extensive destruction of roots and wood during sampling, isotope ecologists have proposed that the average δ^{15}N difference of 2‰ between leaves and roots across a diversity of plant species and ecosystems can integrate intraplant N assimilation and partitioning (Dawson, Mambelli, Plamboeck, Templer, & Tu, 2002; Hogberg, 1997; Houlton et al., 2007; Mayor, Wright, Schuur, Brooks, & Turner, 2014; Shearer & Kohl, 1986). Accordingly, the ε_i value has been evaluated as about 2.0‰ across different ecosystems (Dawson et al., 2002; Hogberg, 1997; Houlton et al., 2007; Shearer & Kohl, 1986). The mean values of $\delta^{15}N_{NH4+}$ and $\delta^{15}N_{NO3-}$ under no invasion, *C. odorata* invasion and *A. adenophpra* invasion (Table 1) were used to calculate f_{NH4+} and f_{NO3-} values (expressed as percentage values (%)) for each plant sample in corresponding plots.

2.5 | Evaluations of plant N preference

Plant NH_4^+ preference over NO_3^- (β_{NH4+}) was evaluated by using the f_{NH4+} minus corresponding proportional contributions of soil NH_4^+ in soil DIN (Equation 2).

$$\beta_{NH4+} = f_{NH4+} - ([NH_4^+]/[DIN]) \qquad (2)$$

where f_{NH4+} values were calculated from Equation 1, $[NH_4^+]$ and [DIN] were mean concentrations of NH_4^+ and DIN in soil of corresponding plots. Positive β_{NH4+} values indicate plant NH_4^+ preference over soil NO_3^-, 0 values indicate no preference, and negative β_{NH4+} indicate a plant preference for NO_3^- over NH_4^+ (more details in Liu et al., 2013).

2.6 | Statistical analysis

Pearson correlation analysis was used to examine the variation relationships of species number, above-ground biomass, leaf N, leaf P, leaf δ^{15}N, f_{NH4+}, β_{NH4+} by plot (overall mean with species lumped) with the invasive pressure, and the variations of leaf δ^{15}N, f_{NH4+}, β_{NH4+} with leaf N for different plants. We used a *T* test to determine significant differences of leaf N and leaf P between invasive plants and native plants under the same invasive pressure. Before analysis of the differences of plot-based soil TN, TP, available P, NH_4^+-N, NO_3^--N, DIN, δ^{15}N between no invasion, *C. odorata* invasion and *A. adenophora* invasion, raw data were assessed for normality and homogeneity using the Shapiro-Wilk's W-test and the Cochran's C-test respectively. Transformations were performed when necessary to satisfy assumptions. Tukey honest significant difference and least significant difference tests were used to identify significant differences between no invasion, *C. odorata* invasion and *A. adenophora* invasion. Statistical analyses were conducted using SPSS 16.0 for Windows (SPSS Inc., Chicago, IL, USA). Statistically significant difference was set at $p < 0.05$ unless otherwise stated.

3 | RESULTS

3.1 | Species richness and above-ground biomass

In total there were 107 species of native plants, belonging to 44 families (mainly Poaceae, Leguminosae, Asteraceae, Rubiaceae, Labiatae, Euphorbiaceae, etc) at the study site. The number of native species in no invasion plots and invasion plots ranged from 15 to 36 and 7 to 24 respectively (Figure 1a). Above-ground biomass of native plants in no invasion plots and invasion plots are 161–536 g/m^2 and 25–681 g/m^2 (Figure 1c). Among invaded plots, the above-ground biomass of *C. odorata* and *A. adenophora* varied distinctly from 207 g/m^2 to 1,868 g/m^2 and from 131 g/m^2 to 1,493 g/m^2 (Figure 1b). The biomass percentages of *C. odorata* or *A. adenophora* in each invaded plot were calculated to express the invasive pressure. The number of native species decreased while total plot-based biomass increased with invasive pressure (Figure 1a,b), and no clear changes were observed for the above-ground biomass of native plants along with invasive pressure (Figure 1c). In total, dominant native plants sampled for nutrient analyses include 35 species in no invasion plots and 25 species in invasion plots (detailed in Table S1). Adjacent plots in the same patches were considered having the same the invasive pressure (detail in Figure 1).

3.2 | Soil N, P concentrations and δ^{15}N values

Concentrations of soil N (NO_3^-, NH_4^+ and TN) and P (available P, TP), δ^{15}N values of soil NO_3^-, NH_4^+ and TN are shown in Table 1, and their variations with the invasive pressure are shown in Figure S1.

No statistical differences were observed for above soil nutrients and δ^{15}N values between no invasion, *C. odorata* invasion and *A. adenophora* invasion (Table 1).

