

A ‘Get-Save-Return’ process continuum runs on phosphorus economy among subtropical tree species

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Abstract

Ecosystem processes interact through trade-offs or legacy effects, yet it remains unclear whether absorption (Get), resorption (Save), and decomposition (Return) are linked to form a ‘Get-Save-Return (GSR)’ continuum and conform to the economics spectrum theory. Here, we tested this hypothesis by synchronously integrating root-nutrient absorption, leaf-nutrient resorption, and leaf-litter decomposition of 15 co-occurring subtropical tree species. There was an active trade-off between phosphorus absorption and resorption, which further caused a passive trade-off between phosphorus resorption and leaf-litter decomposition, indicating that a process-based continuum exists and runs on phosphorus economy. Following the leaf economics spectrum, the acquisitive-strategy species had greater absorption, lower resorption, and faster decomposition, while the conservative-strategy species presented the opposite pattern. The continuum emerged among ectomycorrhizal species rather than arbuscular mycorrhizal species, implying a critical control of mycorrhizal association. Our findings demonstrate the existence of the ‘GSR’ continuum and provide a framework for understanding the whole-plant nutrient economy.

Introduction

The leaf economics spectrum (LES), capturing a suite of key traits provides a useful framework for identifying plant investment strategies (Wright et al. 2004). Species characterised by high specific leaf area (SLA) and nutrient concentration, but low tissue density and lignin concentration, tend to exhibit faster resource absorption (an acquisitive strategy), while species at the opposite end of the LES have a more conservative strategy (Wright et al. 2004; Reich 2014). Plants make a cost-benefit trade-off between root absorption and leaf resorption in nutrient economy (Norby & Jackson 2000; Kou et al. 2017). The acquisitive-strategy species running in a ‘fast lane’ may invest more in root-nutrient absorption but less in leaf-nutrient resorption, while conservative-strategy species running in a ‘slow lane’ may present opposite patterns. This active economic trade-off in nutrient acquisition pathways could cause a subsequent passive trade-off between resorption and decomposition, two primary processes after leaf senescence and fall (Killingbeck 1996; Cornwell et al. 2008). Therefore, a process-based ‘Get (absorption)-Save (resorption)-Return (decomposition)’ continuum (hereafter, the ‘GSR’ continuum; Fig. 1) may emerge. Although trait-based LES is recognised, its linkages with these processes have been less or separately explored (Freschet et al. 2010, 2012; Riva et al. 2019; Rosenfield et al. 2020). Whether the ‘GSR’ continuum exists and conforms to the ‘fast-slow’ leaf economics spectrum has not been tested empirically.

The emergence of the ‘GSR’ continuum may be associated with soil nutrient status and plants’ carbon (C)

investment strategy for nutrient acquisition. In nutrient-poor habitats, acquisitive-strategy species invest more in roots to forage for nutrients and less in leaf nutrient resorption (Hodge 2004; Kramer-Walter & Laughlin 2017; Zhao et al. 2020), leading to nutrient-rich leaf litter and faster decomposition. In contrast, the conservative-strategy species may allocate more effort to leaf nutrient resorption and invest less in the belowground (Deng et al. 2018), leading to nutrient-poor leaf litter and slower decomposition. However, the continuum might not emerge in nutrient-rich habitats where plants acquire nutrients at a relatively low cost. This discontinuity is more likely to occur in the active trade-off between root nutrient absorption and leaf nutrient resorption (Kou et al. 2017), because high nutrient availability may not impel plants to make such an economic trade-off. The legacy effects of resorption on decomposition, i.e. the passive trade-off, however, could persist regardless of soil nutrient availability (Deng et al. 2018), since the nutrient concentration in senesced leaves (resorption proficiency) largely determines the decomposability of leaf litter. Despite this theoretical assumption, our knowledge of the linkage among these processes for plants spanning from acquisitive to conservative strategies remains limited.

The absorptive roots of woody plants are symbiotic with mycorrhizal fungi, which may influence the continuity of these processes. Ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) associations are among the most common mycorrhizal types (Brundrett & Tedersoo 2017), but differ in such processes as nutrient absorption (Chen et al. 2016), nutrient resorption (Zhang et al. 2018), and litter decomposition (Keller et al. 2019; Jiang et al. 2021). Ectomycorrhizal plants utilise organic nutrients directly, as ECM fungi facilitate organic nutrient uptake through secreting extracellular enzymes (Talbot et al. 2008; Lin et al. 2017). However, AM plants mainly scavenge inorganic nutrients mineralised by free-living microbes (Read & Perez-Moreno 2003; Smith & Smith 2011). Moreover, ECM plants have more conservative nutrient cycles and lower leaf nutrient concentrations than AM plants (Chapman et al. 2006; Phillips et al. 2013). Considering the negative relationships between leaf nutrient resorption and green leaf nutrient concentrations (Killingbeck 1996; Kobe et al. 2005; Vergutz et al. 2012), ECM plants may have higher nutrient resorption and slower litter decomposition than AM plants (Keller et al. 2019; Xu et al. 2020). Given the distinct modes of nutrient-cycling processes between ECM and AM plants (Lin et al. 2017), unearthing the mycorrhizal controls over the ‘GSR’ continuum will facilitate predictive and mechanistic understanding of the whole-plant nutrient economy.

