

Article

Phenomenon and Mechanisms of *Sonneratia apetala* Introduction and Spread Promoting Excessive Growth of *Derris trifoliata*

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Abstract: *Sonneratia apetala* Buch., an alien species with strong growth and adaptability, has been introduced and cultivated in Southeastern China. Meanwhile, *Derris trifoliata* Lour., native to coastal and riparian areas in Guangdong, Guangxi, and Fujian provinces, has experienced a rapid surge in population, impacting the health of mangrove ecosystems. Our research focuses on understanding the interactions between Oriental mangroves and *D. trifoliata*, particularly their proliferation and long-term symbiotic relationships. We investigated how Oriental mangrove proliferation promotes excessive *D. trifoliata* growth and explored the underlying mechanisms. In Leizhou Bay, Guangxi, the annual growth rate surged from 12.03% (2005–2015) to 55.36% (2015–2019), indicating a significant acceleration post-2015 and a concerning trend towards overgrowth. *D. trifoliata* failed to produce seeds on sea rockets or bulrushes, instead yielding 10.5 and 97.43 seeds/m² on native red mangroves and Oriental mangroves, respectively. Along riverbanks, 68% of Oriental mangroves hosted *D. trifoliata*, and the suitable regions for these species overlapped significantly. Oriental mangroves reach 15 m tall with 10 × 10 m crown diameters, providing ample vine space, optimal photosynthesis conditions, sturdy support, and convenient dispersal routes. This study offers insights into introduced–native species interactions in mangrove ecosystems, with significance for management and preservation.

Keywords: *Sonneratia apetala*; *Derris trifoliata*; introduction and spread; mangrove; biological invasion

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1. Introduction

Mangrove ecosystems are essential and invaluable components of coastal regions and play a critical role in maintaining ecological balance and biodiversity. The introduction and spread of alien species have significantly affected these mangrove ecosystems [1,2]. *Sonneratia apetala* Buch., native to the coastal regions along the Indian Ocean [3], has found extensive introduction into the southeastern coastal areas of China, encompassing Hainan, Guangdong, Guangxi, and Fujian. This widespread introduction is attributed to its remarkable growth rate and adaptability [4]. This species covers an area of 2968 ha, representing 11.0% of the national mangrove area [5]. Plants thrive in optimal climatic conditions, maximizing their growth and reproduction. Exotic species can swiftly capitalize on additional resources, exhibiting rapid responses [6]. *Sonneratia apetala* has a high growth rate, tall trunks, and abundant sturdy seeds [7]. One distinctive feature is the ab-

sence of deadly herbivores in the regions where it has been introduced, leading to its extensive proliferation, and gradually making it a notable invasive species [8,9]. Following the formation of *S. apetala* forests, local mangrove species encounter challenges penetrating its dense canopy, while seedlings of native mangroves struggle to survive beneath it [10]. Additionally, *S. apetala* exerts allelopathic effects and displays strong interspecific competitiveness, further impeding the growth of native mangrove plants [11].

Derris trifoliata Lour., the fish vine, is another species of concern that has experienced significant spread and excessive growth in mangrove areas [12–14]. The harmful effects of *D. trifoliata* were predominantly noted in communities dominated by *Aegiceras corniculatum* (L.) Blanco. This invasive species ascends to the top of *A. corniculatum*, gradually forming dark green patches that spread from the contact points, leading to the withering, death, and collapse of the affected plant. The natural recovery of the disrupted mangrove ecosystem presents significant challenges [15]. *D. trifoliata* typically forms low-growing communities with heights not exceeding 1.2 m in open areas. Its branches, leaves, and flowers are frequently encrusted with mud, hindering seed formation and reproduction. While *D. trifoliata* inhabits open areas and coexists with native herbaceous plants like reeds and sedges, its spread is relatively gradual. Moreover, it typically undergoes leaf shedding between December and February, constraining its growth cycle.

This study aimed to investigate how the introduction and spread of *S. apetala*, a native species, have contributed to the overgrowth of *D. trifoliata*, a vine species, while uncovering the underlying ecological mechanisms. To achieve this objective, we conducted a detailed analysis of this specific interaction to elucidate general principles regarding the impact of invasive species on mangrove ecosystems. This research provides a scientific foundation for managing and conserving these ecosystems. Our primary hypothesis posits that the introduction and spread of *Sonneratia apetala* indirectly facilitate the overgrowth of *D. trifoliata* by altering the structure and function of the ecosystem. To test this hypothesis, we employed ecological methods and techniques, including field surveys, laboratory analyses, and model simulations, to thoroughly investigate the interactions between these two species and their impacts on the mangrove ecosystem. The contribution of this study is its novel insights into species interactions within mangrove ecosystems and theoretical and practical guidance for the formulation of targeted management strategies. Additionally, by examining the mutual influences of *Sonneratia apetala* and *D. trifoliata*, we provide new perspectives and approaches for protecting and restoring threatened mangrove ecosystems.

