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Research Article

Which traits are necessary to quickly select suitable plant species for ecological restoration?

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Abstract

1. Traditionally, restoration ecologists and land managers have used the trial-and-error method to select candidate restoration species. This method, however, is time consuming (usually more than 3 years) and has a relatively low success rate. Recently, Wang et al. (2020) developed a trait-based species selection framework which can quickly (within 1 month) and successfully select many appropriate species for ecological restoration. They used 28 traits that are associated with tolerance to harsh environmental conditions to select candidate restoration species for a tropical coral island in Hainan Province, China. However, it is likely that some of the 28 traits used in this study may not be very important for species selection, providing the potential use of fewer overall traits. This is important since in many situations land managers will have limited data and resources on species traits.
2. In this study, we used Wang et al. (2020)'s trait data to test which traits are necessary to achieve a similar success rate when screening species for restoration applications. We performed principal component analysis (PCA) to compute each trait's relative contribution. Then, we used the backward stepwise approach where the trait that had the least contribution among all remaining traits was removed one at a time, and the screening model was then run again using the smaller set of traits. Species which are proven very appropriate for ecological restoration in Wang et al. (2020) were the standard to quantify how many and which traits should be used to acquire similar screening results. We also classified all 28 traits into four types of functional traits to test if a small set of traits can mimic Wang et al. (2020)'s selection results.
3. Our results indicate that it is hard to simultaneously reduce trait numbers and maintain the right screening results; especially for tree species. Likewise, vine species and herbaceous species still required most of the original traits used by Wang et al. (2020). Our results also indicate that multiple trait types are required, rather than one single group of functional traits.

4. Our results reject the possibility of using fewer and more targeted traits for species screening. Although investigations in other ecosystems are needed to test the generality of the conclusion, our results suggest that multiple functional traits are still required to be measured to select appropriate plant species for the restoration of tropical coral islands.

KEYWORDS

plant functional traits, response-and-effect trait framework, tropical coral island, vegetation restoration

1 | INTRODUCTION

Intensive land use, human disturbance and climate change have led to an increase in degraded ecosystems across the world (Cardinale et al., 2012; Chapin et al., 2000). These degraded ecosystems are known to seriously affect human economic and social life (Laughlin, 2014). As such, it is very important that we develop effective and efficient methods for restoring them to natural or semi-natural conditions (Dobson et al., 1997; Hobbs & Harris, 2001). The first and most important step in this process is identifying species that are most appropriate and effective for restoration applications (Brown & Amacher, 1999; Fry et al., 2013; Jones, 2013). However, this step requires a comprehensive understanding of the ecological restoration theory, including information on species interactions, successional processes, and resource-use patterns. Because these processes differ greatly across different ecosystems, this remains an enormous challenge. As this type of information is typically lacking, candidate species for restoration purposes are typically chosen using the trial-and-error method (Ostertag et al., 2015; Padilla et al., 2009; Rosenthal, 2003).

Plant functional traits have been shown to be very useful for quickly selecting a number of suitable plant species for the restoration of degraded ecosystems (Laughlin & Laughlin, 2013). The use of functional traits for species selection is based on the idea that only colonizers that possess the appropriate traits to tolerate local environmental conditions and species interactions can succeed long term (Keddy, 1992). Several studies have successfully used functional traits to select suitable plant species for restoring degraded ecosystems (Bochet & García-Fayos, 2015; Guimarães et al., 2018; Matos et al., 2019; Ostertag et al., 2015; Rayome et al., 2019; Wang et al., 2020; Werden et al., 2018). However, each of these studies used different sets of functional traits to select suitable plant species. This is expected since different traits are more or less relevant in different ecosystems. Still, understanding the number and type of traits needed to successfully select restoration species remains an open and important research question.

The majority of restoration practitioners prefer to use a few easy-to-measure traits, such as plant height or specific leaf area (SLA) (Ehleringer & Sandquist, 2006; Padilla et al., 2009; Rosenthal, 2003) to select plant species for restoration. For example, low SLA is thought to help plant species adapt to the stressful environmental conditions found in degraded ecosystems. As such, plant species with low SLA can be selected for planting in these areas. Using a few traits to select candidate plant species for restoration is simple and straightforward. However, this approach can only be effective when there exists a single harsh environmental condition (e.g. high radiation or low soil nutrient) that plant species respond to. When there exist multiple different types of harsh environmental conditions, such as drought, high temperature, low land soil nutrients, this approach may not be effective. For example, if only a single trait were used to select restoration species, it is highly possible that only a few selected plant species would be identified as suitable when tested by the trial-and-error method. Indeed, in a previous study (Wang et al., 2020), only three out of 20 species selected by SLA were proven suitable for restoring an extremely degraded tropical coral island which has multiple harsh environments (e.g. no soil, high UV radiation, drought and so on).

The successful restoration of degraded ecosystems requires restoring properties of the original natural ecosystem and promoting ecosystem functioning (i.e. primary production, litter decomposition, soil respiration, nutrient cycling and soil moisture retention among others) (Suding et al., 2008). Based on this goal, Laughlin (2014) has developed a response-and-effect trait framework which utilizes response traits and effect traits to select appropriate plant species. The goal of this framework is to select species that can adapt well to the specific environment of the degraded ecosystem, while also having a high potential to promote ecosystem functioning. Response traits are those that can help a plant species adjust to the specific environment of the degraded ecosystem. For example, higher leaf proline content can help plant species adapt to stressful environments in degraded ecosystems. Effect traits are those that can directly determine ecosystem functioning, such as N cycling, carbon capture and biomass (Laughlin, 2014). For instance, the plant photosynthetic rate can directly be related to ecosystem productivity (Frolking et al., 1998; Garnier et al., 2004). Given the multiple harsh environmental characteristics and many ecosystems functions that are needed to be recovered in degraded ecosystems, multiple response and effect traits should be used to effectively and efficiently select suitable plant species for the restoration of these systems. It is also highly possible that selecting physiological traits (e.g. photosynthesis rate, leaf proline content and leaf turgor loss point) may be better than using morphological traits (e.g. SLA, leaf dry matter content and leaf anatomical traits), since morphological traits are often used as a proxy for physiological traits (X. Liu et al., 2013). However, physiological traits are often much harder to measure than morphological traits (H. Zhang et al., 2018). As a result, ecologists still have to make a decision regarding how many and which traits should be used to select suitable plant species for restoration.