Here, we present the first empirical evidence of a direct link among these nutrient-associated processes, i.e. absorption, resorption, and decomposition and their relationship with LES in 15 co-occurring subtropical tree species. We determined the associated stoichiometric parameters of four nutrient pools (soils, absorptive roots, green leaves, and senesced leaves) of these species to assess the root absorption and leaf resorption of nitrogen (N) and phosphorus (P). In addition, we simultaneously measured SLA, leaf tissue density (LTD), and lignin concentration in green leaves as well as five morphological and architectural absorptive-root traits: root diameter (RD), specific root length (SRL), root tissue density (RTD), average root length (ARL), and branching intensity (BI) that are closely associated with nutrient absorption. We then performed a microcosm experiment to quantify the leaf-litter decomposition rate. Our previous studies had reported that nutrient foraging strategies (Kou et al. 2018a, b; Li et al. 2019) and litter decomposition (Jiang et al. 2018, 2019) of plants are more driven by P than N in subtropical forests, indicating that P could be the most limiting nutrient for these processes. Our overarching hypothesis is that the ‘GSR’ continuum would exist and run on the P economy and conform to the ‘fast-slow’ LES among these tree species. Based on the mycorrhizal-associated nutrient economy framework (Phillips et al. 2013), the contrasting nutrient economy modes of AM (inorganic-nutrient economy) and ECM (organic-nutrient economy) species can cause divergences in absorption, resorption, and decomposition. Thus, we further hypothesised that the continuum would differ markedly between AM and ECM species.

Materials and methods

Study site and species

The study was conducted at the Qianyanzhou Experimental Station of Red Soil and Hilly Land, Chinese Academy of Sciences (26°44N, 115°03E, 102 m a.s.l.), Jiangxi Province, southeastern China. This area has

a typical subtropical climate, with mean annual temperature and precipitation of 17.9 °C and 1475 mm, respectively (Wen et al. 2010). The parent soil, weathered from red sandstone and mudstone, is classified as Inceptisol, according to the USDA soil taxonomy. The forest was restored in 1985 by planting tree species such as slash pine (*Pinus elliottii* Englem) and Chinese fir (*Cunninghamia lanceolata* Hook) (Wang et al. 2012). In this study, we selected 15 tree species belonging to 13 genera and 9 families, with 8 AM species and 7 ECM species representing the local plant communities (Table S1).

Field sampling and processing

For each tree species, four healthy individuals with a similar diameter at breast height were randomly selected. To ensure sampling independence, the selected individuals were at least 10 m apart. We sampled the green and senesced foliage of these trees in autumn 2018. Specifically, the fully mature and expanded foliage from the most distal branches of each tree was cut from the sun-exposed canopy using a tree trimmer and bamboo extensions. Green foliage with visible biological or physical damage was excluded. More than 60 green leaves from each species were selected for further analysis. Thirty leaves per tree were placed in a valve bag and stored at 4 °C to measure morphological traits. The remaining samples were placed in envelopes to measure chemical traits. Due to the tree height and sampling difficulties, we spent two weeks per month during the whole autumn collecting senesced foliage. The senesced foliage was sampled directly beneath the focal trees from the recently fallen fresh litter on the ground (Huang et al. 2007). The senesced foliage with no visible degradation was well mixed for each species. The first set of subsamples was air-dried for chemical analyses, and the second set of subsamples was used for litter decomposition experiments.

Belowground samples were collected when sampling aboveground foliage. Four 1 × 1 m plots were identified within a 2 m distance from the tree stem in four directions from each target tree. The surface mineral soils (0–20 cm) at the plots were loosened with a pickaxe and spade, and sieved (2-mm mesh size) to sample the initial materials. Meanwhile, intact roots (more than five root orders) were cut from the main lateral roots, following the procedure described by Guo et al. (2008). Each root sample was divided into two subsamples for different analyses. One subsample was gently washed in deionised water to remove adhering organic matter and immediately fixed in formalin-aceto-alcohol solution (90 ml 50% ethanol, 5 ml 100% glacial acetic acid, and 5 ml 37% methanol) to measure anatomical traits. The other subsample was placed into valve bags, incubated with ice bags, and stored at -20 °C for later dissection and analysis of morphological and chemical traits (Guo et al. 2008).

Trait and edaphic variable measurements

The green leaf surface areas were measured by scanning at least five fully expanded leaves using a portable leaf-area meter (Li-3000C, LI-COR, USA), and their area was determined using ImageJ software (NIH Image, Bethesda, USA). For gymnosperm species, 20 leaves per tree were scanned to ensure accuracy. The foliage samples were oven-dried (60 °C, 48 h) and weighed to determine the dry mass. Specific leaf area was expressed as the ratio of leaf area to leaf dry mass. Leaf thickness was measured using digital callipers (SMCTW Company, Shanghai, China) to avoid major veins. Leaf tissue density was then calculated as dry mass divided by the product of leaf area and leaf thickness (Fortunel et al. 2012).

The first- and second-order roots of all species were selected as absorptive roots, because they are considered as belowground resource-acquiring units (Xia et al. 2010; McCormack et al. 2015). To obtain the morphological traits accurately, the dissected root samples were cleaned with deionised water, spread out on glass panes to avoid overlapping, and scanned using an Epson Expression 10000 XL scanner (Seiko Epson Corporation, Japan) at a resolution of 400 dpi. Root diameters and ARL were measured using WINRHIZO version 2012b (Regent Instruments Inc., Quebec City, Quebec, Canada). Subsequently, the scanned samples were oven-dried (60 °C, 48 h) and weighed to calculate SRL (root length divided by its dry mass) and RTD (root dry mass divided by its volume; assuming the root to be a cylinder). We calculated BI as the ratio of the 1st- and 2nd-order root number to the 3rd order root length (Kong et al. 2014).

