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Plant trait-based life strategies of overlapping species vary in different succession stages of subtropical forests, Eastern China

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Plants growing in forests at different succession stages in diverse habitats may adopt various life strategies from the perspective of plant functional traits. However, species composition differs with forest succession, and the effects of forest succession on traits have often been explored without considering the effects of species identity. We comprehensively investigated intraspecific variations in 12 traits of six overlapping species (two tree species and four understory shrub species) in three typical subtropical evergreen broad-leaved forests at different succession stages in eastern China. We found that intraspecific variations differed among traits. Fine root specific length presented large intraspecific variation, leaf area, specific leaf area and fine root tissue density showed medium intraspecific variations, and other traits displayed small intraspecific variations. Trees and understory shrubs in the early-stage forest exhibited higher leaf thickness, dry matter contents and tissue densities of leaves, roots, twigs, and stems and lower leaf area and specific leaf area. Those in the medium- and late-stage forests displayed contrasting trait characteristics. From the perspective of plant functional traits, plants in the early-stage forest formed a series of trait combinations for a resource conservative strategy with a low growth rate to adapt to fragile habitats with poor soil nutrients and changeable soil temperature and humidity, and those in the medium- and late-stage forests (especially the former) formed converse trait combinations for a resource acquisitive strategy with a high growth rate to adapt to low light availability and strongly competitive habitats. Our study reveals that plants in forests at different succession stages adopt various life strategies and provides data to the TRY and China plant trait databases.

KEYWORDS

intraspecific trait variation, forest succession, overlapping species, life history strategy, subtropical forests

Introduction

Plant functional traits are measurable characteristics formed from long-term plant-environment interactions and are closely linked to the growth, reproduction, and survival processes of plants (Violle et al., 2007; Garnier et al., 2016; Kattge et al., 2020). A single trait and the combinations of multiple traits not only respond to plant life history strategy, biodiversity, vegetation, environment, and disturbance changes but also affect ecosystem processes and functions (Cornelissen et al., 2003; Vandewalle et al., 2010; Mensens et al., 2017; Wang et al., 2020). Therefore, the study of plant functional traits is at the forefront of modern ecology and global change ecology (Meng et al., 2007; Liu and Ma, 2015; Blondeel et al., 2020).

Forests are the largest vegetated areas in global terrestrial ecosystems and play important roles in global biodiversity maintenance and climate change mitigation (Melillo et al., 1993; Anderson-Teixeira et al., 2015). Plant functional traits, such as morphological traits and C: N: P ecological stoichiometry of leaves, roots, stems, and twigs (especially leaves) in forests worldwide have been intensively investigated at local, regional and global scales (McGroddy et al., 2004; Chave et al., 2009; Díaz et al., 2016; He et al., 2019; Guerin et al., 2021; Liu et al., 2022). Compared to interspecific trait variations (trait differences among species) of woody plants in forests, intraspecific trait variations (trait differences among independent individuals within a species) are yet to be fully investigated. However, intraspecific trait variations are non-negligible, and they may account for an average of 32% of the total trait variations based on a global database (Siefert et al., 2015). Environmental factors, such as climate, topography, and soil nutrition, greatly affect intraspecific trait variations (Hultine and Marshall, 2000; Thuiller et al., 2004; Quested et al., 2007; Wang et al., 2016a).

In addition, most plant functional trait studies conducted in forests have focused on dominant trees, and understory shrubs have rarely been described. As an important component of forest ecosystems, understory shrubs influence the energy and water cycles of forests and participate in forest renewal, development, and succession (Cao et al., 2020). In limited trait studies on understory shrubs, the latitudinal distribution pattern and driving factors of leaf traits (Luo et al., 2019), the correlation between morphological traits and nitrogen and phosphorus nutrients (Wang et al., 2017), relationships between twigs and leaf traits at different succession stages (Ma, 2014), and different phenotypes of understory shrubs (Wang et al., 2016b) have been reported. Light conditions and canopy coverage are the main environmental factors driving intraspecific variations in leaf traits (Burton et al., 2017). However, studies on intraspecific trait variation in understory shrubs in forests at different succession stages in different habitats are scarce (Kumordzi et al., 2019; Vanneste et al., 2019; Cao et al., 2020).

Environments (or habitats), species composition, and the structure of a forest community change with progressive succession. In early-stage forests, illumination is sufficient, but soil nutrients are poor, and soil temperature and humidity fluctuate. Such forests are committed to gap formation, understory initiation, and regeneration (Moridi et al., 2015; Zhang et al., 2016). In medium-stage forests, soil humidity and nutrients are greatly improved, but light availability is the lowest because of the highest canopy coverage and stand density. Such forests are in volume accumulation, lightning, and stem exclusion phases (Zhang et al., 1999; Wang et al., 2004; Yan et al., 2008; Moridi et al., 2015). Light conditions improve in late-stage forests because of slightly lower canopy coverage and stand density (Moridi et al., 2015; Zhang et al., 2016). Some species (turnover species) only appear in forests at one succession stage and disappear in the next stage, whereas, some species (overlapping species) grow in forests at many succession stages (Yang et al., 2014). Overlapping species in the early-stage forest may form a series of trait combinations for a resource conservative strategy to adapt to fragile habitats with poor soil nutrients and changeable soil temperature and humidity, and those in the medium- and late-stage forests may form converse trait combinations for a resource acquisitive strategy to adapt to low light availability and strongly competitive habitats (Li and Ma, 2002).

