

Article

Changes in Plant Functional Groups during Secondary Succession in a Tropical Montane Rain Forest

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Abstract: Aggregating diverse plant species into a few functional groups based on functional traits provides new insights for promoting landscape planning and conserving biodiversity in species-diverse regions. Ecophysiological traits are the basis of the functioning of an ecosystem. However, studies related to the identification of functional groups based on plant ecophysiological traits in tropical forests are still scarce because of the inherent difficulties in measuring them. In this study, we measured five ecophysiological traits: net photosynthetic capacity (A_{\max}), maximum stomatal conductance (g_{\max}), water use efficiency (WUE), transpiration rate (T_{mmol}), and specific leaf areas (SLA) for 87 plant species dominant in a chronosequence of secondary succession, using four time periods (5 year-primary, 15 year-early, and 40 year-middle successional stages after clear cutting and old growth) in the tropical montane rainforest on Hainan Island, China. These species were grouped using hierarchical cluster analysis and non-metric multidimensional scaling. Finally, the changes in the composition of functional groups and species richness along the chronosequence were analyzed. Results showed that the plant species in the tropical montane rainforest could be classified into eight distinct functional groups. The richness of functional groups was low during the initial early stage and increased as the early and middle stages progressed, and then declined in the late successional stage. The dominant functional groups in the primary stages had the highest A_{\max} , g_{\max} , T_{mmol} , and SLA, as well as the lowest WUE, while those in the early and middle successional stages had functional traits at a moderate level, and at the late stage they had the lowest A_{\max} , g_{\max} , T_{mmol} , and SLA, and highest WUE. Our study showed that the diverse plant species in the tropical montane rainforest could be grouped into a few functional groups according to major ecophysiological traits, and the composition and relative abundance of different groups changed with the successional dynamics of the forest ecosystem.

Keywords: plant functional group; forest dynamics; secondary succession; tropical montane rainforest

1. Introduction

Plant functional groups (PFGs) are groups of species that share similar morphological and physiological attributes, use similar resources, and play similar roles in a particular ecosystem [1]. PFGs can be divided into functional effect and functional response groups based on each group's

function and/or adaptive responses to environmental variables in an ecosystem. The former refers to groups with a similar effect on one or several ecosystem functions such as primary production and nutrient cycling [2,3], and the latter refers to groups with a similar response to particular environmental factors such as resource availability, disturbance, and drought stress [4–6]. Aggregating species into functional groups is a common method useful for reducing the complexity of diverse ecosystems (e.g., tropical rain forest communities) [7,8]. The identification of PFGs has been given priority in international research agendas [9] for two reasons. First, in modeling vegetation under changing climatic conditions, a widely recognized need exists to move away from single-leaf to whole-plant approaches [10]. Second, in doing so, the enormous complexity of individual species and populations needs to be summarized into a relatively small number of general and recurrent patterns [11,12]. Research studies on the characteristics that define the main functional groups of tropical trees and their relationship to forest dynamics and regeneration have proliferated since the mid-1970s [13–15].

PFGs can be defined based on species functional traits, such as life form, maximum potential height, successional status, and seed dispersal pattern [15–17], and on species' associations with particular environmental factors such as light, disturbance [18,19] or on the ecological strategy of species resources use (e.g., competitors (C), stress-tolerators (S), and ruderals (R), C-S-R strategy) [20,21]. PFGs are most commonly defined based on functional traits. The distribution of functional traits in a community and the magnitude of their differences among species can shed light on the relative influence of environmental filtering and competition [22]. Functional traits can be defined as any attributes that have a potentially significant influence on establishment, survival, and fitness of a species [21,23], and plant 'functional traits' are considered to reflect adaptations to variations in the physical environment as well as ecophysiological and/or evolutionary trade-offs among different functions within a plant [24]. Westoby [25] proposed the leaf-height-seed scheme, to define PFGs based on specific leaf area (SLA), canopy height, and seed mass. The output of the PFG method agrees very well with field studies, indicating that a particular functional trait used for PFG identification in this method can fully reflect the survival strategy of plants [20,25].

Based on the definition of a functional group, the most appropriate way to determine the PFG of a species is to group species based on the role of various species in ecosystem processes (e.g., the cycling of carbon, water, and nitrogen). The plant–atmosphere interactions that are of prime interest for regional and global simulations are the carbon, water, and nitrogen cycles. These cycles are strongly linked to the ecophysiological process of different groups of plant species. Although the body of literature available concerning PFGs is substantial, studies focused on tropical forest vegetation are still scarce [26] and few studies were found addressing the identification of functional groups based on ecophysiological attributes, especially in tropical forest ecosystems. Two of the most important reasons why such studies are rarely conducted are that measuring the ecophysiological traits for numerous individual species is difficult, and it is hard to control the comparability between individual plant species. Furthermore, different PFGs are expected to play different roles in ecosystem processes. Therefore, the identification and the estimation of their abundance are relevant to the assessment of ecosystem function [27–29].

Plant communities recover from disturbances through ecological succession, a process that implies sequential changes occur in the community attributes over time [30]. Although many studies have been conducted to aid in understanding the processes of secondary forest succession in the tropics, few studies have applied concepts related to PFGs to plant community succession in tropical forests. Letcher et al. found that successional habitat specialization is a conserved trait for tropical forests, which associate with many different pioneer lineages and a concomitant diversity of functional traits [31]. To assess plant community succession, an assessment of the changes in PFGs based on functional traits during succession is necessary. Through the use of technologies designed to detect changes in plant functional traits, we can also develop tools for inferring the functions and successional status of plant communities [32]. This is especially important for tropical systems, where functional recovery has been poorly explored.

In the present study, we attempted to define functional groups of a tropical montane rain forest (TMRF) on Hainan Island, China, based on five ecophysiological traits: net photosynthetic capacity (A_{\max} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), maximum stomatal conductance (g_{\max} , $\text{mol m}^{-2}\text{s}^{-1}$), water use efficiency (WUE, $\mu\text{mol mol}^{-1}$), transpiration rate (Trmmol , $\text{mmol m}^{-2} \text{s}^{-1}$), and specific leaf area (SLA, $\text{m}^2 \text{kg}^{-1}$). These traits are directly related to plant–atmosphere interactions as well as plant resource acquisition and use. A_{\max} refers to the net photosynthetic rate of a mature leaf under saturated irradiances that directly indicate the interception and assimilation of resources. g_{\max} , WUE, and Trmmol are traits that are directly related to the plant–atmosphere interactions, and plants have to modulate their photosynthetic and transpiration rates in differing environmental conditions by adjusting their stomatal conductance. SLA is the ratio between leaf area and leaf dry mass, and it is related to resource interception and use. This ratio gives a measure of a plant’s investment into photosynthetic processes as well as into a plant’s participation in the carbon and water cycles

PFGs were identified using standard multivariate analysis techniques based on these five ecophysiological traits. Then we explored the variation of functional group compositions during ecological succession. The composition of PFGs and the dynamics along differing successional stages of TMRF were analyzed based on identified functional groups. The objectives of the study were: 1) To aggregate the diverse tree species in the TMRF of Hainan island into a few functional groups based on the field measured functional traits so that future studies related to the ecosystem functioning and their simulation at different scales could be simplified or made more convenient. 2) To understand the change of functional group composition during the process of succession to provide some theoretical bases for the sustainable management and effective restoration of tropical montane forests on Hainan Island, southern China.