The oven-dried samples of green leaves, senesced leaves, and absorptive roots were ground to fine powder using a Retsch MM 400 mixer mill (Retsch GmbH, Haan, Germany) for chemical analyses. The concentrations of C

and N were determined using a Vario MACRO cube elemental analyser (Elementar Analysensysteme GmbH, Langenselbold, Germany). The P concentration was determined using an inductively coupled plasma mass spectrometer (Optima 5300 DV, Perkin Elmer, Waltham, USA). The lignin concentration in green leaves was analysed using the widely used acid detergent lignin method (van Soest & Wine 1968). Ash contents were determined by combusting 40–50 mg of the corresponding samples in a muffle furnace (550°C for 4 h). All initial chemical traits and residual mass of decomposing leaves (see below) were expressed on an ash-free, dry-weight basis.

Soil nitrate (NO_3^-)-N and ammonium (NH_4^+)-N were extracted from the soils (2 mol l^{-1} KCl, 50 ml), and their concentrations were determined using a continuous-flow autoanalyser (Autoanalyzer 3, Bran and Luebbe, Germany). Available P (AP) was extracted with KCl/ NH_4F , and its concentration was determined colourimetrically using ascorbic acid molybdate analysis on a continuous-flow autoanalyser.

Nutrient absorption potential and nutrient resorption

We first defined a new index to assess the nutrient absorption potential of absorptive roots by integrating the key root traits (BI, ARL, and SRL) closely associated with nutrient absorption (Hodge 2004; Kong et al. 2014; Liese et al. 2017) and root-soil accumulation factor (Kou et al. 2017). First, we multiplied BI (tips cm^{-1}) by ARL (cm) to obtain the total length of absorptive roots per unit length of the third-order root. We then divided the total length by SRL (m g^{-1}) to obtain the estimated biomass allocation to absorptive roots per unit length of the third-order root. Lastly, we multiplied the estimated biomass of absorptive roots by a coefficient (i.e. root-soil accumulation factor) to represent the nutrient absorption potential of absorptive roots per unit length of third-order root (g cm^{-1}). Accordingly, the absorption potential of the absorptive roots was calculated using Eqs. (1) for N (nitrogen absorption potential–NAP) and (2) for P (phosphorus absorption potential–PAP), respectively.

$$\text{NAP (g cm}^{-1}\text{)} = \text{BI} \times \text{ARL/SRL} \times [\text{N}_{\text{AR}}/\text{N}_{\text{s}}] \times 10, (1)$$

$$\text{PAP (g cm}^{-1}\text{)} = \text{BI} \times \text{ARL/SRL} \times [\text{P}_{\text{AR}}/\text{P}_{\text{s}}] \times 10, (2)$$

where N_{AR} and P_{AR} are the N and P concentration in absorptive roots, N_{s} and P_{s} are the inorganic N (NH_4^+ -N plus NO_3^- -N) and AP concentration in soils.

The nutrient resorption efficiency was estimated as the percent difference between nutrient concentrations in green and senesced foliage (Aerts et al. 1996; Vergutz et al. 2012), calculated as Eqs. (3) and (4)

$$\text{NRE (\%)} = (\text{N}_{\text{Gr}} - \text{N}_{\text{Se}}) / \text{N}_{\text{Gr}} \times 100 (3)$$

$$\text{PRE (\%)} = (\text{P}_{\text{Gr}} - \text{P}_{\text{Se}}) / \text{P}_{\text{Gr}} \times 100 (4)$$

where NRE and PRE are the N and P resorption efficiency, respectively. N_{Gr} , P_{Gr} , N_{Se} , and P_{Se} are N and P concentrations in green and senesced leaves, respectively.

Nutrient resorption proficiency is defined as the extent to which the nutrient concentration (mg g^{-1}) is reduced in senesced leaves. Lower litter nutrient concentrations correspond to higher nutrient resorption proficiency and *vice versa* (Killingbeck 1996). NRP and PRP are resorption proficiency of N and P, respectively.

Litter decomposition experiments

Referring to the methods described by Jiang et al. (2021), leaf-litter decomposition rates were measured using a laboratory microcosm experiment under standardised conditions (i.e. decomposability). A total of 60 microcosms (15 species $\times$ four replicates) were set up. Each microcosm was constructed using polyvinyl chloride pipe (10 cm in length and 8 cm in diameter) and homogenised fresh soil (100.002 ± 0.003 g) plus oven-dried leaf litter (2.000 ± 0.0002 g) per species. Leaf samples were placed on the soil surface and separated using a nylon net (7×7 cm, 1 mm mesh). These microcosms were incubated in the dark (25 ± 0.02 °C, $70 \pm 5\%$ humidity) throughout the experiment. They were watered with distilled water (once every two weeks) to maintain soil moisture at 60% of water-holding capacity throughout the incubation period. Each microcosm was covered with a perforated adherent film to reduce humidity loss while allowing gaseous exchange. After

a 12-wk incubation, the microcosms were disturbed, and the residual leaf litter was carefully picked up using tweezers, oven-dried at 60 °C, and weighed to determine the mass loss (ML).

Statistical analyses

The data distribution was tested for normality using the Shapiro-Wilk test and log-transformed when necessary for all the measured variables. One-way analysis of variance (ANOVA) was used to test the effects of mycorrhizal type (AM vs ECM) on nutrient absorption potential, nutrient resorption, and mass loss as well as all traits of green leaves and absorptive roots. Significant differences between means were compared using Tukey's honest significant difference test. Correlations among processes and traits were determined by calculating Pearson's correlation coefficients for three categories: all species and species hosting AM and ECM fungi. In order to obtain a proxy for the resource economics of green leaves, principal component analyses (PCA) were performed on a suite of leaf economics traits, including SLA, LTD, concentrations of C, N, P, and lignin in green leaves (Table S2). Based on the first axis of the PCA, we obtained the PC1 scores of each species using the 'psych' package in R. The standard major axis regression was then performed to evaluate the relationships between the PC1 score and nutrient-associated processes (i.e. nutrient absorption potential, nutrient resorption, and decomposition) for the three categories above using the 'SMATR' package in R. Results were considered statistically significant at $P < 0.05$. All statistical analyses were performed using R v.3.4.4 and SAS version 9.4 (SAS Institute Inc., Cary, USA).

