forests

Article

Use of Functional Traits to Distinguish Successional Guilds of Tree Species for Restoring Forest Ecosystems

Benjapan Manohan [1,2], Dia Panitnard Shannon [1,3], Pimonrat Tiansawat [1,3], Sutthathorn Chairuangsri [1,3], Jutatip Jainuan [4] and Stephen Elliott [1,3,*]

[1] Forest Restoration Research Unit, Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai 50200, Thailand
[2] Graduate Master's Degree Program in Biology, Faculty of Science, Chiang Mai University, Chiang Mai 50200, Thailand
[3] Environmental Science Research Centre, Faculty of Science, Chiang Mai University, Chiang Mai 50200, Thailand
[4] The Next Forest Company Limited 228 Moo.1, Tha Sala, Muang, Chiang Mai 50200, Thailand
* Correspondence: stephen_elliott1@yahoo.com

Abstract: Forest ecosystem restoration involves establishing mixes of tree species representing various successional stages of the reference forest. When selecting species, conceptualizing successional status as a gradient of guilds is more appropriate than the conventional binary classification of pioneer and climax species. Therefore, we tested the hypothesis that functional traits can be used to distinguish successional guilds among tree species, planted to test the framework species method of restoration. Values of 13 non-intercorrelated traits of 28 species, derived from field measurements and databases, were analyzed by cluster analysis and rank scoring. Cluster analysis grouped species into six guilds. For rank scoring, negative (from 0 to −2) and positive scores (from 0 to +2) were assigned to each trait, according to their association with early or late succession, respectively. Seven guilds were distinguished from the total scores. This novel technique placed species evenly along a gradient, with 13 and 15 species attaining negative and positive total scores, respectively. Cross-validation between the two techniques was high, signifying the robustness of using functional traits to distinguish successional guilds. Functional traits, therefore, provide a powerful tool to inform species selection when planning forest restoration. However, their wider use depends on greater availability of functional trait data for more tree species.

Keywords: climax species; ecological succession; forest restoration; framework species method; pioneer species

check for updates

Citation: Manohan, B.; Shannon, D.P.; Tiansawat, P.; Chairuangsri, S.; Jainuan, J.; Elliott, S. Use of Functional Traits to Distinguish Successional Guilds of Tree Species for Restoring Forest Ecosystems. *Forests* **2023**, *14*, 1075. https://doi.org/10.3390/f14061075

Academic Editors: Timothy A. Martin, Zhonghua Zhao, Yi Ding and Hongxiang Wang

Received: 5 March 2023
Revised: 13 April 2023
Accepted: 11 May 2023
Published: 23 May 2023

1. Introduction

All over the world, millions of people are planting billions of trees to fulfill the potential of forests to (i) conserve biodiversity, (ii) improve rural livelihoods and (iii) mitigate global climate change (GCC) through carbon sequestration. The role of tropical forest restoration for biodiversity conservation is immense, since such forests are home to an estimated two thirds of Earth's plant species [1]. Such biodiversity generates diversity of economic opportunities, which buffer rural communities against fluctuations in crop prices and climate change-induced reductions in agricultural productivity [2]. In particular, restoration of *tropical* forest ecosystems, is the most efficient land use-based GCC mitigation measure, since it sequesters carbon 40 times more efficiently than conventional tree plantations and 6 times more efficiently than agroforestry systems [3].

Although large-scale tree-planting projects have been enthusiastically embraced by policymakers, governments, corporations and civil society worldwide, such projects do not always fulfil the above-stated ideals [2]. For example, Lewis et al. [3] estimated that only about one third of tree-planting schemes, pledged under the Bonn Challenge (restoration of

350 Mha of forest cover globally by 2030; www.bonnchallenge.org, accessed on 2 February 2023), aim to restore natural forest ecosystems; the rest are monoculture plantations or agroforestry systems, low in both biodiversity and the diversity of products and services that support rural economies, including carbon storage.

One of the reasons why monoculture plantations are favored is that their establishment and management require knowledge of only one or a few tree species. In contrast, practitioners of tropical forest ecosystem restoration must understand complex natural processes of ecological succession and possess expert knowledge about *many* tree species, representative of the reference ecosystem [4]. Such knowledge is traditionally acquired through field trials, during which the relative performance of different tree species is monitored. Such trials may take several years before they yield the data required to refine species-selection decisions. One way to circumvent this may be to use functional traits—"species-specific characteristics that influence performance or fitness of species" [5]—to predict the performance of species and their suitability for inclusion in species mixtures for restoration. Such an approach could make the restoration of diverse tropical forest ecosystems both more practicable and more successful.

One of the most successful methods of restoring tropical forests is the framework trees species method (FSM): "densely planting open sites, close to natural forest, with a group of woody species, characteristic of the reference ecosystem and selected for their ability to accelerate ecological succession" [6]. It is suitable for stage-3 degradation (*sensu* Elliott et al. [7]), where natural regeneration is insufficient to close canopy within 3 years but where seed dispersal from forest remnants remains active. The method involves complementing natural regeneration [8] with the planting of 20–30 tree species, representative of the reference forest ecosystem, and mixing light-loving "pioneer" tree species with shade tolerant "climax" ones (*sensu* Whitmore [9]) to shade out competitive herbaceous weeds and attract seed-dispersing animals [1], resulting in rapid biomass accumulation and recovery of forest structural complexity, biodiversity and ecological functioning.

The system works well on moderately degraded areas that retain some natural regeneration and are within seed-dispersal distance of intact forest remnants ([10]). Experience from early field trials established that the optimal percentage of pioneers to include in the mix was about 15%–25% of the total number of trees planted [6]. However, a limitation to the method's wider application is the difficulty in deciding on ideal species mixtures [6].

According to Turner [1], pioneer species have small seeds, persisting abundantly in the soil seed bank; high seedling mortality and rapid growth; pale-colored, low-density wood; and short-lived, thin leaves with low mass per unit area and with high rates of photosynthesis and respiration and high light-compensation points. Climax trees have the opposite traits. In early FSM trials, some of the tree species tested could be clearly classified as "pioneer" or "climax" species (*sensu* Whitmore [9] and Turner [1]), but most of them combined characteristics of both. For example, several so-called "climax" tree species exhibited *rapid* growth in the exposed conditions of deforested sites [11], being shade-tolerant but not shade-*dependent*.

Ashton et al. [12] proposed a more refined classification system for tree species' successional status in the context of ecosystem restoration. They identified six "regeneration guilds", based on when species dominate successional stages (pioneers of initiation or stem exclusion and late successional species) and their crown positions in the forest canopy (dominant, non-dominant, subcanopy, understory). The system was based on qualitative "life-history traits" [12] but without a procedure to quantify them.

Although studies on the use of plant functional traits in relation to forest regeneration have proliferated since then, most have been subjective and based on qualitative data (see Chazdon's review [13], Chapter 4). Only rarely have researchers applied more quantitative analytical techniques [14,15]. Furthermore, all these studies were carried out in natural forest succession. We know of none that explored how to apply the use functional traits as indicators of successional status of planted trees during forest ecosystem restoration projects in the tropics.

Therefore, this study tested the hypothesis that functional traits can be used to distinguish successional guilds among tree species, planted to test the framework species method of restoration. The aim was to develop a tool to assist with tree-species selection for restoration trials, based on the positioning of species along a successional gradient, as a more precise alternative to the conventional binary division of pioneer and climax species. Such a tool may help to make true, science-based forest-ecosystem restoration (such as the frameworks species method) more practicable and successful in meeting the goals of climate change mitigation and biodiversity conservation [6].

2. Materials and Methods

2.1. Study Site

Restoration trial plots were situated in the upper Mae Sa Valley, Chiang Mai Province, Northern Thailand (at 18°51′46.62″ N, 98°50′58.81″ E, 1200–1325 m above sea level) in Doi Suthep-Pui National Park (Figure 1). The average annual temperature was 22–23 °C. Average annual rainfall was 1736 mm (recorded at the Kog-Ma Watershed Research Station nearest to the study site at a similar altitude [16]). The wet season lasts from May to October. The dry season (mean monthly rainfall < 100 mm) is subdivided into the cool-dry season (November–January) and the hot-dry season (February–April). Annual fires in the dry season are a major hinderance to forest restoration in this landscape.