2. Materials and Methods

2.1. Study Sites and Sampling

The research site was located in the TMRF near the Jianfengling Long-term Research Station of Tropical Forest Ecosystems ($18^{\circ}20'–18^{\circ}57'N$, $108^{\circ}41'–109^{\circ}12'E$) (JRSTF, hereafter) at approximately 800–960 m elevation in Southwest Hainan, China. The region’s tropical monsoon climate has a distinct dry and wet season, a mean annual temperature at the study site of 19.7°C , a mean annual rainfall of 2651.6 mm, and a mean annual potential evaporation of 1303.7 mm [33]. The study site has a lateritic yellow soil [34].

Field measurements were carried out within areas of the TMRF located close to the JFSTF by establishing sampling plots in secondary stands with differing times after clear cutting and in old growth stands. For convenience, four successional stages were arbitrarily defined based on time since harvest: primary (stage I), early (II), middle (III), and late successional or old-growth forest stages (IV) with time since harvest = 5 years, 15 years, 40 years, and old growth (no recent harvest), respectively. A total of 70 plots were previously delimited: three were $10 \times 10 \text{ m}^2$ with abandonment ages of 5 years, 30 were $10 \times 10 \text{ m}^2$ with abandonment ages of 15 years, 12 were $10 \times 10 \text{ m}^2$ with abandonment ages of 40 years, and 25 were $20 \times 20 \text{ m}^2$ old growth sites (Table 1). At the beginning of the study, all free-standing plants (trees, shrubs, and herbs) in each plot were recorded, identified, mapped and measured to the lowest possible taxonomic level between November, 2005 and March, 2006. Based on the results, we selected 87 of the most abundant and representative vascular plant species in the TMRF of JRSTF and measured ecophysiological traits.

Table 1. Sampling plots for the stands of different successional stages.

Successional Stage	Time Years Since Harvest	No. of Plots	Plot Size (m ²)
I Primary	5	3	10 × 10
II Early	15	30	10 × 10
III Middle	40	12	10 × 10
IV Late	Old growth	25	20 × 20

2.2. Measurement of Ecophysiological Traits

Measurements were made on 2–6 individuals for each species and 3–5 leaves per individual in low- to mid-crown positions of trees (≤ 5 m in height). All measurements were taken on fully spread mature leaves and we spent 3–5 min for each leaf in an attempt to ensure that photosynthetic induction had already occurred. Leaf gas-exchange rates were measured in the field in April and May 2006 using an LI-6400 portable photosynthesis measurement system (LI-6400, Li-Cor, Lincoln, NE, USA); A_{\max} , g_{\max} , and T_{trmmol} were measured under ambient CO_2 concentrations and relative humidity [35]. The saturating irradiances ($1000 \mu\text{mol m}^{-2}\text{s}^{-1}$) were obtained using an artificial LED light source (LI-6400). The saturating irradiances were identified by the light response curve of light-demanding species, such as *Sapinum discolor*. The measurements were carried out over 9:00–12:30 and 14:00–15:30 on clear days to minimize the influence of depressed stomatal conductance, which may lead to a reduction in CO_2 assimilation.

Leaves were harvested after measurements were obtained and single-sided leaf areas were measured for each fresh leaf with a leaf area meter (LI-3100, LI-COR) and then leaves were oven dried to a constant weight at 65°C . These data were used for the calculation of SLA. Averaged field parameters of each species or individual were used for statistical analysis. The ecophysiological traits related to photosynthesis of major tree species of differing recovery stages were measured in April–May, 2006.

2.3. Data Analysis

Ecophysiological traits of 87 species were measured in stands of different age, as harvest and averages of parameters for individual species were used for statistical analysis. PFGs were defined based on five functional traits by applying hierarchical cluster analysis. Data were log transformed to meet normality prior to the hierarchical cluster analysis. The relative Euclidean distance and Ward Linkage methods were used in the analysis, and cluster analysis using other distances and linkage methods was also carried out; the results were generally in agreement with each other.

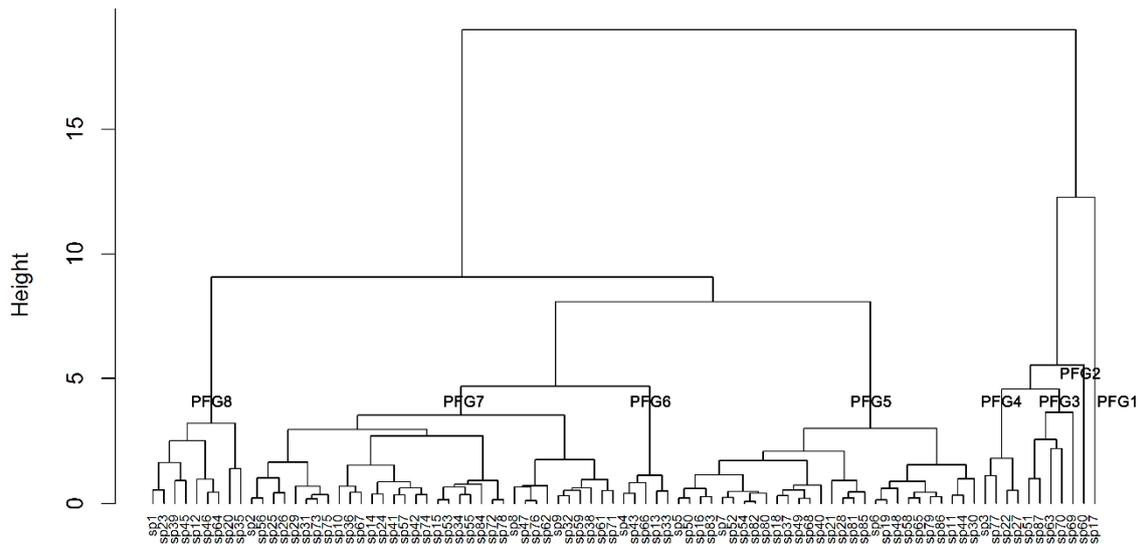
MRPP (multi-response permutation procedures) are non-parametric procedures for testing the hypothesis of no difference between two or more groups of entities. The MRPP algorithm first calculates all pairwise distances in the entire dataset, then calculates δ . It then permutes the sampling units and their associated pairwise distances, and recalculates them based on the permuted data. It repeats the permutation step 999 times. The significance test is the fraction of permuted deltas that are less than the observed delta, with a small sample correction. The function also calculates the change-corrected within-group agreement $A = 1 - \delta E(\delta)$, where $E(\delta)$ is the expected δ assessed as the average of dissimilarities. A value greater than 0 indicates that the difference between groups is greater than the difference within the groups, and less than 0 indicates that the difference within the groups is greater than the difference between groups.