Results

Variations in species-specific root and leaf traits

The morphological and chemical traits of the green leaves varied considerably across the 15 tree species (Table 1). The largest variations in morphological and chemical traits were obtained for LTD (coefficient of variation (CV) = 75%, ranging from 0.02 g cm⁻³ of *Liriodendron chinense* to 0.15 g cm⁻³ of *Pinus elliottii*) and green leaf P concentration (CV = 35%, ranging from 0.6 mg g⁻¹ of *P. elliottii* to 1.9 mg g⁻¹ of *Quercus fabri*), respectively. For senesced leaves, the litter N and P concentrations showed approximately 4-fold variation among species, ranging from 5.7 mg g⁻¹ of *P. elliottii* to 21.1 mg g⁻¹ of *Q. fabri* for N concentration, and from 0.2 mg g⁻¹ of *Schima superba* to 1.0 mg g⁻¹ of *Q. fabri* for P concentration. There were no significant differences in green and senesced leaf traits between the AM and ECM species. The largest variation in absorptive roots was BI (CV = 67%, ranging from 1.1 of *Cinnamomum camphora* to 12.8 of *Q. fabri*). Compared to ECM species, the roots of AM species had larger diameters and ARL, higher N and P concentrations, and lower BI (Table 1).

Variations in species-specific nutrient-associated processes

The nutrient absorption potentials of absorptive roots were 0.23 g cm⁻¹ for N (CV = 64%) and 0.10 g cm⁻¹ for P (CV = 80%) among the 15 woody species (Table 1), respectively. The values of nutrient absorption potential had significant differences only in P element between AM (0.29 g cm⁻¹ for NAP; 0.14 g cm⁻¹ for PAP) and ECM (0.15 g cm⁻¹ for NAP; 0.05 g cm⁻¹ for PAP) species (Table 1; Fig. S1). The average resorption efficiencies were 41% for N (CV = 29%) and 48% (CV = 23%) for P across the 15 woody species (Table 1). Arbuscular mycorrhizal species (48% for NRE and 50% for PRE) exhibited significantly higher resorption efficiencies of leaf N but not P than ECM species (32% for NRE and 46% for PRE) (Table 1; Fig. S1). There were no significant differences in leaf N and P resorption proficiencies between AM (10.5 mg g⁻¹ for leaf-litter N concentration and 0.6 mg g⁻¹ for leaf-litter P concentration) and ECM (13.5 mg g⁻¹ for leaf-litter N concentration and 0.6 mg g⁻¹ for leaf-litter P concentration) species ($P > 0.05$, Table 1; Fig. S1). The mass loss of leaf litter after 12-wk decomposition ranged from 17% for *C. lanceolata* to 35% for *Q. fabri* (CV = 20%, Table 1). Similar to the patterns in nutrient absorption potentials and resorption proficiencies, mass loss was not significantly different between AM (24%) and ECM (28%) species ($P > 0.05$, Table 1; Fig. S1).

Linkages among nutrient-associated processes

Across all species, PAP was negatively correlated with PRP ($R^2 = 0.27$, $P = 0.049$; Fig. 2a), and PRP was negatively correlated with mass loss ($R^2 = 0.30$, $P = 0.035$). Nitrogen absorption potential was only

positively correlated with NRE ($R^2 = 0.48, P = 0.004$), and there were no significant relationships among NAP, NRP, and mass loss ($P > 0.05$). For AM species, PAP had a significant relationship with PRP ($R^2 = 0.74, P = 0.006$; Fig. 2b), and N and P resorption efficiencies were not correlated with mass loss. For ECM species, PAP was negatively correlated with PRP ($R^2 = 0.86, P = 0.003$; Fig. 2c), and PRP was also negatively correlated with mass loss ($R^2 = 0.68, P = 0.022$). Nitrogen resorption efficiency was negatively correlated with mass loss ($R^2 = 0.72, P = 0.015$).

Leaf economics spectrum and its linkage with nutrient-associated processes

For all species, the PCA conducted on the morphological and chemical traits explained 73% of the variation in the first two axes (Fig. 3; Table S2). The first principal component (PC1) captured 54% and was positively correlated with green leaf N and P concentrations and SLA, but negatively correlated with green leaf C and lignin concentrations and LTD.

Across all species, the PC1 axis score was positively correlated with PAP ($R^2 = 0.27, P = 0.047$), litter P concentration ($R^2 = 0.50, P = 0.003$), litter N concentration ($R^2 = 0.29, P = 0.037$), and mass loss ($R^2 = 0.39, P = 0.013$; Figs. 4, S2). For AM species, the PC1 axis score was positively correlated with mass loss ($R^2 = 0.73, P = 0.007$; Figs. 4c, S2). For ECM species, the patterns were similar to all species. The PC1 axis score was positively correlated with PAP ($R^2 = 0.59, P = 0.044$), litter P concentration ($R^2 = 0.77, P = 0.010$), litter N concentration ($R^2 = 0.93, P < 0.001$), and mass loss ($R^2 = 0.62, P = 0.036$; Figs. 4, S2).