2. Materials and Methods

2.1. Distribution Survey of *S. apetala* and *D. trifoliata*

Multiple mangrove sites were selected in river estuaries, including the Lianzhou (109°6'3.59", 21°33'2.52"), Qinzhou (108°34'12.00", 21°44'19.32"), and Dandouhai Bays (109°39'7.20", 21°34'22.44"), and the Dafeng (108°51'36.00", 21°45'40.32"), Maoling (108°28'4.81", 21°50'53.88"), and Beilun Rivers (108°5'9.59", 21°31'52.68"), to include locations with varying degrees of *S. apetala* spread. The distribution of *D. trifoliata* and *S. apetala* in the study area was established through field surveys, which integrated ground reconnaissance with the use of drone aerial images and high-resolution satellite imagery. This approach enabled identifying the locations and extent of *S. apetala* and *D. trifoliata* distributions.

2.2. Comparison of Seed Quantity of *D. trifoliata* on Different Plants

In October 2023, several *D. trifoliata* communities within Lianzhou Bay were chosen for study. These included those found climbing on *Cyperus malaccensis* subsp., *Phragmites australis* (Cav.) Trin., *A. corniculatum*, *Acanthus ilicifolius* L., *Kandelia obovata* Sheue & al., *Excoecaria agallocha* L., as well as *S. apetala* and *D. trifoliata* growing on a sandy shore. Eight types of *D. trifoliata* communities were selected for the study, each with five 1 × 1 m plots.

Representative *D. trifoliata* plants entwined in the crown were selected. The maximum stem diameter, height, and *D. trifoliata* fruit yield per unit area were recorded.

2.3. Survey of *D. trifoliata* Damage on *S. apetala*

The primary tributaries of the Nanliu River (109°4'26.39", 21°36'3.24") in Lianzhou Bay were selected for this survey. A combination of on-site observations and drone imagery was used to assess the extent of *D. trifoliata* damage to *S. apetala* along the banks of the river and record the coordinates of *S. apetala* and the extent of damage to *S. apetala* by *D. trifoliata*. The degree of damage to *S. apetala* was divided into three levels: serious damage (II) when *D. trifoliata* was distributed on the crown of *S. apetala*; slight damage (I) when *D. trifoliata* was distributed on the branches of *S. apetala*; and no *D. trifoliata* damage when *D. trifoliata* was not observed on the trunk.

2.4. MaxEnt Model

The MaxEnt model 3.4.1 (Columbia University in the United States, New York, NY, USA) with the Kuenm package optimization parameters [16] was used to predict the spatial distributions of *D. trifoliata* and *S. apetala*. The sources of environmental data (Table 1) and the selection of environmental factors (Table 2) in this study refer to the research of Li et al. [13]. This study obtained the parameters for the MaxEnt model using the Kuenm package. *D. trifoliata* had a feature class of threshold features (T), product features (T), and linear features (L). *S. apetala* had a feature class of quadratic (Q) and threshold features (T). *D. trifoliata* and *S. apetala* had regulation multipliers of 0.3 and 1.5, respectively.

Table 1. Sources of environmental data.

Data	Year	Data Source	Data Download Website or Reference
Bioclimatic factors	1970–2000	The World Climate Database	www.worldclim.org (accessed on 25 June 2022)
Terrain data	2022	The ETOP01 terrain elevation and ocean seabed terrain data released by the United States Geophysical Center	https://www.ngdc.noaa.gov/mgg/global/global.html (accessed on 14 July 2022)
Sea surface temperature data	2020	National Environmental Information Center of the Oceanic and Atmospheric Administration of the United States (1981–2020 SST data)	https://ftp.emc.ncep.noaa.gov/cmb/sst/oisst_v2/ (accessed on 14 July 2022)
Salinity data	2020	The marine salinity products of the Institute of Atmospheric Physics, Chinese Academy of Sciences.	http://159.226.119.60/cheng/ (accessed on 2 February 2022)
Land-use data	2020	The ESRI 10-m cover data (2020) in the GEE	https://livingatlas.arcgis.com/landcover/ (accessed on 24 June 2022)

Table 2. Environmental variables used to predict the distributions of *D. trifoliata* and *S. apetala* in the Beibu Gulf, Guangxi, China.