Recently, Wang et al. (2020) have expanded on the response and effect framework introduced by Laughlin (2014) to develop a trait-based species screening modelling process that has been shown to effectively and efficiently select many candidate plant species for restoring a highly degraded tropical coral island in Hainan province, China. However, this framework utilized a large suite of 28 traits associated with resisting harsh environmental conditions. It remains highly possible that some of the 28 traits used in this study may not be very important for species selection, providing the potential use of fewer overall traits. This is important since in many situations land managers will not have the time and resources to collect data for such a large number of traits. To test this idea, we used Wang et al. (2020)'s trait data and the selection framework to quantify the minimal number and identities of traits needed for effective species selection. Our goal is to test whether a fewer number of high-quality traits may or may not be feasible for effectively and quickly selecting suitable plant species for ecological restoration.

2 | MATERIALS AND METHODS

2.1 | The framework of trait-based species selection

As described in Wang et al. (2020), the framework for trait-based species selection has the following key steps: (1) Identify target species which have been shown to have high survival rates in the degraded ecosystem. The traditional trial-and-error method may be used to determine the target species. (2) Identify potential species which may be suitable for restoration of the ecosystem. Generally, the potential species pool should include historical native species and non-native species found in regions that have similar environments. (3) identify relevant functional traits associated with the restoration process. (4) Analyse trait data and select species that have high ecological similarity to the target species. These species become candidate species for use in restoration applications. Based on Wang et al. (2020), the maximum entropy (Maxent) model (Shipley & Garnier, 2006), which estimated species relative abundances by choosing the maximum entropy solution to a system of linear constraint equations, was used to compute the similarity index between the target species and the potential species. The input of the Maxent model is the trait value for the target species and the potential species. Then the model returns vectors of relative abundances as the similarity indexes to target species for each potential species. Species with a higher similarity index can directly indicate that their trait spaces are more similar to the target species. (5) The final step is to monitor the survival rates of the selected species and check whether they have comparable survival rates to the target species and have high survival rates than the unselected species.

Wang et al. (2021) also developed a web-based software platform called 'Recover Plant Species Selection (RPSS) Platform' to aid in the modelling procedure. In this study, we will use the software mentioned above to accomplish all the species-screening processes.

2.2 | Study site

Our study site is located in a tropical coral island of Hainan Province (lying between 108°37′–111°03′E and 18°10′–20°10′N), China, where low fertility reef sands are common. The study site has an area of approximately 1 km^2 and its mean elevation is about 5 m. The study site is tropical oceanic monsoon climate with an annual mean temperature of 28°C and about 2800 mm of annual precipitation. Most of the precipitation falls during April and September. The adverse environments in this study site are characterized by high temperatures, intense light, drought and high salinity and alkaline soils in which it is difficult for many plants to colonize and grow (W. Zhang et al., 2019). For human habitation and economic development, developing successful restoration management strategies for this area is exceedingly important (Wang et al., 2020, 2021).

2.3 | Target and potential species

Due to the lack of native plants in the studied tropical coral island, we have identified 20 species on a nearby island with similar environmental conditions to the study site. These species were cultivated in Wenchang City, Hainan Province for 1–3 months and then transplanted to the study site. Three years later, target species were defined as those with survival rates >90% based on the trial-and-error method. As a result, three species *Scaevola sericea* (A), *Ipomoea pes-caprae* (B) and *Cynodon dactylon* 'Yangjiang' (C) were selected as target species for trees, vines and herbs, respectively.

In order to obtain more plant species that can successfully grow in the study site, 66 potential species were selected from four tropical regions, including the South China Sea, the South Pacific Islands and Hawaii, the Indian Ocean Islands, the Caribbean Sea, and the Galapagos Islands. These regions were selected because their climatic and environmental conditions are similar to the study site. The selected 66 species represent a wide range of plant groups containing trees, shrubs, herbs, vines, legumes, semi-mangrove plants and some medicinal and edible plants. The list of the 66 potential species is shown in Table S1 in the Supporting Information. The seedlings of these potential species were cultivated mainly including watering and fertilizing in Wenchang City, Hainan Island, China.

2.4 | Trait selection

We used the same 28 traits as Wang et al. (2020) to select species for restoration. Traits included those associated with the leaf economic traits (e.g. SLA, maximum photosynthetic rate, leaf thickness, leaf area), hydraulic traits (e.g. leaf hydraulic conductivity, stomatal conductance, instantaneous water use efficiency, transpiration rate) and stress-resistant traits (e.g. leaf dry matter content, stomatal density, stomatal pore area index, total antioxidant capacity, superoxide dismutase activity, peroxidase activity, catalase activity, total phenolics content, malondialdehyde content, proline content, water-soluble content). Due to limited leaf samples for some herbs, only 19 traits were used for these species (see Table 1). For the selected target and potential species, traits on mature and healthy leaves of 10 individuals for each species were measured during the growing season. The measurement methods and trait dataset can be obtained from the Supporting Information file.

2.5 | Statistical analysis

Screening results were deemed reliable when the ranges of the target species' trait values were within the range of the potential species. To check whether our trait data met this requirement, we compared trait values of target species A, B and C with the trait values of the 66 potential species based on their median, 25th and 75th percentiles, and most extreme data without outliers.

We performed principal component analysis (PCA) using the 'princomp' function in R (https://www.r-project.org/) to extract the main components of the traits for each target species. In order to determine whether the number of species used affects the results of the PCA, we used different numbers of species and ran multiple PCAs. For example, the PCA for the 28 traits using different samples as 60 species, 50 species, 40 species and 30 species while PCA for 19 traits using different samples as 66 species, 56 species, 46 species, 36 species and 26 species.

The relative contribution of each principal component (PC) was calculated as

$$\text{Contribution of PC}_i = \frac{\text{Variance}\,(\text{PC}_i)}{\sum_{i=1}^{n} \text{variance}\,(\text{PC}_i)} \times 100\%, \quad (1)$$

where n indicates the number of PCs, which was equal to the number of traits in the study. PC_i represents the ith PC. The variance of each PC was also obtained from the 'princomp' function in R.