We used the function “agnes” in the {cluster} R package [36], available on CRAN (<https://svn.r-project.org/R-packages/trunk/cluster>), to accomplish the Hierarchical Cluster analysis. Multi-Response Permutation Procedures (MRPP) were accomplished using the function “MRPP” in the {vegan} R package [37], available on CRAN (<https://cran.r-project.org>, <https://github.com/vegandevs/vegan>).

3. Results

3.1. Plant Functional Groups of the TMRF

The 87 main species in the TMRF in Jianfengling, Hainan Island were aggregated into eight PFGs based on five functional traits (A_{max} , g_{max} , WUE, Trmmol, and SLA) using hierarchical cluster analysis (Figure 1). The results of MRPP showed a significant difference between the groups ($p = 0.001$) and the difference between groups is greater than the difference within the groups ($A = 0.5197$), which indicated that the functional groups classified by the ecophysiological traits were distinct groups.



*Note: Sp1	<i>Blastus cochinchinensis</i> , Lour.	Sp30	<i>Syzygium hancei</i> Merr. et Perry	Sp59	<i>Antidesma montanum</i> Bl.
Sp2	<i>Lithocarpus longipedicellatus</i> (Hick. et A. Camus) A. Camus	Sp31	<i>Phoebe hungmaoensis</i> S. Lee	Sp60	<i>Evodia glabrifolia</i> (Champ. ex Benth.) Huang
Sp3	<i>Elaeocarpus petiolatus</i> (Jack) Wall. ex Kurz	Sp32	<i>Illicium ternstroemioides</i>	Sp61	<i>Helicia formosana</i>
Sp4	<i>Acronychia pedunculata</i> (L.) Miq.	Sp33	<i>Litsea elongata</i> (Wall. ex Nees) Benth. et Hook. f.	Sp62	<i>Eriobotrya deflexa</i> (Hemsl.) Nakai f. koshunensis (Kanehira et Sasaki) Li
Sp5	<i>Ormosia balansae</i> Drake	Sp34	<i>Lasianthus koi</i> Merr. et Chun	Sp63	<i>Sapium discolor</i> (Champ. ex Benth.) Muell. Arg.
Sp6	<i>Chassalia curviflora</i> Thwaites var. <i>longifolia</i>	Sp35	<i>Endospermum chinense</i> Benth.	Sp64	<i>Ampelocalamus actinotrichus</i> (Merr. et Chun) S. L. Chen. T. H. Wen et G. Y. Sheng
Sp7	<i>Neolitsea oblongifolia</i> Merr. et Chun	Sp36	<i>Symplocos paniculata</i> (Thunb.) Miq.	Sp65	<i>Calamus simplicifolius</i> C. F. Wei
Sp8	<i>Mallotus hookerianus</i> (Seem.) Muell. Arg.	Sp37	<i>Dasymaschalon rostratum</i>	Sp66	<i>Rhaphiolepis indica</i> (L.) Lindl. ex Ker
Sp9	<i>Lasianthus chinensis</i> (Champ.) Benth.	Sp38	<i>Lasianthus hirsutus</i> (Roxb.) Merr.	Sp67	<i>Olax wightiana</i> Wall. ex Wight et Arn.
Sp10	<i>Gironniera subaequalis</i> Planch.	Sp39	<i>Sterculia lanceolata</i> Cav.	Sp68	<i>Pygeum topengii</i> Merr.
Sp11	<i>Mastixia pentandra</i> Blume subsp. <i>cambodiana</i> (Pierre) Matthew	Sp40	<i>Symplocos lancifolia</i> Sieb. et Zucc.	Sp69	<i>Miscanthus floridulus</i> (Lab.) Warb. ex Schum. et Laut.

Figure 1. Cont.

Sp12	<i>Winchia calophylla</i> A. DC.	Sp41	<i>Psychotria rubra</i> (Lour.) Poir.	Sp70	<i>Trema angustifolia</i> (Planch.) Bl.
Sp13	<i>Lithocarpus brachystachyus</i> Chun	Sp42	<i>Castanopsis fissa</i> (Champ. ex Benth.) Rehd. et Wils	Sp71	<i>Neolitsea phanerophlebia</i> Merr.
Sp14	<i>Parapyrenaria multisejala</i> (Merr. et Chun) Chang	Sp43	<i>Cyclobalanopsis blakei</i> (Skan) Schott.	Sp72	<i>Dillenia pentagyna</i> Roxb.
Sp15	<i>Ardisia nervosa</i> Walker	Sp44	<i>Ormosia semicastrata</i> Hance f. <i>litchifolia</i> How	Sp73	<i>Castanopsis chinensis</i> Hance
Sp16	<i>Polyosma cambodiana</i> Gagnep.	Sp45	<i>Reevesia pubescens</i> Mast.	Sp74	<i>Artocarpus styracifolius</i> Pierre
Sp17	<i>Eupatorium odoratum</i> L.	Sp46	<i>Pithecellobium lucidum</i> Benth.	Sp75	<i>Glochidion coccineum</i> (Buch.-Ham.) Muell. Arg.
Sp18	<i>Elaeocarpus dubius</i> A. DC.	Sp47	<i>Heliciopsis lobata</i> (Merr.) Sleum.	Sp76	<i>Pinanga discolor</i> Burret
Sp19	<i>Diplospora dubia</i> (Lindl.) Masam.	Sp48	<i>Eurya groffii</i> Merr.	Sp77	<i>Melastoma candidum</i> D. Don
Sp20	<i>Ervatamia hainanensis</i> Tsiang	Sp49	<i>Machilus salicina</i> Hance	Sp78	<i>Olea dioica</i> Roxb.
Sp21	<i>Lasianthus curtisii</i> King et Gamble	Sp50	<i>Ardisia quinquegona</i> Bl.	Sp79	<i>Cinnamomum burmanni</i> (Nees et T.Nees) Blume
Sp22	<i>Lindera kwangtungensis</i> (Liou) Allen	Sp51	<i>Melastoma sanguineum</i> Sims	Sp80	<i>Symplocos pseudobarberina</i> Gontsch.
Sp23	<i>Lithocarpus fenestratus</i> (Roxb.) Rehd.	Sp52	<i>Ilex pubilimba</i> Merr. et Chun	Sp81	<i>Alseodaphne hainanensis</i> Merr.
Sp24	<i>Lindera robusta</i> (Allen) H. P. Tsui	Sp53	<i>Beilschmiedia laevis</i> Allen	Sp82	<i>Canthium dicoccum</i> (Gaertn.) Teysmann et Binnedijk
Sp25	<i>Helicia hainanensis</i>	Sp54	<i>Syzygium jambos</i> (L.) Alston	Sp83	<i>Castanopsis tonkinensis</i> Seem.
Sp26	<i>Nephelium topengii</i> (Merr.) H. S. Lo	Sp55	<i>Cryptocarya chingii</i> Cheng	Sp84	<i>Linociera ramiflora</i> (Roxb.) Wall. ex G. Don
Sp27	<i>Adinandra hainanensis</i> Hayata	Sp56	<i>Pentaphylax euryoides</i> Gardn. et Champ.	Sp85	<i>Cryptocarya chinensis</i> (Hance) Hemsl.
Sp28	<i>Drypetes indica</i> (Muell. Arg.) Pax et Hoffm	Sp57	<i>Evodia leptota</i>	Sp86	<i>Ardisia crenata</i> Sims
Sp29	<i>Lithocarpus fenzelianus</i> A. Camus	Sp58	<i>Prismatomeris tetrandra</i> (Roxb.) K. Schum.	Sp87	<i>Thysanolaena maxima</i> (Roxb.) Kuntze