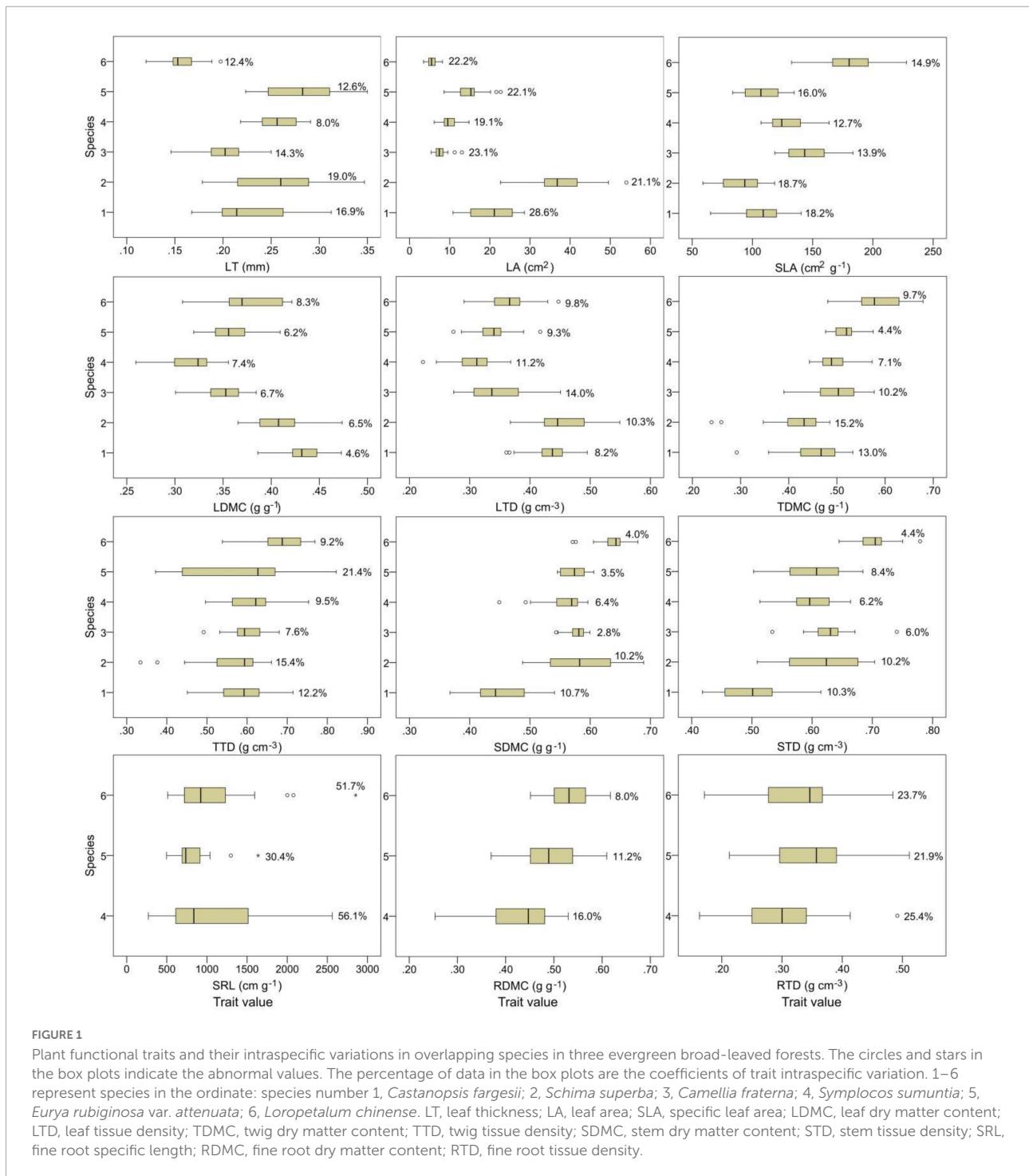
Originating from the uplift of the Qinghai–Tibet Plateau, a broad subtropical evergreen broad-leaved forest was found in China. This forest is a unique vegetation type on Earth and is essential to the global gene pool and regional environments (Song, 2013). In the present study, dominant overlapping species, including tree and understory shrub species, in three evergreen broad-leaved forests at different succession stages in eastern China were investigated as examples. The leaf, twig, stem, and root traits were comprehensively measured. Here, the life strategies of plants growing in forests at different succession stages in various habitats were determined from the perspective of plant functional traits. Specifically, the following predictions were made. (1) Overlapping species in the forests at three succession stages present significant differences in plant functional traits. (2) Plants (trees and understory shrubs) in the early-stage forest form a series of trait combinations with higher leaf thickness (LT), dry matter contents and tissue densities of leaves, roots, twigs, and stems and lower leaf area (LA) and specific leaf area (SLA) for a resource conservative strategy with a low growth rate. Plants in the medium- and late-stage forests form converse trait combinations for a resource acquisitive strategy with a high growth rate. This study provides basic data to global (Kattge et al., 2020) and China (He et al., 2019) plant trait databases and guides the sustainable management and ecological restoration of evergreen broad-leaved forests in eastern China.