Discussion

Ecosystem processes interact via exerting trade-offs or legacy effects (Reich 2014). Disentangling the linkages among processes could improve the predictive and mechanistic understanding of nutrient-cycling responses to changing environments (Cornwell et al. 2008). For the first time, we integrated the vertical (belowground nutrient absorption vs aboveground nutrient resorption) and temporal processes (nutrient flows from green leaf to senesced leaf to leaf litter) associated with the whole-plant nutrient economy among 15 subtropical tree species. Nutrients in new leaves are from two pathways: root absorption from soil ('Get') and resorption from senesced leaves ('Save') (Wright & Westoby 2003). We found that root nutrient absorption potential was negatively correlated with leaf nutrient resorption proficiency (Fig. 2a), indicating a cost-benefit trade-off between belowground absorption and aboveground resorption in nutrient acquisition pathways (Wright & Westoby 2003). Such an economic trade-off has further caused a legacy effect on subsequent leaf-litter decomposition ('Return') as indicated by the negative relationship between nutrient resorption proficiency and mass loss rate (Fig. 2a). The active trade-off between absorption and resorption as well as the passive trade-off between resorption and decomposition jointly indicate the existence of the 'GSR' continuum.

The continuum centred primarily on the P economy when examining the specific nutrients. The PAP was negatively correlated with PRP ($P = 0.048$; Fig. 2a), indicating that greater root nutrient absorption can lead to an increased P concentration in leaf litter (i.e. decreased PRP). Meanwhile, P concentration in leaf litter was positively correlated (i.e. PRP was negatively correlated) with the decomposition rate ($P = 0.035$; Fig. 2a). The resorption proficiency rather than efficiency that emerged in these linkages supports the argument that selection acts upon the residual nutrient concentration in senesced leaves rather than proportional resorption *per se* (Killingbeck 1996; Wright & Westoby 2003). The allocation of effort toward nutrient absorption and resorption depends on both soil nutrient availability and the cost involved in these processes (Kou et al. 2017). The continuity of the P economy could be related to the local edaphic conditions, where soil P availability (6.54 mg kg^{-1} ; Table S3) is relatively low compared to the global level (Zhu et al. 2016). For example, lower P availability can enhance root nutrient foraging strategies (Kou et al. 2018b; Li et al. 2019) and retard leaf-litter decomposition (Jiang et al. 2018, 2019) in P-deficient subtropical forests. Considering that nutrients obtained via resorption also incur a cost, e.g. the hydrolysis of organic compounds (Norby et al. 2000), plants should make an active trade-off between nutrient acquisition pathways by decreasing P resorption (i.e. saving less nutrients) for cost saving.

These processes associated with the N economy were not well linked, as indicated by the decoupling between NAP and NRP ($P > 0.05$; Fig. 2a). The discontinuity in the N economy supports our hypothesis that the

continuum is mainly determined by the trade-off between the two nutrient acquisition pathways. The trade-off disappearance was possibly because N may not be the most limiting nutrient in N-rich subtropical soils (Kou et al. 2018a). The discontinuity may alternatively be related to the diverse forms of N. Unlike P, which is exported in inorganic form (Vance et al. 2003), N can be exported in a diverse array of inorganic and organic forms (Takebayashi et al. 2010). In contrast to ammonium, which must be assimilated in roots, nitrate can be absorbed into organic compounds in roots and leaves (Wang & Macko 2011; Zhou et al. 2020). The dual pathways of nitrate assimilation might influence the assessment of root absorption and leaf resorption, obscuring their linkages. Like the P economy, NRP was marginally negatively correlated with decomposition rate ($P = 0.052$; Fig. 2a), consistent with a recent study showing linkages between leaf nutrient resorption and litter decomposition (Xu et al. 2020). This is unsurprising because the initial nutrient chemistry of leaf litter is closely associated with resorption (Deng et al. 2018) and inherently determines decomposition rates at the local scale (Cornwell et al. 2008).

The continuum conformed to the economics spectrum theory, when linking LES to ‘GSR’ continuum (Fig. 4). The one-dimensional ‘fast-slow’ LES, capturing a suite of key traits, represents species strategies as shaped by their evolutionary history (Reich et al. 1997; Wright et al. 2004) and assumes that the acquisitive-strategy species live fast and die young, while the conservative-strategy species live slow and steady (Wright et al. 2004). We correlated the PC1 scores on the LES with these processes, and found that species at the fast end of the spectrum had higher PAP ($R^2 = 0.27$, $P = 0.047$; Fig. 4a) and litter P concentration ($R^2 = 0.50$, $P = 0.003$; Fig. 4b), while species at the slow end presented the opposite patterns. These results indicate that species at both ends of the LES have contrasting investment strategies regarding nutrient acquisition: acquisitive-strategy species rely more on nutrient absorption but less on nutrient resorption compared to the conservative-strategy species. Less resorption for the acquisitive-strategy species yielded higher-quality leaf litter, and thus faster decomposition ($R^2 = 0.39$, $P = 0.013$; Fig. 4c). Such a passive trade-off implies that selection acts not only upon resorption but also upon decomposability by influencing the residual nutrient concentration in senesced leaves. These findings jointly suggest that the trait-based LES can be extrapolated to the process-based ‘GSR’ continuum.

