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Research Article

The positive interaction between two nonindigenous species, Casuarina (*Casuarina equisetifolia*) and Acacia (*Acacia mangium*), in the tropical coastal zone of south China: stand dynamics and soil nutrients

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Abstract

The role of mixed forests in tropical coastal South China is unclear due to a long history of afforestation with a Casuarina (C*asuarina equisetifolia*) monoculture. In this study, we determined how the stand dynamics and soil nutrients in monoculture stands of C*asuarina equisetifolia* were influenced by Acacia (*Acacia mangium*), a fast-growing pioneer species, when the two tree species were combined in two initial proportions. We also compared the canopy conditions of mixed and monoculture stands of *C. equisetifolia* at the young stage. Over a period of ten years, the density of stems was relatively low in *C. equisetifolia* ×*Acacia mangium* mixed stands compared to *C. equisetifolia* monoculture stands. By contrast, the aboveground biomass, understory diversity and soil nutrients were relatively high in *C. equisetifolia* ×*A. mangium* mixed stands, particularly when the initial mixing proportion of *A. mangium* was greater. Moreover, *C. equisetifolia* can protect *A. mangium in* the windy coastal environment by ensuring evenly distributed crown growth, intact canopy conditions, and high leaf area index (LAI) during the young stage. In conclusion, the two species had a positive interaction in the mixed forests, which suggests that coastal conservation managers need to shift from their traditional focus on *C. equisetifolia* single-species afforestation to multi-tree species mixed afforestation.

Keywords: Mixed afforestation, aboveground biomass, understory dynamic, soil nutrients

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Introduction

Positive interactions, including mutualism, commensalism and facilitation, are traditionally defined as a type of interaction in which one species benefits from the other, without harm and potentially with benefits. These interactions can strongly shape the structure and function of plant communities [2], affecting population growth and fecundity, abundance, geographical range, soil nutrient supply, community diversity and stability [3-5]. For the positive effects of multi-species interactions [6], mixed afforestation was commonly used for forest conservation and restoration in degraded regions over the past two decades [7-8].

Coastal zones, as transition areas between terrestrial and marine ecosystems, are locations of intense exchange of matter and energy. Both waves and winds along the coast erode the ground and impose environmental constraints on forest succession, as well as threaten the restoration of original communities that have been destroyed. Historically, various species grew in the tropical coastal zone of southern China. However, because of the excessive exploitation of natural resources in the early 1900s, these coastal forests were destroyed, leaving a bald coastal landscape for nearly half a century [9]. This situation was not changed until the introduction of the exotic tree species Casuarina (*C. equisetifolia*).

C*. equisetifolia* is a she-oak species of the genus *Casuarina*, with a native range extending from Burma and Vietnam throughout Malaysia; east to French Polynesia, New Caledonia, and Vanuatu; and south to Australia [10]. It was introduced to Hainan Island to reduce coastal erosion in the 1950s and immediately became the dominant species due to its pioneer characteristics, including fast growth, adaptability to barren soils, and ability to resist wind [11]. Unlike normal broadleaf species, *C. equisetifolia* has morphological characteristics, such as a scaly leaf, lance-shaped branchlets, and a tower-shaped morphological structure, that increase its wind resistance and allow it to grow better in hostile coastal environments [12]. However, due to its high tannin content, the litterfall of *C. equisetifolia* decomposes slowly, decreasing the rate of nutrient return and influencing the growth

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of the forest. The litter beneath *C. equisetifolia* consists of fallen cladodes and can accumulate to form thick continuous deposits, which smother and prevent establishment of other species [13-14].

Because of its superior adaptability, Acacia (*Acacia mangium*) became a main plantation species that creates a green and attractive landscape and also contributes to soil improvement and environmental protection of the tropical coastal plain [15]. A large number of afforestation experiments showed that seedlings of *A. mangium* are vulnerable to an oceanic climate, and seedlings planted in a coastal open area will die within approximately two years because of unfavorable conditions if they are not mixed with other nurse plants. Therefore, *A. mangium* plantations were always established behind zones of *C. equisetifolia* to avoid destruction by erosion and winds. Considering the positive effects of mixed afforestation discussed above, we examined the interaction effects between the two tree species during 10 years of succession in the tropical coast. The objectives of this study were to determine: (1) how the vegetation dynamics and soil nutrients in monoculture stands of *C. equisetifolia* were influenced by *A. mangium;* and (2) whether *C. equisetifolia* protects *A. mangium* at the young stage.

