



## Original Research Article

# Effects of *Wollastonia biflora* expansion on the soil seed bank in native forest communities on a tropical coral island



Yao Huang <sup>a,b</sup>, Hai Ren <sup>a,\*</sup>, Jun Wang <sup>a</sup>, Nan Liu <sup>a</sup>, Shuguang Jian <sup>a</sup>,  
Hongyue Cai <sup>a,b</sup>, Dafeng Hui <sup>c</sup>, Qinfeng Guo <sup>d</sup>

<sup>a</sup> Guangdong Provincial Key Laboratory of Applied Botany, CAS Engineering Laboratory for Vegetation Ecosystem Restoration on Islands and Coastal Zones, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, 510650, China

<sup>b</sup> University of Chinese Academy of Sciences, Beijing, 100049, China

<sup>c</sup> Department of Biological Sciences, Tennessee State University, Nashville, TN, 37209, USA

<sup>d</sup> Southern Research Station, USDA Forest Service, RTP, NC, 27709, USA

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## ABSTRACT

Invasive plants and native weeds (i.e., undesirable plant species) often have negative effects on native ecosystems. However, the effects of weed expansion on soil seed banks and seedling emergence in native forests have not been well investigated. In this study, we used a seedling emergence assay to assess the effects of expansion by a native weed, the perennial C<sub>4</sub> herb *Wollastonia biflora*, on the soil seed bank and above-ground vegetation in forests on Yongxing Island, a coral island in the South China Sea. We found that *W. biflora* expansion was associated with a reduced abundance of native species in the soil seed bank, an increased in native species richness in the soil seed bank, and a reduced similarity between the seed bank and the above-ground vegetation. *W. biflora* seeds were more abundant in the surface soil layer than deeper soil layer, and the number of *W. biflora* seeds increases in the degree of *W. biflora* expansion. With *W. biflora* expansion, more species were lost due to growth competition than from seed bank. Overall, the seed bank had more species than the above-ground vegetation regardless of the degree of *W. biflora* expansion. Our findings indicate a high potential for unassisted reestablishment of a species-rich plant community from the seed bank following *W. biflora* removal. The regenerated community could be dominated by a few native tree species or by some invasive species that could prevent subsequent recolonization by native herbs and graminoids. Continued monitoring is required to determine whether and which native species may require assisted reintroduction.

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## 1. Introduction

The protection of forests against harmful invasive species is an important task for ecologists and land managers (Llewellyn et al., 2004; Moreno-Gonzalez et al., 2020; Smethurst et al., 2020). Because of their unique geographical locations and climates, the ecosystems of oceanic islands are vulnerable to invasion and disturbance and their biodiversity is difficult to maintain (Batianoff et al., 2010; Gomes et al., 2020). As a result of the restrictions of climate and soil, the mature forest

\* Corresponding author.

E-mail address: [renhai@scib.ac.cn](mailto:renhai@scib.ac.cn) (H. Ren).

communities on islands may not be the true climax communities ([Exploration Group of Xisha Islands of Institute of Soil Science of Chinese Academy of Sciences CAS, 1977](#)). The structure and ecological resistance of these communities are relatively simple and not stable ([Peng, 1996](#)). Some plant species that would normally be eliminated during forest succession on the mainland constantly invade and alter the mature forests on islands ([Zhang et al., 2011](#)). We refer to such opportunistic plants, whether native or non-native, as weeds. Over the past several decades, the ecosystems on many islands have suffered serious damage as a result of human activities, invasive species and global climate change ([Cordell et al., 2009; Zhang et al., 2011; Prabakaran and Paramasivam, 2014](#)). Ecologists have paid increasing attention to the deterioration of the island ecosystems ([Aston, 1995; Morgan et al., 2014](#)). However, problems persist because many weed species continue to spread in these places and cause harm to native forest communities ([Lohr et al., 2015; Cimadom et al., 2019](#)).

In agricultural fields and plantations, weeds often promote the spread of plant pathogens, resulting in yield losses ([Jezeer et al., 2018](#)). In the early growing season, weeds often grow rapidly and significantly inhibit crop germination and growth ([Kruidhof et al., 2011](#)). In natural settings, weed invasion threatens indigenous biodiversity and species abundance ([Hegde and Miller, 1992; Staver et al., 2020](#)). For example, some weeds have invaded native heathlands in northern Europe due to anthropogenic nitrogen deposition ([Bakker and Berendse, 1999](#)). Similarly, [de la Cretaz and Kelty \(2002\)](#) reported that *Dennstaedia punctiloba*, a native herb and fern species, has increased in abundance and suppressed native forest regenerations, after the eradication of predators of deer by humans. This causes an increase in the abundance of deer that consume plants that compete with the fern.

A challenging and persistent threat to the natural plant communities is the soil seed bank of weeds that produces seedlings that directly compete with native plants and inhibit the above-ground growth of vegetation ([Buhler et al., 1997](#)). Weeds can be temporarily controlled by burning, herbicide application, mechanical removal, and the destruction of their seeds ([Walsh and Newman, 2007; Walsh et al., 2013; Guo et al., 2018](#)). Such management may require a long-term effort, but it may not be possible or practical to destroy weeds every year ([Borger et al., 2016, 2018](#)). Also, the characteristics of weed seeds in the soil bank may significantly differ among weed species ([Gallandt, 2006](#)). Research on the characteristics, dynamics, and distribution of weed seeds in the soil bank may therefore provide information that could help with weed control.