3.3 | Leaf N, P concentrations and δ^{15}N values

No significant difference in leaf N and P concentrations was observed between *C. odorata* and *A. adenophpra* (Table S2). However, both showed higher leaf N and P concentrations than native plants, on average 2.1 times for N and 1.6 times for P when compared with natives under no invasion, and 2.0 times for N and 2.2 times for P when compared with co-occurring natives (Table S2). Leaf N and P of both invasive species increased with invasive pressure, but only leaf N showed such a trend for native plants (Figure 2). Under the same invasive pressure, both invasive plants had generally higher leaf N and P than their co-occurring natives (Figure 2). When leaf N and P differences between invasion and no invasion were calculated for the same native species (using leaf N or P concentrations of native plant samples in invasion plots minus the average leaf N or P concentrations of the same species in no invasion plots), most co-occurring natives showed increased leaf N (by 0.2 ± 0.3% for 17 out of 19 species under *C. odorata* invasion; by 0.2 ± 0.1% for 14 out of 18 species under *A. adenophpra* invasion; Figure 3a), but showed decreased leaf P (by 0.07 ± 0.04% for 16 out of 19 species under *C. odorata* invasion; by 0.06 ± 0.04% for 13 out of 18 species under *A. adenophpra* invasion; Figure 3b). Moreover, most of native plants and invasive plants showed increased leaf N but decreased leaf P concentrations under relatively higher invasive pressures (Figure S2a–d).

Leaf δ^{15}N values did not differ between *C. odorata* (0.2 ± 2.1‰) and *A. adenophora* (1.1 ± 2.8‰). Native plants showed leaf δ^{15}N values of −1.4 ± 1.1‰ under no invasion, −0.5 ± 1.8‰ under *C. odorata* invasion and −1.3 ± 1.3‰ under *A. adenophora* invasion (Table S2). Under the same invasive pressure, both invasive plants had generally similar leaf δ^{15}N values with their co-occurring natives (Figure 4a). With the increases of invasive pressure, however, both invasive species and natives showed increasing leaf δ^{15}N values (Figure 4a). Moreover, leaf δ^{15}N correlated negatively with leaf N for natives under no invasion (Figure 5a). By contrast, there was no clear relationship between leaf δ^{15}N and leaf N for native plants under invasion (Figure 5b), and leaf δ^{15}N correlated positively with leaf N for invasive plants (Figure 5c).

3.4 | Fractional contributions of soil N sources and N preference in plants

The $f_{\mathrm{NH4+}}$ values were 66.8 ± 16.0% for *A. adenophpra* and 63.7 ± 11.9% for *C. odorata*, 50.5 ± 7.9% and 54.6 ± 10.2% for native plants under no invasion and under invasion, respectively

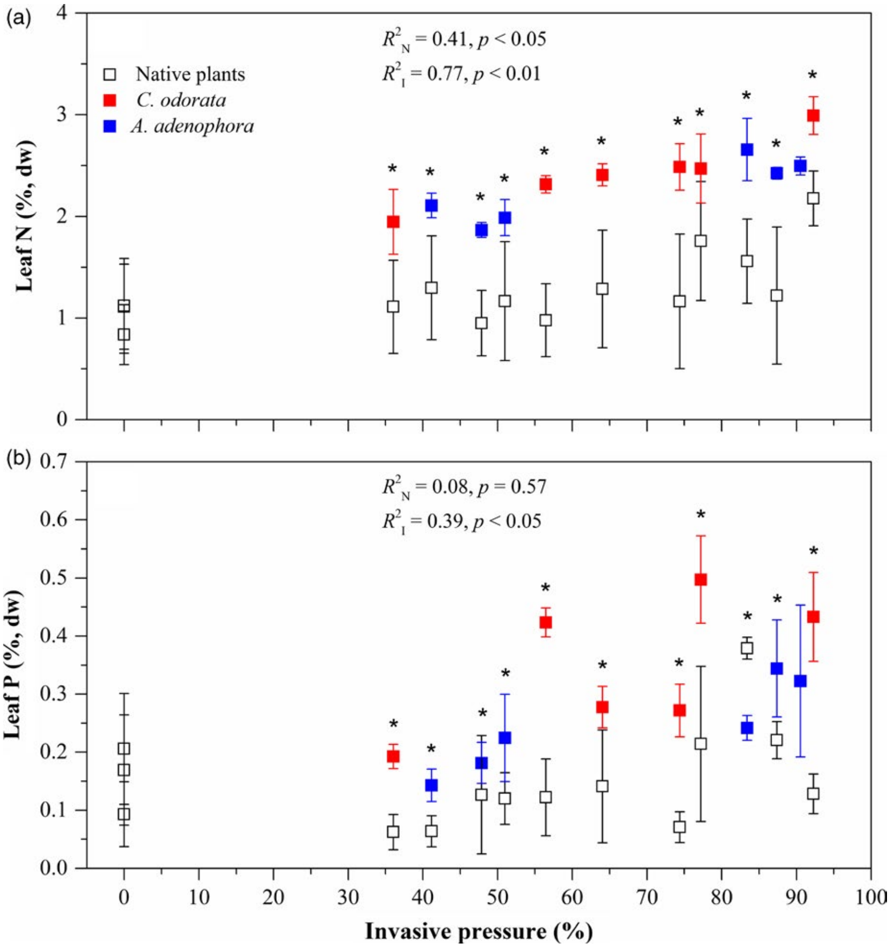

FIGURE 2 Leaf N (a) and P (b) variations of *Ageratina adenophora*, *Chromolaena odorata* and native plants with the invasive pressure. Mean ± *SD* value was calculated for plants (*n* = 3–4 for invasive plants, 2–24 for natives) in each plot. R^2_N and R^2_I show correlation coefficients for native and invasive plants respectively. The asterisk above the error bars indicates a significant difference between values of invasive and co-occurring plants under the same invasive pressure at the level of $p < 0.05$ [Colour figure can be viewed at wileyonlinelibrary.com]