Methods

Study area

The study was conducted in the northeast coastal zone of Wenchang city, Hainan Island, adjacent to the South China Sea, in the monsoon tropics of south China (Fig. 1). The tropical marine climate ensures a plentiful annual rainfall of 1,721.6 mm and mild temperatures averaging 22°C to 24°C. However, the area is also prone to severe typhoons and rain storms. Five to six typhoons occur each year, and some are fatal to replanted forests.

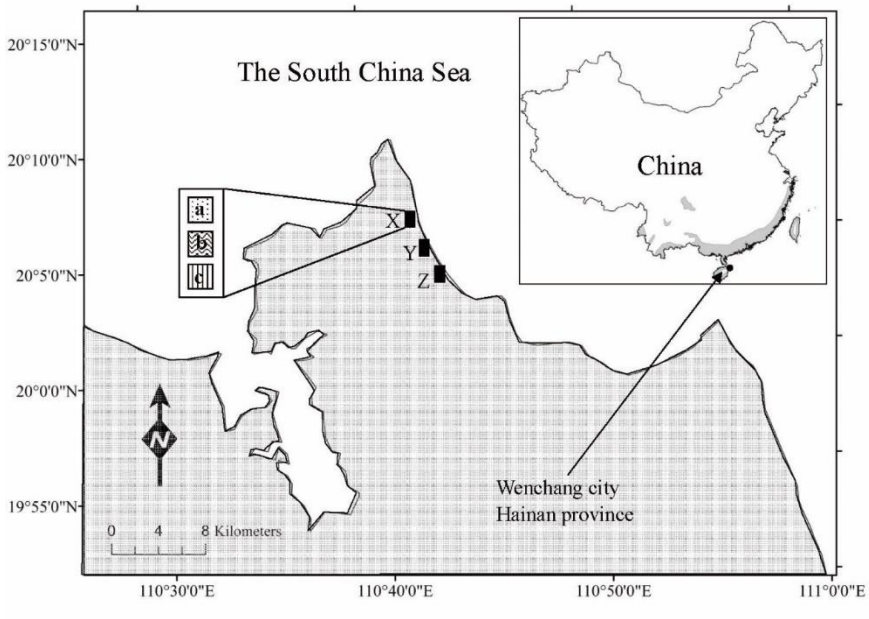


Fig. 1. Study sites in the northeast coastal zone near Wenchang city, Hainan Province, China. X.Y. and Z indicate three experiment blocks (2 hm² each). Three planting treatment plots (a= *Casuarina equisetifolia* only, b= *Acacia mangium* I and c= *Acacia mangium* II) were placed in each block.

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Experimental design

We examined the effects of planting *A. mangium* along with *C. equisetifolia* for tropical coastal forest succession and habitat restoration in an area of 2 hm^2. Both species' seedlings were selected in the nursery and planted systematically using the plant-to-row method on barren land when the plants were one year old in year 1998. Because *A. mangium* monocultures cannot survive in hostile coastal environments, we used three planting levels as follows: *C. equisetifolia* only, *A. mangium* Ⅰ and *A. mangium* Ⅱ (Ⅰ indicates that the mixing proportion of *C. equisetifolia* to *A. mangium* is 1:1, Ⅱ indicates that the mixing proportion of *C. equisetifolia* to *A. mangium* is 2:1). The initial density of afforestation was 2,500 stems per hectare (afforestation spacing=2 m × 2 m). The number of trees in each plot varied with factors such as typhoon, self-thinning, competition, and herbivory. The experimental treatments were determined using a randomized block design with three blocks. Within each block, three plots (plot area: 20 m × 20 m) were established for three planting levels independently, and in each plot, one subplot of 5 m × 5 m was established.

In each experimental plot, the number of trees per hectare was recorded biennially (2000 to 2010) to document survival in the various experimental plantings.

Biennially (2000 to 2010), the DBH (diameter at breast height) and height of trees were measured in each experimental plot and used to calculate the aboveground biomass using two biomass equations from the literature [16-17].

$$C.\ equisetifolia: \ln Y = -0.253 + 0.503 \ln(DBH^2 \bullet H) \quad (1)$$

$$A.\ mangium: \ln Y = -3.212 + 0.905 \ln(DBH^2 \bullet H) \quad (2)$$

where Y is the individual aboveground biomass and *H* is the tree height.

