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CSR Ecological Strategies and Functional Traits of the Co-Existing Species along the Succession in the Tropical Lowland Rain Forest

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Abstract: Trait-based approaches to calculate ecological strategy is important for understanding forest succession dynamics. However, the functional traits and ecological strategy change during succession remain poorly understood. We measured key leaf traits and calculated scores for CSR ecological strategy for 13 co-existing species in different successional stages in tropical lowland rain forests. We analyzed the patterns of functional traits and CSR strategies varied along the succession. The relationship between CSR strategy and environmental factors was examined. Our research results are as follows: (1) In older plots, LDMC was generally lower and SLA was generally higher than younger plots with the succession, the functional traits of the successional co-existing tree species changed, and SLA and LDMC showed significant differences. (2) The co-existing tree species' strategies shifted from S/CS and CS strategies to CS/CSR and CS strategies along the succession. (3) Ecological strategies are linked to different combinations of environmental factors across the four successional stages. Our study suggests that the co-existing tree species in different succession stages of tropical lowland rain forests have a high degree of resistance and a conservative ecological strategy, which is significantly related to canopy openness, soil water content, and soil nutrients.

Keywords: CSR strategy; environmental conditions; trade-offs; plant functional traits; co-existing tree species; forest succession dynamics

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1. Introduction

One of the most prominent focuses in trait-based approaches to ecology is the comprehension of mechanisms that drive patterns of species diversity and species co-existence in forest communities [1,2]. Plant functional traits reflect physiological trade-offs that correspond to different resource acquisition strategies and environmental challenges. Therefore, quantifying functional traits is a powerful index used to measure the life cycle strategies of plants [3,4]. Leaf area (LA) largely determines the light-intercepting capacity of plants [5] and constitutes an indicator of the plant size. The larger values of leaf dry matter content (LDMC) and specific leaf area (SLA) are used to represent the opposite extremes of the plant economic spectrum [6]. The three leaf traits are applicable to all vascular plant life forms worldwide; they represent a wide range of plant functions. Such traits provide an indication of the different ecological strategies adopted by species in response to variation across space and time in the range of abiotic and biological factors [3,6–8]. In particular, how plant traits vary over forest succession has important implications for forest structure and function, especially carbon storage [9].

Succession is the main dynamic process in the ecosystem [10,11]. Using plant functional traits to measure succession can not only reflect the ecological strategy of plants, but can also affect the succession by affecting the survivability of plants. With the succession, the species composition, function, and environment of the community change accordingly [12]. Many studies have shown that during the succession process, the functional traits of plants change, which can reflect the community assembly process of plants, which is related to species ecological strategy, species combination, and environmental conditions [13,14]. During the succession process, the species composition changes, but there are some co-existing species in each stage of succession. They are often highly adaptable to environmental changes, showing strong survival and reproduction ability. Therefore, co-existing species in the succession process deserve our attention. We will use space instead of time to study succession. Understanding the functional traits of co-existing tree species in different successional stages and ecological strategy can provide insights on supporting community assembly and can help us to expand the research on ecosystem functions.

CSR theory is a common approach to understanding the wide variation in plant traits and strategies, in which one thinks of species as competitors, stress tolerators, or ruderals [8,15]. Competitors may allocate resources to plant vegetative growth and large plant organs, occupying relatively stable habitats that are not susceptible to threats, thereby gaining the greatest competitiveness and resources. Stress tolerators typically live in resource-poor and variable environments, and invest resources in durable mechanisms that favor their own protection to adapt to harsh environments. Ruderal-selected plants generally devote resources to their propagules, completing their life cycles quickly to resist repetitive, complex disturbance events. Thus, the CSR strategy synthesizes multiple information on individual traits, making it easier to gain insight into how species might respond to environmental change [3,16].

On the basis of this global CSR synthesis [3,8,17], Pierce [6] et al. used trait variation of 3068 vascular plants to quantify the three primary strategies (competitor, C; stress tolerator, S; and ruderal, R). They found that only three easily accessible leaf traits (leaf area, leaf dry matter content, and specific leaf area) are needed to represent the extremes of a trade-off between large size and conservative vs. acquisitive economics [3]. This method is applicable to vascular plants all over the world, and can be used to compare the functional traits of different ecological scales such as communities [6,13,18], species [19,20], individuals [21,22], and succession stages [19,23], and then calculate ecological strategies [6].