Materials and methods

Study area

Field measurements were conducted in three permanent monitoring plots of the Zhejiang Tiantong Forest Ecosystem National Observation and Research Station (121.783° E,

29.800° N) in the Tiantong National Forest Park, Zhejiang Province, Eastern China. This area is located in mid-subtropical China and controlled by monsoon climates. The mean annual temperature is 16.2°C, with temperatures of 4.2°C and 28.1°C in January and July, respectively. Considerably high and low temperatures are 38.7°C and −8.5°C, respectively. The growing degree days on the base of 10°C is 5,166.2°C. The mean annual



precipitation and evaporation are 1,374.7 and 1,320.1 mm, respectively. The native vegetation is subtropical evergreen broad-leaved forest dominated by *Castanopsis fargesii* Franch. and *Schima superba* Gardn. et Champ. Existing forests in the Tiantong National Forest Park are classified as early-, medium-, and late-stage forests along a secondary succession series because of the intensity of human disturbances (Song and Wang, 1995). Three forest plots (each with an area of 2,500 m², 50 m × 50 m) at three succession stages (i.e., early, medium and late stages) were established and investigated in 2007.

The early-stage forest (121.786° E, 29.801° N) is 20° south of the east and has a 25° slope. This forest is restored from a shrubland with a stand age of 35 y. The height and coverage of the tree layer are 8 m and 70%, respectively. Its dominant tree species is *S. superba*. Another common species in the tree layer is *C. fargesii*. *Loropetalum chinense* (R. Br.) Oliver and *Symplocos sumuntia* Buch. -Ham. ex D. Don are dominant understory shrub species. The medium-stage forest (121.788° E, 29.786° N) is 70° south of the east and has a 20° slope. The stand age is 90 y, and the height and coverage of the tree layer are 15 m and 95%, respectively. This forest is also dominated by *S. superba*, and *C. fargesii* is distributed in the subtree layer. The main understory shrub species are *Eurya rubiginosa* var. *attenuata* H. T. Chang, *Camellia fraterna* Hance, and *S. sumuntia*. The late-stage forest (121.787° E, 29.808° N) is 45° south of the east and has a 26° slope. This forest is in the climax stage with a stand age of 170 y. The height and coverage of the tree layer are 18 m and 90%, respectively. *C. fargesii* is the dominant tree species, and *S. superba* is widely distributed in the subtree layer. *E. rubiginosa*, *C. fraterna*, and *L. chinense* are common in the understory shrub layer.

Measurement of plant functional traits

Overlapping species, including two tree species (*C. fargesii* and *S. superba*) and four understory shrub species (*C. fraterna*, *S. sumuntia*, *E. rubiginosa*, and *L. chinense*), in the three forests were selected for trait measurements. Ten healthy dominant individuals per species in each plot were chosen. From each individual, a branch was collected from the sunlit tree canopy by using a long reach chain saw (tree species) or collected from the upper canopy by using a lopper (understory shrub species). Twenty mature leaves without visible damage were collected. An approximately 20 cm length current-year twig was sampled using a lopper, and a stem sample was determined using a SYCO (trees) or a lopper (shrubs). The roots of trees were difficult to recognize, and *C. fraterna* was grown in rocks in the early-stage forest, so only fine roots (root diameter ≤ 2 mm) of three understory shrub species, that is, *S. sumuntia*, *E. rubiginosa*, and *L. chinense*, were sampled using a hoe.

TABLE 1 Plant functional traits and their abbreviations, units, and calculations.

Plant functional trait	Abbreviations	Unit	Calculation
Specific leaf area	SLA	cm ² g ⁻¹	Leaf area/leaf dry mass
Leaf dry matter content	LDMC	g g ⁻¹	Leaf dry mass/fresh mass
Leaf tissue density	LTD	g cm ⁻³	Leaf dry mass/volume
Twig dry matter content	TDMC	g g ⁻¹	Twig dry mass/fresh mass
Twig tissue density	TTD	g cm ⁻³	Twig dry mass/volume
Stem dry matter content	SDMC	g g ⁻¹	Stem dry mass/fresh mass
Stem tissue density	STD	g cm ⁻³	Stem dry mass/volume
Fine root specific length	SRL	cm g ⁻¹	Fine root length/dry mass
Fine root dry matter content	RDMC	g g ⁻¹	Fine root dry mass/fresh mass
Fine root tissue density	RTD	g cm ⁻³	Fine root dry mass/volume

Fresh masses of leaf, twig, and stem samples were weighed using an electronic balance. Leaf thickness was measured using an electronic Vernier caliper. The length and volume of fine roots and LA were scanned using a WinFOLIA multipurpose leaf area meter (Regent Instruments, Canada). Leaf sample volume was calculated as the product of LA and LT, and twig and stem sample volumes were determined using the drainage method (Cornelissen et al., 2003). All samples were dried in an oven at 80°C for 72 h to determine their dry masses. The values of traits were calculated as shown in Table 1.

Data analysis

The coefficient of intraspecific variation (standard deviation divided by mean) was used to characterize the varying degrees of traits among individuals of a certain species. One-way ANOVA was conducted to determine the trait differences among plant growth forms (trees and understory shrubs) and species in the forests at three succession stages. The principal component analysis (PCA) was done to evaluate the effect of plant species on traits, and show the distributions of traits among plant species. Trait data were log-transformed prior to PCA analysis. Fisher's least significant difference (homogeneity of variance) or Tamhane (heterogeneity of variance) methods were used to conduct *post hoc* tests after the homogeneity test of variances.