The soil samples were collected for nutrient analysis from the different planting levels to evaluate the role of different afforestation types in the soil condition. The baseline soil data were collected in 2000 together with other surveys. Three punch-tube samples of the upper 15 cm of sandy soil were collected and mixed together in each plot. These bulk samples were then analyzed for total N using the micro-Kjeldahl method, and the total organic matter was measured using a modified Walkley-Black procedure [18]. In addition, we began the second survey in 2010.

In each subplot, we assessed the species and number of natural regenerations and shrubs, and also surveyed the grass coverage. All measurements were recorded in late November, biennially, from 2000 to 2010.

Seedlings are vulnerable to oceanic climate. To evaluate the nurse role of *C. equisetifolia* on *A. mangium*, we selected fifteen *C. equisetifolia* and *A. mangium* plants randomly in monocultures of *C. equisetifolia*, *A. mangium* Ⅰ and *A. mangium* Ⅱ in the periphery of these stands in year 2000 (three years old). The LAI was obtained from canopy analysis systems (Hemiview 2.1) by analyzing canopy photos of individual trees in the vertical direction. Crown lengths (W-E-N-S four directions) were measured to demonstrate the lopsided crown phenomenon under continuous environmental stress.

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Statistical analysis

Replicated measurements recorded within one plot were averaged prior to statistical analyses to prevent pseudo-replication. All data (plot averages) were first checked for the homogeneity of variance and normality. We then analyzed data using the planting treatment (three levels) as the fixed effect and the block (three levels) as the random effect. All data were analyzed using SPSS 16.0 (Statistic Package for Social Science). Measurements that were repeated during different years were analyzed using repeated-measures analysis of variance (RANOVA). This analysis takes into account the overall treatment effect, independent of time, as well as the within-treatment effect to determine whether the pattern of the response to treatments changes over time. The three planting levels were then compared using a Tukey test based on the overall effect, independent of time. Because there was no time effect in the analysis of the canopy condition, one way-ANOVA was used.

Results

Vegetation dynamics

The number of planted species in each experimental plot decreased with time because of constant interference from the tropical marine climate. Plots planted with *C. equisetifolia* only had a significantly greater number of plant species than other treatments in 2010 (Fig. 2A; Appendix 1). For the mixed treatments, the average plant number in the plots of *A. mangium* Ⅱ (Number: *C. equisetifolia*: 1,424 /hm^2; *A. mangium* 422/hm^2) was greater than *A. mangium* Ⅰ (Number: *C. equisetifolia*: 998 /hm^2; *A. mangium* 742/hm^2) (Table 1).

The aboveground biomass was, on average, highest in plots of *A. mangium* Ⅰ (71.48 t/hm^2). Next highest was the other mixing type of *A. mangium* Ⅱ (67.53 t/hm^2). The aboveground biomass in plots planted with *C. equisetifolia* was significantly lower (64.64 t/hm^2) than the other two types (Fig. 2B).

The abundance and diversity of natural regenerating saplings differed significantly among the three treatments (Table 1). The average abundance (2,223 /hm^2) and diversity (*H'*: 0.90) in plots of *A. mangium* Ⅰ were significantly higher than the other two treatments. The next highest was *A. mangium* Ⅱ, with a number and diversity (*H'*) of 1,833 /hm^2 and 0.74, respectively. The abundance (1,028 /hm^2) and diversity (0.28) in pure *C. equisetifolia* plots were the lowest (Fig. 2 C and Fig. 2D).

The plots originally planted with *A. mangium* Ⅰ had the highest shrub diversity (*H'*: 1.16) of the three treatments, followed by *A. mangium* Ⅱ (Fig. 2E). The shrub diversity in plots planted only with *C. equisetifolia* was the lowest (0.63).

The grass cover was not significantly different between the two types of mixed plots (Fig. 2F). The pure plots had the lowest grass cover (18%), and much of the floor was covered by *C. equisetifolia* litter (Table 1).

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Table 1. The effects of three planting treatments on community dynamics over a 10-yr period.

Planting treatments	Number of planted species (N/hm^2)	Aboveground biomass of planted species (t/hm^2)	Number of regeneration tree species (N/hm^2)	Shannon-Wiener (Regeneration species)	Shannon-Wiener (shrub species)	Grass coverage (%)
Acacia mangium Ⅰ	1740 ^{c} (45)	71.48 ^{a} (5.53)	2223^{a} (116)	0.90^{a} (0.07)	1.16^{a} (0.11)	31^{a} (3.4)
Acacia mangium Ⅱ	1846 ^{b} (25)	67.53 ^{bc} (4.90)	1833^{b} (95)	0.74^{b} (0.09)	0.88^{b} (0.09)	29^{a} (2.8)
Casuarina equisetifolia pure	2020 ^{a} (16)	64.64^{c} (0.79)	1028^{c} (77)	0.28^{c} (0.05)	0.63^{c} (0.07)	18^{b} (1.9)

Values in parentheses represent the MSE. The means followed by different letters are significant differences ($P < 0.05$) based on ANOVA and the Tukey *post-hoc* test.