In the process of ontogeny, leaves change greatly, including intraspecific variation and interspecific variation [24]. Therefore, the CSR strategy of individual species and vegetation will have a significant change trend. The research [6] shows that the CSR strategy's evidence for species characteristic of primary success, from scree vegetation to siliceous alpine grassland, terminating with alpine *Nardus* pasture, is an initial shift from R- to S-selection. Grime [17] thinks that the early stage of secondary succession is dominated by R-strategy, and S-strategy is dominant in the later stage, while the importance of C-strategy is related to environmental productivity. Therefore, there are many patterns of community succession. The change pattern of vegetation in CSR strategy and the relationship between its environment help to reflect the succession process and its driving force.

There are secondary forests and undisturbed aged forest communities in different succession stages after slash-and-burn disturbance in tropical lowland rain forest of Bawangling, Hainan. This provides good material for us to understand functional traits and ecological strategy from the perspective of co-existing tree species along the successional stages. In this study, we asked the following questions: (1) Do the functional traits of co-existing species change during succession? (2) Is the process of successional forests accompanied by the change of CSR strategy defined by Grime's CSR theory? (3) Are these differences driven by environmental factors? We predict that there are succession co-existing tree species in these forest communities in different succession stages, and their functional traits and ecological strategy will change during succession. The ecological strategy composition for each of the four successional forests was controlled by varied sets of environmental factors. Each ecological strategy at species level was associated with several combinations of environmental factors across all successional forests.

2. Materials and Methods

2.1. Study Site and Species

The study area is located in the mountainous area in the southwest of Hainan Island, in Bawangling (18°52′–19°12′ N, 108°53′–109°20′ E), Hainan Island National Park, China [25]. The park is a tropical monsoon forest that ranges from 100 to 1654 m in elevation. This study was conducted in the tropical lowland rain forest (<800 m asl), where mean annual temperature is 23.6 °C, and annual precipitation is 1677 mm. The study location is characterized as seasonal, with a six-month rainy season from May to October, followed by a six-month dry season during when much of the vegetation is fully to semi-deciduous.

We established eight forest dynamic monitoring sample plots, each with an area of 1 ha (100 m × 100 m). These plots constitute a chronosequence of plots with two plots in each age group: two in the secondary forest abandoned 18 years ago (LSA1, LSA2), two in the secondary forest abandoned 30 years ago (LSB1, LSB2), two in the secondary forest abandoned 60 years ago (LSD1, LSD2), and two in no-disturbance old-growth forest (LOG1, LOG2). Secondary forests were naturally recovered after shifting cultivation. The historical information regarding land use of the plots was obtained from the management records of Bawangling Forestry Bureau of Hainan Province.

Each hectare of plot is subdivided into 25 subplots (20 m × 20 m) for community investigation and environmental factor determination. The species name, diameter at 1.3 m height (DBH), and height of all standing woody stems (excluding lianas) ≥1 cm DBH were recorded in each plot. Through the statistical classification of four succession stages of species, 13 co-existing tree species were found in this study. Thirteen successional co-existing tree species were taken as the research objects for the follow-up study of this paper. See Table 1 below for co-existing species information.

Table 1. The 13 co-existing species among all successional stages and their information (species names, individual numbers of each successional stage).

Family	Species	Stages (Individual Numbers)			
		18-Year-Old	**30-Year-Old**	**60-Year-Old**	**Old-Growth**
Rubiaceae	*Lasianthus hainanensis* Merr.	70	38	383	497
Lauraceae	*Machilus suaveolens* S. Lee	164	119	838	364
Myrsinaceae	*Ardisia quinquegona* Bl.	249	912	1044	893
Fagaceae	*Castanopsis hystrix* J. D.	890	429	110	16
Juglandaceae	*Engelhardia roxburghiana* Wall.	1762	983	1148	65
Euphorbiaceae	*Breynia rostrata* Merr.	123	402	73	17
Rubiaceae	*Psychotria rubra* (Lour.) Poir.	1506	873	2529	235
Gnetaceae	*Gnetum montanum* Markgr.	100	141	88	40
Melastomataceae	*Melastoma sanguineum* Sims.	1919	2304	84	35
Elaeocarpaceae	*Elaeocarpus sylvestris* (Lour.) Poir.	68	393	71	16
Ebenaceae	*Diospyros cathayensis* Steward.	16	23	265	193
Dilleniaceae	*Tetracera asiatica* (Lour.) Hoogland	74	102	247	24
Myrtaceae	*Decaspermum gracilentum* (Hance) Merr. et Perry	37	138	678	17