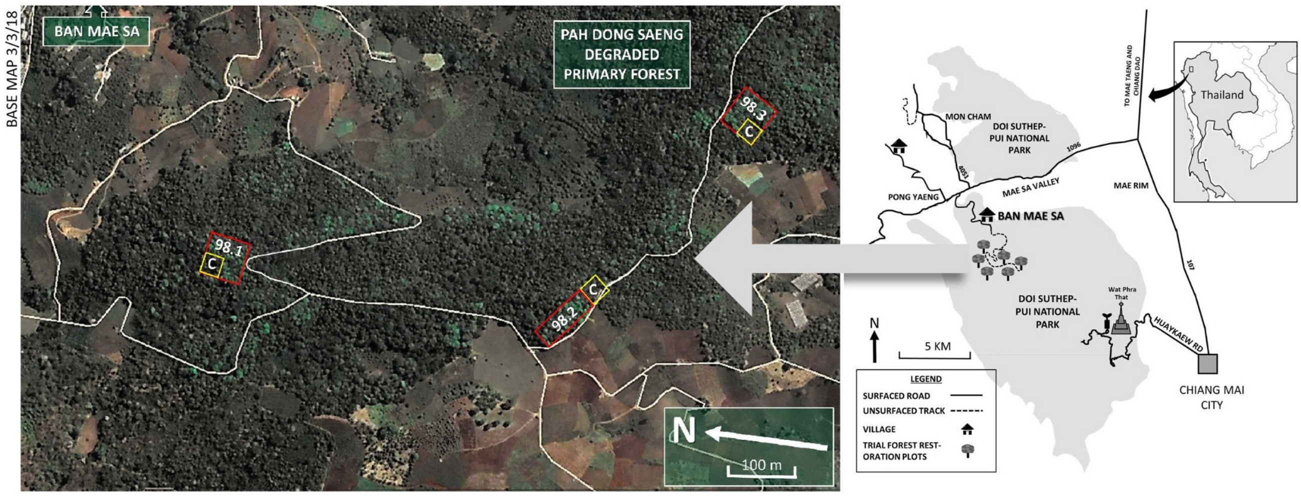

Figure 1. Study location maps. Three replicate framework species trial plots were planted in 1998 (red line, labelled 98.1, 98.2 and 98.3). Control plots "C" indicated by yellow lines. The plot system is located in the upper Mae Sa Valley in northern Thailand. The grey area is Doi Suthep-Pui National Park. Further plot details are available online at restor.eco—https://cmu.to/fSONO (98.1), https://cmu.to/aWMsh (98.2) and https://cmu.to/J04nr (98.3) (all accessed on 10 May 2023).

Formerly, the area had been "primary evergreen, seasonal forest" (*sensu* Maxwell et al., 2001, [17]). Approximately 60 years previously, the forest had been cleared for agriculture (cabbages, litchi, carrots, cut flowers, etc.) and subsequently abandoned and burnt repeatedly. The condition of the area was stage-3 degradation (*sensu* Elliott et al. 2013 [7]), with natural regenerants (saplings taller than 50 cm, live tree stumps and remnant trees) at densities lower than that needed to close canopy within two years (<3100 stems/ha), mostly suppressed by dominant grasses and herbaceous weeds [7]. Remnant patches of intact forest remained within 3 km of the planted plots as potential seed sources. Frugivorous birds and civets remained as potential dispersers of seeds from forest remnants into the trial plots [18,19]. For a more detailed description of the study site, see Elliott et al., 2019 [10].

2.2. Plot Establishment and Monitoring

Chiang Mai University's Forest Restoration Research Unit (FORRU-CMU), in collaboration with Doi Suthep-Pui National Park authority and villagers of Ban Mae Sa, established homogeneous triplicate trial plots in the area, to test the framework species method of forest restoration in 1998, covering 1.44 ha, along with paired control plots. All 28 of the candidate framework tree species, planted on those trial plots, were selected for the present study (Table S4). A total of 1500 saplings 30–50 cm tall were planted in each replicate plot. Plot maps are presented in Figure 1. Before planting, weeds were cleared by slashing and a single application of glyphosate, taking care not to damage pre-existing natural regeneration. Trees were planted approximately 1.8 m apart. After planting, hand weeding and fertilizer application were carried out three times during the first rainy season and three times during the second rainy season, at approximately 6-week intervals. Local villagers implemented fire prevention measures—fire-break cutting and patrols—every hot-dry season.

Before planting day, all saplings were labeled with aluminum tags, each bearing a unique identification number. Trees were monitored for survival and growth at the end of each season from 1998 to 2006 (up to 8 years old) and resurveyed in May 2017 (19 years old) and February 2020 (nearly 22 years old). In early surveys, sapling heights were measured with measuring poles, and root collar diameter (RCD) was measured with Vernier calipers. Crown widths were measured with a tape measure at the widest point. As the trees grew larger, diameter at breast height (DBH) was measured with a tape measure (when DBH > 4.5 cm). In the 2017–2020 surveys, tree heights were measured using a clinometer and telescopic measuring poles.

2.3. Links between Functional Traits and Successional Status Used in This Study

Table 1 summarizes the functional traits used in this study, along with citations on current thinking of how they are related to successional status. These associations form the basis of the analyses used in this study.

Table 1. Association of the final 13 functional traits used in this study with successional status.

Trait	High/Big	Low/Small	References
Ratio of height relative growth rate pre- to post-canopy closure	Pioneer	Climax	[1,20]
Ratio of mortality rates pre- to post-canopy closure	Climax	Pioneer	[1,20]
Half-life	Climax	Pioneer	[1,20]
Wood density	Climax	Pioneer	[1,20]
Leaf size	Pioneer	Climax	[21,22]
Specific leaf area	Pioneer	Climax	[21,23,24]
Leaf dry matter content	Climax	Pioneer	[22,24]
Leaf nitrogen concentration	Pioneer	Climax	[22,25]
Leaf phosphorus concentration	Pioneer	Climax	[22,25]
Dry seed mass	Climax	Pioneer	[1,20,26]
Median length of dormancy	Pioneer	Climax	[1,20,27]
Seedling type	Pioneer, epigeal; climax hypogeal		[26,28]
Germination response to light and shade	Pioneer, requires full sunlight; climax, can germinate in shade		[26,29]

Pioneers tend to have traits that enable them to disperse into recently disturbed sites, the occurrence of which is unpredictable in time and space. Therefore, they tend to produce copious quantities of small seeds that are widely dispersed by bats, birds and wind [1]. Such seeds persist in the soil seed bank until a disturbance event increases light levels and stimulates photosynthesis of the germinating seedlings. High specific leaf area, leaf dry matter content, leaf-nitrogen and leaf phosphorus allow pioneers to take advantage of such conditions [30], achieving high rates of photosynthesis and growth, but at the expense of low wood density and survival [31].

In contrast, late successional, shade-tolerant tree species consolidate their long-term position in ecosystems by carefully budgeting their limited resources, increasing their resilience and persistence and lowering mortality, but at the expense of growth. They survive on accumulated reserves, efficient light usage and by investing in physical and chemical defenses, enabling them to persist in shaded understories [22,32,33].

2.4. Functional Traits Data Collection

A total of 27 tree functional traits were recorded during plot monitoring or derived from secondary sources for each of the 28 planted tree species, following Cornelissen et al.'s protocol [21]. The secondary data sources included Shannon and Tiansawat [34], FORRU's databank [35], CMU herbarium specimens and database and other online databases, such as the Global Wood Density Database [36]. Data sources for each of the 27 traits are detailed in Table S3.

2.4.1. Growth and Survival Traits from Field Measurements

Relative growth rate (RGR) was used to compare growth among species (since it removes the effects of tree size on growth, providing a more species-specific expression of growth potential). It is expressed as a percentage annual increase in a size measurement, relative to the average tree size from the first to the second measurement. In this study, RGRs of height measurements of trees that survived over the census intervals were calculated as:

$$\%\mathrm{RGR} = \frac{\ln[\mathrm{H_i}] - \ln[\mathrm{H_{i-1}}]}{\text{No.days between measurements}} \times 365 \times 100$$

where $\mathrm{H_i}$ is current height, and $\mathrm{H_{i-1}}$ is height at previous monitoring.