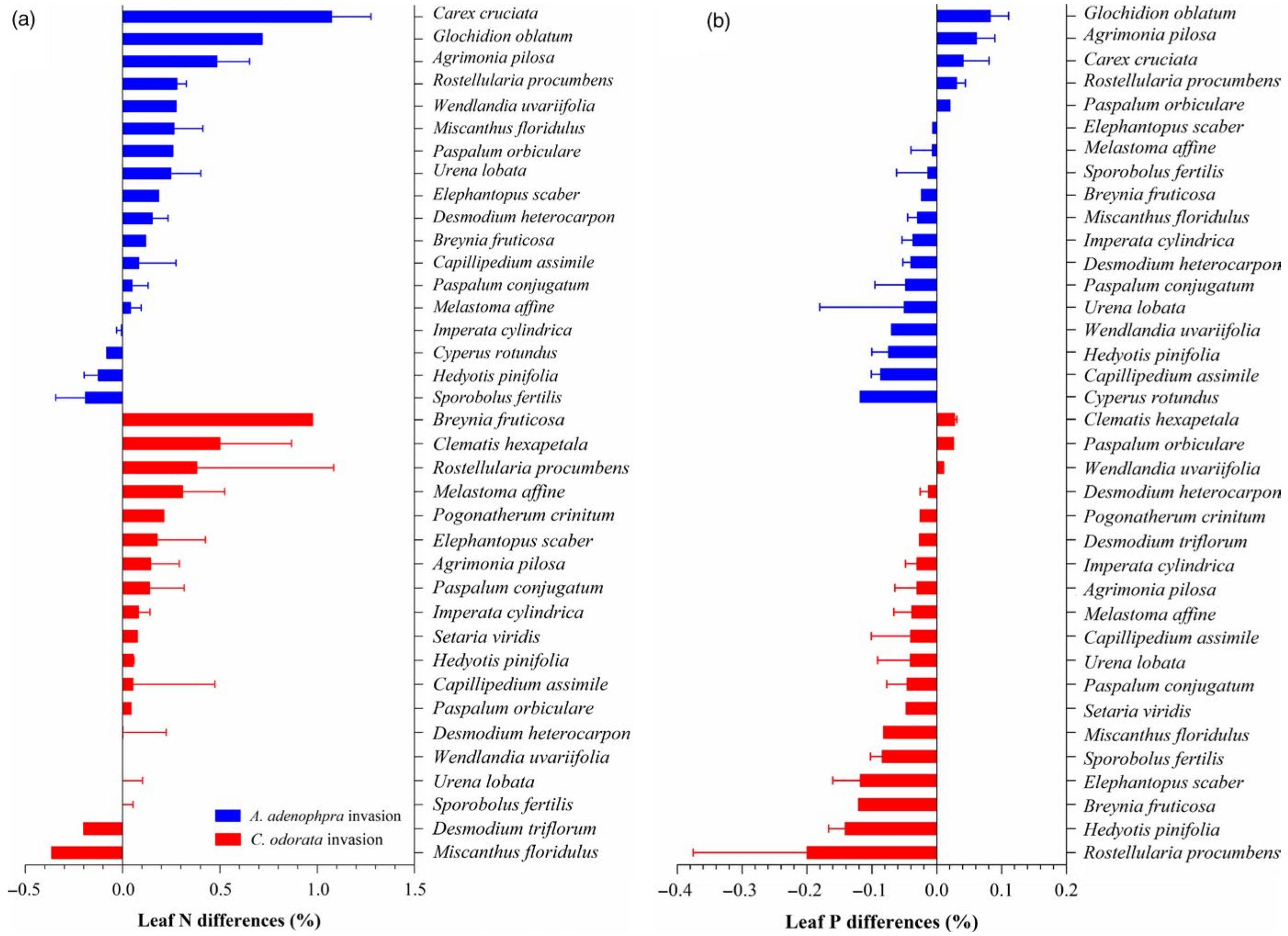

FIGURE 3 Leaf N (a) and P (b) differences of the same native species between invasion and no invasion plots. The values of differences were calculated by using leaf N or P concentrations of native plant samples (*n* = 1 – 6) in invasion plots minus the average leaf N or P concentrations of the same species in no invasion plots. The bars and whiskers show mean and *SD* values, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

(Table S3). Moreover, the $f_{\mathrm{NH4+}}$ values increased with the invasive pressure for both invasive and native plants (Figure 4b). Most of native plants and invasive plants showed increased $f_{\mathrm{NH4+}}$ under relatively higher invasive pressures (Figure S2e,f). Because $\mathrm{NH_4^+}$ also dominated in soil DIN and increased for soils with invasion (Table 1), the $f_{\mathrm{NH4+}}$ and $f_{\mathrm{NO3-}}$ values could not directly be used to evaluate plant preference for $\mathrm{NH_4^+}$ or $\mathrm{NO_3^-}$.