Nutrient return via decomposition provides feedback to the soil matrix and may, in turn, influence root absorption. Perennial plants colonising a habitat may deploy nutrient foraging strategies in multiple dimensions, such as the ‘afterlife’ strategy—decomposition. Based on root trait-decomposition linkages, we found that the acquisitive-strategy species have thinner absorptive roots, but slower root decomposition compared to the conservative-strategy species (Jiang et al. 2021). This finding suggests a potential trade-off between absorptive-root turnover (diameter as a proxy) and decomposition and a possible belowground mechanism underlying species coexistence (Jiang et al. 2021). Despite this, there was no direct link between root absorption and leaf-litter decomposition on the ‘GSR’ continuum ($P > 0.05$; Fig. S3), implying that fast decomposition may not enable the acquisitive-strategy species to preempt the returned nutrients. This asymmetry could be related to two causes. First, leaf litter can decompose away from the home field under physical forces from wind or forest animals (Veen et al. 2019). Second, soil microorganisms or neighbouring plants may compete for and immobilise the returned nutrients (Barbe et al. 2017), which impels the acquisitive-strategy species to run steadily in a fast lane.

The ‘GSR’ continuum running on P economy emerged among ECM species rather than AM species (Fig. 4), supporting our hypothesis that the continuum varied with mycorrhizal type. The contrasting patterns between mycorrhizal types could be because ECM species generally dominate in ‘slow-cycling’ ecosystems with nutrient conservative traits, while AM species dominate ‘fast-cycling’ ecosystems with nutrient acquisitive traits (Philips et al. 2013). Compared to AM species, ECM species may have a strict budget for C investment and thus a tight linkage between root absorption and leaf resorption. Furthermore, AM and ECM species have different degrees of dependence on mycorrhizal fungi based on the root-fungal collaboration gradient globally (Bergmann et al. 2020). From absorptive-root trait comparisons between AM and ECM species, we found that ECM species had greater BI and SRL (marginally significant), and AM species had higher RD (Table 1). These divergences in root traits implied that AM species rely more on mycorrhizal symbiosis, while ECM species rely more on roots themselves when acquiring the limiting nutrients (Bergmann et al.

2020). Therefore, the two pathways of nutrient acquisition could be coupled for the more self-dependent ECM species compared to the more symbiosis-dependent AM species.

While leaf nutrient resorption and leaf-litter decomposition are negatively correlated (Xu et al. 2020), it remains unclear whether the trade-off between the two processes depends on the mycorrhizal type. By partitioning all species into two mycorrhizal groups, we found a tight linkage between these two processes among ECM species ($P = 0.022$; Fig. 2c) rather than AM species ($P > 0.05$; Fig. 2b). This divergent pattern may be related to the contrasting trait controls over leaf-litter decomposition in AM and ECM species (Phillips et al. 2013). Leaf-litter decomposition of ECM species was associated more closely with chemical traits (N and P) (Table S4). In contrast, decomposition of AM species was more correlated with morphological traits (e.g. SLA and LTD; Table S4) rather than chemical traits, although the ‘fast-slow’ LES was linked to decomposition in AM species (Fig. 4c). Despite these findings, the limited number of species makes it difficult to draw robust conclusions when taking a closer look at the mycorrhizal type, although AM ($n = 8$) and ECM ($n = 7$) species were comparable in terms of sample size. Studies incorporating more mycorrhizal tree species are therefore needed to further examine these active and passive trade-offs between nutrient-associated processes.

Overall, our results suggest that there was an active trade-off between root P absorption and leaf P resorption, which caused a passive trade-off between leaf P resorption and leaf-litter decomposition. Based on these findings, we conclude that the ‘GSR’ continuum exists and runs on the P economy among these subtropical tree species, providing a predictive framework for the whole-plant nutrient economy. Importantly, we linked the ‘fast-slow’ leaf economics spectrum to the processes associated with tree nutrient economy on this continuum and revealed that species with acquisitive leaf traits have greater root P absorption, lower leaf P resorption, and faster leaf-litter decomposition, while species with conservative leaf traits presented opposite patterns. These findings imply that the ‘fast-slow’ leaf economics spectrum can be extended to the process-based ‘GSR’ continuum and advance our understanding of the adaptive strategies of acquisitive and conservative species at multi-dimensional scales. Furthermore, the ‘GSR’ continuum emerged among ECM species rather than AM species, demonstrating the importance of mycorrhizal symbiosis in regulating the tree nutrient economy.

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Figure legends

Figure 1 Conceptual framework for ‘Get (absorption)-Save (resorption)-Return (decomposition)’ continuum and its linkage with leaf economics spectrum. **(a)** , the ‘GSR’ continuum comprises an active trade-off between root nutrient absorption and leaf nutrient resorption as well as a passive trade-off between leaf nutrient resorption and leaf-litter decomposition; **(b)** , the acquisitive-strategy species running on a fast lane get more nutrients, resorb less nutrients, and return nutrients fast; **(c)** , the conservative-strategy species running on a slow lane get less nutrients, resorb more nutrients, and return nutrient slowly. In b and c, circle size indicates relative effect strength and grey line indicates no relationship between root absorption and leaf-litter decomposition.

Figure 2 Pairwise correlations among nutrient-associated processes across all species (a, $n = 15$) and species hosting arbuscular mycorrhizal (b, AM, $n = 8$) and ectomycorrhizal (c, ECM, $n = 7$) fungi. The size of the circle is proportional to the correlation coefficient. The cross indicates that the correlations are not significant, $P > 0.05$. NAP is nitrogen acquisitive potential, PAP is phosphorus acquisitive potential, NRE is nitrogen resorption efficiency, NRP is nitrogen resorption proficiency (the negative of nitrogen concentration in leaf

litter was used here), PRE is phosphorus resorption efficiency, PRP is phosphorus resorption proficiency (the negative of phosphorus concentration in leaf litter was used here), and ML is mass loss.

Figure 3 Principal component analysis (PCA) for green leaf traits, including specific leaf area (SLA), leaf tissue density (LTD), green leaf carbon concentration (GCC), green leaf nitrogen concentration (GNC), green leaf phosphorus concentration (GPC), and green leaf lignin concentration (GLC) for all species. (a), trait loading biplot; (b) species distribution in the one-dimensional trait space. AM, arbuscular mycorrhizas; ECM, ectomycorrhizas. See Supporting Information Table S1 for explanation of abbreviations.