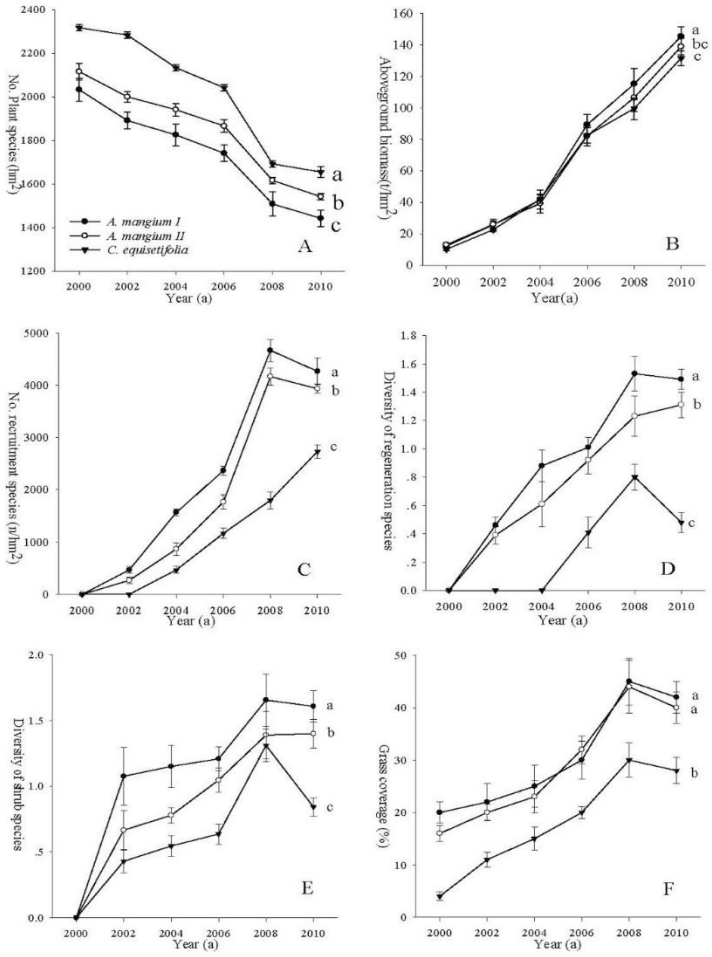


Fig. 2. Plant species/hm^2 (A), aboveground biomass (B), recruitment of native tree species/hm^2 (C), and diversity of regeneration (D) and shrubs (E), grass coverage (%) (F), (mean ± SE, n=3) in plots with 3 planting treatments for the years 2000–2010. (Within each graph, different letters to the right of each line indicate significant differences ($P < 0.05$) based on a Tukey's hsd test following the overall effect analysis of RANOVA. *A. mangium* is the abbreviation for *Acacia mangium* and *C. equisetifolia* is the abbreviation for *Casuarina equisetifolia*.

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Soil conditions

The 10 years of site occupancy by tree plantations significantly altered many soil properties, but the various treatments affected the soils differently.

The soil organic matter (SOM) content, on average, was significantly different among the three treatments ($F_{2, 6}$=85.23; P <0.01). Plots planted with *A. mangium* Ⅰ had the highest SOM (0.73%) in all treatments (Table 2). This was followed by *A. mangium* Ⅱ (0.65%) and the monoculture of *C. equisetifolia* (0.38%).

The variation in SOM was not the same at different treatments during the 10-yr period. The SOM increased significantly in the plots of *A. mangium* Ⅰ (0.40 %) and Ⅱ (0.27 %), but decreased significantly in the monoculture of *C. equisetifolia* (0.09%) (Table 2; Appendix 2-first).

The average totals of N in the plots planted with *A. mangium* (Ⅰ [0.40 g/kg] and Ⅱ [0.37 g/kg]) were significantly higher than the monoculture of *C. equisetifolia*. The variation of the total N in the plots planted with only *C. equisetifolia* (0.09 g/kg) was the lowest, which was significant lower than *A. mangium* Ⅰ and Ⅱ (Table 2 and Appendix 2-second).

Table 2. Soil organic matter and total N in the upper 15 cm of soil after 10 yrs of site occupancy by different plant species.