As succession progresses, tree growth slows, as tree crowns expand and start to compete with each other for light. Pioneer tree species are dependent on high light levels. They grow rapidly in full sunlight and are inhibited by shade, following canopy closure. The situation with later successional species is less clear. Although most are shade-tolerant, they are not necessarily shade-dependent. Many exhibit phenotypic plasticity, growing fast when exposed to full sunlight and out-performing pioneer species after canopy closure [37]. Consequently, the use of RGR to indicate successional status depends on when it is calculated—pre- or post-canopy closure. To overcome this effect, RGR was calculated separately both pre- and post-canopy closure. The ratio of these two RGR values was used in the analyses. In the study plots, canopy closure occurred 3.5 years after planting. The average RGR of each species before canopy closure was divided by the average RGR after canopy closure. A high ratio indicated a strongly pioneer species, whilst a lower one indicated a strongly climax one.

$$\text{RGR ratio} = \frac{\text{average RGR before canopy closure}}{\text{average RGR after canopy closure}}$$

The numbers of surviving trees of each species in each census were recorded and compared with the previous census (or the number originally planted) to derive mortality (%). The mortality rate of pioneers was expected to be relatively low at first, increasing as canopy closure progressed, whilst the reverse was expected of climax species. Therefore, the ratio of mortality pre- to post-canopy closure could be used to distinguish pioneer and climax species, a low ratio indicating pioneers and a higher one indicating climax species:

$$\text{Mortality ratio} = \frac{\text{Mortality}(\%)\text{ before canopy closure}}{\text{Mortality}(\%)\text{ after canopy close}}$$

Pioneer trees species tend to have shorter lifespans than climax species. However, recording tree life span directly is difficult. Consequently, derived half-life was used as the life span trait—the extrapolated time (in years) at which 50% of the trees originally planted died. Pioneer tree species exhibit short half-life, whereas climax species exhibit longer half-life.

2.4.2. Wood Density (WD)

Wood density data for most species were obtained from other research projects, conducted either in the same plot system [38] or the same region [39]. For remaining species, data were extracted from the South-East Asia tropical region database of the Global Wood Density Database [36]. When species-level data were unavailable, genus WD values were used, since WD is a phylogenetically conserved feature [40].

2.4.3. Seed Traits

Seed-trait data for most species were obtained by measuring seeds collected during field surveys or from FORRU-CMU's database [41]. Measurements included seed length (mm), width (mm), volume (mm^3) and mass (g), whereas median length of dormancy (MLD) (days), germination response to light and shade (GRLS) and seedling type (epigeal, hypogeal etc.) had been previously determined in nursery experiments, with the data stored in FORRU-CMU's database.

2.4.4. Leaf Traits

All leaf-traits data were obtained from Shannon and Tiansawat [34], who collected 2 undamaged leaves from each of 10 mature trees (in total, 20 leaves) of 27 species in the same plot system as this study. For the remaining species (*Melia azedarach*), leaves were collected during field surveys. All leaves were measured following Cornelissen et al.'s protocol [21]. Fresh leaves were weighed (LFM, gm) and scanned (including petiole) with a metric reference scale to compute average leaf area (LA, mm^2) using ImageJ (version 1.51 k, Wayne Rasband, National Institutes of Health, USA, http://imagej.nih.gov/ij/ accessed on 10 May 2023). Subsequently, leaves were dried in an oven at 60 °C for 72 h before determining leaf dry mass (LDM, mg) using an electronic balance. The following leaf traits were then computed:

$$\text{Specific leaf area (SLA, mm}^2\text{/mg)} = \text{LA/LDM}$$

$$\text{Leaf mass per area (LMA, mg/mm}^2\text{)} = \text{LDM/LA}$$

$$\text{Leaf dry matter content (LDMC, mg/g)} = \text{LDM/LFM}$$

Leaf nitrogen (LNC) and leaf phosphorus (LPC) concentrations were determined at the Soil Science Laboratory, Faculty of Agriculture, Chiang Mai University. Measurement of leaf thickness and tensile strength testing followed the protocol of Hendry and Grime [42].

2.5. Data Analysis

In total, 27 functional trait variables (including growth and mortality rates) were initially considered for exploring species' successional status. First, they were subjected to data normalization, to allow co-analysis of variables having different ranges and units [43].

The standardized variables were then subjected to pair-wise correlation, using Pearson's correlation coefficient [44]. For each pair of closely correlated variables, one was discarded (following recommendations from the literature [21]), leaving 13 non-correlated variables for further analyses: RGR ratio, mortality ratio, half-life, wood density (WD), dry seed mass (DSM), median length of dormancy (MLD), seedling type, germination response to light and shade (GRLS), leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen and phosphorus concentrations (LNC, LPC).

Two different analytical techniques were then applied to explore how the variables could be used to indicate successional status: (i) rank scoring and (ii) cluster analysis. The former places species along a gradient of successional status, whilst the latter groups together species with similar functional trait values.

For rank-scoring, species were first ranked in descending order of the value of each of the 13 individual non-correlated, functional trait variables (Figures S1–S11, Tables S1 and S2). The ranked distributions were then graded by eyes into 5 classes, with the divisions between classes being drawn where large differences occurred between consecutive values (much like grading student exams). The grades were pioneer (P), intermediate pioneer (IP), intermediate (I), intermediate climax (IC) and climax (C). Each grade was then assigned a score, with those associated with early succession being assigned negative values (−2 to 0) and those associated with late succession being assigned positive values (0 to +2). For example, in the case of seed mass, species with the heaviest seeds (associated with climax species) scored 2, whilst those with the lightest seeds (associated with pioneer species) scored −2. In between these extremes, species were assigned intermediate grade scores according to their relative seed mass. Since there were 13 variables, the maximum total grade score, attainable by any species for all traits combined, was +26 for a perfectly climax species and −26 for a perfectly pioneer species. Species, with total grade scores close to zero, were those with a balanced mix of pioneer and climax traits.

The second analytical technique, hierarchical cluster analysis, was performed using Ward's method [45] to group together species with similar functional trait combinations into successional guilds, visualized as a dendrogram [46]. Ward's method is based on the principle that, at each clustering stage, variance within clusters is minimized with respect to the variance among them. Within-cluster variance is defined as the sums of squares of the distances between species within a cluster and the centroid of that cluster. At each clustering cycle, the two units fused (individual species or species clusters) are those that result in minimum variance increase [47]. Guilds of species with similar trait values were thus derived based on the sizes of differences between successive cluster cycles.

Decentralized standardization, calculation of Pearson's correlation coefficients and hierarchical cluster analysis were performed with R 4.1.3 software [48]. Figure 2 presents a schematic diagram of the workflow.