Data Type	Variable	Description	Unit
Bioclimatic	Bio2	Mean diurnal range [mean of monthly (max. temp–min. temp)]	°C × 10
	Bio3	Isothermality (BIO2/BIO7) (×100)	%
	Bio5	Maximum temperature of warmest month	°C × 10
	Bio6	Minimum temperature of the coldest month	°C × 10
	Bio10	Mean temperature of the warmest quarter	°C × 10
	Bio15	Precipitation seasonality (coefficient of variation)	%

	Bio18	Precipitation in the warmest quarter	mm
	Bio19	Precipitation in the coldest quarter	mm
Terrain	Elevation	Topographic elevation	m
	WTI	Wetland index	--
Ocean salinity	C_sss	Mean sea surface salinity in the coldest season	‰
	W_sss	Mean sea surface salinity in the warmest season	‰
Sea surface temperature	C_sst	Mean sea surface temperature in the coldest season	°C
	W_sst	Mean SST in the warmest season	°C
Substrate type	Substrate	Substrate type	--
Land-use data	Land-use	Land use type	--

The MaxEnt model was utilized to compute the receiver operating characteristic (ROC) curve, with the area under the curve (AUC) serving as the diagnostic test value. AUC values, ranging from 0 to 1, were indicative of prediction accuracy, with higher values indicating greater accuracy. Subsequently, the grid output results were visually converted and analyzed using ArcGIS 10.4 (Environmental Systems Research Institute, Redlands, CA, USA). Each grid's pixel value denoted the probability distribution of mangroves within the grid, varying from 0 to 1. Larger pixel values indicated higher potential distributions and higher habitat suitability of *D. trifoliata* and *S. apetala*. In this study, we used the natural breakpoint method to grade the fitness results as follows: 0–0.2, no fitness; 0.2–0.5, low fitness; 0.5–0.7, medium fitness; and >0.7, high fitness [13,17].

2.5. Data Analysis

The ecological niche overlap between the two species was analyzed using ENMTools 1.3 (University of California, Los Angeles, CA, USA) [18], and the formula was calculated as follows:

$$D(P_X, P_Y) = 1 - \frac{1}{2} \sum_i |P_{X,i} - P_{Y,i}| \quad (1)$$

$$I(P_X, P_Y) = 1 - \frac{1}{2} \sqrt{\sum_i (\sqrt{P_{X,i}} - \sqrt{P_{Y,i}})^2} \quad (2)$$

where $D(P_X, P_Y)$ and $I(P_X, P_Y)$ are the geographical ecological niche overlap of species X and Y ; $P_{X,i}$ and $P_{Y,i}$ are the number of individuals utilizing resource i ($i = 1, 2, \dots, n$) [19]. The D and I values range from 0 to 1, with values closer to 1 indicating a higher ecological niche overlap between the two species.

3. Results and Analysis

3.1. Overgrowth of *D. trifoliata* and Spread of *S. apetala* after Introduction

The area covered by *D. trifoliata* in the mangroves of Leizhou Bay, Guangxi, showed significant variation over different years (Figure 1). In 2005, it covered 11.4 ha, increasing to 35.5 ha by 2015, with an annual growth rate of 12.03%. By 2019, the coverage had expanded rapidly to 206.8 ha, and since 2015, there has been a notable acceleration in the spread of *D. trifoliata* in Leizhou Bay, Guangxi, indicating an overgrowth trend.