Figure 4 Relationships of the PC1 axis score with phosphorus acquisitive potential (a, PAP), leaf-litter phosphorus concentration (b, LPC) and mass loss (c, ML) for all species ($n = 15$, blank circles) and species hosting arbuscular mycorrhizal (AM, $n = 8$, red upper triangles) and ectomycorrhizal (ECM, $n = 7$, purple lower triangles) fungi.

Table 1 Summary of the root and leaf traits and processes for 15 tree species and the pairwise differences between mycorrhizal types.

Trait or process (abbreviation, unit)	Trait or process (abbreviation, unit)	Mean	Min	Max	CV
Absorptive root trait	Root diameter (RD, mm)	0.42	0.34	0.62	22.1
	Specific root length (SRL, m g ⁻¹)	64.36	20.21	119.09	58.1
	Root tissue density (RTD, g cm ⁻³)	0.16	0.09	0.23	25.1
	Average root length (ARL, cm)	0.78	0.35	1.81	61.1
	Branching intensity (BI, tips cm ⁻¹)	5.10	1.07	12.8	67.1
	Root nitrogen concentration (RNC, mg g ⁻¹)	16.55	10.57	24.3	27.1
	Root phosphorus concentration (RPC, mg g ⁻¹)	0.92	0.51	1.33	25.1
Leaf trait	Specific leaf area (SLA, cm ² g ⁻¹)	147.82	50.79	354.51	53.1
	Leaf tissue density (LTD, g cm ⁻³)	0.06	0.02	0.15	75.1
	Green leaf carbon concentration (GCC, mg g ⁻¹)	495.29	460.97	522.80	3.6
	Green leaf nitrogen concentration (GNC, mg g ⁻¹)	20.40	9.15	29.75	30.1
	Green leaf phosphorus concentration (GPC, mg g ⁻¹)	1.15	0.61	1.90	34.1
Nutrient-associated process	Green leaf lignin concentration (GLC, mg g ⁻¹)	401.20	243.54	471.69	15.1
	Nitrogen absorption potential (NAP, g cm ⁻¹)	0.23	0.06	0.49	64.1
	Phosphorus absorption potential (PAP, g cm ⁻¹)	0.10	0.03	0.27	79.1
	Nitrogen resorption efficiency (NRE, %)	40.76	27.43	64.73	28.1
	Leaf-litter nitrogen concentration (LNC, mg g ⁻¹)	11.91	5.70	21.07	35.1
	Phosphorus resorption efficiency (PRE, %)	48.09	27.27	70.80	22.1
	Leaf-litter phosphorus concentration (LPC, mg g ⁻¹)	0.60	0.25	0.96	34.1
	Mass loss (ML, %)	26.09	17.47	34.57	19.1

Min, minimum value; Max, maximum value; CV, coefficient of variation; See Supporting Information Table S1 for more information on species.

Supporting information

Figure S1 Nutrient absorption potential, nutrient resorption and decomposition for species associated with different mycorrhizal types. AM is arbuscular mycorrhizas, ECM is ectomycorrhizas. The violin plot represents the quartile (25%, the bottom dotted line and 75%, the top dotted line) and the middle dotted line represents the mean value. The asterisks indicate significant differences, **, $P < 0.01$; *, $P < 0.05$.

Figure S2 Relationships of the PC1 axis score with nitrogen absorption potential (a, NAP) and leaf-litter nitrogen concentration (b, LNC) for all species ($n = 15$, blank circles) and species hosting arbuscular mycorrhizal (AM, $n = 8$, red upper triangles) and ectomycorrhizal (ECM, $n = 7$, purple lower triangles)

fungi.

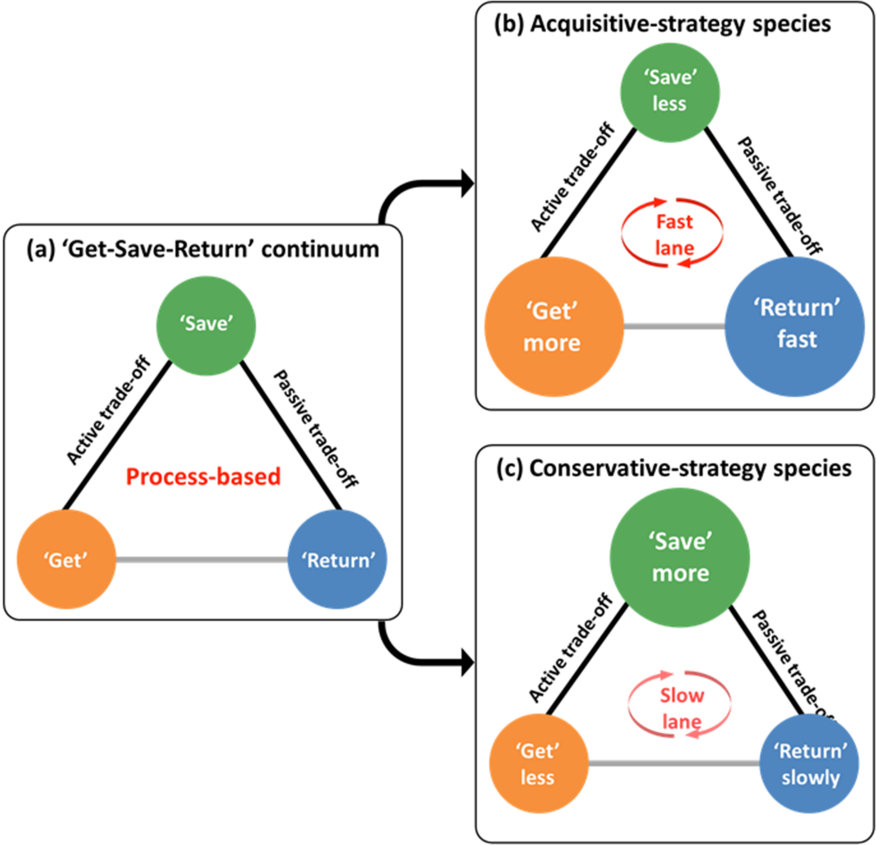
Figure S3 Relationship between phosphorus absorption potential (PAP) and mass loss (ML) for all species ($n = 15$).