All statistical analyses were performed using the SPSS version 20 and the CANOCO 5.

Results

Plant functional traits and their intraspecific variations

The 12 plant functional traits varied among plant species (Figure 1). Among the stem, twig, and leaf traits, *C. fargesii* exhibited the highest leaf dry matter content (LDMC) and the lowest stem dry matter content (SDMC) and stem tissue density (STD). *S. superba* showed the highest LA and leaf tissue density (LTD) and the lowest SLA, twig dry matter content (TDMC), and twig tissue density (TTD). *S. sumuntia* presented the lowest LDMC and LTD, *E. rubiginosa* had the highest LT. *L. chinense* displayed the highest SLA, TDMC, TTD, SDMC, and STD and the lowest LT and LA. *C. fraterna* had intermediate trait values. Among the root traits, *S. sumuntia* presented the lowest fine root dry matter content (RDMC) and fine root tissue density (RTD). *E. rubiginosa* had the highest RTD and the lowest fine root specific length (SRL). *L. chinense* displayed the highest SRL and RDMC.

The intraspecific variations differed among plant functional traits (Figure 1). SRL exhibited the largest intraspecific variations. The intraspecific variations in the SRL of *S. sumuntia* and *L. chinense* were highly variable, indicated by large coefficients of intraspecific variation (56.1 and 51.7%, respectively). The coefficients of intraspecific variation of LA, SLA, and RTD generally ranged from 15 to 35%. Other traits displayed small intraspecific variations, indicated by small coefficients of intraspecific variation, especially for LDMC, SDMC, and STD, whose coefficients of intraspecific variation were generally less than 10%.

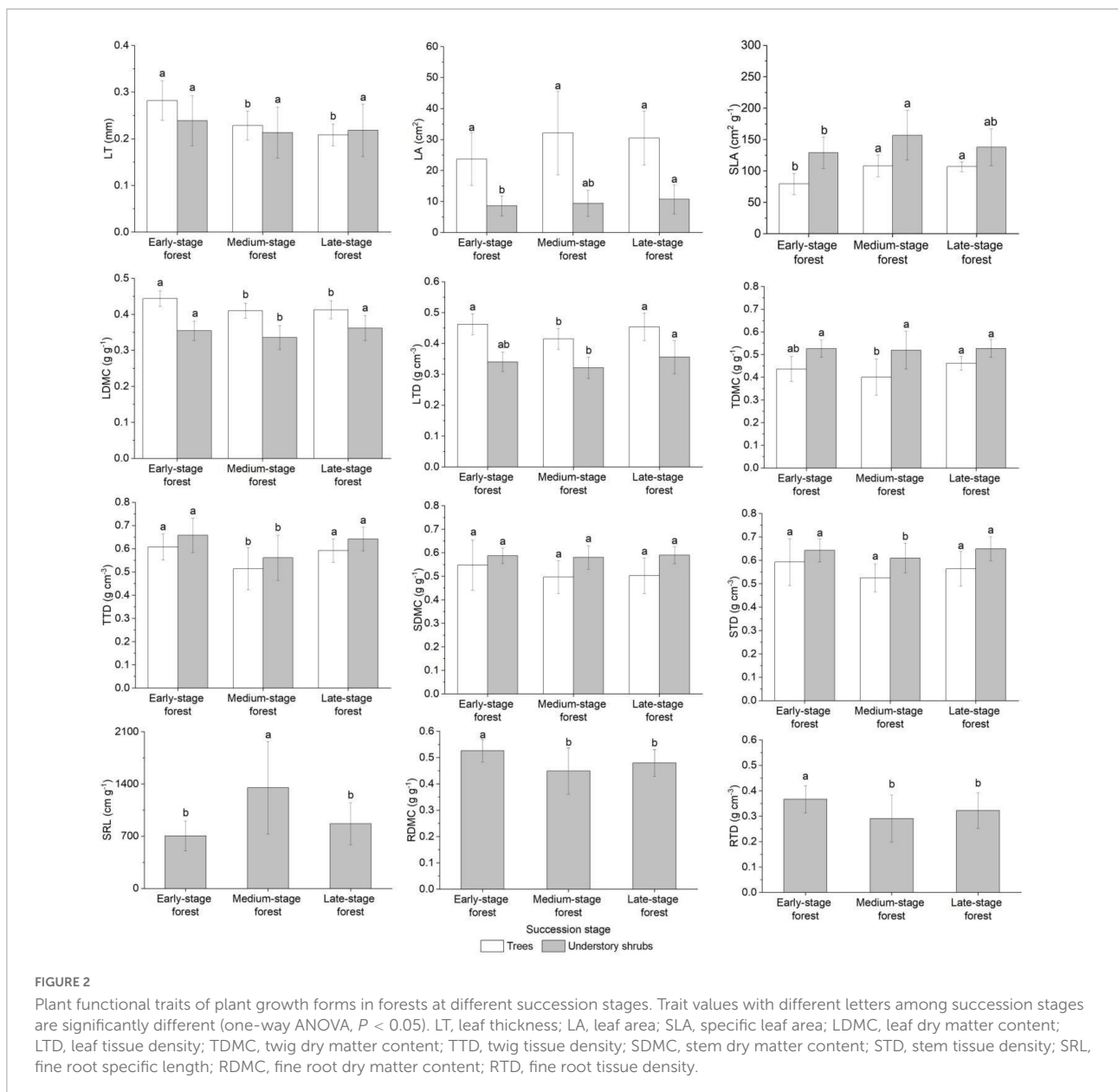
Plant functional traits of plant growth forms at different succession stages