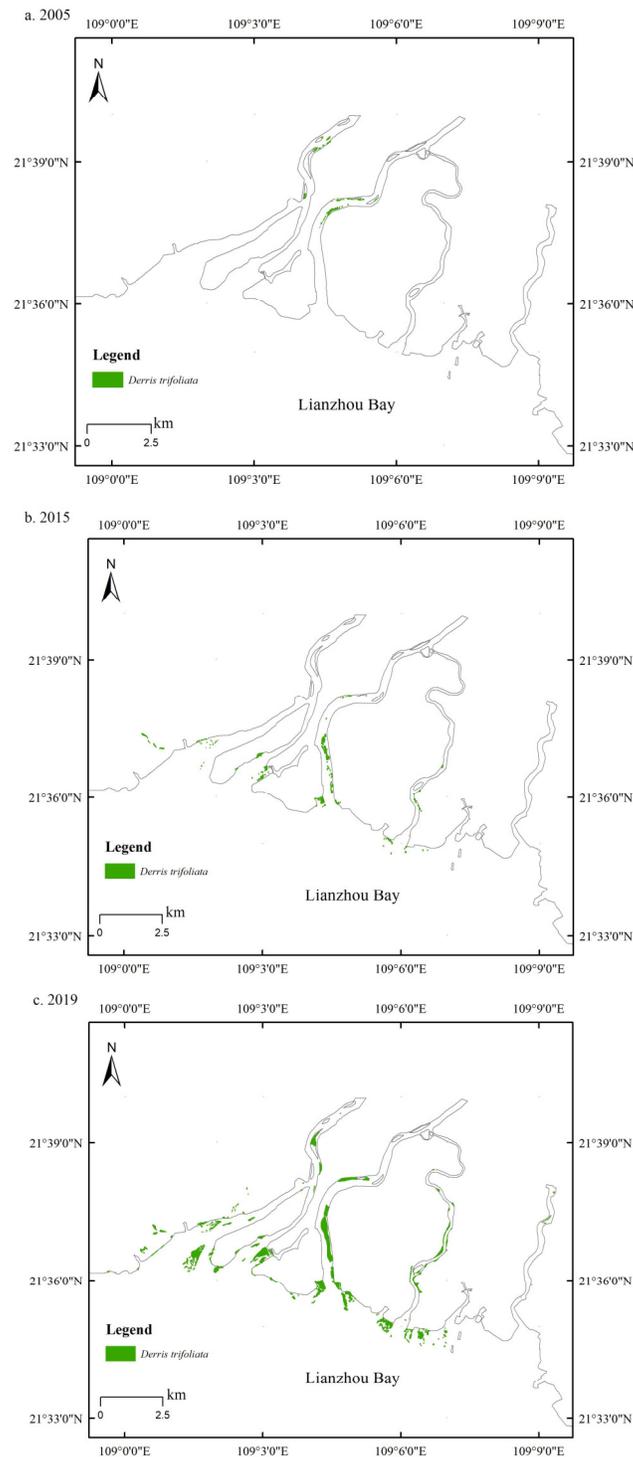


Figure 1. Distribution of *Derris trifoliata* in Lianzhou Bay, Guangxi Province, in 2005, 2015, and 2019.

In 2004, *S. apetala* was first introduced in Leizhou Bay, Guangxi, China, with an initial area of approximately 0.7 ha. Despite the absence of large-scale artificial planting activities, *S. apetala* has rapidly spread through natural propagation in the estuarine areas of Leizhou Bay. The natural expansion of *S. apetala* plants was observed along all rivers entering the sea in Leizhou Bay. Preliminary statistics indicate that by 2023, the number of

mature *S. apetala* plants will have reached no less than 2000, which is expected to continue increasing. This suggests rapid natural spread of *S. apetala* in the Leizhou Bay area of Guangxi following its introduction.

3.2. Long-Term Seed Production of *D. trifoliata* on *S. apetala*

Figure 1 shows that the area covered by *D. trifoliata* in the Leizhou Bay mangrove forest exhibited significant variation in different years. In 2005, the *D. trifoliata* area was 11.4 ha, which increased to 35.5 ha by 2015, with an average annual growth rate of 12.03%. Subsequently, in 2019, the *D. trifoliata* area sharply increased to 206.8 ha, with an extraordinarily high average annual growth rate of 55.36%. Thus, since 2015, the expansion of *D. trifoliata* in Leizhou Bay has accelerated significantly, manifesting an overgrowth trend.

Derris trifoliata exhibited variations in seed production and stem diameter in different plant species, including herbaceous, shrub, and tree species in the Lianzhou Bay mangrove forest (Table 3). From the herbaceous species to the shrubs and then the tree species, both the fruit production and stem diameter of *D. trifoliata* gradually increased (Table 1).

Table 3. Comparative analysis of the damage and seed output of *Derris trifoliata* on different plants.

Host Tree	Vegetation Type	Average Height and Crown Diameter of Adult Plants (m)	Coverage Area	Coverage Time (a)	Seed Output (ind./m ²)	Maximum Base Diameter (mm)	Damage Degrees
<i>Cyperus malaccensis</i>	herbaceous	1.60 c, ≤1	Small	≤1	0 c	12.3	Mild
<i>Phragmites australis</i>	herbaceous	1.77 c, ≤1	Small	≤1	1.60 c	5.3	Mild
<i>Acanthus ilicifolius</i>	shrub	1.11 c, ≤1	Moderate	≤3	1.50 c	11.1	Moderate
<i>Aegiceras corniculatum</i>	shrub	1.80 c, 2–3	Big	≤3	10.50 c	15.2	Serious
<i>Kandelia obovata</i>	tree	1.93 c, 2–3	Moderate	≤5	21.55 bc	15.9	Moderate
<i>Excoecaria agallocha</i>	tree	3.20 b, 2–3	Moderate	≤5	53.17 b	16.8	Moderate
<i>Sonneratia apetala</i>	tree	7.86 a, 4–5	Big	≥5	97.43 a	28.4	Serious

(Note: means followed by the same letter are not significantly different ($p > 0.05$)).

When *D. trifoliata* adhered to herbaceous plants such as *C. malaccensis* and *P. australis*, it produced no fruits and 1.6 fruits/m², respectively. These herbaceous plants often wither and collapse during winter, and considering their limited structural support, they cannot withstand the extensive growth of *D. trifoliata*. This phenomenon frequently results in the collapse of both the herbaceous plants and *D. trifoliata*. Consequently, the growth and propagation of *D. trifoliata* on *C. malaccensis* and *P. australis* was limited.