*Wollastonia biflora* is a perennial, C<sub>4</sub>, climbing grass (Compositae) that originated on tropical and subtropical coastline and offshore islands of China ([Chinese Academy of Science Flora of China Editorial Board, 1988](#)). Recent studies of *W. biflora* have focused on its physiology ([Idris et al., 2018](#)) and metabolic components (e.g., antimicrobial activity of essential oils, see [Ahmed et al., 2018](#)). In mainland ecosystems, *W. biflora* gradually disappears with forest succession. On coral islands, however, *W. biflora* has grown abundantly and expanded into native forest communities ([Tong et al., 2013](#)). Yongxing Island is a coral island in the South China Sea. In 1970s, Yongxing Island had not been seriously disturbed and its forest communities were intact. *W. biflora* was scattered and occupied less than 5% in the forests ([Exploration Group of Xisha Islands of Institute of Soil Science of Chinese Academy of Sciences CAS, 1977](#)). With land development and construction in the past decades, the native forest communities on Yongxing Island have been destroyed ([Zhang et al., 2011; Liao et al., 2013](#)). At the same time, invasive species have appeared on the edges of the damaged natural forest ([Li et al., 2004](#)). The area of *W. biflora* expansion in the native forest communities on the island often exceeds 50% ([Cai et al., 2020](#)). Its strong climbing ability enables *W. biflora* to wrap around trees and reduce their growth. The prolonged isolation of coral islands has led to unique flora and fauna, which are difficult to maintain due to frequent natural disasters (typhoons and tides) and limited availability of soil nutrients and fresh water ([Lugo, 1988; Gibbs et al., 2010](#)). The expansion of *W. biflora*, which is tolerant of low soil nutrients and drought, could destroy the original habitat and inhibit the germination of other native plants ([Drake, 1998](#)).

We used a seedling emergence assay to investigate the effects of *W. biflora* invasion on the soil seed bank on Yongxing Island in the South China Sea. The expansion of this species has received little attention as a potential threat to the environment, probably because it is an endemic species and produces an oil with antibacterial activity ([Ahmed et al., 2018](#)). At the outset of this study, *W. biflora* had expanded to occupy 20–50% of the areas of the native forest communities on Yongxing Island. In the current study, we selected areas on Yongxing Island that differed in the degree of *W. biflora* expansion to answer the following questions:

(1) How has the expansion of *W. biflora* affected the species richness, abundance, composition, and diversity, of the soil seed bank and the above-ground vegetation, and do these effects differ among seasons? (2) How does *W. biflora* expansion affect the contributions of the seed banks in the surface soil layer (0–5 cm) and a deeper soil layer (5–10 cm) to the above-ground plant community? (3) How do the richness and abundance of alien species in the seed bank change along a *W. biflora* expansion gradient and does the control of *W. biflora* increase the probability of invasion by these alien species?

## 2. Materials and methods

### 2.1. Study area and habitat

This study was carried out on Yongxing Island (16°49'N–16°50'N, 112°20' E–112°21'E), a coral island of Paracel Islands in the South China Sea. The island is located in the central tropics, and has a typical tropical marine climate with both a year-round high temperature and an annual mean temperature ranging from 26 to 27 °C, the annual total precipitation is 1500 mm, and the annual evaporation capacity is 2400 mm. About 353 plant species grow on the island, of which 187 are wild species ([Tong et al., 2013](#)). The island has mainly guano phosphatic coral-sand soils and the remaining immature soils are predominantly composed of coral sands ([Exploration Group of Xisha Islands of Institute of Soil Science of Chinese Academy of](#)

[Sciences CAS, 1977](#)). The vegetation is characterized by the dominant native tree species *Pisonia grandis* and *Guettarda speciosa*, with a sparse shrub layer and a dense groundcover of herbs and graminoids, such as *Scaevola taccada*, *Stenotaphrum micranthum*, and other species typical of coral Paracel Islands ([Zhang et al., 2011](#)).

Except for *W. biflora*, only a few Asteraceae are grow on the Paracel Islands, and those that do grow on the islands have small ranges. With the development of Yongxing Island, native forest communities have been destroyed, and *W. biflora*-dominated communities have appeared on the newly damaged forest land, the mono-dominated community of *W. biflora* appeared ([Cai et al., 2020](#)). *W. biflora* can grow to more than 3 m in height, has a strong climbing ability, and as noted earlier, is very harmful to the native forest community. The areas with and without *W. biflora* expansion often have similar biological, physical and disturbance characteristics (i.e., a similar richness of alien species, tree densities and covers of the herb, shrub and tree canopy layers in the above-ground vegetation) (personal observations). A map of the region and detailed information on the structural and floral attributes of the endangered community and on the climatic and geological characteristics of the region are provided in [Exploration Group of Xisha Islands of Institute of Soil Science of Chinese Academy of Sciences CAS \(1977\)](#) and [Tong et al. \(2013\)](#).