Figure 1. Dendrogram depicting functional groups derived from data of 87 species. Variables used to create cluster include net photosynthetic capacity (A_{max}), maximum stomatal conductance (g_{max}), water use efficiency (WUE), transpiration rate (Trmmol), and specific leaf areas (SLA). Plant functional groups (PFGs).

The composition and functional traits of different PFGs varied greatly (Table 2). PFG1 included one species: *Eupatorium odoratum* L., an invasive ruderal in deforested areas in tropical forest areas. Their main functional traits were comparatively high A_{max} , g_{max} , Trmmol, SLA, and low WUE. PFG2 also included one species: *Evodia glabrifolia* (Champ. ex Benth.) Huang, a fast-growing species, had comparatively high A_{max} , Trmmol, and SLA but moderate g_{max} and low WUE. The group PFG3 was mainly composed of shrubs and tall grasses of the *Poaceae*, along with pioneer species with higher than average A_{max} , moderate g_{max} , Trmmol, WUE, and SLA. The group PFG4 was mainly composed of evergreen trees and shrubs, such as *Elaeocarpus petiolatus* (Jack) Wall. ex Kurz and *Adinandra hainanensis*, characterized by comparatively lower g_{max} , moderate A_{max} , WUE, Trmmol, and lower SLA. PFG5 and PFG6 included most of the tree species in the genera and families typical of the TMRF. Representative species such as *Cryptocarya chinensis* (Hance) Hemsl., *Diplospora dubia* (Lindl.) Masam, and *Lithocarpus brachystachyus* Chun, were mostly common species in the middle successional stages. Functional traits of these two groups were low A_{max} , g_{max} , Trmmol, and moderate SLA, while the WUE of PFG5 was generally higher in contrast with PFG6. The groups PFG7 and PFG8 were mainly composed of late successional species, such as *Dillenia pentagyna* Roxb. and *Nephelium topengii* (Merr.) H. S. Lo. They had

similar functional traits such as low A_{max} , g_{max} , and Trmmol values and higher WUE, while the SLA of PFG8 were relatively higher than that of PFG7.

Table 2. The distributions of the five traits in each plant functional group (Number of species in each PFGs indicated in brackets).

PFGs	Growth Form	Characteristic of Functional Traits	Representative Species
PFG1(1)	Perennial herbs	High A_{max} (>10), High g_{max} (>10), Low WUE (<10), High Trmmol (>5), High SLA (>20).	<i>Eupatorium odoratum</i> L.
PFG2(1)	Trees	High A_{max} (>10), Middle g_{max} (1–10), low WUE (<10), High Trmmol (>5), High SLA (>20).	<i>Eoodia glabrifolia</i> (Champ. ex Benth.) Huang
PFG3(5)	Shrubs and herbs	High A_{max} (>10), Middle g_{max} (1–10), Middle WUE (10–20), High Trmmol (>5), Middle SLA (10–20).	<i>Sapium discolor</i> (Champ. ex Benth.) Muell. Arg. <i>Thysanolaena maxima</i>
PFG4(4)	Evergreen Trees and shrubs	Middle A_{max} (5–10), Low g_{max} (<1), Middle WUE (10–20), Middle Trmmol (2–5), Middle SLA (10–20).	<i>Elaeocarpus petiolatus</i> (Jack) Wall. ex Kurz <i>Adinandra hainanensis</i>
PFG5(28)	Shrubs, Trees and Liana	Low A_{max} (<5), Low g_{max} (<1), High WUE (>20), Low Trmmol (<2), Middle SLA (10–20).	<i>Cryptocarya chinensis</i> (Hance) Hemsl. <i>Diplospora dubia</i> (Lindl.) Masam.
PFG6(5)	Evergreen Trees and Shrubs	Low A_{max} (<5), Low g_{max} (<1), Low WUE (<10), Low Trmmol (<2), Middle SLA (10–20).	<i>Lithocarpus brachystachyus</i> Chun <i>Cyclobalanopsis blakei</i> (Skan) Schott.
PFG7(34)	Shrubs or small trees	Low A_{max} (<5), Low g_{max} (<1), High WUE (>20), Low Trmmol (<2), Middle SLA (10–20).	<i>Dillenia pentagyna</i> Roxb. <i>Nephelium topengii</i> (Merr.) H. S. Lo
PFG8(9)	Shrubs or saplings	Low A_{max} (<5), Low g_{max} (<1), High WUE (>20), Low Trmmol (<2), High SLA (>20).	<i>Blastus cochinchinensis</i> Lour. <i>Ervatamia hainanensis</i> Tsiang

3.2. Analysis of Species Richness and Occurrence Frequency of PFGs

The occurrence frequency in the plots at different times after harvest for the different functional groups of TMRF was analyzed (Figure 2, table S). The result showed that almost all high occurrence species were present in PFG5 and PFG7.

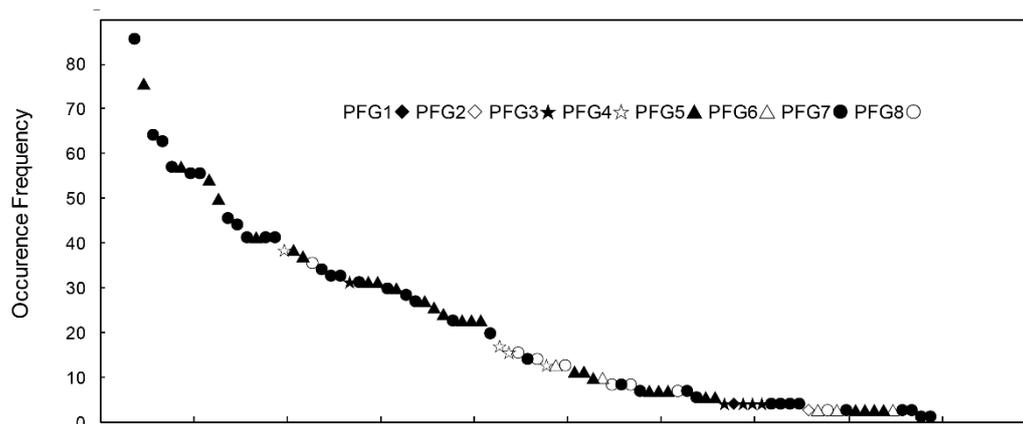


Figure 2. The occurrence frequency of 87 species belonging to different plant functional groups. The 87 species corresponding to each symbol in Figure 2 are listed in Table S1.