On the other hand, when *D. trifoliata* adheres to shrubs such as *A. corniculatum* and *Sonneratia caseolaris*, it produces 1.50 and 10.5 seed/m², respectively. This suggests that *D. trifoliata* can generate seeds for propagation when grown on supportive plants like *A. corniculatum* and *S. caseolaris*. However, shrubs, especially *A. corniculatum*, often die relatively quickly, causing *D. trifoliata* to lose its support structure and subsequently die or form low shrub-like patches. In such cases, *D. trifoliata* does not produce or generate few seeds. Thus, *D. trifoliata* experienced self-limitation when growing on native shrub mangrove plants.

When *D. trifoliata* clung to trees, such as *K. obovata* and *E. agallocha*, it produced 21.55 and 53.17 seed/m², respectively. *D. trifoliata* has more space to grow and reproduce sexually when climbing trees than herbaceous and shrub vegetation do. *K. obovata* and *E.*

agallocha are native plants with relatively few natural herbivores. This reduces the likelihood of *D. trifoliata* clinging to these plants, decreasing the opportunities for further expansion.

The fruit production of *D. trifoliata* on *S. apetala* (97.43 seed/m²) exceeded that of native plants (Table 1). *D. trifoliata* readily attaches to *S. apetala*, capitalizing on ample sunlight that fosters efficient photosynthesis, thereby boosting both the quantity and quality of seeds (see Figure 2). Consequently, the introduction and propagation of *S. apetala* promoted sexual reproduction in *D. trifoliata*, thereby aiding its external expansion. *S. apetala*, which bears fruit twice a year, yields a notable number of seeds and exhibits remarkable adaptability to the environment, thereby enhancing its dispersal capabilities [20]. These features enabled the rapid propagation of *S. apetala* in the estuarine areas of Leizhou Bay, providing favorable conditions for the growth of *D. trifoliata*. *D. trifoliata* has clung to *S. apetala* for over five years (Table 1), allowing for their long-term symbiosis and providing *D. trifoliata* with opportunities to produce seeds and expand through creeping stems.

In summary, the introduced species *S. apetala* was more conducive to *D. trifoliata* overgrowth than native mangrove plants.



Figure 2. Seeds of *Derris trifoliata* growing on *Sonneratia apetala*.

3.3. Active Propagation of *S. apetala* and Its Rapid Growth Facilitate the Expansion of *D. trifoliata*

The introduction and propagation of *S. apetala* has led to its extensive distribution in estuarine areas, allowing it to preferentially occupy the growth zones of native plants, such as *C. malaccensis* and *S. grossus* (Figure 3). This provides an opportunity for *D. trifoliata* to thrive and expand beyond its original habitats. Additionally, the natural spread of *S. apetala* in estuarine regions has established pathways and corridors that facilitate the spread of *D. trifoliata* to new areas, promoting its overgrowth. With the extensive propagation of *S. apetala*, *D. trifoliata* plants can now climb into the crowns of *S. apetala* trees, providing them with additional growing space and reproductive opportunities, further facilitating their expansion.

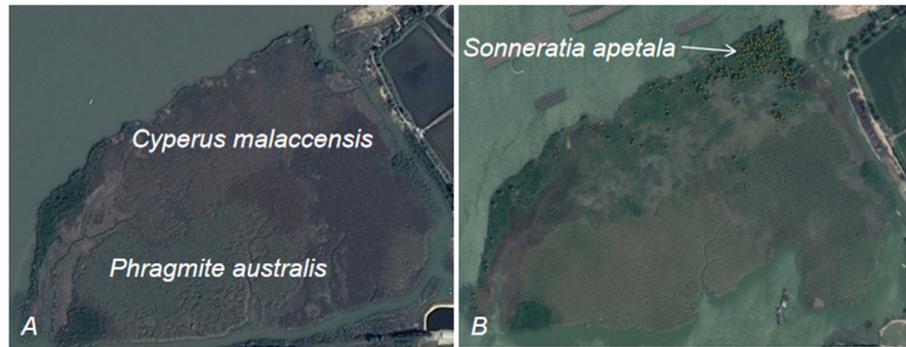


Figure 3. *Sonneratia apetala* rapidly invades habitats of *Cyperus malaccensis* and *Phragmites australis*. ((A) native salt algae plants (B) *Sonneratia apetala* diffuses into native salt algae plants).

Sonneratia apetala, as an introduced fast-growing tree species, can grow up to 0.8–3.4 m annually [21]. In the Leizhou Bay area, the average height of *S. apetala* stands at 7.86 m, surpassing that of other native mangrove plants (see Table 1). Additionally, the maximum stem diameter of *D. trifoliata* clinging to *S. apetala* measures 28.4 mm, significantly larger than that of *D. trifoliata* on native plants (Table 1). The distribution of *S. apetala* and *D. trifoliata* along the Nanliu River is shown in Figure 4 and Table 4, where mature *S. apetala* with *D. trifoliata* displaying mild damage (I) reached 32.97%, and those with moderate damage (II) accounted for 27.33%. The percentage of young *S. apetala* with mild damage (I) was 14.43%, and no young *S. apetala* with moderate damage was observed. Surveys of *S. apetala* and *D. trifoliata* on both banks of the Nanliu River revealed that the rate of *D. trifoliata* attachment to mature *S. apetala* was 60.30%. The attachment rate for young *S. apetala* was 14.43%, resulting in a combined attachment rate of 68% for *S. apetala* on both banks of the Nanliu River.