2.2. Functional Trait Collection

In the four succession stages, 13 successional coexisting species were studied. After data screening, for each study species, we located at least eight individuals for each species in the study growing within the National Park and carried out trait collection, following methods and criteria of Pérez-Harguindeguy [26]. From each individual, we collected two recently expanded, non-senescent leaves from multiple branches. We determined leaf fresh weight (LFW, mg). Each leaf was scanned using a flatbed scanner and leaf area (LA, mm^2) was measured for each leaf or leaflet using ImageJ (from the US National Institutes of Health; http://www.nih.gov/, accessed on 22 February 2013). Each leaf was then placed in a drying oven for a minimum of 48 h at 80 °C and the final dry mass was recorded (LDW, mg). From these measurements, we calculated leaf dry matter content (LDMC, the ratio of leaf dry mass to fresh mass, %) and specific leaf area (SLA, mm^2 mg^{-1}).

2.3. Measurements of Environmental Factors

In the center of each 20 m × 20 m subplot, we collected two samples of soil, one of which was used to measure soil water content. The other soil sample was used for nutrient analysis; it was collected in the rainy season and dried at ambient temperature in the lab to prevent the volatilization of N compounds that can occur when samples are dried at high temperatures. Soil total phosphorus (TP, g kg^{-1}), total potassium (TK, g kg^{-1}), soil available phosphorus (AP, mg kg^{-1}), available nitrogen (AN, mg kg^{-1}), available potassium (AK, mg kg^{-1}), soil water content (SWC, %), and soil organic matter (SOM, g kg^{-1}) were measured according to standard methods [27].

To assess light irradiance in the understory at different successional stages, we used a Hem iView canopy analysis system (HMV1v8, Delta-T Devices Ltd., Cambridge, UK) to take hemispherical photographs at a height of 1.5 m at the center of each 10 m × 10 m quadrat center. Canopy cover was calculated from each photograph as the percentage of closed-canopy pixels using the Gap Light Analyzer (Version 2.0) software (Burnaby, British Columbia, Canada, https://www.sfu.ca/rem/forestry/downloads/gap-light-analyzer.html, accessed on 20 February 2013), following Comita et al. [28]. Canopy openness (CO, %) was then obtained from the formula Canopy Openness = 1 − Canopy Cover.

2.4. Data and Statistical Analyses

We determined Grime's competitive–stress-tolerant–ruderal (CSR) strategies by inputting each species' LA, LDMC, and SLA values into the "StrateFy" strategy classification tool6. This classification method represents the extent of C-, S-, and R-selection using trade-offs between traits (LA, SLA, and LDMC), integrated and compared with trade-offs from over 3000 species from a variety of biomes. We estimated the species values of LA, LDMC, SLA, C, S, and R. We used ternary plots to visualize the patterns of species ecological strategies' distribution change among successional stages. Ternary plots were drawn in SigmaPlot. To allow for parametric statistical analyses, we log-transformed traits values before analysis. Differences in the distribution of species functional traits and ecological strategy among successional stages were tested using an analysis of variance (ANOVA) and post hoc Tukey's test.

To explore the influence of environmental variables on each ecological strategy (C, S, or R), we used linear mixed-effect models [29]. We performed individual models for each ecological strategy and environmental variables in each single successional stage, using the environmental variables as fixed effect and the species as a random effect. The random effect was included in order to control for non-accounted differences between groups [29]. At last, we generated a full set of models using the dredge function in the MuMIn package in R [30]. These models were ranked using the Akaike information criterion corrected for small sample size (AICc); the model with the lowest AICc value was selected as the best model. All statistical analyses were performed in R [31].

Data of environmental factors, functional traits, and CSR strategy values of coexisting species can be found in the Supplementary Materials.