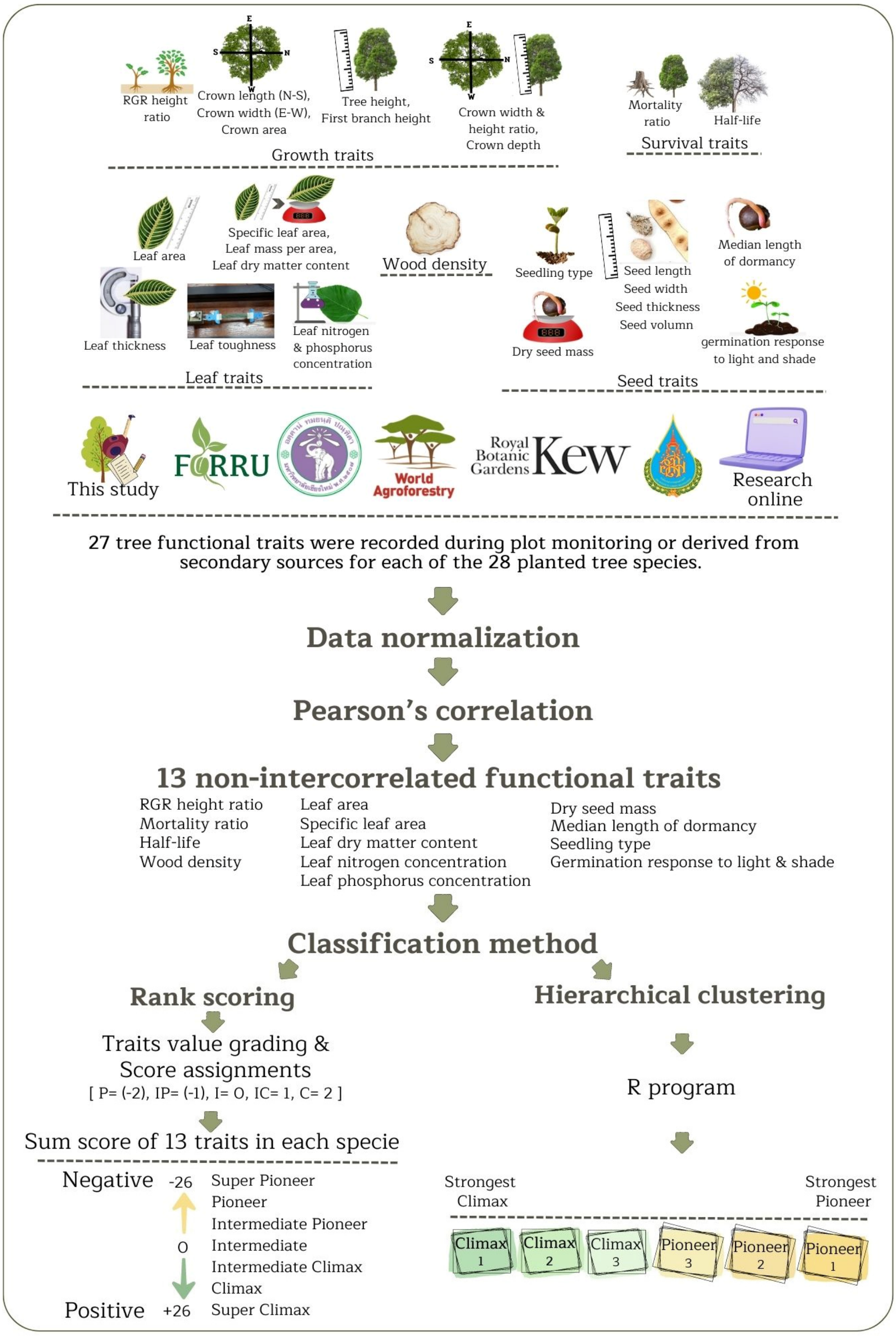

Figure 2. A schematic diagram of the study processes: P = pioneer; IP = intermediate pioneer; I = intermediate; IC = intermediate climax; C = climax.

3. Results

3.1. Rank Scoring

The sources and mean values of the 13 non-correlated variable data are presented in Tables S3 and S4, respectively. All species studied shared both pioneer and climax traits to varying degrees. None achieved the perfect climax total grade score (+26) nor the perfect pioneer grade score (−26). The grade score divisions are presented in Table 2, whilst the calculations and summed scores are presented in Table 3. The most extreme scores ranged from −57.7% of the maximum possible negative pioneer score (*Erythrina subumbrans*) to +61.5% of the maximum possible positive climax score (*Syzygium albiflorum*). The top five most strongly pioneer species were *E. subumbrans*, *G. arborea*, *H. dulcis*, *M. azedarach* and *F. altissima*. The top five most strongly climax species were *S. albiflorum*, *Q. semiserrata*, *Q. kerrii*, *P. lanceolata* and *S. arboretum*. Rank scoring resulted in a remarkably even distribution of species along a gradient (Figure 3) with slightly less than half (13 species) attaining a negative total grade score (indicating early successional status) and slightly more than half (15 species) attaining a positive total grade score (indicating later successional status).

Table 2. Grade score divisions.

No.	The Successional Guilds	Percent of Score
1	Super pioneer	−100% to −60%
2	Pioneer	−59% to −40%
3	Intermediate pioneer	−39% to −20%
4	Intermediate	−19% to 19%
5	Intermediate climax	20% to 39%
6	Climax	40% to 59%
7	Super climax	60% to 100%

3.2. Hierarchical Clustering

Results of hierarchical cluster analysis are presented in Figure 4. The first clustering round divided species neatly into two primary clusters: pioneer and climax species. Subsequent rounds produced three sub-clusters within the pioneer cluster and another three within the climax cluster. *E. subumbrans* and *M. azedarach* were the first to be grouped together within the pioneer cluster (Pioneer 1). The remaining pioneer species were subsequently clustered into two groups. The Pioneer 2 sub-cluster comprised *G. arborea*, *H. dulcis*, *M. stipulata*, *N. javanica*, *P. cerasoides* and *S. rarak*, whilst the Pioneer 3 sub-cluster comprised *C. axillaris*, *D. glandulosa*, *F. altissima*, *H. trijuga* and *M. gerrettii*.

In the climax cluster, three sub-clusters could be distinguished: Climax 1, comprising *E. acuminata*, *G. mckeaniana*, *Q. kerrii*, *Q. semiserrata* and *S. albiflorum*; Climax 2, comprising *A. andersonii*, *C. calathiformis* and *P. lanceolata*; and Climax 3, comprising *A. lawii*, *A. polystachya*, *B. javanica*, *C. iners*, *H. nilagirica*, *H. amygdalina* and *S. arboreum*.

Table 3. Sum of 13 functional trait grade scores of 28 species, ranked from most strongly pioneer to most strongly climax species: RGR = relative growth rate; WD = wood density; SLA = specific leaf area; LDMC = leaf dry matter content; LNC = leaf nitrogen content; LPC = leaf phosphorus content; MLD = median length of dormancy; GRLS germination response to light and shade; P = pioneer; IP = intermediate pioneer; I = intermediate; IC = intermediate climax; C = climax.

Rank number	Species	RGR of height ratio	Mortality ratio	Half-life	WD	LA (cm^2)	SLA (mm^2/mg)	LDMC (mg/g)	LNC (%)	LPC (%)	Dry seed mass (g)	MLD (day)	Seedling type	GRLS	Number of occurrences					Sum score	Percent of graded maximum score	Successional guilds
															P (-2)	IP (-1)	I (0)	IC (+1)	C (+2)			
1	*Erythrina subumbrans*	P	P	IP	P	IC	P	P	P	P	IP	C	I	P	8	2	1	1	1	-15	-57.69	Pioneer
2	*Gmelina arborea*	I	P	IP	IP	I	P	P	IP	I	IP	IC	P	P	5	4	3	1	0	-13	-50.00	
3	*Hovenia dulcis*	I	P	IP	IP	IC	P	IP	IP	IP	P	IP	P	I	4	6	2	1	0	-13	-50.00	
4	*Melia azedarach*	P	P	IP	P	P	C	IC	P	I	P	IC	P	P	8	1	1	2	1	-13	-50.00	
5	*Ficus altissima*	IP	P	IC	P	IP	C	IP	IC	I	P	I	P	P	5	3	2	2	1	-9	-34.62	Intermediate Pioneer
6	*Diospyros glandulosa*	C	I	P	IP	IC	IP	I	IP	IC	P	IP	P	P	4	4	2	2	1	-8	-30.77	
7	*Prunus cerasoides*	I	IP	I	IP	C	P	IC	P	I	P	IC	P	P	5	2	3	2	1	-8	-30.77	
8	*Markhamia stipulata*	IC	IC	IP	IC	I	IP	IP	P	P	P	C	P	I	4	3	2	3	1	-6	-23.08	
9	*Sapindus rarak*	IP	IP	I	I	IC	IP	IP	IP	IP	IC	I	P	I	1	6	4	2	0	-6	-23.08	
10	*Choerospondias axillaris*	IC	P	IC	P	C	IP	IC	P	I	IC	P	P	I	5	1	2	4	1	-5	-19.23	Intermediate
11	*Magnolia garrettii*	C	IC	I	IP	I	I	I	I	I	P	IP	P	P	3	2	6	1	1	-5	-19.23	
12	*Heynea trijuga*	C	P	I	IP	IC	I	IC	IP	I	P	IP	C	P	3	3	3	2	2	-3	-11.54	
13	*Nyssa javanica*	IC	IP	I	IP	IC	I	IC	I	P	P	C	P	I	3	2	4	3	1	-3	-11.54	
14	*Aphanamixis polystachya*	C	IC	P	I	I	I	IP	I	I	I	IC	C	I	1	1	7	2	2	3	11.54	
15	*Aglaia lawii*	C	I	P	IC	IC	I	I	IP	IP	IP	C	C	C	1	3	3	2	4	5	19.23	
16	*Bischofia javanica*	IC	P	IC	I	IC	IC	I	IC	C	P	C	P	C	3	0	2	5	3	5	19.23	
17	*Eurya acuminata*	C	C	IC	I	C	I	IC	IC	C	P	I	P	P	3	0	3	3	4	5	19.23	
18	*Castanopsis calathiformis*	I	P	C	IC	I	I	IC	P	I	C	C	C	I	2	0	5	2	4	6	23.08	Intermediate Climax
19	*Horsfieldia amygdalina*	C	IC	IP	P	IC	I	P	IC	IC	IC	IC	C	C	2	1	1	6	3	7	26.92	
20	*Cinnamomum iners*	C	IP	IC	IP	IC	IC	IC	IC	IC	P	C	C	I	1	2	1	6	3	8	30.77	
21	*Alseodaphnopsis andersonii*	IC	IP	C	I	IP	IC	IC	IC	C	C	IC	I	I	0	2	3	5	3	9	34.62	
22	*Garcinia mckeaniana*	C	C	P	C	I	IC	I	C	C	I	I	C	P	2	0	4	1	6	9	34.62	
23	*Helicia nilagirica*	C	I	I	IC	IC	I	I	IC	IC	IC	IP	C	C	0	1	4	5	3	10	38.46	
24	*Sarcosperma arboreum*	C	IC	IC	P	IC	IC	IC	IC	IC	I	IP	C	C	1	1	1	7	3	10	38.46	
25	*Phoebe lanceolata*	C	C	C	IC	IC	I	IC	I	IC	C	P	C	I	1	0	3	4	5	12	46.15	Climax
26	*Quercus kerrii*	C	IC	I	IC	IC	IC	C	IC	IC	I	C	C	I	0	0	3	6	4	14	53.85	
27	*Quercus semiserrata*	C	IC	I	C	C	I	C	I	I	IC	C	C	I	0	0	5	2	6	14	53.85	
28	*Syzygium albiflorum*	C	IP	IC	C	C	IC	C	C	C	IC	C	C	P	1	1	0	3	8	16	61.54	Super Climax