3.3. PFGs Richness and Functional Composition in Different Successional Stages

The richness of PFGs varied significantly within differing successional stages ($\chi^2 = 213.774$, $df = 21$, $p < 0.001$). The statistical analysis showed that the richness of PFGs was lowest in the primary stage. The dominant PFGs of this stage were PFG3 and PFG4 (high relative abundance), while PFG5, PFG6, PFG7, and PFG8 were not found. PFG richness increased rapidly after the restoration of the forest

environment and PFG richness of the early and middle successional stages were highest; the dominant PFGs of these stages were PFG5 and PFG7. The richness of PFGs decreased in the late successional stage as a result of the disappearance of pioneer species; the dominant PFGs of this stage were PFG5 and PFG7 (Figure 3).

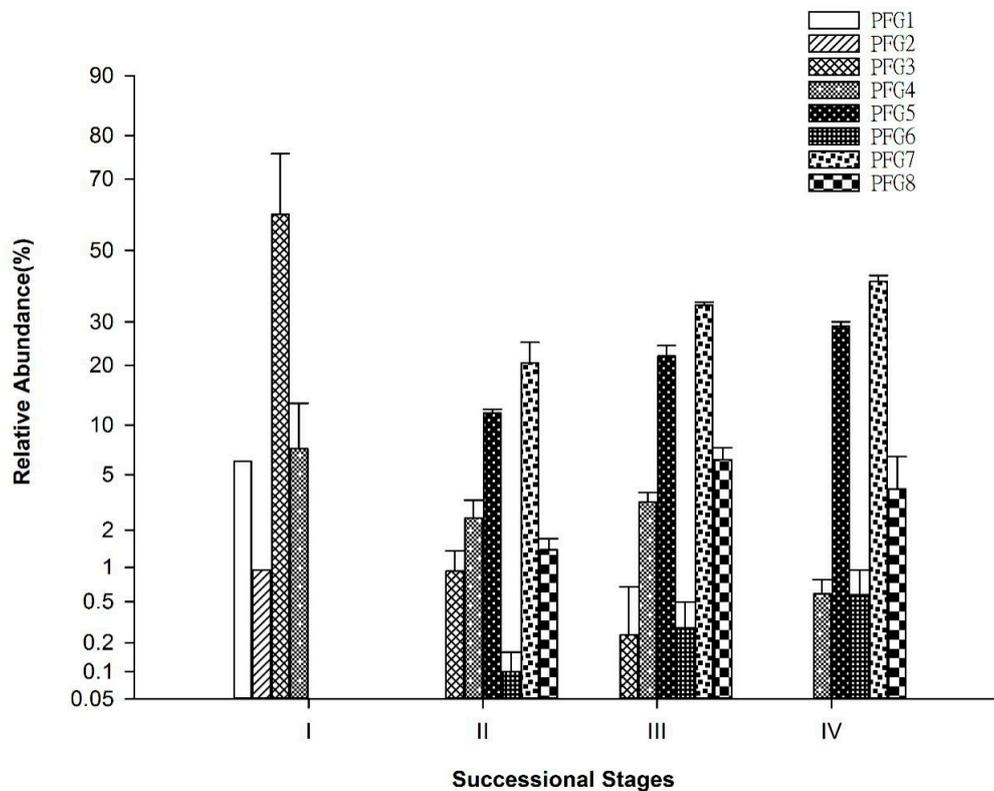


Figure 3. PFG richness and functional composition in different successional stages. Table 1 lists the successional stages.

3.4. Relative Abundance of PFGs along the Successional Stages

Generally, the relative abundance of PFG1, PFG2, PFG3, and PFG4 decreased as time progressed through the successional stages, and that of PFG5 peaked at late stage while the relative abundance of PFG6, PFG7, and PFG8 increased during the successional stages (Figure 4). The PFG1 and PFG2 occurred only in the primary stage, while PFG3 and PFG4 were dominant in the primary stage. The species found in these four stages were most found in the early and middle successional stages. The relative abundance of PFG5, PFG6, PFG7, and PFG8 increased gradually as time progressed through, PFG5, PFG6, and PFG7 dominated PFGs of the late successional stages, while PFG8 dominated in the middle stage.

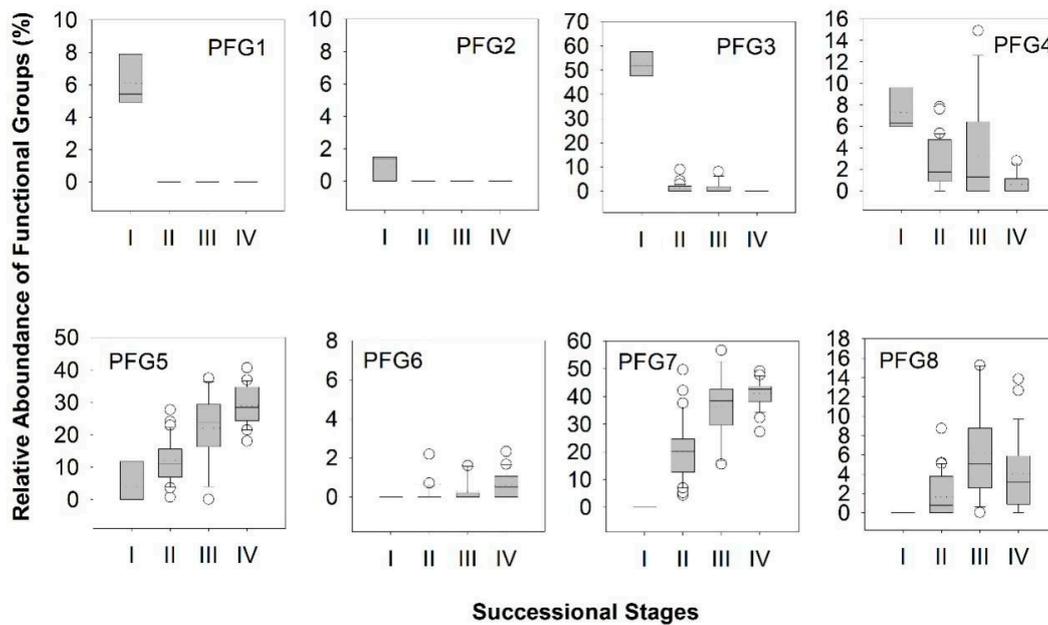


Figure 4. Box plot of relative abundance of PFGs in difference successional stages of tropical montane rain forest (TMRF). Table 1 lists the successional stages.