Planting treatments	Soil organic matter (%)			Soil total N (g kg^{-1})		
	2000	2010	variation	2000	2010	variation
Acacia mangium Ⅰ	0.53 (0.05)	0.93 (0.09)	0.40 a	0.24 (0.03)	0.56 (0.02)	0.32 a
Acacia mangium Ⅱ	0.51 (0.03)	0.78 (0.05)	0.27 b	0.21 (0.01)	0.52 (0.02)	0.31 a
Casuarina equisetifolia pure	0.42 (0.05)	0.33 (0.03)	-0.09 c	0.15 (0.01)	0.24 (0.01)	0.09 b

Values in parentheses represent the MSE. Different letters represent significant differences (P<0.05) using ANOVA and the Tukey *post-hoc* test.

Canopy condition

The LAI values were significantly different among the three treatments (LAI: P<0.01, F=15.832). The LAI value of *C. equisetifolia* in *A. mangium* Ⅱ was higher than the other four, whereas the *A. mangium* in *A. mangium* Ⅰ was the smallest (Table 3).

Generally, the crowns grew evenly along the four directions. Crowns formed the shape of an ellipse or were nearly tapered unless influenced by a continuous external force. The results showed that the crown lengths of *A. mangium* individuals in the four directions were highly significantly different (P=5.9 ×10^{-7}, F=14.084) in *A. mangium* Ⅰ (the ratio of *A. mangium* was high). The crown length in south and west directions was over three meters, which was significant longer than in the east and north directions (less than two m). However, the *A. mangium* crown length exhibited few differences in *A. mangium* Ⅱ, and only the west crown showed a slight difference.

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Table 3. Leaf area index and crown length in different types of 3-year-old forests.

Individual types	LAI	Crown length (m)			
		East	South	West	North
15 Ca-Eq in pure forest	1.10 a	1.57	1.72	1.70	1.54
15 Ca-Eq in *A. mangium* Ⅰ	1.07 a	1.55	1.67	1.65	1.53
15 Ca-Eq in *A. mangium* Ⅱ	1.12 a	1.60	1.73	1.78	1.63
15 Ac-Ma in *A. mangium* Ⅰ	0.82 b	1.79	3.32	3.03	1.58
15 Ac-Ma in *A. mangium* Ⅱ	1.01 a	2.30	2.11	2.65	2.10

Ca-Eq indicates *Casuarina equisetifolia* individuals and Ac-Ma indicates *Acacia mangium* individuals. The LAI is the leaf area index. a, b represent for significance at 0.05.

Discussion

Although the roles of interactions are recognized throughout the field of ecology, the effect of positive interactions between nonindigenous species is a controversial topic in restoration and conservation [19]. Our comparative trial revealed that nonindigenous *A. mangium* could improve the aboveground biomass, understory richness and diversity, and soil nutrients when combined with *C. equisetifolia*. *C. equisetifolia* could protect *A. mangium* effectively under variable maritime climate conditions.

Species respond differently to environmental stresses, and each species has a survival strategy for a hostile environment. Unlike *C. equisetifolia*, *A. mangium* is more likely to live in a protected environment. Compared to *C. equisetifolia*, *A. mangium* seedlings are vulnerable to death in the open, but their recruitment improved under *C. equisetifolia*, which provides shelter against a harsh maritime environment. Our study shows that the number of individuals in each treatment group depends significantly on the initial density of *C. equisetifolia. A. mangium* Ⅱ benefitted from the protective effect from *C. equisetifolia*, and had higher survivorship than *A. mangium* Ⅰ during the 10-yr period.

Beyond any maximum-yield density, interactions occur as component species strive to capture resources from a shared location [20]. Compared to a monoculture of *C. equisetifolia, A. mangium* has more capacity to accumulate biomass because it grows quickly. The biomass accumulation in the mixed forest was clearly improved, particularly when the proportion of *A. mangium* was high.

Natural regeneration plays a key role in vegetation restoration and development. In our experiment, *A. mangium* planted at different ratios to *C. equisetifolia* influenced the long-term understory characteristics, such as diversity and grass coverage. All of the understory layers (regeneration, shrubs, and grass) were improved in the mixed treatments (Ⅰ and Ⅱ). For the *C. equisetifolia* mixed forest, understory vegetation improved more under level Ⅰ than Ⅱ. However, we provide no direct evidence to explain the role of *A. mangium* on recruitment, regeneration and shrub development. Nevertheless, the long-term development of different species assemblages can profoundly affect understory vegetation dynamics and produce results similar to those of Bezemer et al. [21]. Many previous studies were performed on short time scales and used artificial management, such as weeding [22]. Therefore, data on the influence of mixed afforestation on understory vegetation restoration in the absence of human interference over 10 years are important for coastal vegetation management.