Table S1 List of 15 tree species and their characteristics.

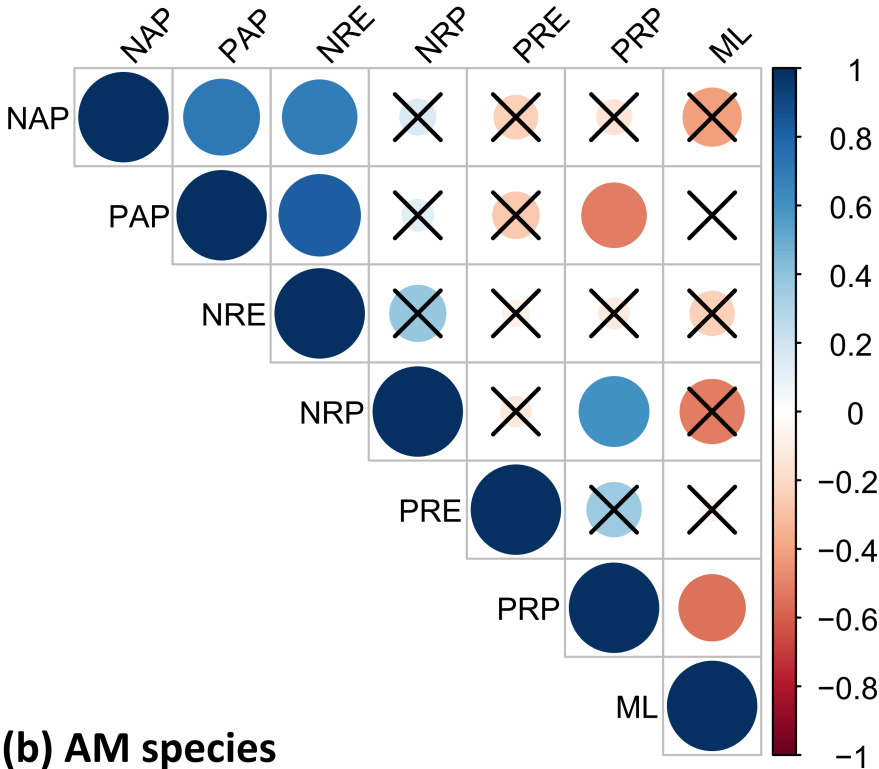
Table S2 Loading scores of six green leaf traits on each component of the principal components analysis (PCA) for all species ($n = 15$).

Table S3 Soil nitrogen and phosphorus properties for each species.

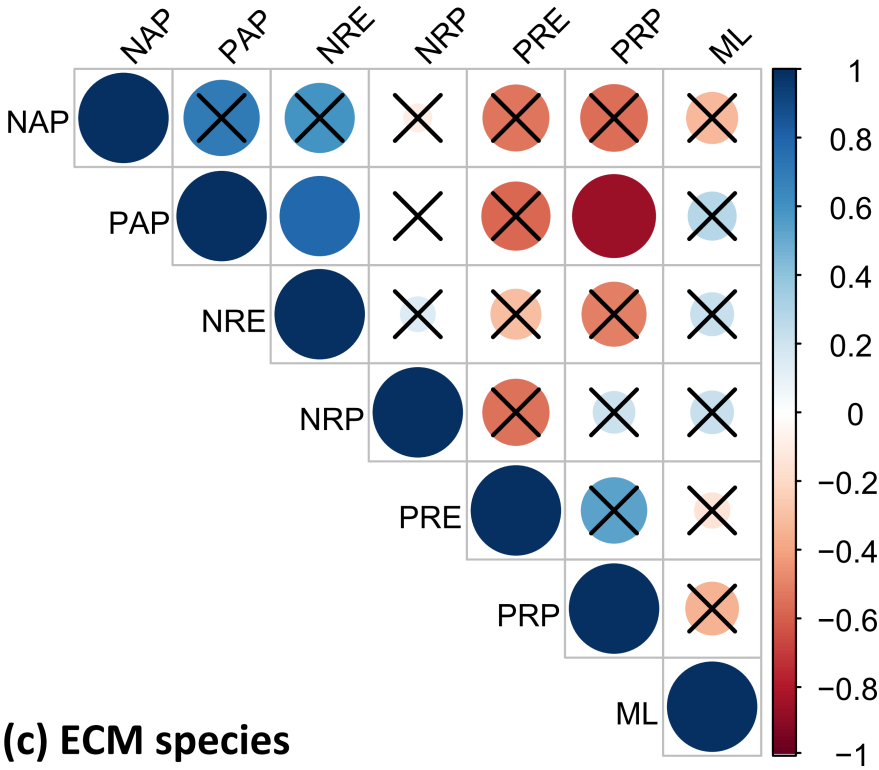
Table S4 Relationships of mass loss with green-leaf and leaf-litter traits.



(a) All species



(b) AM species



(c) ECM species