## 2.2. Experimental design

The experimental areas were selected based on two criteria: 1) The forest communities have not been disturbed over 5 years by human activities. 2) *W. biflora* has expanded into the forest communities in different degrees. The experiment used a completely randomized design with 25 replications for each of the three treatments of *W. biflora* expansion. A total of 75 plots (5 m × 5 m each) were established in the studied community in November 2018. These included 25 plots with a high degree of *W. biflora* expansion (H-exp, *W. biflora* foliage cover ≥50%), 25 plots with a light degree of *W. biflora* expansion (L-exp, *W. biflora* foliage cover 20%), and 25 plots without *W. biflora* (Un-exp). The numbers of native and alien plant species of the above-ground vegetation were recorded in each plot. The effects of *W. biflora* expansion were assessed using a correlative, multi-site comparative procedure in which the seedlings that emerged from soil seed bank samples were assessed ([Cabin et al., 1998](#); [Wang et al., 2009](#)). Seed banks were sampled in 2 m × 2 m subplots (one subplot for each of the 75 plots) at the same plots and times (between April and November 2018). Above-ground vegetation was assessed for species abundance (number of individuals per plot), composition of above-ground plants (number of plant species), the coverage of above-ground plants (matrix vegetation cover), the coverage of trees (canopy cover), and the ground cover of *W. biflora*.

## 2.3. Sampling and seedling emergence

The effects of *W. biflora* expansion on the density and richness of viable propagules in the soil seed bank were assessed using a seedling emergence assay ([Mason et al., 2007](#)). Although the seedling emergence assay cannot be used to detect dormant seed, it is useful for rapidly assessing the viable component of the seed bank and the species that are therefore likely to contribute to vegetation regeneration ([Brown, 1992](#)). Within each 2 m × 2 m subplot, we used a soil corer (63 mm diameter) to collect soil samples from 10 random points (excluding litter) and at two layers, i.e., the surface soil layer (0–5 cm) and deep soil layer (5–10 cm). The soil was passed through a 6 mm × 6 mm mesh sieve to remove stones, woody debris, and other contaminants.

Soil samples were spread evenly to a depth of about 2 cm over a propagation medium of sterilized coarse sand within 22 cm × 18 cm propagation trays, which were positioned randomly in glasshouses at the South China Botanical Garden, Guangzhou, China. Tap water was applied to each tray twice daily for 5 min. Seedling emergence was assessed once every 14 days for the first 3 months and then monthly for 1 year. Seedlings were removed from trays upon identification, or were transferred to individual pots for future identification. The number and species composition of plants in each tray were determined ([Thompson and Band, 1997](#)).

## 2.4. Data analysis

### 2.4.1. Comparison of soil seed bank and above-ground vegetation

We grouped all plant species into three categories: *W. biflora*, native species (excluding *W. biflora*) and alien species.

We first compared the assemblage of species between the above-ground vegetation and the seed bank (both soil layers) using Sørensen's quotient of similarity ([Ikeda et al., 2014](#)), which was calculated as:

$$SQ = [2C / (A + B)] \times 100$$

where A is the number of species in the soil seed bank, B is the number of species in above-ground vegetation, and C is the number of species common to the seed bank and above-ground vegetation.

The Shannon-Wiener index (SWI) and Pielou index (PI) of the above-ground vegetation and the soil seed bank were used to measure the species diversity and evenness, respectively, of the forest community ([Wang et al., 2019](#)). SWI and PI were calculated as followings:

$$SWI = - \sum_{i=1}^s P_i \ln P_i \quad (i = 1, 2, 3, \dots, s)$$

$$PI = - (\sum_{i=1}^s P_i \ln P_i) \ln S \quad (i = 1, 2, 3, \dots, s)$$

where  $P_i$  is the relative importance value of species  $i$ , and  $S$  is the total number of species.

Two-way analysis of variance (ANOVA) was used to assess the differences in native and alien species richness (response variables) between the seed bank and above-ground vegetation across habitats with different degrees of *W. biflora* expansion (H-exp, L-exp, and Un-exp). A one-way ANOVA was used to compare the SQ values for the seed bank vs. above-ground vegetation QS across habitats with different degrees of *W. biflora* expansion degrees. We used the Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980) to analyze community species composition. We obtained the total germination density for each plot, and used DCA to evaluate the differences in seed germination between different habitats.

Compositional differences between the seed bank and above-ground vegetation were assessed using distance-based permutational multivariate analysis of variance (PERMANOVAs) (Anderson, 2001) with R 3.5.3. PERMANOVAs were based on Bray-Curtis similarity indices and were calculated using species presence/absence data for all possible combinations of sample pairs (McArdle and Anderson, 2001). Subplots containing no species were removed from analyses because Bray-Curtis indices cannot be calculated with 0 species. Compositional differences were examined by generating non-metric multidimensional scaling ordination plots (Clarke, 1993).

#### 2.4.2. Effects of *W. biflora* expansion on the soil seed bank

General linear models (GLMs) were used to assess the effects of *W. biflora* expansion, as well as the extrinsic physical, biological and disturbance characteristics of the surrounding community on the germinant density and richness of native and alien species in the seed bank of the surface soil layer, deep soil layer, and both soil layers combined (Field, 2010).