In this study, $\beta_{\mathrm{NH4+}}$ values were 0.01 ± 0.17 for *A. adenophpra*, 0.02 ± 0.13 for *C. odorata*, −0.04 ± 0.13 and −0.07 ± 0.11 for native plants under no invasion and under invasion respectively (Table S3). The $\beta_{\mathrm{NH4+}}$ values increased with the invasive pressure for invasive plants, but not for native plants (Figure 4c).

4 | DISCUSSION

4.1 | Species richness and productivity

In nondisturbed ecosystems, net primary productivity often increases with species richness and functional group diversity, due to the differentiation of niche and resources utilization (Hooper et al., 2005; McKane et al., 2002). Here, the invasion of *C. odorata* and *A. adenophora* had a dramatic effect causing a reduction in the number of native species but increased the above-ground productivity as invasive pressure increased (Figure 1). Invasive plants are often highly productive and dominate the net primary productivity in invaded ecosystems, which causes the decreases of native plants even to the extreme of no co-occurrence under severe invasion (Ehrenfeld, 2003). Mechanically, soil nutrient availabilities are often enhanced in the invaded ecosystems (Rout & Callaway, 2009; Sardans et al., 2017). Furthermore, we have not conducted long-term monitoring on the invasion, but according to our observations of species number and biomass (Figure 1), we infer that the invasive pressure might generally increase with the invasion history, which is an important factor in shaping ecosystem nutrient dynamics (Evans & Belnap, 1999; Funk & Vitousek, 2007). The spatial patterns of nutrient dynamics and plant nutrient use observed under different invasive pressures are likely to reflect their variations with the history of invasion. However, the nutrient utilization of invasive and