The LA, SDMC, and STD of trees were close in the forests at three succession stages ($F_{LA} = 2.904$, $F_{SDMC} = 1.694$, $F_{STD} = 2.892$, $P > 0.05$), whereas other traits showed significant differences ($F_{LT} = 20.858$, $F_{SLA} = 20.012$, $F_{LDMC} = 11.176$, $F_{LTD} = 7.204$, $F_{TDMC} = 4.497$, $F_{TTD} = 8.709$, $P < 0.05$; Figure 2). Trees in the early-stage forest presented the highest LT, LDMC, LTD, TTD, SDMC, and STD and the lowest LA and SLA; trees in the medium-stage forest exhibited the highest LA and SLA and the lowest LDMC, TDMC, TTD, SDMC, and STD; and those in the late-stage forest generally displayed intermediate trait values (Figure 2). Understory shrubs in the forests at three succession stages showed small discrepancies in LT, TDMC, and SDMC ($F_{LT} = 1.934$, $F_{TDMC} = 0.169$, $F_{SDMC} = 0.477$, $P > 0.05$), but

they exhibited significant differences in other traits ($F_{LA} = 2.082$, $F_{SLA} = 6.294$, $F_{LDMC} = 5.716$, $F_{LTD} = 5.642$, $F_{TTD} = 14.524$, $F_{STD} = 4.676$, $F_{SRL} = 15.995$, $F_{RDMC} = 9.023$, $F_{RTD} = 6.521$, $P < 0.05$; Figure 2). Shrubs in the early-stage forest presented the highest LT, TTD, RDMC, and RTD and the lowest LA, SLA, and SRL; shrubs in the medium-stage forest exhibited the highest SLA and SRL and the lowest LT, LDMC, LTD, TDMC, TTD, SDMC, STD, RDMC, and RTD; and those in the late-stage forest also displayed intermediate trait values (Figure 2).

Plant functional traits of overlapping species at different succession stages

The traits of overlapping species in forests at three succession stages differed to varying degrees (Figures 3, 4 and Supplementary Table 1). In general, plants in the early-stage forest exhibited high LT, LDMC, LTD, TDMC, TTD, SDMC, STD, RDMC, and RTD and low SLA and SRL; plants in the medium-stage forest presented contrary trait characteristics compared with those in the early-stage forest; and those in the late-stage forest displayed intermediate trait values except high LA (Figure 4). Specifically, the LA, TDMC, TTD, SDMC, and STD of *C. fargesii* exhibited small discrepancies in the forests at three succession stages ($F_{LA} = 1.851$, $F_{TDMC} = 2.945$, $F_{TTD} = 0.649$, $F_{SDMC} = 0.183$, $F_{STD} = 0.424$, $P > 0.05$). However, *C. fargesii* in the early-stage forest exhibited significantly higher LT, LDMC, and LTD and significantly lower SLA ($F_{LT} = 7.101$, $F_{LDMC} = 7.469$, $F_{LTD} = 4.041$, $F_{SLA} = 12.254$, $P < 0.05$; Figure 4). All traits of *S. superba* showed significant differences in the forests at three succession stages ($P < 0.05$). *S. superba* in the early-stage forest showed significantly higher LT, LDMC, SDMC, and STD and significantly lower LA and SLA ($F_{LT} = 64.481$, $F_{LDMC} = 10.140$, $F_{SDMC} = 15.454$, $F_{STD} = 19.011$, $F_{LA} = 11.506$, $F_{SLA} = 41.995$, $P < 0.05$); *S. superba* in the medium-stage forest showed significantly lower LTD, TDMC, and TTD ($F_{LTD} = 5.079$, $F_{TDMC} = 16.451$, $F_{TTD} = 17.975$, $P < 0.05$; Figure 4). The LA, SDMC, and STD of *C. fraterna* did not differ in the forests at three succession stages ($F_{LA} = 3.021$, $F_{SDMC} = 0.318$, $F_{STD} = 0.243$, $P > 0.05$). Conversely, *C. fraterna* in the early-stage forest had significantly higher LT and TDMC ($F_{LT} = 11.128$, $F_{TDMC} = 15.314$, $P < 0.05$); *C. fraterna* in the medium-stage forest had significantly higher SLA and significantly lower LDMC ($F_{SLA} = 8.543$, $F_{LDMC} = 13.261$, $P < 0.05$); and *C. fraterna* in the late-stage forest had significantly higher LTD and TTD ($F_{LTD} = 27.678$, $F_{TTD} = 9.051$, $P < 0.05$; Figure 4). The LDMC, LTD, and TDMC of *S. sumuntia* presented small discrepancies in the forests at three succession stages ($F_{LDMC} = 2.181$, $F_{LTD} = 1.721$, $F_{TDMC} = 5.545$, $P > 0.05$). However, *S. sumuntia* in the early-stage forest presented significantly higher LT, TTD, and RTD and significantly lower SLA ($F_{LT} = 2.999$, $F_{TTD} = 3.754$, $F_{RTD} = 6.109$, $F_{SLA} = 6.277$, $P < 0.05$); *S. sumuntia* in the medium-stage forest presented