3. Results

3.1. Patterns of Leaf Trait Distribution among Successional Stages

At different successional stages, the values of the species traits LA, LDMC, and SLA showed different distribution patterns (Figure 1). Values of LA for the selected species in each stage did not differ significantly among the four successional stages ($p > 0.05$). However, there were significant differences in LDMC and SLA (Figure 1). In older plots, LDMC was generally lower and SLA was generally higher than younger plots.

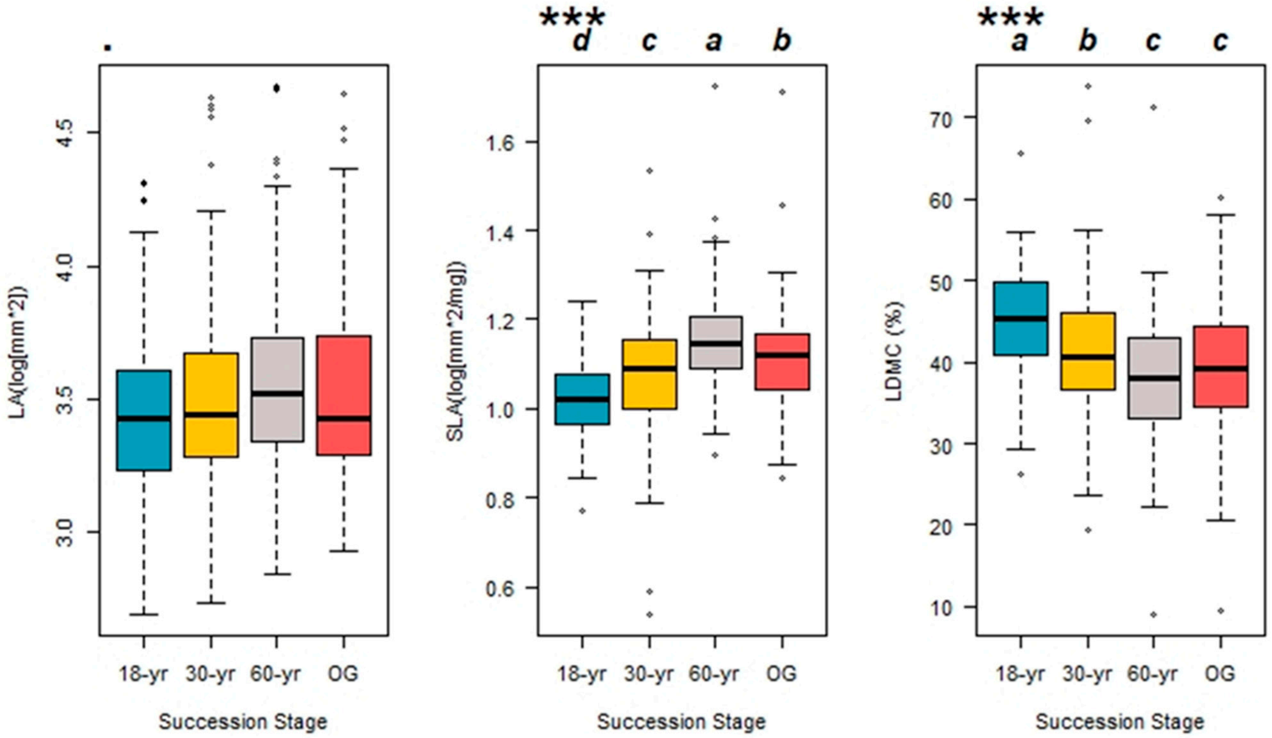

Figure 1. Changes of functional traits of co-existing tree species in different succession stages of tropical lowland rain forests in Hainan. Where LA is leaf area, SLA is specific leaf area, and LDMC is dry matter content of leaves. (Blue, 18-year-old forest; yellow, 30-year-old forest; gray, 60-year-old forest; red, old-growth forest.) One-way ANOVA test, $p > 0.05$ indicates non-significant difference among different stages, ***, $p < 0.001$ indicates the significant difference. A post hoc Tukey test was performed to test difference of combinations of functional traits: different letters indicated significant differences among the succession stages ($p < 0.05$).