The possible multicollinearity among three uncorrelated community-level predictors (e.g. number of native species of above-ground vegetation within a 400 m<sup>2</sup> quadrat, percentage cover of *W. biflora* and canopy vegetation layers) was assessed by generating a matrix of Pearson correlation coefficients. One landscape-level predictor (i.e. percentage cover of vegetation in the matrix surrounding each site) was included in the models. GLMs were then constructed using a backward variable elimination procedure, whereby non-significant predictors ( $p > 0.05$ ) were successively removed from the models (i.e. all predictors and their first-order interactions included). Model fit was verified at each stage of variable elimination by calculating Akaike's Information Criterion (Akaike, 1974). GLMs were also used to assess the variation in the species richness and density of other native species as related to the degree of *W. biflora* expansion and other extrinsic environmental factors. Poisson regression, using the same backward selection procedure as used for the GLMs, was used to simulate the response of woody species richness to *W. biflora* expansion; due to that woody species were rare, and data transformations were unable to improve the normality of the data.

PERMANOVAs were also used to assess the dissimilarity in seed bank compositions of native and alien species in habitats with different degrees of *W. biflora* expansion. Analyses were done using both species abundance data (i.e., the density of germinants) and presence/absence data. Analyses using presence/absence data allowed us to detect the contributions of rare and less abundant species to community change.

### 3. Results

#### 3.1. Species richness, abundance, and diversity of above-ground vegetation and the soil seed bank in habitats with different degrees of *W. biflora* expansion

A total of 48 species were recorded in the soil seed bank ( $n = 42$ ) and above-ground vegetation ( $n = 26$ ) in the 75 plots. Six (13%) and 22 (47%) species were unique to the seed bank and above-ground vegetation, respectively. Among the 48 species, 17% were trees, 6% were shrubs, and 77% were herbs (Supplementary Table S1). One-way ANOVA revealed that the density of non-*W. biflora* plants, total native species richness, native species diversity, and *W. biflora* abundance in the soil seed bank had the same trends in November 2018 and April 2018. In the soil seed bank, total species richness, total species Shannon diversity index, total species Pielou evenness index and the density of *W. biflora* increased but the density and species richness of native species decreased with the degree of *W. biflora* expansion (Table 1). In the H-exp plots, the total species richness, Shannon diversity index, and Pielou evenness index in the soil seed bank were significantly higher in the deep soil layer (5–10 cm) than in the surface soil layer (0–5 cm). However, the densities of native species and *W. biflora* in the soil seed bank were significantly higher in the surface soil layer than in the deep soil layer in the H-exp plots.

#### 3.2. Similarities of species composition between the above-ground vegetation and the soil seed bank

A two-way ANOVA revealed that the mean ( $\pm$ SE) native species richness pooled across all plots was significantly higher in the soil seed bank ( $12.8 \pm 2.03$  species) than in the above-ground vegetation ( $5.13 \pm 1.25$  species). The native above-ground vegetation and seed bank assemblages were also different based on species identity (i.e. presence/absence) (Fig. 1). Across all

**Table 1**

Numbers of non-*W. biflora* plants, species richness, species diversity, and numbers of *W. biflora* plants that emerged as seedlings from the soil seed banks in the Un-exp, L-exp, and H-exp (Un-exp, no expansion; L-exp, 20% coverage by *W. biflora*; and H-exp, ≥50% coverage by *W. biflora*) plots at 0–5 and 5–10 cm depth. Values are means ± SE of 25 replicate subplots.

Month	Gradient	Soil depth (cm)	Native species density (individual/m <sup>2</sup> )	Total species richness	Native species richness	Total species diversity index	Total species evenness index	<i>W. biflora</i> density (individual/m <sup>2</sup> )
April	Unexp	0–5	8.5 ± 0.5a	12.2 ± 2.3a	12.2 ± 1.8a	1.84 ± 0.29a	0.69 ± 0.06a	0.21 ± 0.2a
		5–10	2.9 ± 0.5 b	13.4 ± 0.8 a	8.4 ± 0.5b	2.13 ± 0.12 ab	0.88 ± 0.02 ab	—
	L-exp	0–5	7.9 ± 1.6 a	15.6 ± 2.9 ab	11 ± 2.8a	2.21 ± 0.25 ab	0.78 ± 0.05a	1.16 ± 0.36b
		5–10	3.0 ± 0.5 b	15.4 ± 2.2 ab	8.8 ± 0.4b	2.33 ± 0.13b	0.88 ± 0.03b	0.12 ± 0.04a
	H-exp	0–5	8.2 ± 1.9 a	17.8 ± 1.9 b	6.8 ± 0.75b	2.04 ± 0.09 ab	0.7 ± 0.02a	2.56 ± 0.93c
		5–10	3.3 ± 0.5 b	13.8 ± 1.7 a	7.6 ± 1.5b	2.31 ± 0.11b	0.9 ± 0.03b	0.18 ± 0.06a
	November	Unexp	0–5	7.3 ± 1.1 a	11.8 ± 1.5 a	11.8 ± 1.5a	1.55 ± 0.26a	0.63 ± 0.09a
		5–10	3.3 ± 0.3 a	13.2 ± 1.2 a	8.2 ± 0.4b	2.06 ± 0.13 ab	0.8 ± 0.05 ab	—
		L-exp	0–5	6.0 ± 0.79 a	15.4 ± 1.5 ab	12.2 ± 1.3a	2.03 ± 0.32 ab	0.74 ± 0.03a
		5–10	3.4 ± 0.1 b	15.9 ± 2.5 ab	8.6 ± 0.6b	2.35 ± 0.18b	0.84 ± 0.03a	0.21 ± 0.09a
		H-exp	0–5	6.6 ± 1.5 a	17.6 ± 2.2 b	7.4 ± 0.5b	2.1 ± 0.13 ab	0.73 ± 0.04a
			5–10	4.6 ± 0.6 ab	18.1 ± 1.3 b	7 ± 1.1b	2.55 ± 0.08b	0.87 ± 0.03b