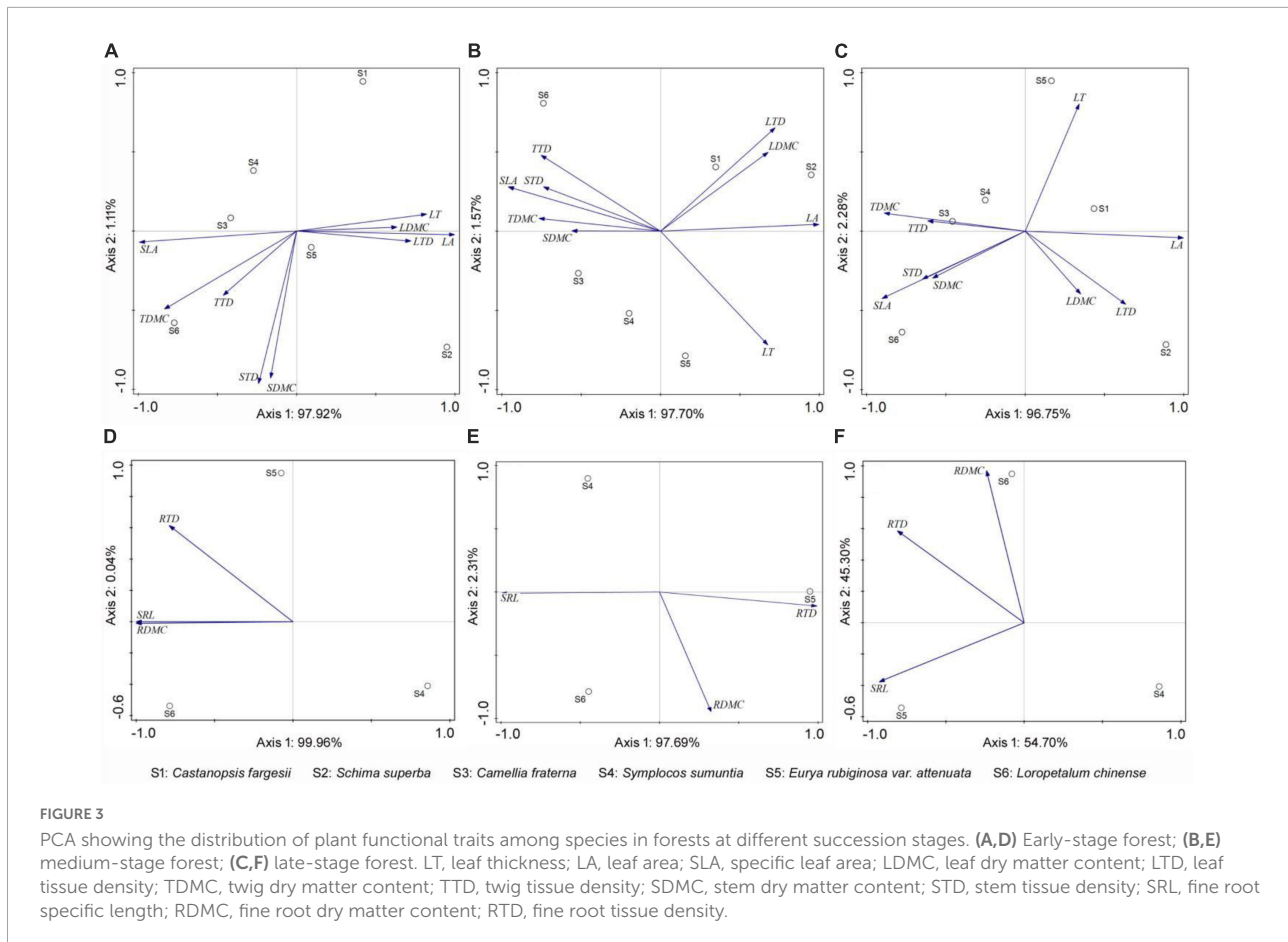


significantly higher SRL and significantly lower SDMC, STD, and RDMC ($F_{SRL} = 12.966$, $F_{SDMC} = 10.480$, $F_{STD} = 5.873$, $F_{RDMC} = 30.602$, $P < 0.05$); and *S. sumuntia* in the late-stage forest presented significantly higher LA ($F_{LA} = 4.846$, $P < 0.05$; **Figure 4**). The LT, SLA, LDMC, LTD, SRL, and RTD of *E. rubiginosa* exhibited no differences in the forests at three succession stages ($F_{LT} = 0.745$, $F_{SLA} = 1.043$, $F_{LDMC} = 0.566$, $F_{LTD} = 2.468$, $F_{SRL} = 1.329$, $F_{RTD} = 0.453$, $P > 0.05$). By comparison, *E. rubiginosa* in the medium-stage forest exhibited significantly higher TDMC and SDMC and significantly lower TTD and STD ($F_{TDMC} = 3.110$, $F_{SDMC} = 4.452$, $F_{TTD} = 49.393$, $F_{STD} = 22.889$, $P < 0.05$). *E. rubiginosa* in the late-stage forest exhibited significantly higher LA and significantly lower RDMC ($F_{LA} = 3.057$, $F_{RDMC} = 4.201$, $P < 0.05$; **Figure 4**). The LA,