Table 4. Damage percentage of *Sonneratia apetala*.

<i>Sonneratia apetala</i>	Number of <i>S. apetala</i>				Damage Percentage		
	All	Mild Damage	Moderate Dam- age	Damage	Mild Damage	Moderate Dam- age	Damage
Adult	534	234	88	322	43.82%	27.33%	60.30%
Seedling	97	14	0	14	14.43%	0.00%	14.43%



Figure 4. *Sonneratia apetala* covered with *Derris trifoliata* on the outer edge of a beach at Nanliu River in mid-October 2023.

Derris trifoliata effectively utilizes support structures for climbing, expanding its growth space alongside tall support trees (see Figure 5). As it ascends, *D. trifoliata* distances itself from periodically inundated and highly saline environments, favoring optimal growth conditions. This indicates that *S. apetala* provides a more conducive environment for *D. trifoliata* growth compared to other native mangrove plants. Simultaneously, the extensive propagation of *S. apetala* in the estuarine regions provided substantial sup-

port for the growth of *D. trifoliata* (Figure 4). *D. trifoliata* uses *S. apetala* as climbing structures to grow and reproduce abundantly, resulting in a rapid increase in the number of *D. trifoliata* plants and, consequently, overgrowth. This phenomenon strongly supports the hypothesis that the introduction and propagation of *S. apetala* promotes the overgrowth of *D. trifoliata*.

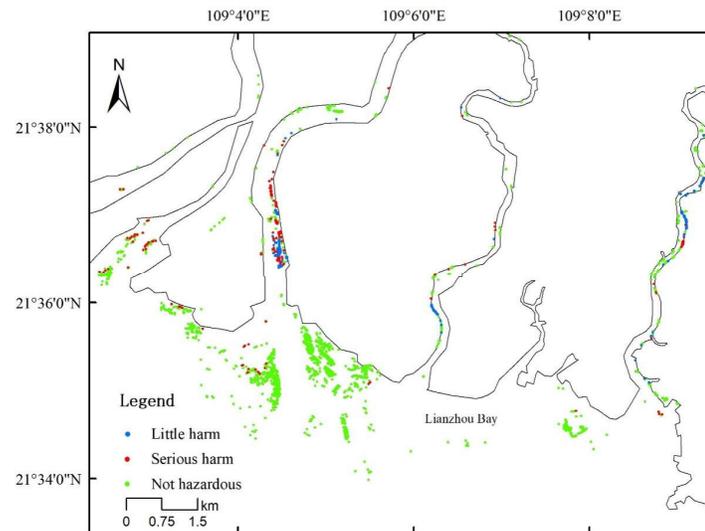


Figure 5. *Sonneratia apetala* damaged by *Derris trifoliata* in Lianzhou Bay in mid-October 2023.

Sonneratia apetala relies on hydrodynamics for dispersal [22], typically spreading to locations along estuaries, coastlines, and water edges where its expansion is more susceptible to the influence of tides and water currents (Figure 4). Moreover, these aquatic edges allow the waterborne dispersal of *D. trifoliata* seeds due to the transportation of seeds to distant areas by tides and water currents, facilitating their rapid spread to other locations.

Synchronized growth between *S. apetala* and *D. trifoliata* also contributes to their cooperative dissemination. The fruit maturation period of *S. apetala* aligns with that of *D. trifoliata* owing to their shared tidal cycle. This synchrony facilitates their joint spread, fostering interactions.

In summary, the introduction and propagation of *S. apetala* have enhanced the growth of *D. trifoliata*. This includes increasing the likelihood of *D. trifoliata* attachment, boosting seed quantity per unit area, and resulting in significant variations in *D. trifoliata* stem diameters among different tree species. This improvement allows *D. trifoliata* to grow and reproduce under improved conditions while promoting interactions and ecological balance among species within the mangrove ecosystem. This is of considerable significance for understanding the complex interactions between introduced and native species and for the conservation and management of mangrove ecosystems.

3.4. High Overlap in the Suitable Areas for *D. trifoliata* and *S. apetala*

This study unveiled a correlation between a higher abundance of *D. trifoliata* and an increased number of *S. apetala* individuals, with *D. trifoliata* commonly entwining around *S. apetala* trees. In regions like Guangxi Lianzhou and Qinzhou Bays, as well as the Dandouhai, Maoling, and Fengjia Rivers, severe infestations of *D. trifoliata* were observed, indicating its detrimental impact on the stability of these ecosystems. However, in these areas, we observed the natural expansion of *S. apetala*, providing strong support for the excessive growth of *D. trifoliata*. In these regions, *S. apetala* naturally expands over a wide range, and the habitats suitable for *S. apetala* and *D. trifoliata* exhibit significant overlap.