4. Discussion

The concept of PFGs has been regarded as a framework for predicting ecosystem response to environmental changes on a global scale, without detailed information about each species [8,38]. Therefore, research related to PFGs is strongly tied to the modeling of ecosystem processes [39]. The challenge in functional grouping is how to find the most appropriate indices and methods to use for the aggregation of PFGs. PFGs are commonly defined based on a series of related quantitative traits [39–41]. Theoretically, one can properly define PFGs based on ecophysiological traits related to plant–atmosphere interactions. A study of shrub vegetation in Florida showed that PFGs based on physiological traits were spatially and temporally robust [42]. A study in the eastern Amazonian region demonstrated that ecophysiological traits were significantly different between functional groups. Additionally, PFGs identified by combining hard traits (ecophysiological traits) with soft traits (e.g., leaf chemical, anatomical characteristics) were highly consistent with groups based on life forms [26]. One can reasonably, practically, and feasibly define functional groups using ecophysiological traits [43]. However, measuring large sets of ecophysiological parameters in the field for grouping is time intensive and expensive, making it necessary to find one or a set of easy-to-measure soft traits that can be used as substitutes of ecophysiological traits, and the grouping result based on these indicators are expected to agree with that of the ecophysiological traits. A study of shrub habitat in Florida [44] showed that groups defined by life forms were similar to ecophysiological-based groups. We attempted to identify PFGs based on a set of ecophysiological traits related to photosynthetic parameters obtained from field measurements. These traits are indices of plant–atmosphere interaction (gas and water exchange), and are therefore directly related to plant use of light, water, and other resources. Thus, this grouping is expected to enable successful prediction of responses to environmental variations in climate, atmospheric chemistry, or site disturbances.

Community structure can strongly influence ecosystem function [44], and the functions of species in ecosystems are highly related to the size and density of the individual species [45]. According to López-Martínez’s study [46], variation in floristic composition was greatest for shrubs and lowest for trees. We found that most of the species with higher occurrence frequency were smaller than the relatively rare species in the same group. For example, in group 7, *Heliciopsis lobata* (Merr.) Sleum, *Cryptocarya chingii* Cheng, and *Antidesma montanum* Bl. occurred only in the middle and

late successional stages were larger than relatively found shrubs like *Lasianthus chinensis* (Champ.) Benth., *Symplocos paniculata* (Thunb.) Miq., and *Pentaphragma eurycoides*. Meanwhile, we can interpret varied community characteristics along the succession gradient by studying key functional traits of dominant species. Similarly, community characteristics can be interpreted by studying their functional compositions and the main characteristics of functional groups [8]. We attempted to study succession by comparing sites of various ages in the montane rain forest in Jianfengling using an approach called a “space for time substitution.” Our results indicate that the richness of PFGs is lowest in the primary successional stage, increases rapidly after the restoration of a forested environment, and peaks during the early and middle stages then decreases in the late stage. The results indicate that the influence of an established species in its habitat is the main force driving succession [47] and the establishment and growth of new species strongly depends on particular physical environments created by earlier species [48]. The establishment of new species will cause changes to the existing habitats. Lucía et al. found that although almost all species can be established along the complete environmental gradient, species that dominated early in succession had acquisitive functional traits, while those that dominated at later successional ages and hills showed more conservative traits [24]. The establishment of PFGs during the primary stage facilitates the establishment and growth of new PFGs, which conversely inhibit the survival of former; the decrease in functional richness during the late successional stage is probably caused mainly by the heavily shaded original forest environment, which is unfavorable for the growth and regeneration of light-demanding pioneer species. This constitutes a foundation for further exploration of the application of remote sensing technologies to the study of tropical succession.

Community changes during succession include not only the increase in functional group richness but also changes in the composition of PFGs. Statistical results show that the relative abundance of PFG1, PFG2, PFG3, and PFG4 decrease as ecological succession progresses and that PFG5 peaks at the late stage while the relative abundances of PFG6, PFG7, and PFG8 increase as succession continues. Analysis shows that the dominant PFGs of the primary stage are those with higher photosynthetic capacity, fast-growing rates, and low water use efficiency. These PFGs appear to be associated with relative high values of A_{max} , $Trmmol$, and SLA, as well as with lower values of WUE. This particular combination of traits generally occurs as a response to a particular combination of environmental conditions: low water availability, high light availability, and high temperature [49]. Dominant PFGs of the early and middle stages were those with moderate photosynthetic capacity and WUE and comparatively high growth rates; the main PFGs of the late successional stage were those with low A_{max} , high WUE, and low growth rates.

We found that the SLA, which had been above average throughout the succession, rose above 20 in group 8 again, possibly because group 8 was mainly composed of shade tolerant species in the middle and late succession. The facilitation and inhibition model of succession proposes that early successional species are more vulnerable to variety of physical and biological factors that cause mortality. Thus, the relative abundance of PFGs with pioneer species (gap species) decreases during succession, while that of PFGs, mainly composed of shade-tolerant species, increases during ecological succession. Surprisingly, in PFG3, a shrub-like herbaceous C4 plant *thysanolaena maxima*, which looks like bamboo, is grouped with three other shrub species. This may be part of the reason, as it may have some important leaf trait differences with shrubs. This difference points to a potential problem, in that using leaf traits to define PFGs is somewhat limited. It may be more meaningful and useful to add dimensions to the leaf traits we studied such as heights and seeds; these could perhaps be used in addition to leaf traits to define them [42]. Zhang and Zang [13] classified tropical forest vegetation of Hainan Island, China into six functional groups based on successional status and potential maximum height. There is still much room for research and in-depth exploration on leaf traits in the future. Variation of dominant PFGs in differing stages indicates that what really determines the occurrence and relative abundance of PFGs in a particular community is the diversity of microhabitats and the abundance of shaded and gap habitats in the meta community over long periods of time. The replacement of species will cause variations in the functional groups present and the variations

in the richness and relative abundances of PFGs and in the progress of ecological succession of a community are cause and effect related.

5. Conclusions

Based on five field measured ecophysiological traits, major plant species in the TMRF of Jianfengling, Hainan Island, were grouped into eight PFGs by applying quantitative techniques. MRPP tests indicated that the identified PFGs are distinct groups with high heterogeneity between groups but high homogeneity within each group. The richness of PFGs and functional groups composition of TMRF in the Jianfengling areas varied significantly during ecological succession. Species composition and PFGs richness were relatively low in the primary stage as the closed canopy forested environment was lacking, and because the plant community of this stage was dominated by fast-growing pioneer groups with high A_{max} and low WUE. The richness of PFGs increased rapidly after establishment of a forested environment and reached a peak in the middle successional stages. Additionally, the related dominant PFGs of both these stages were faster-growing species with moderate A_{max} and lower WUE. The richness of PFGs decreased in the late successional stage because the dense canopy limited the regeneration of light-demanding species, and the dominant PFGs of this stage were slow-growing species with low A_{max} , but high WUE. A functional approach should be incorporated as a regular descriptor of forest succession because it provides a richer understanding of vegetation dynamics than is offered by either the floristic or structural approach alone.

Tropical montane rainforests are one of the most highly diverse types of forests in the world, and they are considered extremely vulnerable to disturbance and climate changes. Our study, which aggregated the diverse plant species into a few functional groups based on ecophysiological functional traits, provided new insights elucidating the structure and function of tropical forest ecosystems [13]. It is also an effective way of making further landscape planning, improving forest conservation planning and conserving biodiversity in species-rich tropical forests [50].