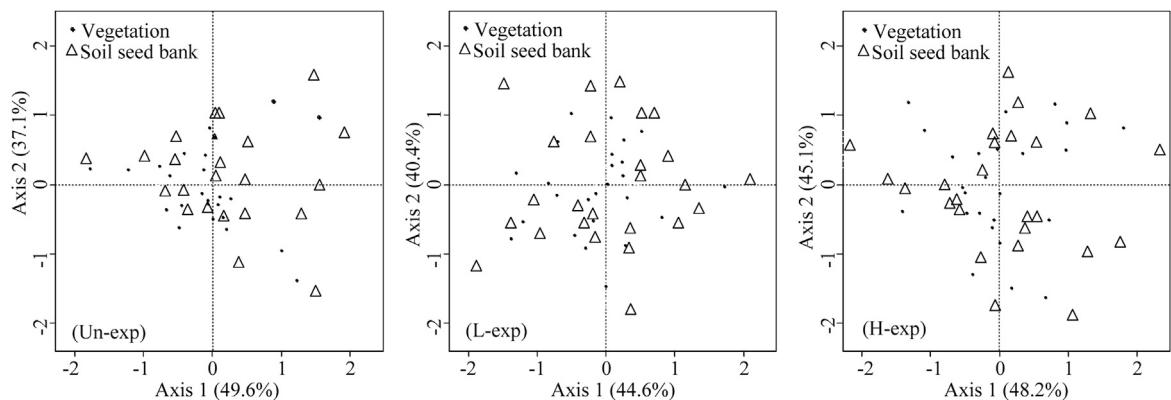


**Fig. 1.** Photographs of *W. biflora* growing within (top) and on the edge (bottom) of the forest on Yongxing Island.

plots, the mean ( $\pm$ SE) Sørensen's quotient of similarity between the seed bank and above-ground vegetation was 37.6% ( $\pm$ 8.8%). The degree of similarity between the above-ground vegetation and seed bank was significantly lower for sites with than without *W. biflora* expansion: the respective mean ( $\pm$ SE) SQ values for the above-ground vegetation vs. the seed bank were 27.1% ( $\pm$ 5.7%) in the H-exp plots, 32.1% ( $\pm$ 3.2%) in the L-exp plots and 53.6% ( $\pm$ 24.8%) in the Un-exp plots (one-way,  $P_{H-L} > 0.05$ ,  $P_{U-L}$  &  $P_{U-H} < 0.01$ ). The seed bank assemblage was more homogeneous than the above-ground vegetation, because plots were more tightly clustered within the DCA space (Fig. 2).

### 3.3. Effects of *W. biflora* expansion on the native seed bank

In total, 8269 germinants, consisting of 40 native and 8 alien species, were recorded from the combined surface layer and deep layer soil seed banks. Over 83% of the germinants were native, and the majority of these were recorded in the Un-exp plots (Supplementary Table S1). The deep soil layer contributed very little to the alien species seed bank, i.e., only 6% of the alien germinants emerged from the deep layer soil.



**Fig. 2.** Detrended Correspondence Analysis (DCA) of species composition between above-ground vegetation and the soil seed bank as related to the degree of *W. biflora* expansion (Un-exp, no expansion; L-exp, 20% coverage; and H-exp,  $\geq 50\%$  coverage) on the coral island.

A total of 6930 native germinants (excluding *W. biflora*) were recorded from the soil seed bank. Both the richness and density of native germinants in the soil seed bank were significantly lower at plots with than without *W. biflora* expansion (Table 2). The density of native germinants was positively related to both native community richness and canopy cover, but species richness also significant increased with decreasing canopy cover and increasing matrix vegetation cover (i.e., 20 m  $\times$  20 m plot).

The species richness of native germinants was not affected by *W. biflora* expansion, and the density of native germinants was affected by native vegetation canopy cover and the coverage of *W. biflora* in the deep layer soil seed bank (Table 2).