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Soil organic matter is the main source of nutrients for plant growth and soil development. It can improve the soil physical properties and accelerate the activities of microorganisms. Because *C. equisetifolia* litter decomposes very slowly, the organic matter content is low and easily lost in coastal sandy soils [13]. In our experiment, the SOM increased significantly in plots planted with *A. mangium* Ⅰ and Ⅱ over 10 years. The *A. mangium* used in our study are nitrogen-fixing plants and effectively increase the soil total N when interplanted with the other nitrogen-fixing plant, *C. equisetifolia*.

Unlike most broadleaf species, *C. equisetifolia* has special canopy characteristics, such as degraded scaly leaves, lance-shaped branchlets, and tower-shaped morphological structures. These phenotypic traits increase wind resistance and allow for better growth in the hostile coastal environment, particularly during the young growth stages [11]. Because of the continual influence of the northeastern marine monsoon, the morphological characteristics of tree species generate differentiation, predominantly during the young stages. Lopsided crowns are a universal phenomenon for the majority of species and significantly affect growth. However, this phenomenon was not observed for *C. equisetifolia*. Its adaptive features allow *C. equisetifolia* to resist strong winds and protect other species from hurricane influences, decrease the crown damage from hurricanes, and maintain normal photosynthetic capacity. Evenly distributed crown growth, intact canopy conditions, and high LAI provide advantages for interacting with other species.

Implications for conservation

The complexity of the community structure, species richness and diversity, and soil fertility are the main factors in forest vegetation dynamics [23]. Plant facilitation plays an important role in these factors and may promote early succession in abandoned fields [8, 24]. Our 10-year experiment on the species configuration shows how different species change a community dominated by *C. equisetifolia*. As a fast-growing pioneer species, *A. mangium* showed better effects on the development of both stands (aboveground biomass and species diversity) and soil conditions (organic matter and total N) when combined with *C. equisetifolia*. Our results indicate that mixed afforestation could solve several problems caused by species such as *C. equisetifolia,* and may improve the structure and function of coastal forest ecosystems and promote the process of forest succession.

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Appendix 1. Results of repeated-measures ANOVA for the characteristics of *Casuarina equisetifolia* plots interplanted with *Acacia mangium*. Shown are the F and P values for the overall ANOVA planting treatment and block effects and for the interaction with time.

Variable	planting treatment		Block		planting treatment × year		Block × year	
	$F_{2,6}$	*P*	$F_{2,6}$	*P*	$F_{12,45}$	*P*	$F_{10,45}$	*P*
No. of planted species	42.25	<0.001	0.046	0.978	8.23	<0.001	0.05	1
aboveground biomass of planted species	69.13	<0.001	0.332	0.721	27.52	<0.001	0.042	1
No. of regeneration species	29.28	<0.001	1.051	0.408	5.31	<0.001	0.506	0.882
Diversity (H') (Regeneration)	13.58	<0.001	0.828	0.492	6.58	<0.001	0.225	0.976
Diversity (H') (shrub)	10.36	<0.001	0.571	0.623	4.82	<0.001	0.121	1
Grass coverage	7.55	<0.001	0.353	0.696	3.71	<0.001	0.07	1

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Appendix 2. Results of repeated-measures ANOVA for soil characteristics *Casuarina equisetifolia* plots interplanted with *Acacia mangium*. Shown are the F and P values for the overall ANOVA, planting treatment and block effects, and for the interaction with time. First: The results of repeated-measures ANOVA for the D-value between 2000 and 2010. Second: The results of repeated-measures ANOVA for the average value between 2000 and 2010.

First	planting treatment		Block	
Variable	$F_{2,6}$	*P*	$F_{2,6}$	*P*
OM change	42.05	<0.001	0.132	0.877
TN change	35.14	<0.001	0.026	0.974

Second	planting treatment		Block		planting treatment × year		Block × year	
Variable	$F_{2,6}$	*P*	$F_{2,6}$	*P*	$F_{2,12}$	*P*	$F_{2,12}$	*P*
OM average	85.23	<0.001	0.10	0.905	19.68	<0.001	0.05	0.918
TN average	151.12	<0.001	0.03	0.970	22.53	<0.001	0.01	0.993

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