During the 18- to 30-year-old stage of secondary succession, tree species showed higher leaf economic structure (the higher LDMC and lower SLA), and their leaves were relatively conservative. In the 60-year-old stage of secondary succession, they showed relatively acquisitive leaf economics trait values, with the highest SLA and lowest LDMC, with higher growth rate and resource acquisition ability, and the old-growth forest was similar to that. There was also a shift from conservative towards acquisitive strategies.

3.2. Spectrum of CSR Strategies Varied along the Succession

Locating all 13 co-existing tree species in CSR strategy space showed that when the average CSR value of each species is characteristic, the strategic positioning of the four succession stages is along the C–S axis of the CSR triangle, and the R component contributes little (Figure 2). The S and C components were strongly negatively correlated, and were also negatively correlated with the R component. Co-existing tree species from the 18-year-old plots were mainly concentrated around the S/CS region of the triangle (mean C:S:R strategy = 34:63:3%; Figure 2), whereas tree species from the 30-year-old plots were mainly CS (36:57:6%; Figure 2). Tree species from the 60-year-old plots exhibited a mean strategy of CS/CSR (39:49:11%; Figure 2) and the old-growth forest exhibited a mean strategy of CS (39:53:8%; Figure 2).

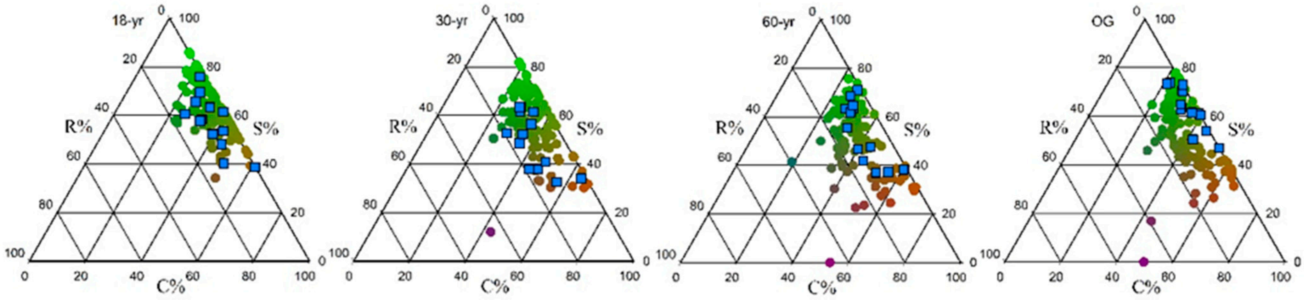

Figure 2. A ternary diagram showing CSR strategy values of co-existing tree species in different successional stages of tropical rain forest. The blue square represents the strategic average of each species feature ($n = 13$), while the circle represents the individual strategic value of a single species ($n = 104$). C (%), S (%), and R (%) respectively represent the scores of C, S, and R in the C-S-R triangle. Ecological strategies are represented by red (C), green (S), and blue (R) ecological strategies, and mixed colors represent mixed strategies (e.g., red/green = CS strategy).

When taking a closer look (Figure 2), we found a separation between values across forest succession stages. Indeed, when evaluating differences between succession stages for each ecological strategy component separately (Figure 3), we found significant differences across most values, especially between the 18-year-old forest and the 60-year-old forest. For components C ($p < 0.01$), we found significant differences between most succession stages (Figure 3), except for 60-year-old and old-growth forests. For component S ($p < 0.001$), differences were significant among all stages (Figure 3). For components R ($p < 0.001$), we found significant differences between most succession stages, except for the 30-year-old forest and old-growth forests (Figure 3). With the change of the succession process, the ecological strategy of co-existing tree species in tropical rain forest shifts was characterized mainly by changes from S/CS, CS towards CS/SCR, and finally a return to the CS strategies.