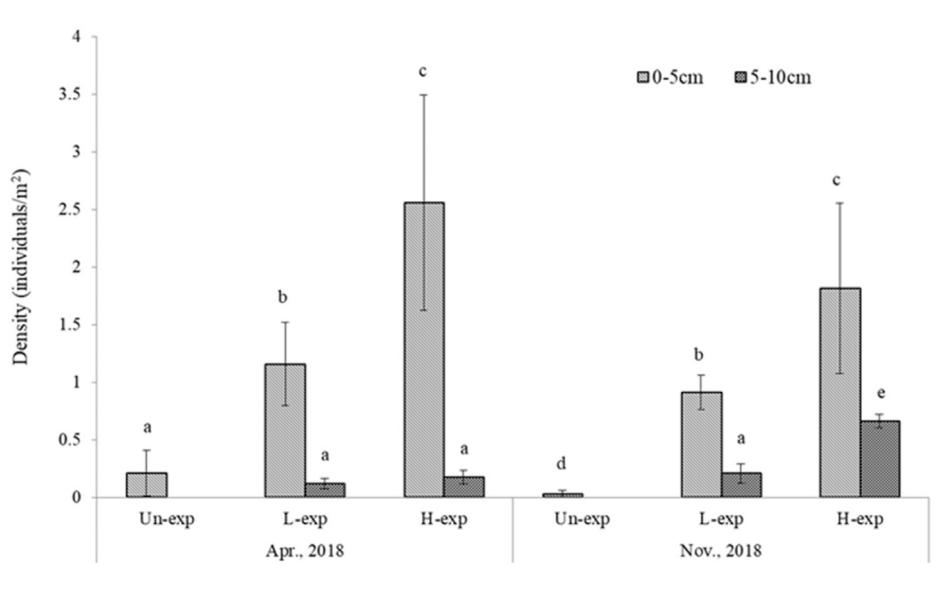
### 3.4. Distribution of *W. biflora* in the soil seed bank

Fewer *W. biflora* germinants were produced by soil seed bank samples of both the 0–5 cm and 5–10 cm layers in November than in April of 2018 (Fig. 3). In both months, the number of *W. biflora* germinants was greater in 0–5 cm samples

**Table 2**

The richness and density of native germinants in the soil seed bank of the (a) surface layer, (b) deep layer, and (c) total (both soil layers) in native forest communities as affected by *W. biflora* expansion and other independent variables and as determined by general linear models. Values in bold are statistically significant. Models presented provide the 'best fit' for each response variable based on the backwards step-wise elimination procedure, in which the elimination of non-influential predictors at each step was verified using the Akaike Information Criterion (AIC).

Seed bank sample type	Estimate	Std	t value	p	$r^2$
(a) 0–5 cm seed bank					
<i>Density</i>					
Model	244.7	33.4	7.34	<0.001	0.967
Canopy cover (%)	1.27	0.34	3.70	<0.001	
Expansion degree	-10.5	0.58	-2.30	0.024	
Native community richness	7.56	0.56	13.6	<0.001	
Ground cover (%)	-2.32	0.46	-5.07	<0.001	
Expansion degree $\times$ Native community richness	-2.56	0.18	-14.1	<0.001	
<i>Richness</i>					
Model	39.4	27.5	1.43	0.0156	0.669
Canopy cover (%)	-1.09	0.13	-8.41	<0.001	
Expansion degree	-10.7	1.21	-8.85	<0.001	
Matrix vegetation cover (%)	0.83	0.24	3.53	<0.001	
(b) 5–10 cm seed bank					
<i>Density</i>					
Model	-123.1	56.2	-2.19	0.032	0.224
Canopy cover (%)	-2.07	0.59	-3.57	<0.001	
Ground cover (%)	1.91	0.53	3.66	<0.001	
<i>Richness</i>					
Model non-significant	-0.082	28.17	-0.003	0.997	0.762
(c) Total seed bank					
<i>Density</i>					
Model non-significant	201.46	507.31	0.397	0.693	0.515
<i>Richness</i>					
Model	65.52	8.55	7.67	<0.001	0.743
Expansion degree	-0.51	0.089	-5.69	<0.001	
Native community richness	5.87	0.821	7.15	<0.001	



**Fig. 3.** Numbers of *W. biflora* germinants produced by the soil seed bank at 0–5 cm and 5–10 cm soil depth as affected by month and the degree of *W. biflora* expansion (Un-exp, no expansion; L-exp, 20% coverage; and H-exp, ≥50% coverage) on the coral island. Values are means ± SE.

than in 5–10 cm samples (Fig. 3). The expansion of *W. biflora* significantly influenced the number of *W. biflora* germinants in the 0–5 cm layer but not in the 5–10 cm layer of the soil seed bank (Table 1; Fig. 3). The number of *W. biflora* germinants produced by the seed bank in the surface layer increased with the degree of *W. biflora* expansion, and *W. biflora* germinants even appeared in the surface layer of the Un-exp plots. However, the number of *W. biflora* germinants produced did not significantly differ between the soil seed banks in the deep soil layer of the L-exp and H-exp plots, and *W. biflora* germinants rarely appeared in the soil seed bank of the deep soil layer samples from the Un-exp plots.

### 3.5. Potential for expansion of alien species as affected by *W. biflora* expansion

Eight alien species were recorded in the 75 plots (Supplementary Table S1). A two-way ANOVA revealed that the above-ground vegetation had significantly fewer alien species than the seed bank; the mean (±SE) species richness was 3.12 (±0.31) for above-ground vegetation and 5.17 (±0.01) for the seed bank. Alien species richness was affected by *W. biflora* expansion (Table 3).

In total, 892 alien germinants were recorded from the seed bank, 90.2% of which emerged from surface soil samples. The density of alien germinants in the surface layer increased with *W. biflora* expansion (Table 4) and was negatively associated with native species canopy coverage and the interaction between the degree of *W. biflora* expansion and the coverage of *W. biflora*. However, the density of alien germinants in the deep layer was unaffected by *W. biflora* expansion.