Based on the PCA results, we calculated each trait's contribution as

$$\text{Contribution of trait}\,(i) = \sum_{j=1}^{m} |\text{loadings}\,(trait\,(i, j))| \times \text{contribution of PC}_j, \quad (2)$$

where PC_j is the jth PC, $trait(i)$ is the ith trait. Loadings are the weights of the eigenvector, which is the variance–covariance matrix of the original trait data. They describe how each trait contributes to each PC. When a trait has high loading (positive or negative) on one PC, that means, the variable contributes a large amount to the overall PC. We defined each trait's contribution as the trait's contributions to each PC multiply each PC's relative contribution.

In order to test how many and which traits are needed to obtain the accurate screening results, we used a backward stepwise approach where individual traits were removed one at a time, and the screening model was run again using the smaller set of trait combinations (hereafter short as a combination). At each step, one trait (or two/three, if the two/three traits have very similar contributions) which has the least contribution among all remaining traits is removed to form a new combination. Separate analyses were computed for the three target species. Traits were removed until the stop criterion is reached (in this study, we defined the stop criterion as there are only three functional traits left). As described in Wang et al. (2020), the species screening model returns a vector of similarity indexes for potential species. We sorted the potential species based on their similarity index to the target species from largest to smallest. In Wang et al. (2020), only the top-five ranking screened plant species were proven appropriate for restoration. As a result, in order to facilitate the analysis process, the top-five ranking screened plant species were selected to compare with the top five species of Wang et al. (2020)'s screening results. The more similar the top five screened plant species with the previous study (Wang et al., 2020), the better the screening result of this combination is. It should be noted that the higher the ranking of the screening results, the closer the selected species were to the target species. This means for all combinations, it is more important to select the top one ranking of the original experiment's screening result than the topfive.

Next, we tested which kinds of traits had a greater influence on the screening results. We first classified the 28 traits into four functional groups (i.e. structural traits, biochemical traits, hydraulic traits, and gas exchange traits; see Table 2). Then, according to different structural locations and different physiological functions, we divided the structural traits into three subgroups (e.g. leaf anatomical traits, leaf morphological traits and leaf stomatal traits) and divided the biochemical traits into three subgroups (e.g. leaf antioxidant traits, leaf osmotic traits and leaf chlorophyll traits) (see Table 2; Violle et al., 2007). For each experiment, we deleted traits from one group or one subgroup and ran the screening process again. The new screening results will be compared with the original screening results which using all traits.

3 | RESULTS

3.1 | Trait values between target species and potential species

For all three target species, most of the measured trait (27 out of 28 traits for target tree species, 28 out of 28 traits for target vine species and 18 out of 19 traits for target herb species) values were within the range of traits values measured for the potential species. The only exception was for palisade tissue width (PW) of species A (tree) and instantaneous water use efficiency (WUEi) of species C (herb) (Figures S1–S3 in the Supporting Information). As a result, we are confident that our trait datasets are useful for carrying out trait-based species screening.

TABLE 1 Descriptions of the selected plant traits and abbreviations used in this study. Sources and physiological functions are also shown

Leaf trait category	Trait	Abbreviation	Unit	Information compilation source	Ecological relevance	Ecophysiological mechanism
Structural traits	Leaf/palisade/spongy tissue thickness	LT/PT/ST	μm	Field sampling and laboratory measurements	Radiation and drought tolerance	Thicker LT/PT/ST could tolerate higher radiation and hold more water
	Leaf palisade/spongy tissue thickness ratio	PST	-	Field sampling and laboratory measurements	Radiation and drought tolerance	Higher PST could enhance the photosynthetic capacity
	Palisade tissue width	PW	μm	Field sampling and laboratory measurements	Radiation and drought tolerance	A larger PW could enhance the photosynthetic capacity
	Upper epidermis thickness	UE	μm	Field sampling and laboratory measurements	Radiation and drought tolerance	Thicker UE could prevent from water loss
	Leaf dry matter content	LDMC	mg g^{-1}	Field sampling and laboratory measurements	Nutrient acquisition and retention of resources	Larger LDMC is related to more carbon allocation
	Specific leaf area	SLA	cm^2 g^{-1}	Field sampling and laboratory measurements	Resource capture and environment adaptability	SLA is related to photosynthetic capacity and leaf nutrient allocation
	Leaf area	LA	cm^2	Field measurements	Water retention and drought tolerance	LA is related to photosynthetic capacity and leaf transpiration
	Guard cell length	SL	μm	Field sampling and laboratory measurements	Water retention and drought tolerance	Larger SL potentially has higher stomatal conductance and water loss
	Stomatal density	SD	n mm^2	Field sampling and laboratory measurements	Water retention and drought tolerance	Higher SD potentially has higher stomatal conductance and water loss
	Stomatal area index	SPI	%	Field sampling and laboratory measurements	Photosynthesis and evaporation intensity	Higher SPI potentially has higher stomatal conductance and water loss
Biochemical traits	Total antioxidant capacity	AOC	U g^{-1}	Field sampling and laboratory measurements	Antioxidant capacity	Higher AOC could reduce oxidation damages from stresses such as high UV radiation
	Superoxide dismutase activity	SOD	U g^{-1}	Field sampling and laboratory measurements	Antioxidant capacity	Higher SOD could reduce oxidation damages from stresses such as high UV radiation
	Peroxidase activity	POD	U g^{-1}	Field sampling and laboratory measurements	Antioxidant capacity	Higher POD could reduce oxidation damages from stresses such as high UV radiation

(Continues)

TABLE 1 (Continued)