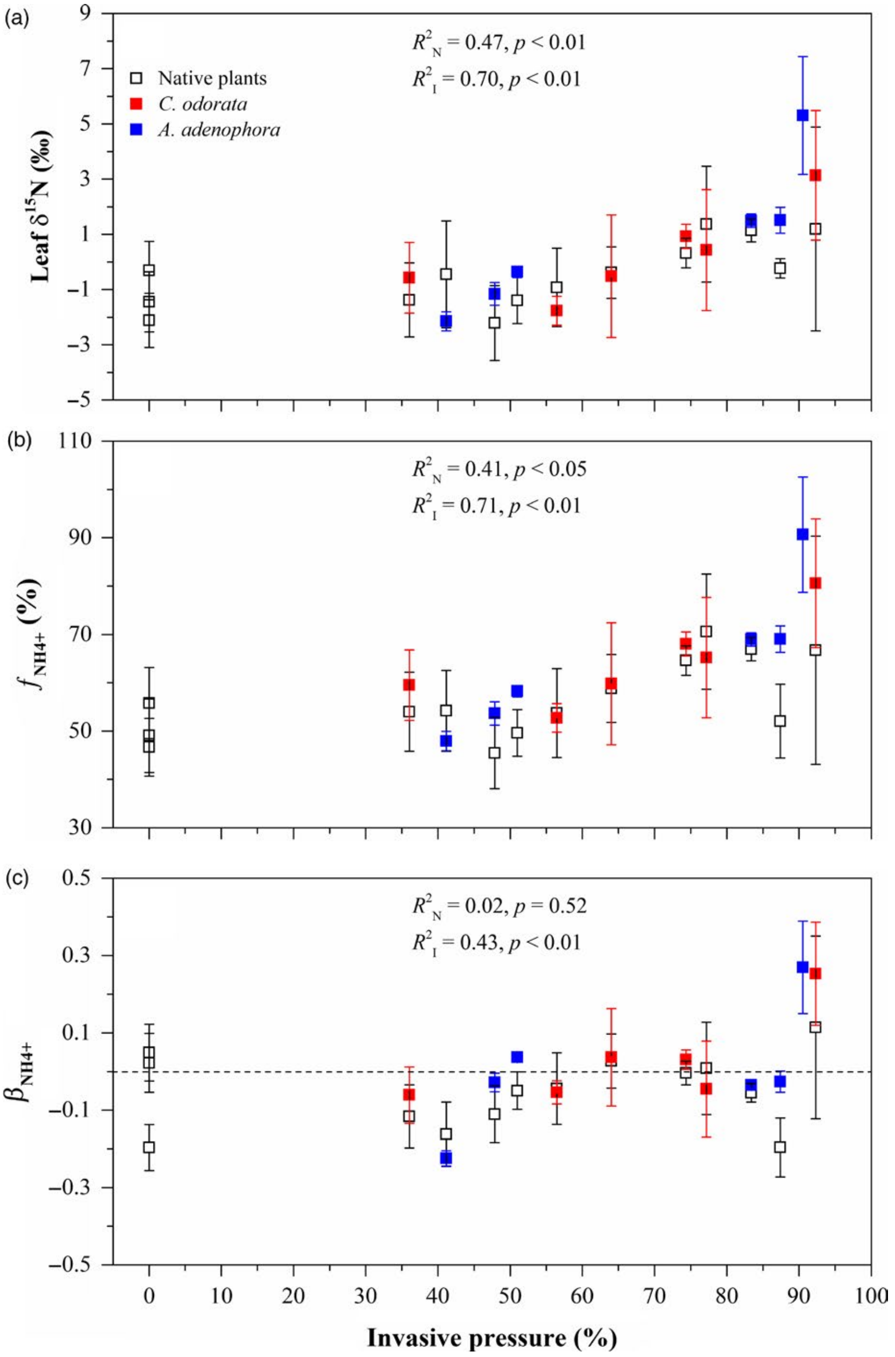

FIGURE 4 Variations of leaf δ^{15}N values (a), proportional contributions of soil NH$_4^+$ to plant N (f_{NH4+}) (b) and plant NH$_4^+$ preference over NO$_3^-$ (β_{NH4+}) (c) of *Ageratina adenophora*, *Chromolaena odorata* and native plants with the invasive pressure. Mean ± *SD* value was calculated for plants (*n* = 3–4 for invasive plants, 2–26 for natives) in each plot. R^2_N and R^2_I show correlation coefficients for native and invasive plants respectively [Colour figure can be viewed at wileyonlinelibrary.com]

native plants changes with invasive pressure has not been understood adequately and explicitly.

4.2 | Soil N and P status

Soil TN in this study (0.3 ± 0.0%; Table 1) distributed in high N levels of soils among China and other regions (Han, Fang, Guo, & Zhang, 2005; Yu et al., 2017), which is significantly higher than TN levels of natural soils reported in tropical and subtropical China (*c*. 0.1 ± 0.0%; reviewed by Tian, Chen, Zhang, Melillo, & Hall, 2010). However, soil TP in this study (*c*. 0.60 ± 0.30 mg/g; Table 1) was distinctly lower than those of other regions (e.g. 0.70 mg/g for the USA, Han et al., 2005; Reich & Oleksyn, 2004; US Geological Survey, 2001). Actually, soil TP in the whole of tropical and subtropical China (*c*. 0.58 ± 0.04 mg/g, Tian et al., 2010) are generally low, especially in southwestern China (<0.52 mg/g; Han et al., 2005), which has been attributed to high P leaching and occlusion associated with soil weathering in a warm, high precipitation climate (similar to the situation in Hawaii, Vitousek et al., 2010). Soil P was less abundant relative to N, which determined their availabilities to plants with different functional traits.

In this study, increased plant N and P availabilities in invaded ecosystems were shown by the increasing of soil available P (mainly under *A. adenophora* invasion) and NH$_4^+$ than noninvaded