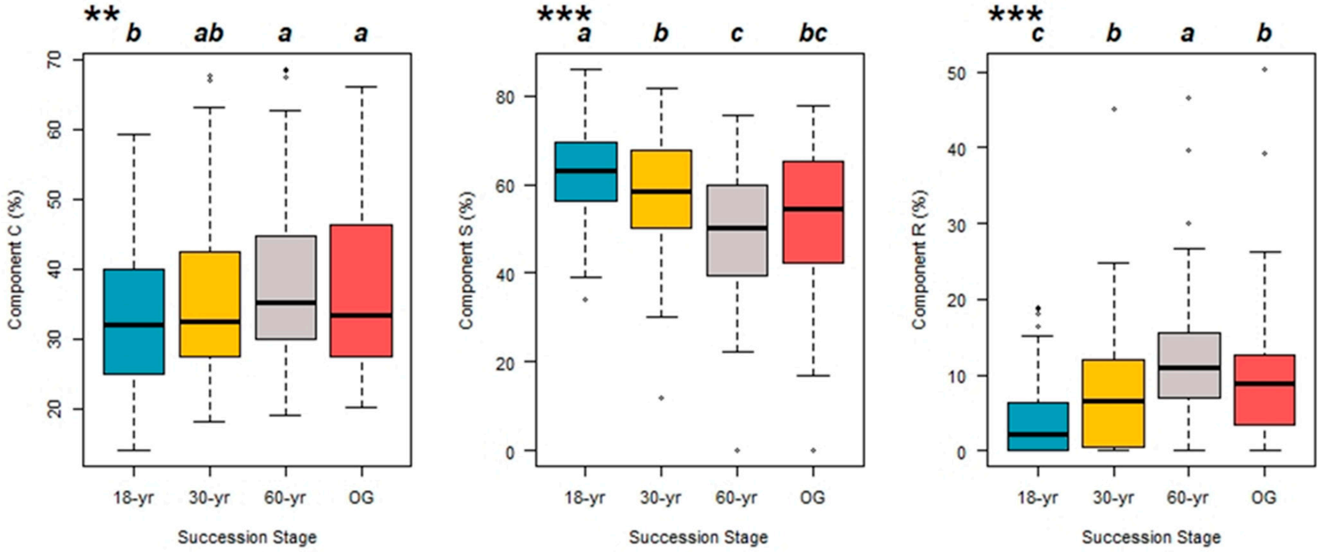

Figure 3. Changes in CSR ecological strategy values of co-existing tree species in different succession stages of tropical lowland rain forests in Hainan. The box represents the strategy values of 13 species. (Blue, 18-year-old forest; yellow, 30-year-old forest; gray, 60-year-old forest; red, old-growth forest.) One-way ANOVA test **, $p < 0.01$, ***, $p < 0.001$ indicates significant difference. A post hoc Tukey test was performed to test difference of combinations within each component: different letters indicate significant difference among successional stages ($p < 0.05$).

3.3. Relationship between CSR Strategy and Environmental Factors

Linear mixed-effects models indicated that correlations between different plant ecological strategies and the measured environmental factors varied with the successional stages (Table 2). In the 18-year-old forest, component C was positively correlated with TP and CO; component S was positively correlated with AP but negatively correlated with TP and SWC; component R was positively correlated with SWC. In the 30-year-old forest, component C was positively correlated with AP and SOM but negatively correlated with TP; component S was positively correlated with TN but negatively correlated with AP and SOM; component R was positively correlated with AP and SOM. In the 60-year-old forest, component C was positively correlated with SOM, while it was negatively correlated with CO and AP; component S was positively correlated with CO. In old-growth forest, component C was negatively correlated with SOM; component S was positively correlated with SOM.

Table 2. Linear mixed-effects models analysis between species-level plant ecological strategy values and environmental factors in the different successional forests. (Available potassium (AK, mg kg^{-1}), available nitrogen (AN, mg kg^{-1}), soil available phosphorus (AP, mg kg^{-1}), total potassium (TK, g kg^{-1}), soil total phosphorus (TP, g kg^{-1}), canopy openness (CO, %), soil water content (SWC, %), and soil organic matter (SOM, g kg^{-1})).

Successional Stages Traits	**Environmental Factors**								**Parameters**	
	AK	**AN**	**AP**	**TK**	**TP**	**CO**	**SWC**	**SOM**	**AICc**	***p*<**
18-year-old										
Component C					1.19	1.00			677.73	0.00
Component S			1.05		−2.40		−2.88		730.90	0.00
Component R							2.26		603.64	0.00
30-year-old										
Component C			2.26		−1.48			2.15	689.70	0.00
Component S			−3.98					−4.89	759.90	0.00
Component R			1.96					3.27	680.90	0.00
60-year-old										
Component C		−1.95				−1.80		1.95	652.70	0.00
Component S						2.12			756.10	0.00
Component R									703.90	0.00
Old-Growth										
Component C								−1.69	674.40	0.00
Component S								2.55	778.80	0.00
Component R									715.00	0.00