Leaf trait category	Trait	Abbreviation	Unit	Information compilation source	Ecological relevance	Ecophysiological mechanism
	Catalase activity	CAT	$U\ g^{-1}$	Field sampling and laboratory measurements	Antioxidant capacity	Higher CAT could reduce oxidation damages from stresses such as high UV radiation
	Total phenolics content	TP	$mg\ g^{-1}$	Field sampling and laboratory measurements	Antioxidant capacity	Higher TP could reduce oxidation damages from stresses such as high UV radiation
	Water-soluble protein	CPR	$mg\ g^{-1}$	Field sampling and laboratory measurements	Osmotic adjustment and nutrient retention	Higher CPR could increase osmotic concentration thus drought tolerance
	Malondialdehyde content	MDA	$nmol\ g^{-1}$	Field sampling and laboratory measurements	Lipid peroxidation degree	Higher MDA could reduce lipid oxidation damages from stresses such as high UV radiation
	Proline content	PRO	$\mu g\ g^{-1}$	Field sampling and laboratory measurements	Osmotic adjustment	Higher PRO could increase osmotic concentration thus drought tolerance
	Chlorophyll *a*/ chlorophyll *b*/ total chlorophyll content	CHLa/ CHLb/ CHLt	$mg\ g^{-1}$	Field sampling and laboratory measurements	Light capture and photosynthetic capacity	Higher CHLa/CHLb/ CHLt could increase light capture and photosynthetic capacity
Hydraulic traits	Leaf hydraulic conductance	K_{leaf}	$mmol\ s^{-1}\ m^{-2}\ MPa^{-1}$	Field sampling and laboratory measurements	Water retention and acquisition capacity	Higher K_{leaf} could transport water more efficiently
Gas exchange traits	Maximum photosynthetic rate	A_{max}	$\mu mol\ m^{-2}\ s^{-1}$	Field measurements	Photosynthetic capacity	Directly reflect carbon fixation rate
	Stomatal conductivity	g_s	$mol\ m^{-2}\ s^{-1}$	Field measurements	Stomatal adjustment and water retention	Directly reflect gas exchange rates of water and oxygen
	Instantaneous water use efficiency	WUEi	$\mu mol\ mol^{-1}$	Field measurements	Leaf carbon and water utilization capacity	Directly reflect leaf carbon and water utilization
	Transpiration rate	*E*	$mmol\ m^{-2}\ s^{-1}$	Field measurements	Leaf water utilization	Directly reflect leaf water loss

For target species C *Cynodon dactylon* 'Yangjiang', LT, PT, ST, PST, PW, UE, SL, SD and SPI are not measured due to the limitation of fresh leaf samples.

3.2 | PCA and trait contribution results

The results of the PCA were found to be robust, since using a different number of species led to similar results (Figures 1 and 2). Ten PCs for the 28 traits and eight PCs for the 19 traits contained roughly 80% of the total contribution from all variables, suggesting low overlap among the measured traits. As for trait contributions, most traits showed similarly high contributions, except for stomatal area index (SPI) and malondialdehyde content (MDA) (Figure 3).

3.3 | The influence of using fewer traits when screening

All three target species required a large number of traits to match the original results (the top five species of the screening results are the same as with the top five species of Wang et al., 2020,'s screening results). Species A required 27 traits, while species B and C required 23 and 14 traits, respectively (see Table 3).

TABLE 2 Categories of 28 leaf traits based on different functions

Group	Subgroup	Trait abbreviation
Structural traits (group A)	Leaf anatomical traits (subgroup a1)	LT/PT/ST, PST, PW, UE
	Leaf morphological traits (subgroup a2)	LDMC, SLA, LA
	Leaf stomatal traits (subgroup a3)	SL, SD, SPI
Biochemical traits (group B)	Leaf antioxidant traits (subgroup b1)	AOC, SOD, POD, CAT, TP, MDA
	Leaf osmotic traits (subgroup b2)	CPR, PRO
	Leaf chlorophyll traits (subgroup b3)	CHLa/CHLb/CHLt
Hydraulic trait (group C)	/	Kleaf
Gas exchange traits (group D)	/	Amax, gs, WUE, E

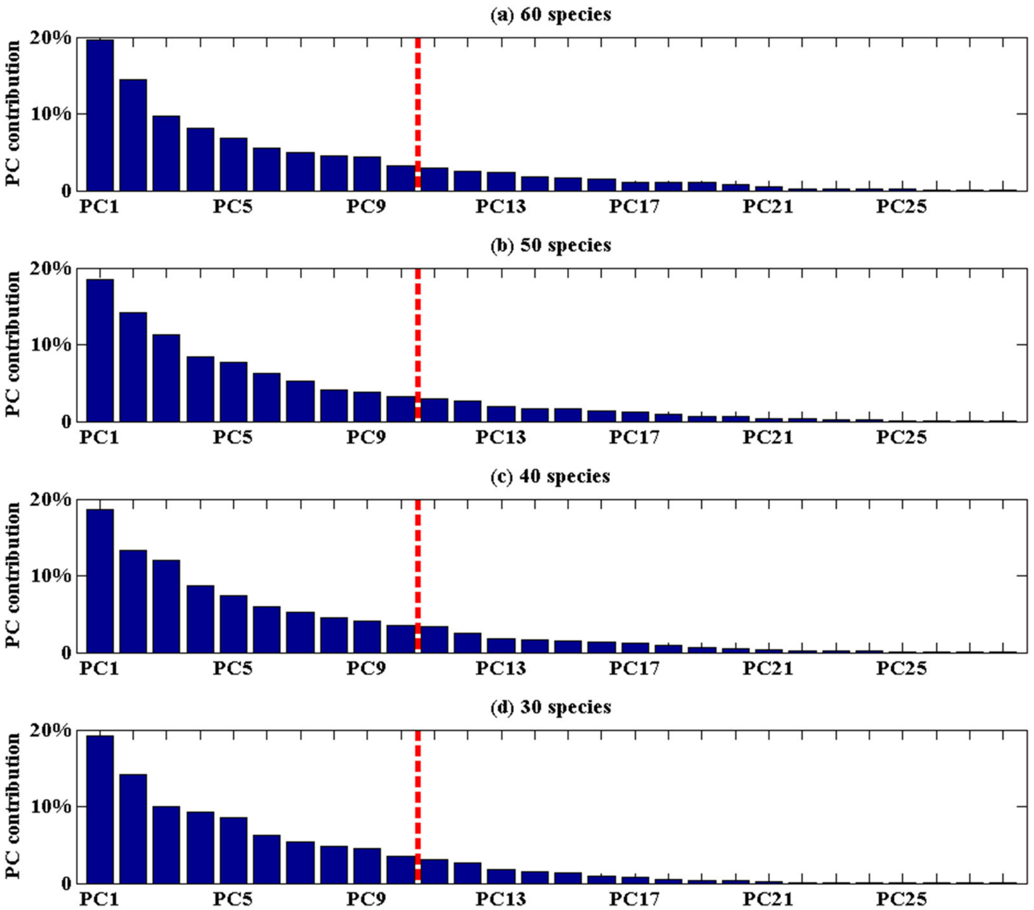

FIGURE 1 PCA results for 28 selected traits of (a) 60 species, (b) 50 species, (c) 40 species and (d) 30 species. The red dash lines mean that the total contribution rates of all the front PCs are reached 80%. Among all 66 potential species, only 60 species have all 28-trait data, some herb potential species only measured 19 traits. Thus, we use a maximum of 60 potential species in this figure. Because PCA requires the number of species must higher than the number of traits (28 traits), we cannot use 20 species to repeat the PCA process