Supplementary Materials: The following are available online at <http://www.mdpi.com/1999-4907/10/12/1134/s1>, Figure S1: Box plot for the distributions of the five traits in each plant functional group, Table S1: The 87 species corresponding to each symbol.

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References

1. Hawkins, C.P.; MacMahon, J.A. Guilds: The multiple meanings of a concept. *Annu. Rev. Entomol.* **1989**, *34*, 423–451. [[CrossRef](#)]
2. Gitay, H.; Noble, I.R.; Connell, J.H. Deriving functional types for rain-forest trees. *J. Veg. Sci.* **1999**, *10*, 641–650. [[CrossRef](#)]
3. Pos, E.; Guevara Andino, J.E.; Sabatier, D.; Molino, J.F.; Pitman, N.; Mogollón, H.; Neill, D.; Cerón, C.; Rivas-Torres, G.; Di, F.A.J.E.; et al. Estimating and interpreting migration of Amazonian forests using spatially implicit and semi-explicit neutral models. *Ecol. Evol.* **2017**, *7*, 4254–4265. [[CrossRef](#)] [[PubMed](#)]

4. García-Palacios, P.; Maestre, F.T.; Gallardo, A. Soil nutrient heterogeneity modulates ecosystem responses to changes in the identity and richness of plant functional groups. *J. Ecol.* **2011**, *99*, 551–562. [[CrossRef](#)] [[PubMed](#)]
5. Lavorel, S.; Díaz, S.; Cornelissen, J.H.C.; Garnier, E.; Harrison, S.P.; McIntyre, S.; Pausas, J.G.; Pérezharguindeguy, N.; Roumet, C.; Urcelay, C. Plant Functional Types: Are We Getting Any Closer to the Holy Grail? *Terr. Ecosyst. Chang. World* **2007**, *17*, 149–164.
6. Muler, A.L.; Canham, C.A.; Etten, E.J.B.V.; Stock, W.D.; Froend, R.H.J.F.E. Using a functional ecology approach to assist plant selection for restoration of Mediterranean woodlands. *For. Ecol. Manag.* **2018**, *424*, 1–10. [[CrossRef](#)]
7. Hubbell, S.P. Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct. Ecol.* **2005**, *19*, 166–172. [[CrossRef](#)]
8. McLaren, J.R.; Turkington, R. Ecosystem properties determined by plant functional group identity. *J. Ecol.* **2010**, *98*, 459–469. [[CrossRef](#)]
9. Kooyman, R.; Rossetto, M. Definition of plant functional groups for informing implementation scenarios in resource-limited multi-species recovery planning. *Biodivers. Conserv.* **2008**, *17*, 2917–2937. [[CrossRef](#)]
10. Körner, C. CO₂ Fertilization: The Great Uncertainty in Future Vegetation Development. In *Vegetation Dynamics Global Change*; Solomon, A., Shugart, H., Eds.; Springer: New York, NY, USA, 1993; pp. 53–70. [[CrossRef](#)]
11. Díaz, S.; Noy-Meir, I.; Cabido, M. Can grazing response of herbaceous plants be predicted from simple vegetative traits? *J. Appl. Ecol.* **2010**, *38*, 497–508. [[CrossRef](#)]
12. Barradas, M.C.D.; Zunzunegui, M.; Tirado, R.; Ain-Lhout, F.; Novo, F.G. Plant functional types and ecosystem function in Mediterranean shrubland. *J. Veg. Sci.* **2010**, *10*, 709–716. [[CrossRef](#)]
13. Zhang, Z.; Zang, R. Relationship between species richness of plant functional groups and landscape patterns in a tropical forest of Hainan Island, China. *J. Trop. For. Sci.* **2011**, *23*, 289–298.
14. Li, N.; He, N.; Yu, G.; Wang, Q.; Jian, S. Leaf non-structural carbohydrates regulated by plant functional groups and climate: Evidences from a tropical to cold-temperate forest transect. *Ecol. Indic.* **2016**, *62*, 22–31. [[CrossRef](#)]
15. Chazdon, R.L.; Finegan, B.; Capers, R.S.; Salgado-Negret, B.; Casanoves, F.; Boukili, V.; Norden, N. Composition and dynamics of functional groups of trees during tropical forest succession in northeastern Costa Rica. *Biotropica* **2010**, *42*, 31–40. [[CrossRef](#)]
16. Eisenhauer, N.; Scheu, S. Invasibility of experimental grassland communities: The role of earthworms, plant functional group identity and seed size. *Oikos* **2008**, *117*, 1026–1036. [[CrossRef](#)]
17. Spasojevic, M.J.; Harline, K.; Stein, C.; Mangan, S.A.; Myers, J.A. Landscape context mediates the relationship between plant functional traits and decomposition. *Plant Soil* **2019**, *438*, 377–391. [[CrossRef](#)]
18. Katabuchi, M.; Kurokawa, H.; Davies, S.J.; Tan, S.; Nakashizuka, T. Soil resource availability shapes community trait structure in a species-rich dipterocarp forest. *J. Ecol.* **2012**, *100*, 643–651. [[CrossRef](#)]
19. Hong, H.N.; Uria-Diez, J.; Wiegand, K. Spatial distribution and association patterns in a tropical evergreen broad-leaved forest of north-central Vietnam: Official organ of the International Association for Vegetation Science. *J. Veg. Sci.* **2016**, *27*, 318–327.
20. Brym, Z.T.; Lake, J.K.; Allen, D.; Ostling, A. Plant functional traits suggest novel ecological strategy for an invasive shrub in an understorey woody plant community. *J. Appl. Ecol.* **2011**, *48*, 1098–1106. [[CrossRef](#)]
21. Reich, P.B.; Buschena, C.; Tjoelker, M.G.; Wrage, K.; Knops, J.; Tilman, D.; Machado, J.L. Variation in growth rate and ecophysiology among 34 grassland and savanna species under contrasting N supply: A test of functional group differences. *New Phytol.* **2003**, *157*, 617–631. [[CrossRef](#)]
22. Lucía, S.V.; Juan, D.; José, A.; Casandra, R.-G.; Horacio, P.; Paula, J. Functional Diversity of Small and Large Trees along Secondary Succession in a Tropical Dry Forest. *Forests* **2016**, *7*, 163.
23. Storkey, J.; Brooks, D.; Haughton, A.; Hawes, C.; Smith, B.M.; Holland, J.M.; Lavorel, S. Using functional traits to quantify the value of plant communities to invertebrate ecosystem service providers in arable landscapes. *J. Ecol.* **2013**, *101*, 38–46. [[CrossRef](#)]
24. Sanaphre-Villanueva, L.; Dupuy, J.M.; Andrade, J.L.; Reyes-García, C.; Jackson, P.C.; Paz, H. Patterns of plant functional variation and specialization along secondary succession and topography in a tropical dry forest. *Environ. Res. Lett.* **2017**, *12*, 055004. [[CrossRef](#)]