The alien species richness in the soil surface layer increased with *W. biflora* expansion (Table 4). However, alien species richness in the surface layer was negatively associated with the coverage of trees (native species), but was positively associated with the interaction between the degree of *W. biflora* expansion and alien community richness. *W. biflora* expansion significantly affected the composition of the alien species seed bank (PERMANOVA: presence/absence, pseudo F = 1.850, p = 0.01; germinant density, pseudo F = 7.381, p = 0.001).

## 4. Discussion

### 4.1. Changes in the soil seed bank associated with *W. biflora* expansion

Our data from Yongxing Island, a coral island in the South China Sea, suggest that total species richness, Shannon diversity index, Pielou evenness index, and the number of *W. biflora* seeds in the soil seed bank increased while the numerical abundance of native species in the soil seed bank decreased with *W. biflora* expansion. The effects of *W. biflora* expansion on the soil seed bank were qualitatively similar in April and November but were quantitatively greater in April (Supplementary Table S1; Table 1). These findings are consistent with earlier reports that *W. biflora* expansion reduced the abundance of native species (Kundel et al., 2014). Species diversity and the evenness index of all species increased with the degree of *W. biflora* expansion, which was inconsistent with many previous studies that found that the expansion of weeds decreases the diversity and richness of species in the native communities (Woods, 1993; Scharfy et al., 2009). However, Yongxing Island has

**Table 3**

Alien species richness as affected by *W. biflora* expansion (three treatment levels: Un-exp, no expansion; L-exp, 20% coverage; and H-exp,  $\geq 50\%$  coverage) and sample type (two treatment levels: above-ground vegetation vs. seed bank) and as determined by two-way ANOVAs. Bold P-values are statistically significant.

Source of variation	DF	SS	MS	F	p	$r^2$
Expansion degree	2	62.60	31.300	64.759	<b>&lt;0.001</b>	0.85
Sample Type	1	0.03	0.033	0.069	0.7951	
ID $\times$ ST	2	2.47	1.233	2.552	0.0989	
Error	24	11.6	0.483			

**Table 4**

The richness and density of alien germinants in the seed banks of the (a) surface soil layer (0–5 cm), (b) deep soil layer (5–10 cm), and (c) both layers (0–10 cm) in native forest communities as affected by *W. biflora* expansion and other independent variables and as determined by general linear models. Values in bold are statistically significant. The presented models provided the 'best fit' for each response variable based on the backward variable elimination procedure, in which the elimination of predictors at each step was verified using the Akaike Information Criterion (AIC).

Seed bank sample type	Estimate	Std	t value	p	$r^2$
(a) 0–5 cm seed bank					
<i>Density</i>					
Model	47.58	16.84	2.83	<b>0.006</b>	0.982
Canopy cover (%)	−0.41	0.18	−2.33	<b>0.023</b>	
Expansion degree	5.31	1.85	2.88	<b>0.005</b>	
Ground cover (%)	−0.31	0.21	−1.47	<b>0.147</b>	
Expansion degree $\times$ Ground cover (%)	0.05	0.01	3.99	<b>&lt;0.001</b>	
<i>Richness</i>					
Model	7.58	2.20	3.44	<b>0.002</b>	0.422
Canopy cover (%)	−0.08	0.02	−3.38	<b>0.002</b>	
Expansion degree	0.94	0.44	2.15	<b>0.038</b>	
Alien community Richness	0.90	0.16	5.71	<b>&lt;0.001</b>	
Expansion degree $\times$ Alien community Richness	0.09	0.16	2.78	<b>0.008</b>	
(b) 5–10 cm seed bank					
<i>Density</i>					
Model non-significant	−13.13	37.85	−0.35	0.738	0.416
<i>Richness</i>					
Model non-significant	0.58	0.15	3.91	0.069	0.232
(c) Total seed bank (0–10 cm)					
<i>Density</i>					
Model	15.35	18.43	0.83	<b>0.041</b>	0.984
Canopy cover (%)	−0.05	0.19	−0.28	0.78	
Expansion degree	13.04	2.39	5.45	<b>&lt;0.001</b>	
Canopy cover $\times$ Expansion degree	−0.07	0.016	−4.48	<b>&lt;0.001</b>	
<i>Richness</i>					
Model	7.91	1.91	4.15	<b>&lt;0.001</b>	0.952
Canopy cover (%)	−0.08	0.02	−4.01	<b>&lt;0.001</b>	
Alien Community Richness	0.99	0.14	7.24	<b>&lt;0.001</b>	
Alien Community Richness $\times$ Expansion degree	−0.12	0.03	−4.08	<b>&lt;0.001</b>	

substantial habitat heterogeneity due to ocean currents and monsoons, among other factors, which affect the structure and distribution of vegetation. Because of the coral island environment, coral islands support monodominant communities that cannot advance to climax communities (Kohn and Walsh, 1994). The seeds of many pioneer species remain in the soil seed bank and do not germinate in unsuitable environment. Once the area occupied by *W. biflora* expanded, the original community structure was altered, many species began to emerge (Mouillot et al., 2011), and the overall species diversity increased.