3.4 | The influences of different types of traits on screening results

We found that for target species A (tree) and C (herb), each of the four trait categories (i.e. structural traits, biochemical traits, hydraulic traits and gas exchange traits) were needed for matching the original screening results (Tables 4 and 6, Exp 1–4). Omitting any trait category led to significant differences when compared to the original results. However, for target species B (vine), removing any one of the structural, hydraulic and gas exchange trait categories led to the same list of species as found in the original experiment, although in a different order (Table 5, Exp 1, 3, 4). However, if the biochemical traits were removed, the

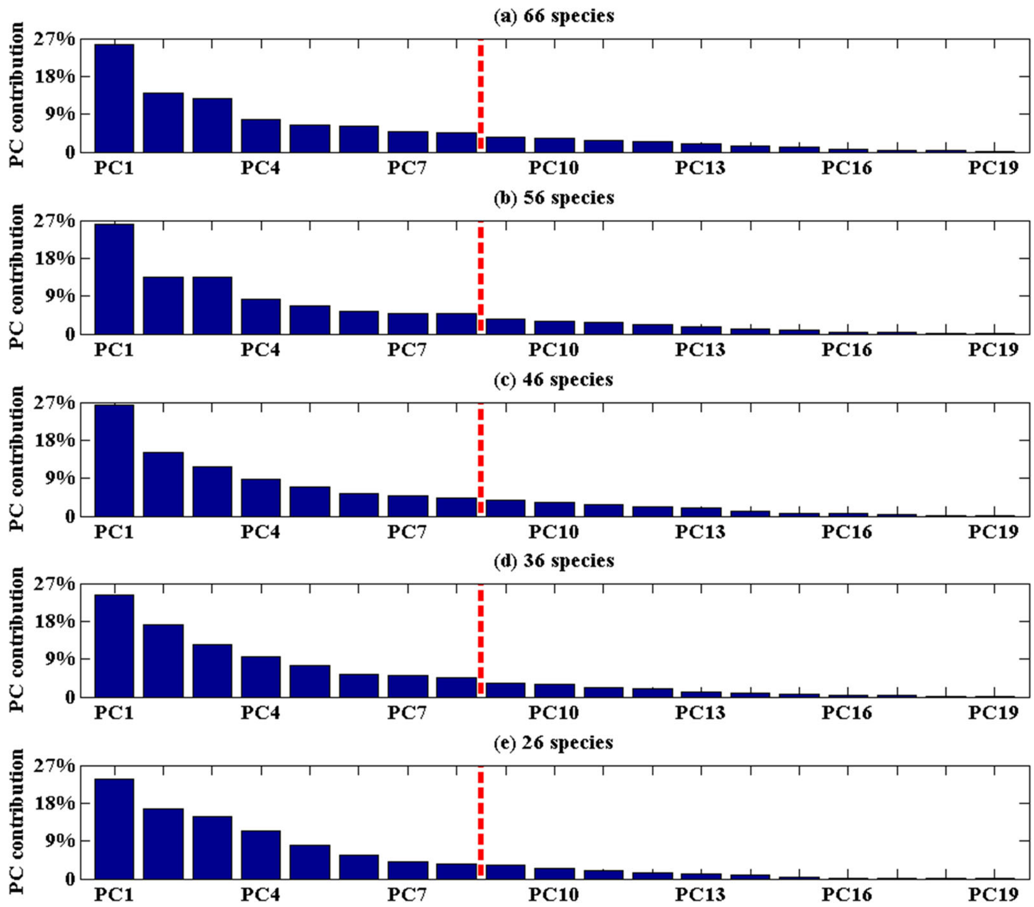

FIGURE 2 PCA results for 19 selected traits of (a) 66 species, (b) 56 species, (c) 46 species, (d) 36 species and (e) 26 species. Because PCA requires the number of species must higher than the number of traits (19 traits), we cannot use 16 species to repeat the PCA process

TABLE 3 PCA-based reduce functional traits screening results for target species A (tree), target species B (vine), and target species C (herb). S1, S2, S3, and so on indicate serial numbers of different potential species

Species A (tree)		Species B (vine)		Species C (herb)	
Traits	Screening results	Traits	Screening results	Traits	Screening results
28 traits (original)	**S11, S23, S5, S48, S58**	28 traits (original)	**S51, S11, S13, S5, S27**	19 traits (original)	**S63, S64, S66, S6, S31**
27 traits	**S11, S23, S5, S48, S58**	27 traits	**S51, S11, S13, S5, S27**	18 traits	**S63, S64, S66, S6, S31**
26 traits	S8, **S23, S11**, S43, S20	26 traits	**S51, S11, S13, S5, S27**	16 traits	**S63, S64, S6, S66, S31**
24 traits	S8, **S23, S11**, S43, S20	24 traits	**S51, S5, S13, S11, S27**	15 traits	**S63, S64, S6, S66, S31**
22 traits	S8, **S23, S11**, S43, S20	23 traits	**S51, S5, S13, S11, S27**	14 traits	**S63, S64, S6, S66, S31**
19 traits	S8, S37, **S23, S5, S11**	22 traits	**S51, S5, S13, S11**, S52	13 traits	**S63, S64, S66, S6**, S16
16 traits	**S5, S23**, S37, S8, S20	19 traits	**S51**, S1, S52, **S13, S11**	12 traits	**S63, S6, S64**, S17, S9
12 traits	**S23**, S8, S51, S20, S43	16 traits	**S51**, S12, **S13**, S52, S1	10 traits	**S63, S6**, S17, **S64**, S18
9 traits	**S23**, S51, S20, S52, S24	12 traits	**S51, S13**, S52, S1, S20	8 traits	**S63, S6, S64**, S18, S17
7 traits	S25, S55, **S23**, S20, S22	9 traits	**S51, S11**, S52, **S13**, S55	6 traits	**S64**, S13, S20, S55, S38
3 traits	S20, S52, S22, S24, S25	7 traits	S22, **S13**, S55, S43, S52	3 traits	S13, S7, **S64, S63**, S20
		3 traits	S23, S52, S43, S24, S26		

Bold font indicates that the screened species is one of the results from the original experiment.