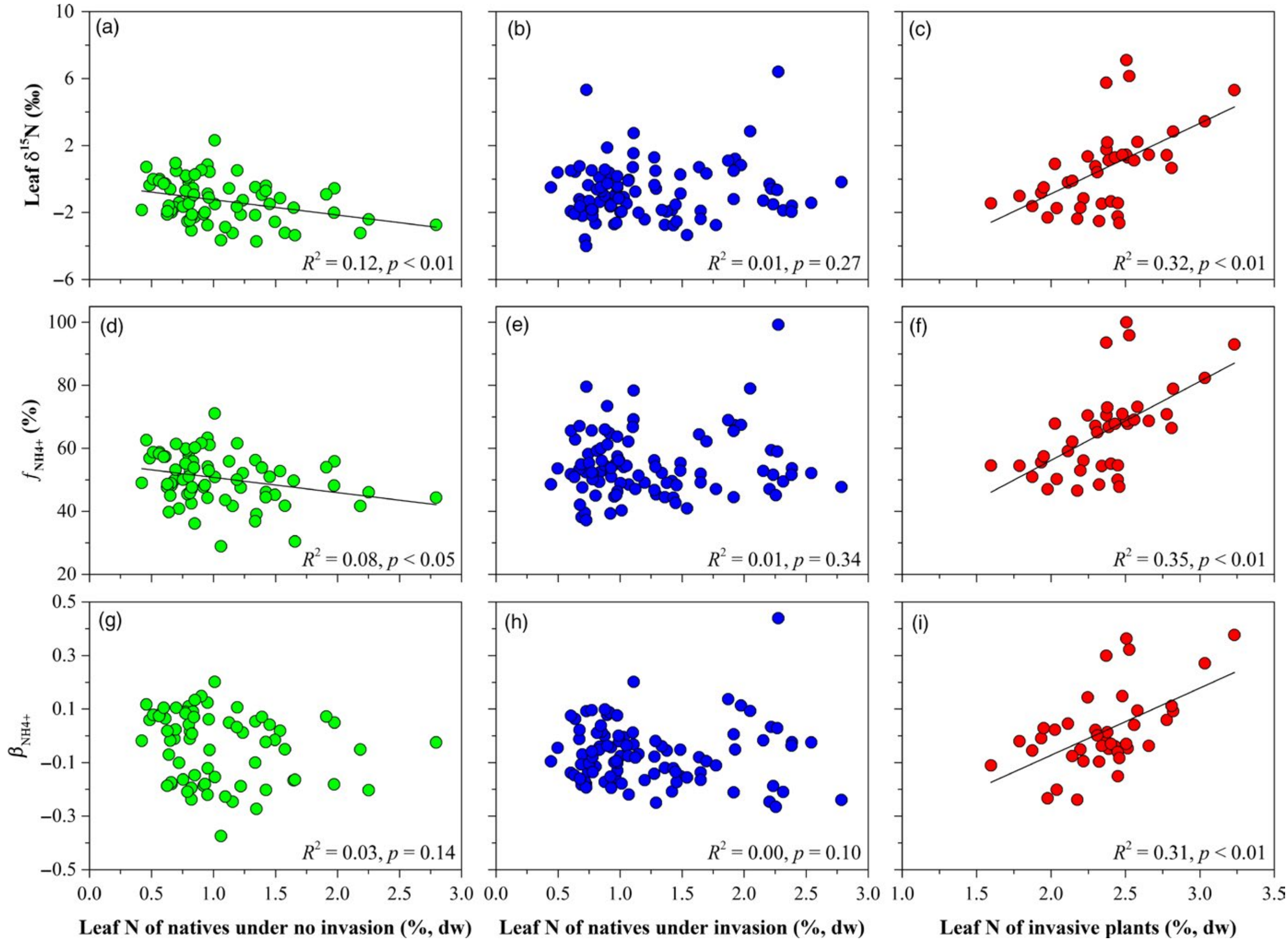

FIGURE 5 Variations of leaf $\delta^{15}N$ values, proportional contributions of soil NH_4^+ to plant N (f_{NH4+}) and plant NH_4^+ preference over NO_3^- (β_{NH4+}) with leaf N concentrations for native plants under no invasion (*n* = 70 for 30 species in total; a, d and g), native plants under invasion (*n* = 94 for 26 species in total; b, e and h) and invasive plants (*n* = 40; c, f and i) [Colour figure can be viewed at wileyonlinelibrary.com]

ecosystems (Table 1, Figure S1c–f). This is consistent with higher soil inorganic N and available P integrated for different invaded ecosystems at a global scale (see the meta-analysis of Sardans et al., 2017), and with microbial and enzymatic evidence from controlled experiments (Hawkes et al., 2005; Lee et al., 2012; McLeod et al., 2016). Our results are supported by the presence of more abundant microbial communities involved in soil N mineralization under the invasion of *A. adenophora* in SW China (Niu et al., 2007; Xiao et al., 2014; Yu et al., 2005). Elevated N mineralization was driven by increases in above-ground productivity (Figure 1b) and hence litter inputs in invaded ecosystems (Jo et al., 2017; Lee et al., 2017). For soil NO_3^-, higher concentrations in invaded ecosystems should have occurred due to the increasing of soil NH_4^+ (Table 1, Figure S1e,f) and higher abundance of ammonia-oxidizing bacteria which generate enhanced NO_3^- production rates in experimental simulation of *A. adenophora* invasion (Niu et al., 2007; Xiao et al., 2014; Yu et al., 2005). Unexpectedly, enhanced soil NO_3^- was not associated with invasion of this study (Table 1, Figure S1d). A possible mechanism could be loss of mobile NO_3^- from the invaded ecosystems via denitrification and leaching (Fang et al., 2015; Houlton, Sigman, & Hedin, 2006). Particularly, high precipitation in the study area may cause leaching to dominate NO_3^- losses from the surface soil and therefore no clear accumulation of NO_3^- in soils under invasion.

The increasing of soil $\delta^{15}N$ under invasion supported increased NO_3^- losses compared to no invasion (Table 1, Figure S1g). Mechanically, NO_3^- is typically depleted in ^{15}N due to the strong ^{15}N discriminations during nitrification (Denk et al., 2017; Koba et al., 2010). Our results also suggest nitrification as a major process regulating $\delta^{15}N$ signatures and the differences between NO_3^- and NH_4^+ (Table 1). Potentially, NO_3^- losses caused ^{15}N enrichment in soils under invasion because of enhanced mineralization, nitrification and plant preference for NH_4^+ (Amundson et al., 2003; Craine et al., 2015; Ometto et al., 2006). Similarly, soil $\delta^{15}N$ was increased by *Bromus* invasion because of faster litter decomposition, greater NO_3^- leaching from the invaded ecosystems and consequently higher NH_4^+ but stable NO_3^- concentrations were observed in surface soils (Sperry et al., 2006). The ^{15}N enrichment in soil N pools due to the losses of ^{15}N-depleted NO_3^- has also been observed in forests of the same region with our study site in tropical China (Fang et al., 2015). The increasing of soil NH_4^+ under invasion (but not for NO_3^-; Table 1, Figure S1d,e) is an important determinant of N use of co-occurring plants.