25. Cornelissen, J.H.C.; Cerabolini, B.; Castro-Díez, P.; Villar-Salvador, P.; Montserrat-Martí, G.; Puyravaud, J.P.; Maestro, M.; Werger, M.J.A.; Aerts, R. Functional traits of woody plants: Correspondence of species rankings between field adults and laboratory-grown seedlings? *J. Veg. Sci.* **2003**, *14*, 311–322. [[CrossRef](#)]
26. Westoby, M. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* **1998**, *199*, 213–227. [[CrossRef](#)]
27. Domingues, T.F.; Martinelli, L.A.; Ehleringer, J.R. Ecophysiological traits of plant functional groups in forest and pasture ecosystems from eastern Amazonia, Brazil. *Plant Ecol.* **2007**, *193*, 101–112. [[CrossRef](#)]
28. Díaz, S.; Cabido, M. Plant functional types and ecosystem function in relation to global change. *J. Veg. Sci.* **1997**, *8*, 463–474. [[CrossRef](#)]
29. Meers, T.L.; Bell, T.L.; Enright, N.J.; Kasel, S. Role of plant functional traits in determining vegetation composition of abandoned grazing land in north-eastern Victoria, Australia. *J. Veg. Sci.* **2008**, *19*, 515–524. [[CrossRef](#)]
30. Mechelen, C.V.; Dutoit, T.; Kattge, J.; Hermy, M.J.E.E. Plant trait analysis delivers an extensive list of potential green roof species for Mediterranean France. *Ecol. Eng.* **2014**, *67*, 48–59. [[CrossRef](#)]
31. Lima, T.A.; Vieira, G. High plant species richness in monospecific tree plantations in the Central Amazon. *For. Ecol. Manag.* **2013**, *295*, 77–86. [[CrossRef](#)]
32. Letcher, S.G.; Lasky, J.R.; Chazdon, R.L.; Norden, N.; Wright, S.J.; Meave, J.A.; Pérez-García, E.A.; Muñoz, R.; Romero-Pérez, E.; Andrade, A.; et al. Environmental gradients and the evolution of successional habitat specialization: A test case with 14 Neotropical forest sites. *J. Ecol.* **2015**, *103*, 1276–1290. [[CrossRef](#)]
33. Zeng, Q.B.; Li, Y.D.; Chen, B.F.; Wu., Z.M.; Zhou, G.Y. *Research and Management of Tropical Ecosystem*; China Forestry Press: Beijing, China, 1997. (In Chinese)
34. Jiang, Y.X.; Lu, J.P. *Tropical Forest Ecosystem in Jianfengling, Hainan Island, China*; Science Press: Beijing, China, 1991. (In Chinese)
35. Alvarez-Anorve, M.Y.; Quesada, M.; Sanchez-Azofeifa, G.A.; Avila-Cabadilla, L.D.; Gamon, J.A. Functional regeneration and spectral reflectance of trees during succession in a highly diverse tropical dry forest ecosystem. *Am. J. Bot.* **2012**, *99*, 816–826. [[CrossRef](#)] [[PubMed](#)]
36. Maechler, M.; Rousseeuw, P.; Struyf, A.; Hubert, M.; Hornik, K. cluster: Cluster Analysis Basics and Extensions. *R Package Version* **2012**, *1*, 56.
37. Jari Oksanen, F.; Blanchet, G.; Friendly, M.; Kindt, R.; Legendre, P.; McGlinn, D.; Minchin, P.R.; O'Hara, R.B.; Simpson, G.L.; Solymos, P.; et al. vegan: Community Ecology Package. R Package Version 2.5-5. Available online: <https://CRAN.R-project.org/package=vegan> (accessed on 1 September 2019).
38. McLaren, J.R.; Novoplansky, A.; Turkington, R.J.P.E. Few effects of plant functional group identity on ecosystem properties in an annual desert community. *Plant. Ecol.* **2016**, *217*, 1–15. [[CrossRef](#)]
39. Holl, K.D.; Zahawi, R.A.; Cole, R.J.; Ostertag, R.; Cordell, S. Planting Seedlings in Tree Islands Versus Plantations as a Large-Scale Tropical Forest Restoration Strategy. *Restor. Ecol.* **2011**, *19*, 470–479. [[CrossRef](#)]
40. Reich, P.B.; Walters, M.B.; Ellsworth, D.S. From tropics to tundra: Global convergence in plant functioning. *Proc. Natl. Acad. Sci. USA* **1997**, *94*, 13730–13734. [[CrossRef](#)]
41. Craine, J.; Tilman, D.; Wedin, D.; Reich, P.; Tjoelker, M.; Knops, J. Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Funct. Ecol.* **2002**, *16*, 563–574. [[CrossRef](#)]
42. Westoby, M.; Falster, D.; Moles, A.; Vesk, P.; Wright, I. Plant ecological strategies: Some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* **2002**, *33*, 125–159. [[CrossRef](#)]
43. Foster, T.E.; Brooks, J.R. Functional groups based on leaf physiology: Are they spatially and temporally robust? *Oecologia* **2005**, *144*, 337–352. [[CrossRef](#)]
44. Hérault, B.; Bachelot, B.; Poorter, L.; Rossi, V.; Bongers, F.; Chave, J.; Paine, C.E.T.; Wagner, F.; Baraloto, C. Functional traits shape ontogenetic growth trajectories of rain forest tree species. *J. Ecol.* **2011**, *99*, 1431–1440. [[CrossRef](#)]
45. Risser, P.G. Biodiversity and ecosystem function. *Conserv. Biol.* **1995**, *9*, 742–746. [[CrossRef](#)]
46. López-Martínez, J.; Sanaphre-Villanueva, L.; Dupuy, J.; Hernandez-Stefanoni, J.L.; Meave, J.; Gallardo, A. β -Diversity of Functional Groups of Woody Plants in a Tropical Dry Forest in Yucatan. *PLoS ONE* **2013**, *8*, e73660. [[CrossRef](#)] [[PubMed](#)]
47. Chapin, F. Physiological controls over plant establishment in primary succession. In *Primary Succession on Land*; Miles, J., Walton, D.W.H., Eds.; Blackwell Scientific Publications: Oxford, UK, 1993; pp. 161–178.
48. Pickett, S.; Collins, S.; Armesto, J. A hierarchical consideration of causes and mechanisms of succession. *Vegetatio* **1987**, *69*, 109–114. [[CrossRef](#)]

49. Lebrija-Trejos, E.; Pérez-García, E.A.; Meave, J.A.; Poorter, L.; Bongers, F. Environmental changes during secondary succession in a tropical dry forest in Mexico. *J. Trop. Ecol.* **2011**, *27*, 477–489. [[CrossRef](#)]
50. Zhang, Z.-D.; Zang, R.-G.; Convertino, M. Predicting the distribution of potential natural vegetation based on species functional groups in fragmented and species-rich forests. *Plant Ecol. Evol.* **2013**, *146*, 261–271. [[CrossRef](#)]



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