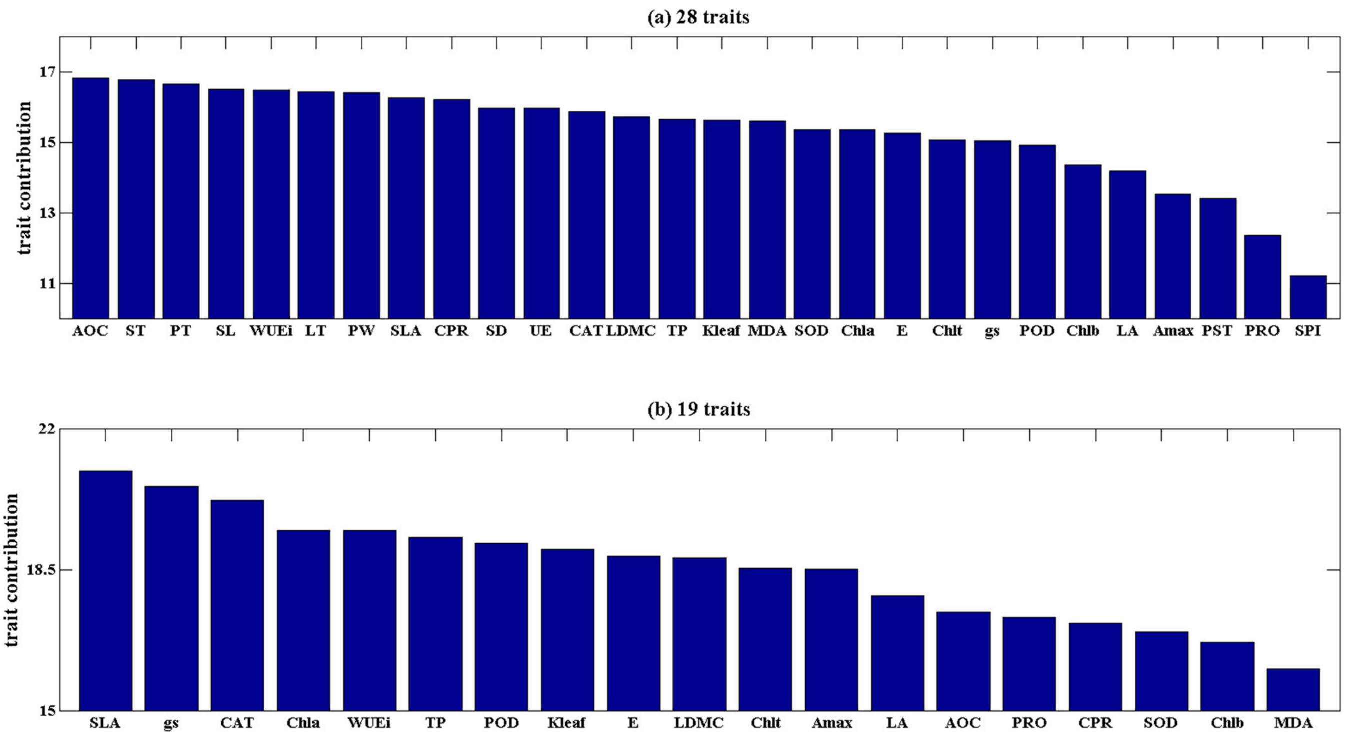

FIGURE 3 Trait contributions for (a) 28 traits and (b) 19 traits. The order of the traits is from large to small based on trait contributions

TABLE 4 Experience-based reduce functional traits screening results for species A (tree). The details of trait groups/subgroups can be found in Table 2. S1, S2, S3, and so on indicate serial numbers of different potential species

	Traits	Screening results
Original Exp	(A), (B), (C), (D)	**S11**, **S23**, **S5**, **S48**, **S58**
Exp 1 Delete group A	(B), (C), (D)	**S11**, **S23**, S25, S43, **S58**
Exp 2 Delete group B	(A), (C), (D)	S8, S12, S55, S19, S46
Exp 3 Delete group C	(A), (B), (D)	**S11**, **S23**, **S5**, S57, S34
Exp 4 Delete group D	(A), (B), (C)	**S11**, S20, **S23**, S13, S37
Exp 5 Most simplified (one trait for each group/subgroup)	*Structural traits*: LT, SLA, SL *Biochemical traits*: AOC, CPR, CHLt *Hydraulic trait*: Kleaf *Gas exchange traits*: Amax	S24, **S5**, **S23**, **S58**, S52
Exp 6 Delete subgroup a1	(a2, a3), (B), (C), (D)	**S11**, S26, **S5**, **S23**, S13
Exp 7 Delete subgroup a2	(a1, a3), (B) (C), (D)	**S11**, **S23**, **S58**, S1, S9
Exp 8 Delete subgroup a3	(a1, a2), (B) (C), (D)	**S11**, **S23**, **S5**, **S48**, **S58**
Exp 9 Delete subgroup b1	(A), (b2, b3) (C), (D)	**S58**, **S5**, S55, S38, S6
Exp 10 Delete subgroup b2	(A), (b1, b3) (C), (D)	S8, **S23**, **S11**, S43, S20
Exp 11 Delete subgroup b3	(A), (b1, b2) (C), (D)	**S11**, **S23**, **S5**, **S48**, **S58**

Bold font indicates that the screened species is one of the results from the original experiment.

screening results ended up significantly different from the original experiment (Table 5, Exp 2). Nevertheless, the correct screening results could not be attained by merely using biochemical traits alone (Table 5, Exp 12).