For example, *S. apetala* has spread naturally over a wide area in Lianzhou Bay. *S. apetala* both heavily and mildly infested with *D. trifoliata* were observed in this region (Figure 5).

The Maximum Entropy Model was employed to predict the distribution of *D. trifoliata* and *S. apetala*. The AUC values for *S. apetala* in both the training and test sets were 0.973 and 0.968, while for *D. trifoliata*, the corresponding AUC values were 0.979 and 0.978, respectively. Thus, the model demonstrated high reliability. The optimal suitable habitat area for *S. apetala* was 1800 hm² (Figure 6 and Table 5), and for *D. trifoliata*, it was 3000 hm² (Figure 7 and Table 5). Regions with a high degree of suitability for both species were mainly located in Lianzhou Bay, the Guangxi Shankou Mangrove Nature Reserve, and the Guangxi Maowei Sea Provincial Mangrove Nature Reserve, showing similar spatial suitability. Using ENMTools 1.3 software to analyze the ecological niche overlap between *D. trifoliata* and *S. apetala* revealed that the ecological overlap value was 0.7559, the geographical distribution overlap (I) was 0.7988, and the D value was 0.5955. These findings indicate a significant habitat similarity between the two species. These results further confirm the observed interaction between *D. trifoliata* and *S. apetala*, where *S. apetala* provided a growth structure that promoted the growth of *D. trifoliata*.

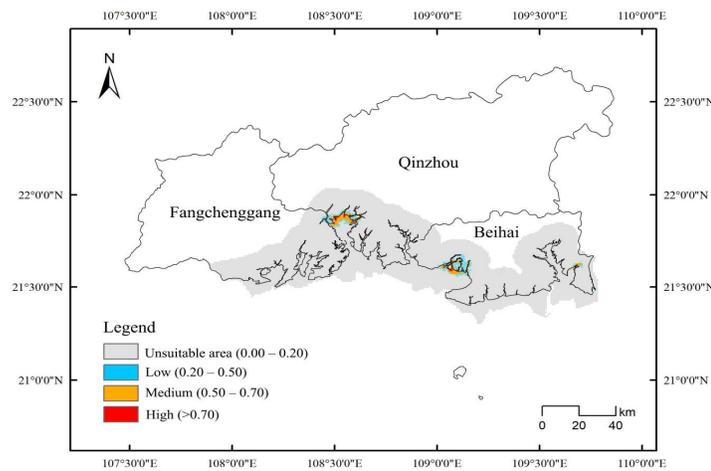


Figure 6. Predicted distribution map of *Sonneratia apetala*.

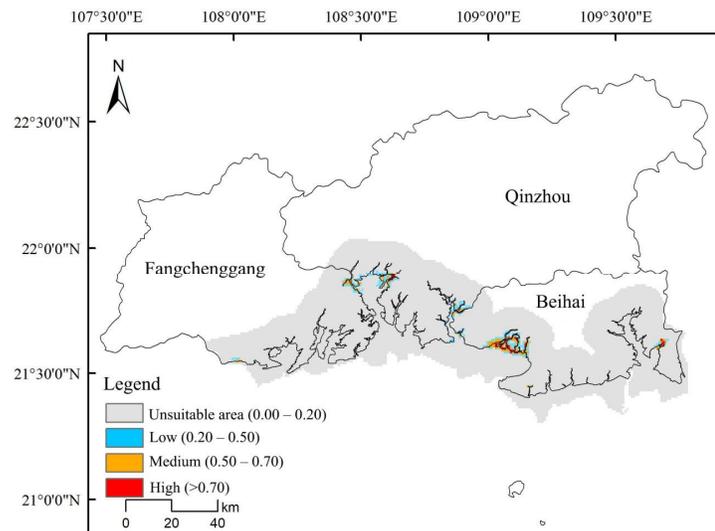


Figure 7. Predicted distribution map of *Derris trifoliata*.

Table 5. Suitable area for *D. trifoliata* and *S. apetala*.

Plant Species	Optimal Suitable Area (hm ²)	Medium Suitable Area (hm ²)
<i>D. trifoliata</i>	3000	11,900
<i>S. apetala</i>	1800	14,000

These spatial distribution results further support our hypothesis that a strong association exists between the introduction and spread of *S. apetala* and *D. trifoliata* overgrowth, emphasizing the importance of their mutually symbiotic relationship within the mangrove ecosystem.

Through observing and analyzing their spatial distribution, we have provided compelling evidence that enhances the understanding of the complex ecological interactions between these two species. These findings have significant implications for mangroves and other ecological conservation.