4.3 | Plants N and P uptake abilities

Leaf N and P levels are controlled by their availabilities in soil and the uptake abilities of specific plants (Ehrenfeld, 2003; Elser et al., 2007). Leaf N and P of *C. odorata* (2.4 ± 0.3% and 0.33 ± 0.11% respectively) and *A. adenophpra* (2.3 ± 0.3% and 0.24 ± 0.08% respectively; Table S2) were higher than those of terrestrial plants (1.9 ± 0.8% and 0.12 ± 0.10% for 753 species respectively) in China (Han et al., 2005), and plants globally 1,251 plants (1.8 ± 0.9% and 0.14 ± 0.11% respectively; Reich & Oleksyn, 2004). For *A. adenophpra*, the leaf N levels we observed resembled that observed in India (2.4 ± 0.2%), both of which were significantly higher than that observed in Mexico as a native species (2.0 ± 0.1%; Feng et al., 2011). Moreover, the higher uptake abilities of invasive plants were also confirmed by distinctly higher leaf N and P levels than natives under the same soil N and P conditions (Figure 2).

Previously, increased soil N availability, N uptake and photosynthetic N use efficiency have been recognized to promote the biomass accumulation and invasion of exotic plants (Baruch & Goldstein, 1999; Ehrenfeld, 2003; Fargione & Tilman, 2005; Gilliam, 2006). These strategies and mechanisms were also demonstrated in the growing study of *A. adenophpra* (Feng et al., 2009). However, increased soil N availability and N uptake in plants would enhance the demand for other nutrients especially P (Eller & Oliveira, 2017; Valliere et al., 2017; Wanek & Zotz, 2011). In our study, both productivities and leaf N and P levels of invasive plants increased with the invasive pressure (Figures 1b and 2). Presumably, this should have resulted in lower leaf N and P levels for natives. However, leaf N increased but leaf P decreased in co-occurring natives under relatively higher invasive pressures (Figure 3 and Figure S2), indicating that they have benefited in N availability and N uptake under the invasion. Most likely, the N competition between invasive and co-occurring plants was not exacerbated but both enhanced by the invasion. In contrast, P availability for co-occurring natives was lowered suggesting that P competition between invasive and native plants was exacerbated by the invasion. The P deficiency relative to N in the soil at our study sites supported the stronger P competition than N competition. Our results provide new evidence on lowered P availability for co-occurring plants due to the luxury consumption of soil N and P by invasive plants under P-poor conditions, which was proposed in a controlled study (Eller & Oliveira, 2017).

4.4 | Plants N sources and preference

Leaf N uptake and hence N concentrations would change with the availability of plant N sources (Ehrenfeld, 2003; Elser et al., 2007). Exotic plant invasion altered soil N availabilities thereby influencing the distribution of leaf N levels among co-occurring species (Hawkes et al., 2005; Lee et al., 2012). Both the N concentrations and $\delta^{15}N$ values of coexisting plants increased with the increasing of invasive pressure (Figures 2a and 4a) suggesting that both the uptake abilities and fractional contributions of ^{15}N-enriched N sources in plants increased with added invasive pressure. Clearly, the mean values of f_{NH4+} were higher than 50% for both native and invasive plants (Table S3) suggesting that soil NH_4^+ was the dominant N source for the plants investigated. Generally, invasive plants showed higher f_{NH4+} values than native plants, indicating the increased ability of invasive species to use soil NH_4^+. Increasing f_{NH4+} for both invasive and native plants indicates increasing soil NH_4^+ assimilation with increased invasive pressure (Figure 4b). Moreover, invasive plants showed positive β_{NH4+} values, but native plants showed negative β_{NH4+} values under both invasion and no invasion (Table S3). These results clearly suggested that invasive plants preferred NH_4^+ over NO_3^-, and native plants preferred NO_3^- over NH_4^+. Resembling the pattern of f_{NH4+} values (Figure 4b), the β_{NH4+} values increased with the invasive pressure only for invasive plants, but not for native plants (Figure 4c). This reveals a positive feedback of NH_4^+ assimilation and NH_4^+ preference of invasive plants to the invasive pressure. Previously, the NH_4^+ preference of invasive plants has been observed in few controlled experiments (Rossiter-Rachor et al., 2009). Excessive NH_4^+ uptake and assimilation can lead to intracellular pH decreases and ionic imbalance in plants (Britto & Kronzucker, 2002). Growing experiments with crops or model plants have observed chlorosis under high levels of NH_4^+ fertilization (Britto & Kronzucker, 2002). However, the importance of NH_4^+ toxicity remains unclear for plants in natural ecosystems, given that many plants are relying on NH_4^+ as a major N source and NH_4^+ was universally observed in the xylem saps to be transported from roots to shoots (Peuke, Gessler, & Tcherkez, 2013; Schjoerring, Husted, Mäck, & Mattsson, 2002). Mechanically, preferential NH_4^+ uptake and assimilation were associated with the high energy cost of NO_3^- reduction and the potential for avoiding excessive NH_4^+ accumulation (Kronzucker, Glass, & Siddiqi, 1999). In contrast, increases of soil N availability in many invaded ecosystems occurred in NO_3^- with preferential NO_3^- uptake in invasive plants (Ehrenfeld, Kourtev, & Huang, 2001; Gilliam, 2006; Kourtev, Huang, & Ehrenfeld, 1999), not NH_4^+. The mechanisms of plant N use such as N preference between NH_4^+ and NO_3^- are important in driving invasion and influencing the potential coexistence of native species (Gilliam, 2006). Our results underscore plant NH_4^+ preference over NO_3^- as an important strategy for invaders because of its responsiveness to the invasive pressure and thereby enrich the understanding of exotic plant invasion from the perspective of plant N dynamics. In previous studies, plant N preference under invasion was more often evaluated by short-term ^{15}N labelling or inferred from higher production rates in soils, higher reduction rates in plant tissues, and higher biomass under higher supply of NH_4^+ and/or NO_3^- (Ehrenfeld et al., 2001; Fargione &