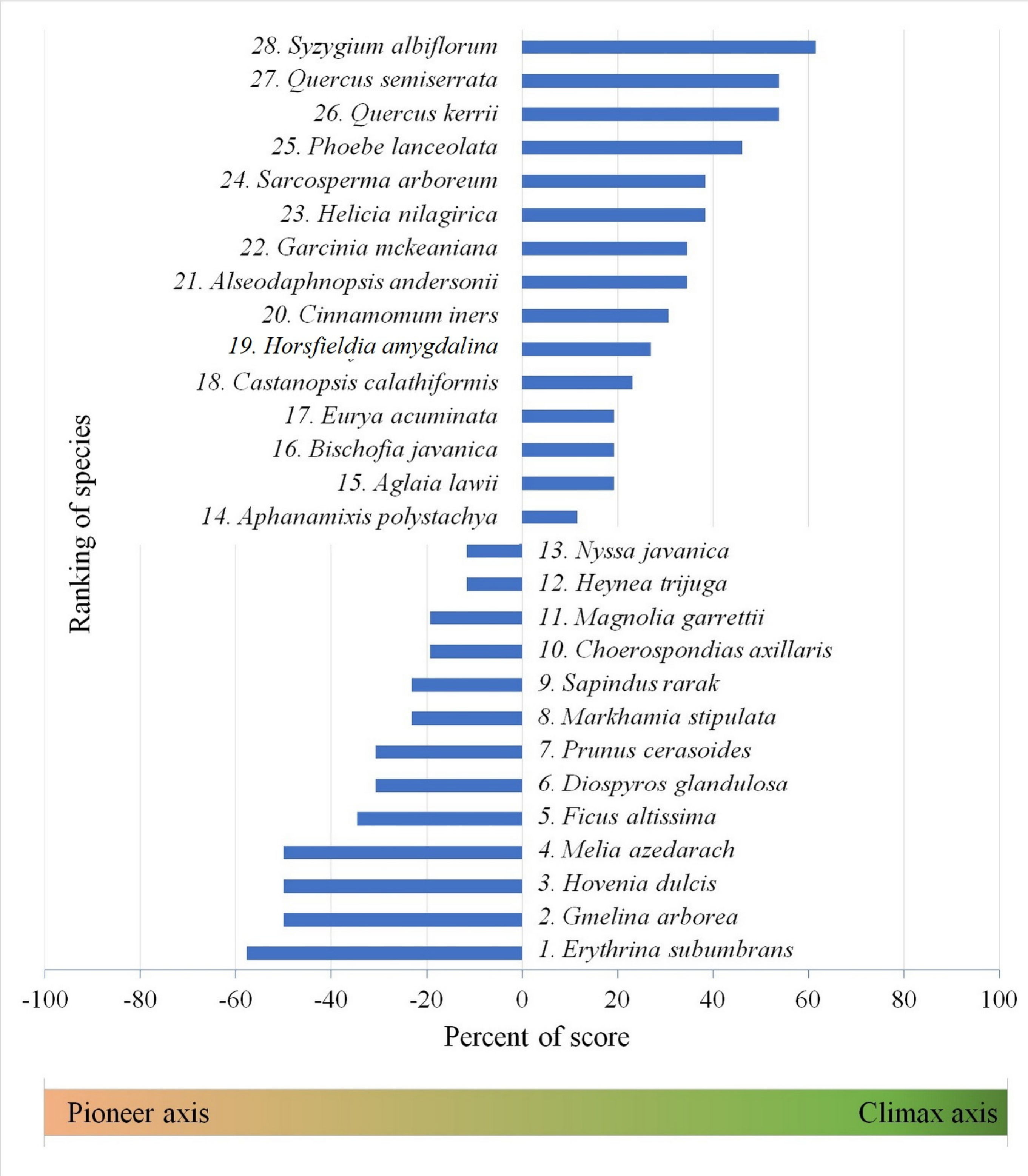

Figure 3. Even distribution of species, ranked by total grade score, along a gradient from pioneer status (negative scores) to climax status (positive scores).