4. Discussion

Pierce et al.'s prediction [6] that the "StrateFy" tool could more easily classify plant ecological strategies has been well supported by experimental studies [32–34]. However, to our knowledge, this quantitative approach to determine the CSR strategies of co-existing tree species in tropical lowland rain forests has remained rather limited. In this study, we found significant differences in ecological strategies along the succession stage. The 30-year-old forest and old-growth forest were associated with the strategy of competition/stress tolerance (C/S); whereas, 18-year-old forest was more associated with the stress-tolerance strategy (S). However, the 60-year-old forest not only showed intermediate values for components C and S, but also showed higher values for component R. Overall, among the 13 plant species considered in this study, CSR strategy varied along the C-S axis, and only the component R contributed little. The low contribution of the ruderal component resulted in a strong (negative) correlation between C and S in the co-existing tree species studied here. The opposition between competitiveness and stress tolerance was also found in different forest types (along a short latitudinal gradient) [35]. Related studies have shown woody tree species seem to be filtered against the R strategy (R-selected species are mostly represented by annual herbs) and tropical tree species tend toward more conservative or competitive strategies [21,35].

We recorded differences in co-existing tree species ecological strategies along the succession stage and functional group formation shaped by the environmental gradient, with plants investing in conservative traits (lower SLA/higher stress tolerance) in 18- and 30-year-old, whereas more acquisitive traits (higher LA/higher competitive) were predominantly recorded for plants in late succession (60-year-old). The old-growth forest showed significant changes from acquisitive (60-year-old) to conservative values (higher stress tolerance). As expected, species showed different strategies along the chronosequence, and even different individuals of species at the same succession stage are not the same (for example, *Lasianthus hainanensis* showed S/CS, CS, and CS/CSR strategy). This may suggest that within-species variation in CSR strategy is common [24]. The diversity of ecological strategies among species is conducive to maintaining biodiversity and ecosystem functions, and it is the basis of species coexistence. The diversity of intra-species ecological strategies can enhance the adaptability of species to the environment and enhance the ability of species to survive and reproduce [34].

In this study, we consistently found a strong and significant association between environmental factors and CSR strategies for the tropical lowland rain forest region. High light availability increased the S component directly, as well as indirectly via decreasing soil water content and soil available phosphorus. In contrast, high light had a negative effect on C and R. High phosphorus increased the C component, and high soil water content had a positive effect on R. In the tropical forests, which are often limited by p [36–38], canopy openness is reported to be a more important variable in explaining species with higher stress tolerance (S%) across successional stage [39]. As succession proceeds, canopy openness and light availability decrease [40,41], and the optimal ecological strategy shifts from fast growth in high light to competing for light and persisting in deep shade [42].

Few studies have focused on variation in CSR strategy across successional forests [19,23], although many have examined how the changing microhabitat leads to changes in co-existing tree species' adaptive strategies [43,44]. As we expected, environmental factors were significantly associated with ecological strategies along the chronosequence. Related studies have shown that environmental filters (e.g., soil and abiotic conditions) lead to a convergence of ecological strategies towards stress tolerance [45–47]. The majority of previous studies have examined intra- and interspecific variation in plant functional traits [42,48] or relationships between functional traits of trees and seedlings along a successional gradient [49]. Previous studies indicate that directional changes in environmental conditions along successional gradients affect not only the plant community natural regeneration [48], but also leaf functional traits [40] and ecological strategy [19]. Plants acclimate or adapt to the different habitat conditions along secondary succession, resulting in specific CSR strategies.