Tilman, 2005; Kourtev et al., 1999; McKane et al., 2002; Rossiter-Rachor et al., 2009). Methodologically, combining soil inorganic N compositions and natural N isotopes in plant and soil can provide more straightforward evidence on in situ plant N preference in invaded ecosystems.

Correlations between N concentrations and δ^{15}N values in leaves provided further insights into N utilization among invasive plants, native plants under invasion and no invasion (Figure 5). So far, positive correlations between leaf N and δ^{15}N have been constructed at different spatial scales for arctic tundra, temperate and tropical forest, and grassland ecosystems (Craine et al., 2009; Martinelli et al., 1999), which suggested increasing N availability and ^{15}N enrichment in plant-available N sources associated with the “openness” of the ecosystem N cycle (Amundson et al., 2003; Craine et al., 2009, 2015; Koba et al., 2012). However, for plant species or communities under the same soil N status in a given ecosystem, different uptake or preferences between NH_4^+ and NO_3^- can determine the relationships between leaf N contents and δ^{15}N values at species or community levels (Craine et al., 2015; Takebayashi, Koba, Sasaki, Fang, & Yoh, 2010). In our study, there were three cases. First, leaf N contents decreased with leaf δ^{15}N (Figure 5a) and f_{NH4+} (Figure 5d) values for natives (30 species) under no invasion, indicating a wide and diverse differentiation between NH_4^+ and NO_3^- assimilations among native plants. In generally, native species with relatively high NO_3^- assimilation showed higher leaf N contents under no invasion (Figure 5d). Second, natives under invasion showed no clear relationship between leaf N and δ^{15}N, f_{NH4+} or β_{NH4+} values (Figure 5b,e,h). When comparing the same species at different gradients of invasive pressure, native plants under relatively higher invasive pressures had generally higher NH_4^+ contributions (Figure S2e,f). This supports the importance of NH_4^+ assimilation for the coexistence of native plants. Third, for both *C. odorata* and *A. adenophpra*, leaf N concentrations were positively correlated with both leaf δ^{15}N (Figure 5c), f_{NH4+} and β_{NH4+} values (Figure 5f,i). This verified the increasing preference of ^{15}N-enriched NH_4^+ to the enhanced N assimilation for these high-productive invaders.

5 | CONCLUSIONS

Exotic plant invasion has been changing the vegetation composition and function in many of global terrestrial ecosystems. Based on in situ evidence on plant N and P use mechanisms under different invasive pressures, this study provides new insights into plant invasion and coexistence in invaded ecosystems. Enhanced soil NH_4^+ availability under invasion contributed to preferential NH_4^+ utilization of invasive plants, which also possessed high P uptake ability and consumed a large fraction of available P in the relatively P-poor soil. The N availability of co-occurring plants has profited from exotic plant invasion, but unfortunately P availability for natives was lowered by the invasion. Consequently, leaf P levels of co-occurring species decreased under invasion. Our results supported the hypothesis that invasive plants have higher uptake thus occupation of soil nutrients, achieving increasing above-ground productivity along with the invasive pressure. In parallel, native plants changed, either passively or actively, their nutrients use strategies for achieving a co-occurrence under altered soil nutrients status under invasion. However, most species will disappear due partly to the exacerbated nutrient competition. As N and P are often the main limiting nutrients for terrestrial plants, all the above findings are of broad significance for understanding nutrient dynamics in different plant–soil systems.

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AUTHORS’ CONTRIBUTIONS

X.-Y.L. and Y.-B.L. planned and designed the research; X.-Y.L., Y.-B.L. and Y.-H.T. conducted fieldwork; C.-C.H. and X.-Y.L. conducted experiments and performed data collection and analyses, wrote the manuscript; all authors commented on data interpretation and the whole manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1656nr6 (Hu et al., 2018).

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