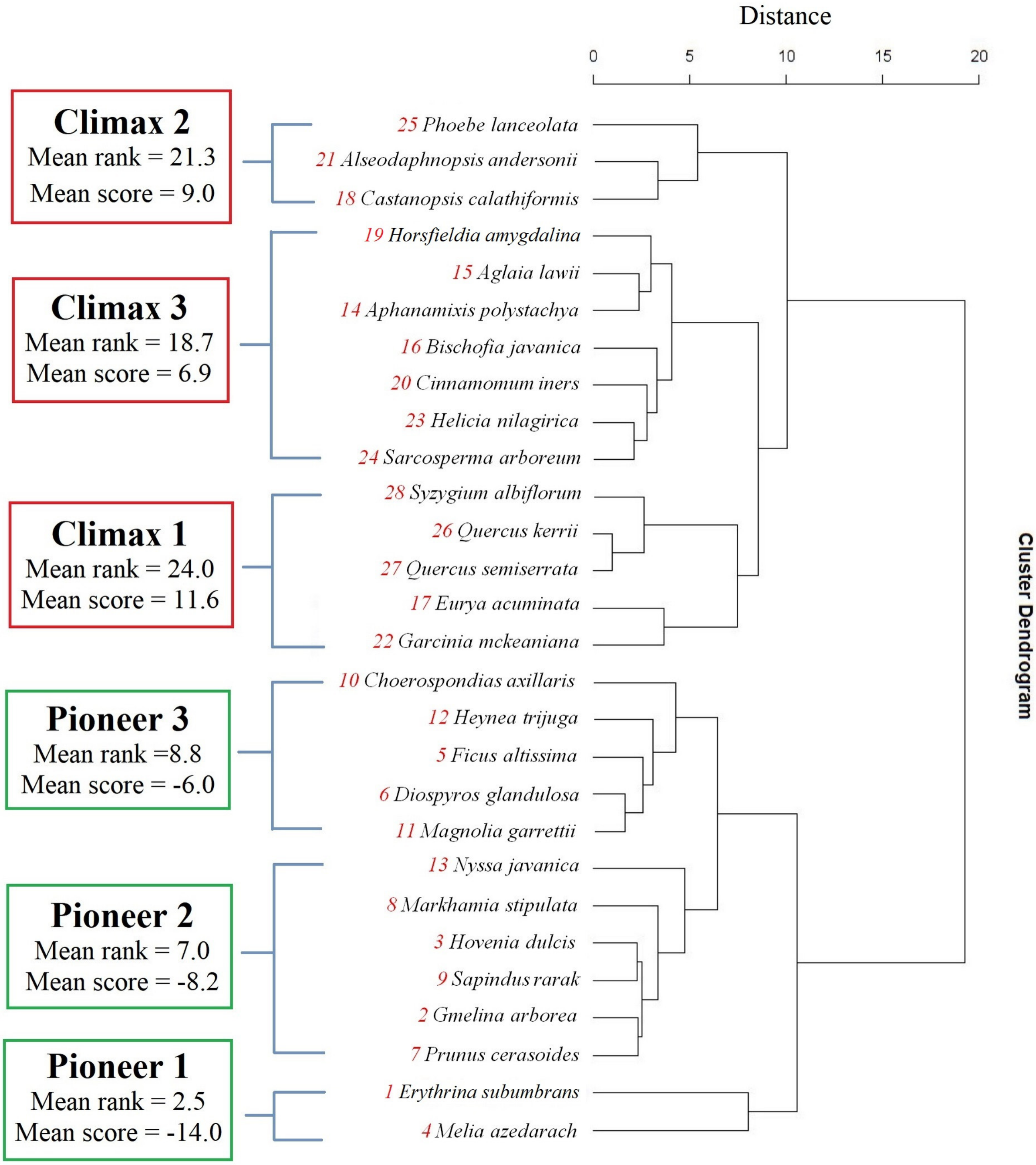

Figure 4. Dendrogram of hierarchical clustering by Ward's method. The red numbers are the species ranks from Table 3. Mean rank and score are averages of all species in each sub-cluster, calculated from Table 3, columns 1 and 21, respectively.

4. Discussion

4.1. Comparison between the Score Ranking System and Hierarchical Cluster Analysis

The processes of rank scoring and cluster analysis were mathematically distinct, yet the successional guilds that emerged from both techniques were strikingly similar. Both approaches involved a combination of objective quantitative analysis and subjective decisions.

The rank scoring system operated on the gross grade scores that were assigned to each species variable in a partially subjective manner, with the ranking itself being a purely mathematical procedure. In contrast, cluster analysis was performed on the individual variable values after centralized standardization. The subjective element came into play at the end of the process, when the dendrogram was examined for cluster assignment. Overall, the ability of both techniques to distinguish similar successional guilds demonstrates the power of combining quantitative analysis with subjective interpretation.

Most notably, cluster analysis placed all those species with negative rank scores (13 species) in the pioneer primary cluster and all those with positive rank scores (15 species) in the climax primary cluster. Examining the sub-clusters, the match between the two techniques was not so absolute. However, examining the mean rank numbers and scores of the species within each sub-cluster, it is notable that mean rank numbers increased in a progression from 2.5 to 7.0 and 8.8 for Pioneer 1, 2 and 3, respectively, whilst mean grade scores also progressed from −14 to −8.2 and −6.0, respectively. The climax sub-clusters followed the same pattern. Mean rank numbers for all species in the Climax 1, 2 and 3 sub-clusters declined from 24.0 to 21.3 and 18.7, respectively, whilst mean grade scores also declined in similar progression from 11.6 to 9.0 and 6.9, respectively. This demonstrates alignment of the hierarchical cluster analysis with the gradation achieved by rank scoring (Figure 4), from pioneer to intermediate and from climax to intermediate (Table 3). Overall, our findings demonstrate the importance of using multiple techniques to distinguish successional guilds.

4.2. Successional Guilds

Eleven previously published accounts of the successional status of the species examined in this study are summarized in Table S5. In general, the classification of species at either end of the succession gradient matched exactly with previously published reports. For example, the assignment of *E. subumbrans*, *G. arborea*, *M. azedarach* and *P. cerasoides* as pioneers and of *H. amygdalina*, *Q. kerrii*, *Q. semiserrata*, *S. arboretum* and *S. albiflorum* as climax species agreed with all studies summarized in Table S5.

However, moving towards the center of the successional gradient, some differences with published studies emerged. For example, PROSEA et al. [49] and Gardner [50] defined *E. acuminata*, and *C. axillaris* as pioneer species due to their occurrence in open areas. The difficulty in assigning *E. acuminata* to a successional guild was also evident in the current study, since cluster analysis placed it in the Climax 1 sub-cluster, whilst rank scoring labelled it "intermediate". It was the most divergent species between the two analytical methods. Both species exhibited some climax characteristics, such as low mortality; they lived longer than other pioneer species and had high LDMC (Figures S2, S3 and S9).

The successional status of *H. dulcis* is also debatable. Waiboonya [51] and Pothong [39] described it as a climax species because mature trees are found near streams in primary forest. In contrast, Betts [52] and Shannon and Tiansawat [34] considered it to be a pioneer species because it grows rapidly at the seedling/sapling stage on exposed sites. Cluster analysis placed *H. dulcis* in the Pioneer 2 sub-cluster, whilst rank scoring placed it firmly in the pioneer guild (rank 3, score −50%) mostly due to low survival post-canopy closure (50% survival over 8 years) and because most of its other traits matched those of pioneer species.

Moreover, Pakkad (pers. comm. 23 May 2021) and Gardner [50] labeled *F. altissima* and *N. javanica* as climax species because of their longevity and occurrence in primary forest. In contrast, Betts [52] and Shannon and Tiansawat [34] classified both as pioneers because they can grow rapidly in open areas. In this study, however, although more than half of the traits of *F. altissima* matched those of pioneer species (including low RGR, high mortality and low wood density), the rest were more typical of climax species. Consequently, *F. altissima* was identified as a weakly pioneer species (sub-cluster Pioneer 3, rank score −35% = intermediate pioneer). The traits of *N. javanica* variously matched those of pioneer, intermediate and climax species. So, unsurprisingly, rank scoring classed it as "intermediate", and cluster analysis placed it in the Pioneer 2 sub-cluster.

4.3. Practical Applications

Ashton's study [12] demonstrated that during the early forest regeneration on open sites, all successional guilds may be present due to the randomness of seed-dispersal. Light-dependent early-successional species grow up first but then decline, as an understory of slower growing shade-tolerant late-successional species rise to dominance. Therefore, planting an even mix of trees representing *all* successional guilds of the reference forest type, in a single step, closely mimics and truncates natural forest succession. It avoids the delay inherent in relying upon natural dispersal mechanisms to deliver seeds from the range of successional guilds to restoration sites.

The benefits of planting both pioneer and climax trees, in a single step, when implementing the framework species method of forest restation was first recognized by Goosem and Tucker [37]. Experience from their early field trials in Australia established that the optimal percentage of pioneers to include in the mix was about 15%–25% of the total number of planted stems [6], with the rest representing later successional stages. For the specific case of using the framework species method to restore evergreen forest in northern Thailand, the species guilds, identified by this study, allow fine tuning of species mixes that could accelerate recovery of forest biomass, structural complexity, biodiversity and ecological functioning. More generally, where sufficient data are available, the generic approaches demonstrated above could be used to guide the design of optimal species mixes to restore other tropical forest ecosystems in other areas.

However, when deciding on the proportion of each successional guild to include in the original planting mix, the initial level of degradation must be considered. For example, where pioneer tree species have already colonized a site, the proportion of trees representing the early pioneer guilds could be reduced, whilst those representing later successional guilds could be increased. On the other hand, restoration on severely degraded sites would likely benefit from increased representation of trees from early pioneer guilds.

5. Conclusions

High cross validation between the two analytical techniques demonstrated the robustness of using functional traits to distinguish successional guilds and to inform species-selection decisions when planning forest restoration projects. The study also demonstrated the value of a pragmatic approach that combines quantitative and subjective elements within the analyses performed. Between the two techniques, rank scoring is recommended because, conceptually, it placed species along a continuous linear gradient mirroring the continuous linear nature of succession, using quantitative data right from the start of the calculation process. Furthermore, it is highly intuitive and easy to calculate. In contrast, cluster analysis is a grouping (rather than a linear grading) process, which is difficult to grasp conceptually. Furthermore, it involves more complex and less intuitive mathematical procedures.