LTD, TDMC, TTD, SDMC, and STD of *L. chinense* displayed small discrepancies in the forests at three succession stages ($F_{LA} = 1.863$, $F_{LTD} = 1.427$, $F_{TDMC} = 3.032$, $F_{TTD} = 3.858$, $F_{SDMC} = 0.534$, $F_{STD} = 1.092$, $P > 0.05$). Conversely, *L. chinense* in the medium-stage forest exhibited significantly higher SRL and significantly lower LT, SLA, LDMC, RDMC, and RTD ($F_{SRL} = 9.020$, $F_{LT} = 6.386$, $F_{SLA} = 14.432$, $F_{LDMC} = 7.311$, $F_{RDMC} = 2.477$, $F_{RTD} = 6.157$, $P < 0.05$; **Figure 4**).

Discussion

Few studies on intraspecific trait variations have been conducted compared with studies on interspecific trait variation

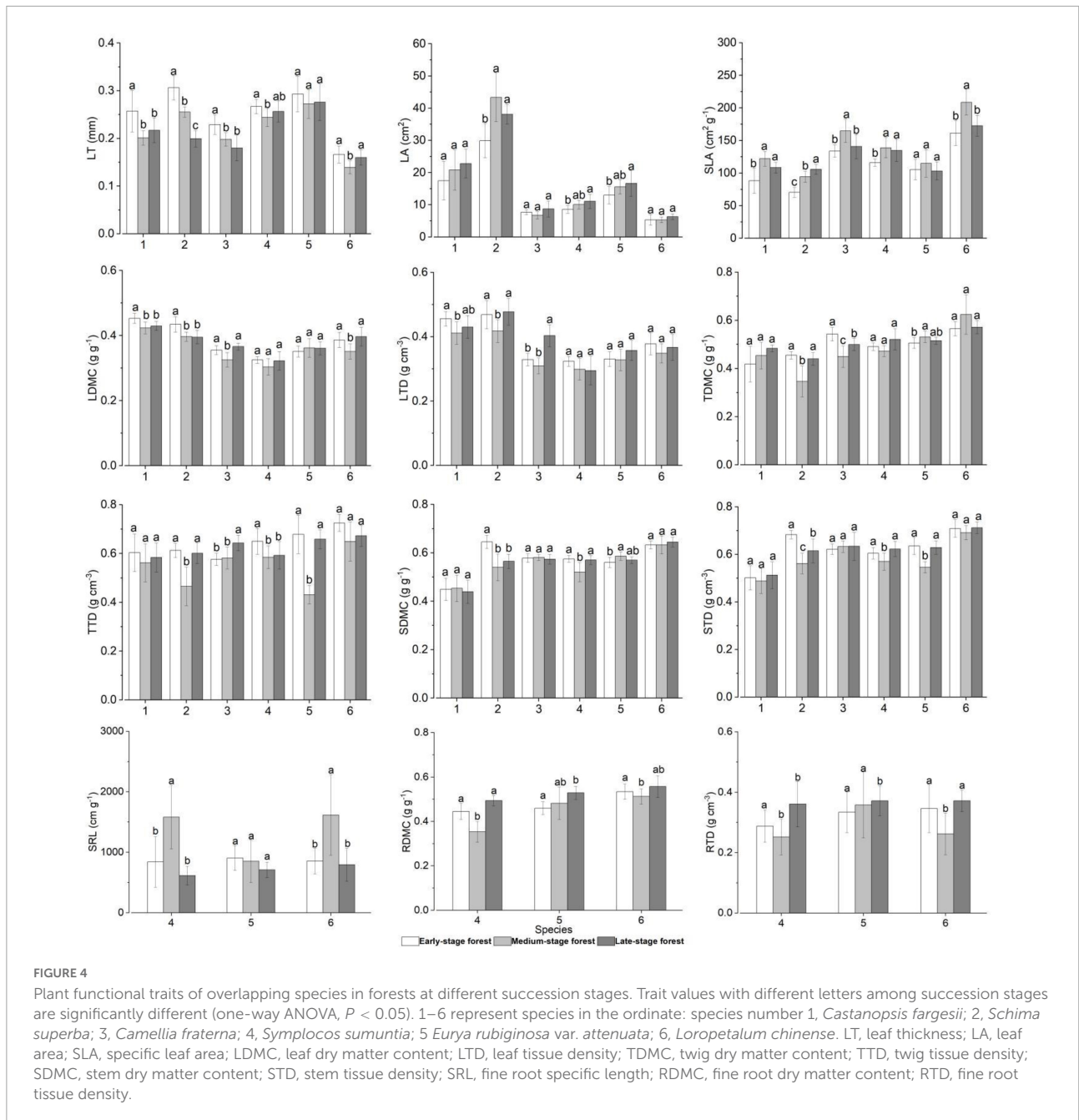


in the world's forests, and most trait studies have focused on trees and their leaf traits, such as LA, LDMC, and SLA (Rosbakh et al., 2015; Siefert et al., 2015; Zhou, 2016; Heilmeyer, 2019; Zhang et al., 2019). The intraspecific trait variation characteristics of understory shrubs and those of the twigs, stems, and roots of trees have rarely been reported (Burton et al., 2017; Zhong et al., 2018; Cao et al., 2020). The present study comprehensively investigated the intraspecific variation characteristics of 12 traits of leaves, twigs, stems, and roots of six common species (two tree species and four understory shrub species) in three typical subtropical evergreen broad-leaved forests in eastern China. This study could fill the gap in plant functional trait studies in subtropical China.