For the trait subgroups, leaf anatomical and morphological traits were more important than leaf stomatal traits for selecting ecological similar species of target species A (tree) (Table 4, Exp 6–8). Leaf antioxidant traits were more significant for screening results of species A

TABLE 5 Experience-based reduce functional traits screening results for species B (vine). S1, S2, S3, and so on indicate serial numbers of different potential species

	Traits	Screening results
Original	(A), (B), (C), (D)	**S51**, **S11**, **S13**, **S5**, **S27**
Exp 1 Delete group A	(B), (C), (D)	**S11**, **S51**, **S5**, **S27**, **S13**
Exp 2 Delete group B	(A), (C), (D)	S1, S15, S55, **S13**, **S51**
Exp 3 Delete group C	(A), (B), (D)	**S51**, **S11**, **S13**, **S5**, **S27**
Exp 4 Delete group D	(A), (B), (C)	**S51**, **S13**, **S11**, **S5**, **S27**
Exp 5 Most simplified (one trait for each group)	*Structural traits*: LT, SLA, SL *Biochemical traits*: AOC, CPR, CHLt *Hydraulic trait*: Kleaf *Gas exchange traits*: Amax	S37, **S51**, **S11**, S52, S28
Exp 6 Delete subgroup b1	(A), (b2, b3), (C), (D)	**S51**, S55, S15, **S11**, S3
Exp 7 Delete subgroup b2	(A), (b1, b3), (C), (D)	**S51**, **S11**, **S13**, **S5**, **S27**
Exp 8 Delete subgroup b3	(A), (b1, b2), (C), (D)	**S51**, **S5**, **S13**, S1, S52
Exp 9 Delete group A and C	(B), (D)	**S11**, **S51**, **S5**, **S27**, **S13**
Exp 10 Delete group A and D	(B), (C)	**S5**, **S51**, **S27**, **S11**, S28
Exp 11 Delete group C and D	(A), (B)	**S51**, **S13**, **S11**, **S5**, **S27**
Exp 12 Delete group A, C, and D	(B)	**S5**, **S51**, S58, S28, **S27**

Bold font indicates that the screened species is one of the results from the original experiment.

TABLE 6 Experience-based reduce functional traits screening results for species C (herb). S1, S2, S3, and so on indicate serial numbers of different potential species

	Traits	Screening results
Original	(A), (B), (C), (D)	**S63**, **S64**, **S66**, **S6**, **S31**
Exp 1 Delete group A	(B), (C), (D)	S9, **S64**, **S66**, **S6**, S18
Exp 2 Delete group B	(A), (C), (D)	**S63**, **S64**, **S66**, S61, **S6**
Exp 3 Delete group C	(A), (B), (D)	**S64**, **S63**, S20, S32, **S66**
Exp 4 Delete group D	(A), (B), (C)	**S63**, **S66**, **S31**, S36, S11
Exp 5 Most simplified (one trait for each)	*Structural traits*: SLA *Biochemical traits*: AOC, CPR, CHLt *Hydraulic trait*: Kleaf *Gas exchange traits*: Amax	**S66**, S61, S36, S9, **S63**
Exp 6 Delete subgroup b1	(A), (b2, b3), (C), (D)	**S63**, **S64**, **S66**, S16, **S6**
Exp 7 Delete subgroup b2	(A), (b1, b3), (C), (D)	**S63**, **S66**, **S64**, **S6**, **S31**
Exp 8 Delete subgroup b3	(A), (b1, b2), (C), (D)	**S63**, **S64**, **S66**, **S6**, S36

Bold font indicates that the screened species is one of the results from the original experiment.

(tree) than leaf osmotic and chlorophyll traits (Table 4, Exp 9–11). For target species B (vine) and C (herb), leaf antioxidant and chlorophyll traits were more effective than leaf osmotic traits (Tables 5 and 6, Exp 6–8).

4 | DISCUSSION

Here, we quantified whether it was feasible to use fewer but more targeted functional traits when selecting suitable plant species for ecological restoration. We found that many different types of functional traits, but not a fewer number of high-quality traits, are feasible for successfully selecting plant species for restoration purposes.

Trait-based approaches have been proven to be effective at finding suitable species for restoration purposes (Bochet & García-Fayos, 2015; Ostertag et al., 2015), but we still need to improve these frameworks so as to balance the work required to measure traits with the accuracy of the results. This is because some physiological traits are harder to measure than others and because certain traits may not be crucial for species living in the target environment (Wang et al., 2020).

The initial 28 traits were carefully selected to include various functional responses to different environmental stresses (e.g. high light, UV radiation, drought, and salinity). We determined that most of these traits are nearly equally important (Figure 3), thus traits representing multiple functions are needed to select suitable species for restoration. This is biologically reasonable since traits tend to have multiple functions and interactions. As a result, complex plant trait networks likely reflect plant adaptations and responses to different disturbance regimes and global changes (He et al., 2020). However, we also found that some traits have less contributions to the selection process. These traits either were calculated from other trait values such as SPI or represented multiple functions that overlapped with other traits. For example, MDA is functionally similar to superoxide dismutase activity (SOD) and peroxidase activity (POD), whereby each trait reduces oxidation damage from stress (here high UV radiation). This is a common problem in studies using multiple autocorrelated traits (Dirnböck & Dullinger, 2004) and when using PCAs to reduce trait/variable numbers (Liu et al., 2019).

There is the potential to select fewer but more accurate traits from our initial 28 traits. However, we found that it was hard to simultaneously reduce trait number and maintain the right screening results; especially for tree species (27 out of 28 traits are needed). Compared to tree species, fewer traits are needed for vine species (23 out of 28 traits) and herbaceous species (14 out of 19 traits). Because vines and herbs were less diverse overall than trees, thus they occupy fewer ecological niches in the communities (van der Sande et al., 2019) and may require fewer functional traits to distinguish among species within different life forms (Santiago & Wright, 2007). It is also possible that for the harsh environments of the tropical coral islands in our study, herbs are more functionally convergent than trees. For example, most herbs in our study showed tough leaves with very high SLA (*Spinifex littoreus* and *Lepturus repens*), whereas leaves of candidate tree species showed greater variation in SLA, likely because trees can adjust other organs/traits to adapt to stress (F. Liu et al., 2010). However, 82% (= 23/28) and 74% (= 14/19) of total functional traits were still necessary to keep for vine and herbaceous species. Moreover, the low-ranking traits selected by PCA maybe not indeed less important in the selection model. For example, the second lowest ranking trait for tree species A (proline content [PRO]) is a not only key trait in indicating higher leaf antioxidant capacities (N. Liu et al., 2014) but also indicates leaf tolerance to general environmental stresses. In our dataset, *Artocarpus heterophyllus* is a selected tree species with typically higher PRO content than other trees. Thus, many traits remain the best choice for using Wang et al. (2020)'s trait-based species screening model.