The study yielded immediate benefits to practitioners of the framework species method in the seasonally dry tropical forests of SE Asia as an aid for species selection. However, wider application of the generic approach of using functional traits to select candidate framework tree species for restoring other forest ecosystems depends on data availability. Although databases of several of the functional traits used in this study can now be accessed online (e.g., the Global Wood Density Database [36], TRY plant trait database [53] and the Royal Botanic Gardens, Kew Database [54]), data are incomplete and/or are sometimes difficult to access. In particular, growth and survival data (which doubtless added to the robustness our results) from restoration field trials are rarely made available online, except as Supplementary Materials in a few papers [41]. Therefore, managers of forest restoration-trial-plot systems are encouraged to share more monitoring data online. Ideally, a central repository of such data would be extremely useful to widen use of trait-based data to inform species-selection decisions when planning forest-restoration projects [55,56].

To sum up, our study shows that the use of functional traits could be a powerful tool to plan ideal mixes of successional guilds when selecting tree species for forest restoration trials. However, its wider application depends on greater availability of easily accessible functional trait data of a wide range of indigenous forest tree species.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14061075/s1, Figures S1–S11: Ranked individual functional trait data as indicators of successional status.; Table S1: Seedling types; Table S2: Germination response to light and shade (GRLS); Table S3: Data sources for the for functional trait variables; Table S4: Data for 27 functional traits of 28 framework tree species; Table S5: Previous reports of the successional status of the framework tree species.

Author Contributions: Conceptualization, B.M., P.T. and S.E.; data curation, B.M. and J.J.; formal analysis, B.M., P.T., J.J. and S.E.; funding acquisition, D.P.S. and S.C.; investigation, B.M., J.J. and S.E.; methodology, B.M., P.T. and S.E.; project administration, D.P.S., P.T., S.C. and S.E.; resources, D.P.S., S.C. and S.E.; supervision, D.P.S., P.T., S.C. and S.E.; writing—original draft, B.M.; writing—review and editing, S.E. All authors have read and agreed to the published version of the manuscript.

Funding: University fees of B.M. were supported by the National Science and Technology Development Agency (NSTDA) Scholarship (P-17-50564). Research costs were partially supported by the Center of Excellence on Biodiversity (BDC-PG3-160019) and the National Research Council of Thailand (Project no. 347588). The work of D.P.S., P.T., S.C. and S.E on this research and manuscript was partially supported by Chiang Mai University.

Data Availability Statement: The data are presented in the Supplementary Materials.

Acknowledgments: We gratefully acknowledge the contributions of indigenous knowledge and labor of the villagers of Ban Mae Sa Mai/Noi in establishing and maintaining the plot system over many years. We also thank all the many FORRU-CMU staff, students and interns who participated in plot maintenance, monitoring, data collection and data processing over many years. Greuk Pakkad is thanked for his curation of the FORRU-CMU database.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Turner, I.M. *The Ecology of Trees in the Tropical Rain Forest*; Cambridge University Press: Cambridge, UK, 2001. [CrossRef]
2. Di Sacco, A.; Hardwick, K.A.; Blakesley, D.; Brancalion, P.H.S.; Breman, E.; Cecilio Rebola, L.; Chomba, S.; Dixon, K.; Elliott, S.; Ruyonga, G.; et al. Ten golden rules for reforestation to optimize carbon sequestration, biodiversity recovery and livelihood benefits. *Glob. Chang. Biol.* **2021**, *27*, 1328–1348. [CrossRef] [PubMed]
3. Lewis, S.L.; Wheeler, C.; Mitchard, E.T.A.; Koch, A. Regenerate natural forests to store carbon. *Nature* **2019**, *568*, 25–28. [CrossRef] [PubMed]
4. Gann, G.D.; McDonald, T.; Walder, B.; Aronson, J.; Nelson, C.R.; Jonson, J.; Hallett, J.G.; Eisenberg, C.; Guariguata, M.R.; Liu, J.; et al. International principles and standards for the practice of ecological restoration. Second edition. *Restor. Ecol.* **2019**, *27*, S1–S46. [CrossRef]
5. Nock, C.A.; Vogt, R.J.; Beisner, B.E. *Functional Traits*; Wiley: Hoboken, NJ, USA, 2016.
6. Elliott, S.; Tucker, N.I.J.; Shannon, D.P.; Tiansawat, P. The framework species method: Harnessing natural regeneration to restore tropical forest ecosystems. *Philos. Trans. R. Soc. B Biol. Sci.* **2022**, *378*, 20210073. [CrossRef] [PubMed]
7. Elliott, S.; Blakesley, D.; Hardwick, K. *Restoring Tropical Forest: A Practical Guide*; Royal Botanic Gardens, Kew: Richmon, UK, 2013.
8. Chazdon, R.L. Landscape Restoration, Natural Regeneration, and the Forests of the Future. *Ann. Mo. Bot. Gard.* **2017**, *102*, 251–257. [CrossRef]
9. Whitmore, T. *Tropical Rainforests of the Far East*; Clarendon Press: Oxford, UK, 1984.
10. Elliott, S.; Chairuangsri, S.; Kuaraksa, C.; Sangkum, S.; Sinhaseni, K.; Shannon, D.; Nippanon, P.; Manohan, B. Collaboration and Conflict—Developing Forest Restoration Techniques for Northern Thailand's Upper Watersheds Whilst Meeting the Needs of Science and Communities. *Forests* **2019**, *10*, 732. [CrossRef]
11. Elliott, S.; Navakitbumrung, P.; Kuarak, C.; Zangkum, S.; Anusarnsunthorn, V.; Blakesley, D. Selecting framework tree species for restoring seasonally dry tropical forests in northern Thailand based on field performance. *For. Ecol. Manag.* **2003**, *184*, 177–191. [CrossRef]
12. Ashton, M.; Gunatilleke, C.V.S.; Singhakumara, B.; Gunatilleke, N. Restoration pathways for rain forest in southwest Sri Lanka: A review of concepts and models. *For. Ecol. Manag.* **2001**, *154*, 409–430. [CrossRef]
13. Chazdon, R.L. *Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation*; University of Chicago Press: Chicago, IL, USA, 2014.