Since the application of succession in plant ecology research, studies on vegetation succession have been widely performed. Biodiversity and carbon storage were often used as indicators to evaluate vegetation succession processes in early studies (Ni et al., 2015; Capellesso et al., 2021). Plant functional traits and trait-based community ecology (a theory using trait-based approaches to determine community composition, structures and functions) offer an alternative approach to reveal the colonization, survival, growth, and death processes of plants and plant communities in different succession vegetation

(Song et al., 2018). However, species compositions vary in different succession vegetations, and traits of different species were measured in previous studies. Rather than considering several dominant species in different succession vegetation (Chazdon, 2008; Muscarella et al., 2017), the present study focused on overlapping species and provided another pathway to understand the interaction of plant functional traits and vegetation succession.

Plant functional traits are codetermined by species identity (genetic factors) and environment (Scheiner and Lyman, 1991; Weiher and Keddy, 1995). Environments promote the coexistence of species with similar functional traits in local habitats, but intraspecific trait variations cause differences in the life history strategy of a certain species or different species (Ackerly and Cornwell, 2007; Auger and Shipley, 2013; Siefert et al., 2015; Kumordzi et al., 2019). However, the species composition of a plant community differs with the environment. The effects of environments on traits are often discussed without considering the effects of species identity, or some statistical analysis methods, such as two-way ANOVA, are used in species–environment interactive analysis in other studies (Zhong et al., 2018; Cao et al., 2020). In the present study, overlapping species in three typical subtropical evergreen



broad-leaved forests with different habitats in eastern China are investigated as an example to explore the effects of the environment on traits. This investigation method is preferred because of the direct exclusion of the effects of species identity.

Root traits often exhibit the largest interspecific and intraspecific variations resulting from complex and diverse below-ground habitats (Comas and Eissenstat, 2004). Leaf traits display larger interspecific and intraspecific variations than twig and stem traits (Ackerly and Reich, 1999; Garnier et al., 2001; Zhong et al., 2018). In the present study, variations in the

intraspecific traits of overlapping species in the forests at three succession stages with different habitats ranged from 2.8% to 56.1%, with an average of 13.5%. Some traits of roots and leaves considerably varied. SRL, RTD, LA, and SLA also differed, but RDMC, LT, LTD, and LDMC (especially the last leaf trait) slightly varied. Consistent with early studies (Garnier et al., 2001), our study showed that intraspecific variations in twig and stem traits slightly differed.

A single trait and the combinations of multiple traits can indicate the adaptation and response of plants to certain environments, expose the plant trade-off strategies of resource

acquisition and utilization, and reveal the different life history strategies of plants in different environments (Wright et al., 2004; Diaz et al., 2016). Some species (resource acquisitive strategy adopters) present a high SLA, leaf nitrogen content, photosynthetic and respiratory rates, and short lifespans. Some other species (resource conservative strategy adopters) display low SLA, leaf nitrogen content, photosynthetic and respiratory rates, and long lifespan (Chen and Xu, 2014). Such plant and trait combinations favor niche overlap and competition reduction, rich biodiversity maintenance, and ecosystem stability enhancement (Liu and Ma, 2015). In the present study, the early-stage forest is a relatively fragile ecosystem with poor soil nutrients and fluctuating soil temperature and humidity. Trees and understory shrubs in such forests allocate more nutrients to resist adverse environments. Thus, they adopt a slow investment-return (resource conservation) strategy and form a series of trait combinations with higher LT, LDMC, LTD, TDMC, TTD, SDMC, STD, RDMC, and RTD and lower SLA and SRL for storing more nutrients and growing slower. However, in the medium- and late-stage forests, trees and understory shrubs are exposed to lower light availability and stronger competition. They adopt a quick investment-return (resource acquisitive) strategy and are associated with a series of trait combinations with higher LA, SLA, and SRL and lower LT, LDMC, LTD, TDMC, TTD, SDMC, STD, RDMC, and RTD for faster growth. Plants in medium-stage forests are more resource acquisitive for lower light availability and stronger competition than those in late-stage forests.

The remaining primary evergreen broad-leaved forests only account for 4% of its total distribution area in eastern China because of intensive human disturbances. Degraded secondary forests, shrub and grass communities, and bare land are distributed everywhere. However, excellent hydrothermal conditions promote secondary forest succession once human disturbances stop. Evergreen broad-leaved forests may recover gradually in this area. Therefore, research on the secondary succession mechanism and restoration ecology of evergreen broad-leaved forests should be strengthened (Song, 2013). Understanding the trend of changes in trait characteristics with vegetation succession and the life strategies of plants adapted to different succession vegetation is important not only for providing data to the global and China plant trait databases but also for establishing regional forest management and restoration in eastern China.

Data availability statement

The original contributions presented in this study are included in the article/**Supplementary material**, further inquiries can be directed to the corresponding author.

Author contributions

LL and YW conceived and designed the research. LL and HX analyzed the data. XQ contributed to the field work. LL wrote the first draft with substantial input from YW. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.1103937/full#supplementary-material>

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