Despite the stressful conditions of the tropical lowland rain forest environment, we found relatively high diversity of ecological strategies, but most species lay between the S and C strategies. We also found significant differences between successional stages for C, S, and R values, indicating that species can combine traits in different ways, leading to different ecological strategies over succession. Plant ecological strategies are linked to different combinations of environmental factors across the four successional forests. In the 18-year-old forest, the plants under these relatively harsher environmental conditions (higher canopy openness and poorer soils) presented a mean strategy of S/CS. They had relatively high S scores, suggesting that low phosphorous is more of a constraint than an opportunity for resource acquisition [50]. At the same time, they also had high C values, which may be explained by higher CO. Low SLA (i.e., higher S) is often found under phosphorus-limited conditions [51]. The 18- and 30-year-old forests showed similar environmental conditions, but the 30-year-old site had lower CO than the 18-year-old site. In these stages, the co-existing tree species exhibited stress-tolerant and competitive strategies. In later successional stages (60-year-old), species exhibited a mean of CS/CSR strategy, with a higher component of R than the earlier two successional stages, which indicated that the plant ecological strategy had changed. In order to adapt and respond to environmental changes, plants have made more complicated trade-offs to maintain the most competitive position, which perhaps reflects species with higher leaf construction and defense costs in habitats with lower light availability and higher competition for nutrients. The old-growth forest is somewhat similar to the 30-year-old forest, with low light levels and low soil-available phosphorus. Overall, vegetation across the chronosequence showed different strategies, varying from higher stress tolerance (S) in younger forest, to CS strategy, and finally to higher competitive ability C in old-growth forest. Our results do not support Grime's prediction of secondary succession ecological strategy. First of all, the R-strategy does not have a dominant position in the early stage of succession. The reason for this difference may be that the early succession in this study started from a secondary forest, while Grime's early succession was from bare soil. In this study, we mainly focus on woody plants, which are generally considered to change between C and S selection. Secondly, in our research, the S-strategy is not dominant in the late succession stage, but there are more advantages of the C-strategy. Therefore, we speculate that with the succession, the forest has been well restored and environmental productivity has improved.

The heterogeneity in ecological strategies across successional stages suggests that distinct CSR strategies may coexist within the many microhabitats of tropical lowland rain forests [6,19]. Furthermore, phenotypic plasticity could broaden the range of strategic variation observed for a given species and could also result in more complete resource use [52–54]. This result could be interpreted as supporting the following idea: the greater the range of ecological strategies, the greater the opportunity for more efficient resource use in a temporally variable environment [16]. As such, the fine-scale variability in canopy openness, soil water content, and soil nutrients of the different successional stages, combined with interspecific differences in traits related to resource use, could enable the development of different strategies in tropical lowland rain forest plant communities.

5. Conclusions

This study assessed, for the first-time, variation in the competitive–stress tolerator–ruderal (CSR) ecological strategies of co-existing tree species in a tropical lowland rain forest chronosequence, and quantitatively evaluated variation in these strategies caused by differences in microhabitat canopy openness and soil water and nutrients. We showed that tropical tree species are highly stress-tolerant and showed many conservative strategies. Ecological strategies varied across the chronosequence, from more conservative to more acquisitive, with marked differences between 18-year-old, 30-year-old, 60-year-old, and old-growth forests. Different CSR ecological strategies are associated with each tree species' ability to deal with resource limitation under distinct environmental filters.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13081272/s1, Table S1: Environmental data (mean and standard deviation) of four succession stages (Total potassium (TK, g kg^{-1}), available nitrogen (AN, mg kg^{-1}), Available potassium (AK, mg kg^{-1}), canopy openness (CO, %), soil water content (SWC, %), and soil organic matter (SOM, g kg^{-1}), soil available phosphorus (AP, mg kg^{-1}), soil total phosphorus (TP, g kg^{-1})); Table S2: Functional traits and CSR strategy values (mean and standard deviation) of 13 coexisting species in four succession stages. (LA, leaf area, (mm^2); LDMC, leaf dry matter content, (%); SLA, specific leaf area, (mm^2 mg^{-1}); C, S and R are the CSR scores of species based on three leaf traits and CSR calculation tool—"Stratefy"); Figure S1: Community proportion of 13 coexisting species in four succession stages.

Author Contributions: Conceptualization, X.L.; methodology, X.L.; formal analysis, Y.W. and C.C.; investigation, Y.W., C.C. and B.H.; writing—original draft preparation, Y.W.; writing—review and editing, X.L.; visualization, Y.W. and C.C.; project administration, X.L.; funding acquisition, X.L. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The datasets generated and/or analyzed during the current study are not publicly available due to privacy or ethical restrictions, but are available from the corresponding author on reasonable request.

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Conflicts of Interest: The authors declare that they have no known competing financial interest or personal relationships that could have appeared to influence the work reported in this paper.

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