14. 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]
15. Herrera-Peraza, R.; Bever, J.; Garcinuño, J.M.; Sal, A.; Herrera, P.; García, E.; Oviedo, R.; Torres-Arias, Y.; Delgado, F.; Valdés-Lafont, O.; et al. A new hypothesis on humid and dry tropical forests succession. *Acta Botánica Cuba* **2016**, *215*, 232–280.
16. Glomvinya, S.; Tantasirin, C.; Tongdeenok, P.; Tanaka, N. Changes in Rainfall Characteristics at Huai Kog-Ma Watershed, Chiang Mai Province. *Thai J. For.* **2016**, *35*, 66–77.
17. Maxwell, J.F.; Elliott, S. Vegetation and Vascular Flora of Doi Sutep-Pui National Park, Northern Thailand. In *Thai Studies in Biodiversity*; Biodiversity Research and Training Program (BRT): Bangkok, Thailand, 2001.
18. Sinhaseni, K. *Natural Establishment of Tree Seedling in Forest Restoration Trials at Ban Mae Sa Mai*; Chiang Mai Province Chiangmai, Chiangmai University: Chiang Mai, Thailand, 2008.
19. Toktang, T. *The Effects of Forest Restoration on the Species Diversity and Composition of a Bird Community in Doi Suthep-Pui National Park Thailand from 2002–2003*; Graduate School, Chiang Mai University: Chiang Mai, Thailand, 2005.
20. Swaine, M.D.; Whitmore, T.; Swaine, M.D.; Whitmore, T.C. On the definition of ecological species groups in tropical forests. Vegetatio. *Plant Ecol.* **1988**, *75*, 81–86. [CrossRef]
21. Cornelissen, J.H.C.; Lavorel, S.; Garnier, E.; Díaz, S.; Buchmann, N.; Gurvich, D.E.; Reich, P.B.; Steege, H.T.; Morgan, H.D.; Van Der Heijden, M.G.A.; et al. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* **2003**, *51*, 335–380. [CrossRef]
22. Poorter, L.; Bongers, F. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* **2006**, *87*, 1733–1743. [CrossRef] [PubMed]
23. Rijkers, T.; Pons, T.L.; Bongers, F. The effect of tree height and light availability on photosynthetic leaf traits of four neotropical species differing in shade tolerance. *Funct. Ecol.* **2000**, *14*, 77–86. [CrossRef]
24. Wright, I.J.; Reich, P.B.; Westoby, M.; Ackerly, D.D.; Baruch, Z.; Bongers, F.; Cavender-Bares, J.; Chapin, T.; Cornelissen, J.H.C.; Diemer, M.; et al. The worldwide leaf economics spectrum. *Nature* **2004**, *428*, 821–827. [CrossRef]
25. Zhang, G.; Zhang, L.; Wen, D. Photosynthesis of subtropical forest species from different successional status in relation to foliar nutrients and phosphorus fractions. *Sci. Rep.* **2018**, *8*, 10455. [CrossRef]
26. Baraloto, C.; Forget, P.-M. Seed size, seedling morphology, and response to deep shade and damage in neotropical rain forest trees. *Am. J. Bot.* **2007**, *94*, 901–911. [CrossRef]
27. Dalling, J.W.; Hubbell, S.P.; Silvera, K. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *J. Ecol.* **1998**, *86*, 674–689. [CrossRef]
28. Ibarra-Manríquez, G.; Martinez-Ramos, M.; Oyama, K. Seedling Functional Types in a Lowland Rain Forest in Mexico. *Am. J. Bot.* **2001**, *88*, 1801–1812. [CrossRef]
29. Pearson, T.R.H.; Burslem, D.F.R.P.; Mullins, C.E.; Dalling, J.W. Functional significance of photoblastic germination in neotropical pioneer trees: A seed's eye view. *Funct. Ecol.* **2003**, *17*, 394–402. [CrossRef]
30. Bonal, D.; Born, C.; Brechet, C.; Coste, S.; Marcon, E.; Roggy, J.-C.; Guehl, J.-M. The successional status of tropical rainforest tree species is associated with differences in leaf carbon isotope discrimination and functional traits. *Ann. For. Sci.* **2007**, *64*, 169–176. [CrossRef]
31. Selaya, G.N.; Anten, N.P.R. Leaves of pioneer and later-successional trees have similar lifetime carbon gain in tropical secondary forest. *Ecology* **2010**, *91*, 1102–1113. [CrossRef]
32. Prado Júnior, J.; Schiavini, I.; Vale, V.; Raymundo, D.; Lopes, S.; Poorter, L. Functional traits shape size-dependent growth and mortality rates of dry forest tree species. *J. Plant Ecol.* **2017**, *10*, 895–906. [CrossRef]
33. Wright, S.J.; Kitajima, K.; Kraft, N.; Reich, P.; Wright, I.; Bunker, D.; Condit, R.; Dalling, J.; Davies, S.; Diaz, S.; et al. Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* **2010**, *91*, 3664–3674. [CrossRef]
34. Shannon, D.P.; Tiansawat, P. *Using Functional Traits to Determine Success in Forest Restoration*; Faculty of Science, Chiang Mai University: Chiang Mai, Thailand, 2019.
35. FORRU. *FORRU Main Databank*; Biology, Faculty of Science Chiang, Mai University: Chiang Mai, Thailand, 2023.
36. Zanne, A.E.; Lopez-Gonzalez, G.; Coomes, D.A.; Ilic, J.; Jansen, S.; Lewis, S.L.; Miller, R.B.; Swenson, N.G.; Wiemann, M.C.; Chave, J. Data from: Towards a Worldwide Wood Economics Spectrum. Global Wood Density Database. Dryad Identifier, 2009. Available online: https://doi.org/10.5061/dryad.234 (accessed on 10 May 2023). [CrossRef]
37. Goosem, S.; Tucker, N.I.J. *Repairing the Rainforest*, 2nd ed.; Wet Tropics Management Authority and Biotropica Australia Pty. Ltd.: Cairns, QLD, Australia, 2013.
38. Jantawong, K.; Elliott, S.; Wangpakapattanawong, P. Above-Ground Carbon Sequestration during Restoration of Upland Evergreen Forest in Northern Thailand. *Open J. For.* **2017**, *7*, 157–171. [CrossRef]
39. Pothong, T. *New Allometric Equations for Tree Biomass and Carbon Calculations in Secondary Hill Evergreen Forest in Northern Thailand*; Chiang Mai University: Chiang Mai, Thailand, 2019.
40. Chave, J.; Muller-Landau, H.C.; Baker, T.R.; Easdale, T.A.; ter Steege, H.; Webb, C.O. Regional and phylogenetic variation of wood density across 2456 Neotropical tree species. *Ecol. Appl.* **2006**, *16*, 2356–2367. [CrossRef]
41. Pakkad, G. Morphological Database of Fruits and Seeds of Trees in Doi Suthep-Pui National Park. Master's Thesis, Graduate School, Chiang Mai University, Chiang Mai, Thailand, 1997.

42. Hendry, G.A.F.; Grime, J.P. *Methods in Comparative Plant Ecology: A Laboratory Manual*; Chapman & Hall: Boca Raton, FL, USA, 1993.
43. Schneider, F.D.; Fichtmueller, D.; Gossner, M.M.; Güntsch, A.; Jochum, M.; König-Ries, B.; Le Provost, G.; Manning, P.; Ostrowski, A.; Penone, C.; et al. Towards an ecological trait-data standard. *Methods Ecol. Evol.* **2019**, *10*, 2006–2019. [CrossRef]
44. Flörchinger, M.; Braun, J.; Böhning-Gaese, K.; Schaefer, H.M. Fruit size, crop mass, and plant height explain differential fruit choice of primates and birds. *Oecologia* **2010**, *164*, 151–161. [CrossRef]
45. Ward, J.H. Hierarchical Grouping to Optimize an Objective Function. *J. Am. Stat. Assoc.* **1963**, *58*, 236–244. [CrossRef]
46. Teichgraeber, H.; Brandt, A.R. Systematic Comparison of Aggregation Methods for Input Data Time Series Aggregation of Energy Systems Optimization Problems. In *Computer Aided Chemical Engineering*; Eden, M.R., Ierapetritou, M.G., Towler, G.P., Eds.; Elsevier: Amsterdam, The Netherlands, 2018; Volume 44, pp. 955–960.
47. Ludwig, J.A.; Reynolds, J.F. Statistical ecology: A primer on methods & computing. *J. Appl. Ecol.* **1988**, *26*, 1099.
48. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2020; Available online: https://www.R-project.org/ (accessed on 10 May 2023).
49. PROSEA. *Plant Resources of South-East Asia: Timber Trees; Lesser-Known Timbers*; Backhuys Publishers: Leiden, The Netherlands, 1998.
50. Gardner, S.; Sidisunthorn, P.; Anusarnsunthorn, V. *A Field Guide to Forest Trees of Northern Thailand*; Kobfai Publishing Project: Bangkok, Thailand, 2007.
51. Waiboonya, P.; Elliott, S.; Tiansawat, P. Seed Storage Behaviour of Native Forest Tree Species of Northern Thailand. *Environ. Asia* **2019**, *12*, 104–111. [CrossRef]
52. Betts, H. The Framework Species Approach to Forest Restoration: Using Functional Traits as Predictors of Species Performance. Ph.D. Thesis, University of Liverpool, Liverpool, UK, 2013.
53. Kattge, J.; Bönisch, G.; Díaz, S.; Lavorel, S.; Prentice, I.C.; Leadley, P.; Tautenhahn, S.; Werner, G.D.A.; Aakala, T.; Abedi, M.; et al. TRY plant trait database—Enhanced coverage and open access. *Glob. Chang. Biol.* **2020**, *26*, 119–188. [CrossRef] [PubMed]
54. Royal Botanic Gardens, K. Royal Botanic Gardens, Kew—Herbarium Specimens. 2021. Available online: https://www.gbif.org/dataset/cd6e21c8-9e8a-493a-8a76-fbf7862069e5 (accessed on 19 August 2022).
55. Banin, L.F.; Raine, E.H.; Rowland, L.M.; Chazdon, R.L.; Smith, S.W.; Rahman, N.E.B.; Butler, A.; Philipson, C.; Applegate, G.G.; Axelsson, E.P.; et al. The road to recovery: A synthesis of outcomes from ecosystem restoration in tropical and sub-tropical Asian forests. *Philos. Trans. R. Soc. B Biol. Sci.* **2023**, *378*, 20210090. [CrossRef]
56. Gornish, E.S.; McCormick, M.; Begay, M.; Nsikani, M.M. Sharing knowledge to improve ecological restoration outcomes. *Restor. Ecol.* **2021**, e13417. [CrossRef]