4. Discussion

This study explored the impact of the introduction of *Sonneratia apetala* on the overgrowth of *D. trifoliata*, revealing the profound effects of their interaction on mangrove ecosystems. Our results indicate a significant correlation between the introduction of *Sonneratia apetala* and the overgrowth of *D. trifoliata*. This finding aligns with ecological theories suggesting that introducing invasive species can alter species interactions and competitive dynamics within ecosystems, thereby influencing their structure and function [23,24].

While some scholars believe that *S. apetala* has increased the fixation rate of N₂, which is significant for the sustainable management and restoration of mangrove ecosystems [24], the negative impact of *S. apetala* has not been fully considered. Our results provide insights into the potential adverse effects of invasive species introduction on mangrove ecosystems, contrasting with findings in the literature [25]. Existing research mainly focuses on the ecological impacts of a single invasive species [26], yet our study offers a comprehensive perspective on the interactions between two species, thereby expanding our understanding of ecosystem impacts.

These findings offer strong support for existing theories, particularly regarding the impact of invasive species introduction on ecosystem health [9]. The rapid spread of *Sonneratia apetala* provides additional space for the survival and reproduction of *D. trifoliata*, promoting its overgrowth. This interaction may exacerbate the degradation of native mangrove ecosystems, affecting the habitat and ecological services they provide to native species [27].

Our results not only deepen the understanding of species interactions within mangrove ecosystems but also offer practical guidance for managers in developing effective ecosystem management and conservation strategies. By understanding the relationship between the introduction of *S. apetala* and the overgrowth of *D. trifoliata*, targeted measures can be implemented to control or mitigate the spread of these species, protecting and restoring mangrove ecosystems.

While this study offers valuable insights, it also has limitations. For instance, it focuses on species interactions within a specific region, which may not fully represent situations in different areas. For example, in areas lacking rivers, certain dynamics may not be as apparent [28]. Additionally, owing to the limited duration of this study, we may not have captured changes in long-term ecological processes, such as mudflat elevation [29], soil nutrient accumulation [30–33], allelopathy [34], light impact [35,36], adaptability to salinity [37–39], natural enemy factors [40,41], gene differentiation [42], etc. Hence, further research should encompass a broader geographical scope and longer time scales to obtain a more comprehensive understanding.

Moreover, future research should incorporate additional ecological factors, such as pollution [43], biological characteristics of species [32], and external disturbances, such as

climate change [39] and human activities [44], to assess their combined effects on ecosystems. Furthermore, long-term monitoring and interdisciplinary approaches are crucial for comprehending and managing the interactions between invasive and native species in mangrove ecosystems.

In summary, our study underscores the importance of understanding and managing species interactions in mangrove ecosystems, especially in the context of invasive species introduction. By examining the interactions between *S. apetala* and *D. trifoliata*, we enhanced the understanding of the function and health of this specific ecosystem and provided practical insights and strategies for ecosystem management to overcome the challenges posed by introducing invasive species.

5. Conclusions

Based on our findings, we examined the relationship and underlying mechanisms between the introduction and spread of *S. apetala* and the proliferation of *D. trifoliata*. In the mangrove forests of Liangzhou Bay, Guangxi, the area covered by *D. trifoliata* experienced a notable annual average growth rate of 12.03% from 2005 to 2015. Subsequently, from 2015 to 2019, this rate surged to 55.36%, indicating a pronounced phase of overgrowth. This suggests a significant acceleration in the spread of *D. trifoliata* after 2015.

We also observed that *D. trifoliata* rarely produces seeds when climbing on native plants, such as *C. malaccensis* and *P. australis*. By contrast, on native mangrove plants, such as *S. apetala*, the seed density of *D. trifoliata* reached 97.43 seeds/m². This study further revealed that 68% of the *S. apetala* trees were affected by *D. trifoliata*, and the natural spread of *S. apetala* was observed in several regions, including Liangzhou Bay, Guangxi. The analysis indicated a high ecological and geographic distribution overlap between *D. trifoliata* and *S. apetala*, highlighting the substantial spatial similarity in their habitats.

This study also revealed that the tall *S. apetala* provides more climbing space for *D. trifoliata*, photosynthesis conditions, a stable support structure, and more convenient pathways for dispersion, increasing the duration for which *D. trifoliata* grow on them, increasing seed production, and promoting dispersion. A unique finding of this study is the identification of a neglected phenomenon, where *D. trifoliata* wraps around *S. apetala* and stably produces many seeds over a long period, the dispersion of which promotes the excessive growth of *D. trifoliata*. However, because *S. apetala* is relatively tall, *D. trifoliata* generally does not cause its death; thus, the control of *D. trifoliata* on *S. apetala* is often overlooked. Additionally, a synergistic dispersion phenomenon between the seeds of *D. trifoliata* and *S. apetala* was discovered, indicating that the seeds of both often disperse together to new areas. This study provides important insights into the complex interactions between introduced and local species in mangrove ecosystems, offering scientific value for the management and conservation of mangrove ecosystems.

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