#### 4.2. Effects of *W. biflora* expansion on the relationship between the soil seed bank and the above-ground vegetation

The relationship between the species composition of the above-ground vegetation and of the soil seed bank differed depending on the degree of *W. biflora* expansion. As *W. biflora* expansion increased, more new species became part of the above-ground native plant community and the similarity between the above-ground vegetation and the soil seed bank decreased; these findings were consistent with a previous report (Brown, 1992). Many species in the soil seed banks were not present in the above-ground vegetation, and the proportion of seed bank species that were not present in the above-ground vegetation increased with *W. biflora* expansion. Our results are inconsistent with previous results that showed that expansion by an invasive species leads to species loss (Gooden et al., 2009). In addition, we found that as *W. biflora* expansion increased, many new species entered the soil seed bank, such as *Tridax procumbens*, *Sphagneticola trilobata*, and *Praxelis clematidea*. Consistent with a previous report (Tozer et al., 2010), we found that most of the species that appeared in the soil seed bank

with *W. biflora* expansion were invasive and they might be opportunistic. Our results suggest that although such species did not appear in the aboveground vegetation, more seeds of new species will enter the soil seed bank as *W. biflora* expands its coverage (Coleman and Levine, 2007).

Researchers have suggested that a mature forest with a complex hierarchical structure and closed canopy that reduces wind speeds would prevent the invasion of wind-pollinated herbs (Cheng et al., 2020). However, *W. biflora* expansion can increase canopy openness and promote the propagation of perennial herbs in the windy environment on the coral island. Wind pollination and the large numbers of small seeds produced by these herbs facilitate their spread throughout the forest (Thompson et al., 1993).

#### 4.3. Effects of *W. biflora* expansion on numbers of *W. biflora* seeds in the soil seed bank

We found that the number of *W. biflora* seeds in the seed bank in the surface soil layer but not in the deep soil layer increased with the degree of *W. biflora* expansion (Fig. 3). In contrast, there were almost no *W. biflora* seeds in the soil seed bank of plots without *W. biflora* (see also del Fabbro et al., 2014). The increase in its seed numbers in the surface soil but not in the deeper soil suggests that expansion by *W. biflora* may be a recent event (Kundel et al., 2014). It is also possible that *W. biflora* seeds do not remain viable in the deep soil layer (Thompson et al., 1997). Some species known to have more persistent seeds were more abundant in areas with substantial *W. biflora* expansion than in neighbouring areas without *W. biflora* expansion, and such patterns may explain the slight shifts observed in seed bank composition. For example, *Oxalis corniculata* and *Digitaria sanguinalis* were more abundant in plots with a high degree of *W. biflora* expansion than in plots without *W. biflora* expansion (Supplementary Table S1).

#### 4.4. Preventing the next invasion is essential following weed management

The seed bank and above-ground vegetation assemblages differed substantially, with only 37.6% similarity in species composition. The low level of similarity is consistent with other studies of seed banks (Holmes and Cowling, 1997; Mason et al., 2007; Vilà and Gimeno, 2007). In the current study, > 80% of the species were unique to the seed bank and never emerged into the above-ground vegetation. Even though seeds of alien species were substantial and persistent components of the soil seed banks, few invasive alien species appeared in the above-ground vegetation and the coverage of them was much smaller than the coverage of native species. Although the alien propagules had little effects on the existing above-ground vegetation, we suspect that they may germinate and establish if certain conditions are met. The diversity of the forest is limited by low rates of post-settlement recruitment rather than by reductions in the arrival of propagules. Although *W. biflora* expansion resulted in reductions in the number of individuals of native species, the seed bank still contained significantly more species (most of which were unique) than the above-ground vegetation. There may be a high potential for unassisted reestablishment of a species-rich above-ground vegetation from the seed bank on Yongxing Island although the reestablished plant community is unlikely to resemble the original community in structure, function, or species composition.

Assuming that *W. biflora* is removed, our study has several implications for the subsequent regeneration or restoration of native vegetation. First, several native species, such as the trees *P. grandis*, *M. citrifolia*, and *F. superba*, may require supplemented reintroduction because their propagules are rare in seed bank. Such species are likely to be underrepresented in regenerating communities dominated by herbs. *G. speciose*, a native tree species, may be the only woody species in regenerating communities because of its abundance in the soil seed banks in both areas without and with *W. biflora* expansion.

Alien species were abundant in the soil seed bank (they represented about 11% of the total number of species recorded) and therefore pose a significant threat of plant invasion to the regenerating community. The risk of invasion following *W. biflora* removal could be reduced by the targeted application of herbicides. (Mason and French, 2007). Furthermore, although the soil seed bank represents the regeneration potential of a community following weed or invader removal (Holmes and Cowling, 1997), the contribution of the seed bank and the restoration trajectory of the regenerating community may be influenced by the removal method. Long-term monitoring of the regenerating vegetation will be required to identify species that are unable to recolonize. In some cases, supplemented reintroduction may be needed to ensure that invasive species do not dominate the emergent vegetation.

### 5. Conclusions

We found that *W. biflora* expansion altered the characteristics of the soil seed bank and above-ground vegetation on Yongxing Island. The density of native species other than *W. biflora* in the above-ground vegetation decreased with the degree of *W. biflora* expansion although overall species richness increased. The dissimilarity between above-ground vegetation and the soil seed bank also increased with the degree of *W. biflora* expansion. If *W. biflora* is removed, the forest on the island could be dominated by *G. speciose* or could be susceptible to invasion by alien species. Continuous monitoring is essential for effective restoration of the forests on Yongxing Island.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01403>.

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