We also classified all of the traits into four important functional groups (i.e. structural traits, biochemical traits, hydraulic traits and gas exchange traits) to determine whether certain groups were more important than others. Consistent with a PCA-based trait combination, we found that multiple function-based trait combinations are required rather than one single functional group of traits. The likely reason is that the four functional groups and/or subgroups of the initial 28 traits correspond to different aspects of plant adaptation (Bush et al., 2018; Fry et al., 2013). Thus, the relative impact of each trait group on the screening results may reveal the importance of different functions.

Furthermore, we identified which subgroups of traits were more important in selecting the right target species. We found that all subgroups of traits are indispensable for getting original species screening results for species A (tree), B (vine) and C (herb). However, these subgroups of traits have different influences on species screening results for species A (tree), B (vine) and C (herb), respectively. Overall, leaf antioxidant traits are more informative than other leaf biochemical traits for all three target species. It is true that antioxidant traits are highly sensitive to high light, UV radiation and salinity (Ashraf & Foolad, 2007), which are exactly the environmental conditions for tropical coral islands in this study. In addition, for species A (tree), leaf stomatal traits are not as important as other leaf structural traits (Table 2, Exp 6–8). This might be because that leaf anatomical and morphological traits are synthesized adaptive traits and physical bases for all functions relating to growth, water maintenance and nutrient allocation (Wright et al., 2004), while stomatal traits only reflected small-scale level responses. For species B (vine) and C (herb), besides leaf antioxidant traits as detected for species A (tree), leaf chlorophyll traits are also important, compared with leaf osmotic traits. We supposed that leaf chlorophyll traits are long-term indicators of leaf health, directly linked with photosynthetic capability, and thus are more tightly related with vine/herb survival than for trees. As a result, leaf antioxidant and chlorophyll traits are crucial for selecting suitable vine and herb species for restoration, while additive leaf anatomical and morphological traits are needed to be considered for tree species.

Another potential reason for requiring multiple traits to select appropriate species is that Wang et al.'s (2020) species sorting framework is built on the basis of the response-and-effect traits framework of Laughlin (2014). However, many traits used in our study can be classified as both response and effect traits. For example, our measured biochemical, hydraulic and gas exchange traits can be seen as good response traits that can help plants adapt to stressful environments (Wang et al., 2020). In the meantime, they can also be good effect traits that can determine ecosystem functioning, including soil water, nutrient and C cycling (Anderegg et al., 2018; Bernacchi et al., 2013; Lavorel & Garnier, 2002). Moreover, species across different life forms (tree, vine and herbaceous species) are highly impossible to have the same appropriate response and effect traits. In addition, Wang et al.'s (2020) species sorting framework utilized Shipley's maximum entropy (Maxent) model, which used a system of linear constraint equations to calculate species similarity index to select suitable species. By using multiple traits simultaneously, the Maxent model can make a system of linear constraint equations more efficient, as multiple traits can produce more additional species relative abundance distributions than one or two types of traits (Laughlin, 2014). As a result, if we still wish to use few traits (e.g. less than 10 traits) to select appropriate species for restoration, future experiments are necessary to determine which traits are the best response and effect traits for helping in selecting species across different life forms.

We noted that our whole analysis is based on the prerequisite that species selected by the whole 28 traits in Wang et al. (2020) are the most suitable species for ecological restoration. We have to admit that this prerequisite may not be perfect, as this only comes from a single study, and confirmation regarding the real-world application of these species to restoration remains unknown. However, Wang et al. (2020) have clearly demonstrated that species selected by the 28 traits are indeed the most suitable species for restoration, as after using the trial-and-error, the survival rates of selected species are much higher than those for all unselected species. The key reason may be attributed to the harsh conditions of the study island, which in turn make plants to develop many different traits coding for many different functions. Nevertheless, it remains highly possible suitable plant species can be selected by fewer and more targeted traits in less harsh conditions. That is because limiting factors (e.g. soil nitrogen, phosphorus limitation, and so on) can be found in less harsh conditions, which in turn merely force a plant to develop some key functional traits (i.e. high SLA, leaf nitrogen and phosphorus content) to adapt to these specific limiting factors. This merits future research to verify this assumption. Last but not the least, more target traits should be selected to maintain long-term high plant diversity. That is because, progressively increased plant diversity will result in different types of niche partitioning and coexistence of mechanisms (i.e. habitat filtering or biotic interactions dominated), which can only be reflected by several key traits. Thus, selecting traits that can reflect niche partitioning and community assembly can be more reasonable to select appropriate plant species to ensure long-term diversity and ecosystem function.

5 | CONCLUSIONS

In summary, our results clearly reject the possibility that using fewer and highly relevant traits can be just as effective and efficient as using a large suite of diverse traits for selecting restoration species, especially for tree species. Thus, multiple functional traits will likely remain necessary. Although some physiological traits (e.g. leaf turgor loss point) are indeed hard and time consuming to measure, we found that these trait measurements can usually be obtained within a single month. Compared to the trial-and-error method that takes at least several years, our species screening framework based on multiple types of traits is still the best choice for restoration ecologists and land managers. Even though investigations in other ecosystems are needed to test the generality of the conclusion, our study provides advice for future trait-based species selection experiments that selecting and measuring multiple functional traits is the most cost-effective choice for successfully screening out the required restoration plant species, especially in tropical coral islands.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTION

C. W., H. Z. and H. L. conceived the ideas and designed methodology; C. W. analysed the data; C. W., H. Z. and H. L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.6q573n5w0 (Wang et al., 2020b).

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