

RESEARCH

Quantitative Classification and Environmental Interpretation of Secondary Forests 18 Years After the Invasion of Pine Forests by *Bursaphelenchus xylophilus* (Nematoda: Aphelenchoididae) in China

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ABSTRACT. With growing concerns over the serious ecological problems in pine forests (*Pinus massoniana*, *P. thunbergii*) caused by the invasion of *Bursaphelenchus xylophilus* (the pine wood nematode), a particular challenge is to determine the succession and restoration of damaged pine forests in Asia. We used two-way indicator species analysis and canonical correlation analysis for the hierarchical classification of existing secondary forests that have been restored since the invasion of *B. xylophilus* 18 years ago. Biserial correlation analysis was used to relate the spatial distribution of species to environmental factors. After 18 years of natural recovery, the original pine forest had evolved into seven types of secondary forest. Seven environmental factors, namely soil depth, humus depth, soil pH, aspect, slope position, bare rock ratio, and distance to the sea, were significantly correlated with species distribution. Furthermore, we proposed specific reform measures and suggestions for the different types of secondary forest formed after the damage and identified the factors driving the various forms of restoration. These results suggest that it is possible to predict the restoration paths of damaged pine forests, which would reduce the negative impact of *B. xylophilus* invasions.

Key Words: *Bursaphelenchus xylophilus*, ecological restoration, forest transformation, quantitative classification, environmental interpretation

Many scholars believe that the pine wood nematode *Bursaphelenchus xylophilus* (Steiner and Buhner) Nickle, which causes pine wilt disease, may have originated in North America (Dropkin et al. 1981, Bergdahl 1988). In 1982, the first occurrence of pine wilt disease in mainland China was found on *Pinus thunbergii* in the area of Sun Yat-sen Mausoleum, Nanjing (Eastern China). At that time, only 256 dead trees were found (Sun 1982, Chen et al. 1983). Just 30 years later, the epidemic had rapidly expanded and spread to 16 provinces, including Anhui, Chongqing, Fujian, Guangdong, Guangxi, Guizhou, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Shandong, Shanxi, Sichuan, Yunnan, and Zhejiang (Zhang and Luo 2003, Wu 2004, State Forestry Administration 2014). The epidemic has caused, both directly and indirectly, an accumulated loss of hundreds of billions of yuan. At present, the epidemic is moving closer to famous scenic spots, such as Huangshan, which is a World Natural Heritage Site (Zhang et al. 2004).

In Japan, *P. thunbergii* forests have been the most heavily affected by *B. xylophilus*; many pine trees have died since 1905, when the first dead tree was found in Kyushu, and pine wilt disease has become a national concern (Mamiya, 1972, 1988; Maehara and Futai 2000; Kanzaki and Futai 2006). *B. xylophilus* was also found for the first time in 1988 in Busan, South Korea, in 1999 in Portugal, and in 2011 in Spain (Enda 1997, Mota et al. 1999, Mota and Vieira 2008, Robertson et al. 2011). At present, pine wilt disease caused by *B. xylophilus* poses a large threat to the pine forests of Asia and Europe (Evans et al. 1996, Kulnich and Orlinskii 1998, Sousa et al. 2002).

In China, forests of *Pinus massoniana* and *P. thunbergii* have sustained the most serious damage, and pine wilt disease of these species is of major concern (Chai and Jiang 2003; Zhao et al. 2003, 2007; Shi et al. 2007a,b). Of these two species, *P. massoniana* is more widely distributed and accounts for a large proportion of the pine trees in China. It is the primary coniferous species in subtropical regions. Under natural conditions, it is usually distributed in poor geological environments,

such as hills, steep slopes, and sites with poor, dry soils. The long-term geological and environmental conditions in these environments have formed its site-specific ecological characteristics, namely high seed germination, strong seedlings, resistance to infertility, attraction to sunlight, and strong reproductive ability. In places where native evergreen broadleaf forests are under intensive human disturbance, the evergreen broadleaf species have had difficulty in self-renewing and recovering in a short period of time; however, the introduction of *P. massoniana* seeds has been very successful for reforestation. These areas are called pioneer pine forests or pioneer communities (Anonymous 1991, Tian 2005).

P. thunbergii originated from the east coast of Japan and the Korean Peninsula and is widely distributed in the coastal provinces of China, such as Shandong, Jiangsu, Anhui, Zhejiang, and Fujian. *P. thunbergii* likes light, is resistant to drought and infertility, is susceptible to water logging and cold temperatures, and grows well in areas with a warm and moist maritime climate. It grows best in deep and loose sandy soil layers containing humus. Because of its resistance to sea fog and wind, it can also grow on beach areas with saline soil. Due to the high vulnerability of *P. thunbergii* to pine wilt disease, *B. xylophilus* has devastated *P. thunbergii* forests in Asian countries, such as Japan and China, from the 1980s to the present (Kuroda 2004). Zhejiang Province has 2.6×10^6 hm² of *P. thunbergii* forest, which accounts for 49.7% of the forest area and 59.2% of the stock volume of the province. It is the primary landscape resource for many scenic areas in China (Anonymous 1980).

The first incidence of pine wilt disease in Zhejiang Province was discovered in August 1991. In recent years, the degree of damage in Zhejiang Province has been increasing and the damaged area has expanded to 2.7×10^4 hm², which accounts for >60% of the total damaged area in China. The main forests on Zhoushan Island, which is part of Zhejiang Province, were primarily pure *P. massoniana* and

P. thunbergii forests before 1990 and were seriously damaged by *B. xylophilus* around 1993. Therefore, Zhoushan City, Zhejiang, was an ideal location for the present study.

There are many reports of the evolution and restoration of *P. massoniana* and *P. thunbergii* forest systems (Jing and Cai 2005, Ou et al. 2005). However, there has been no specific study of pine forest restoration after the invasion of *B. xylophilus*. This knowledge deficit is due to the lack of preinvasion plant community composition data (remote-sensing imagery can acquire data only for the canopy and not for the understory layers). To solve this problem, we analyzed resource inventory data from a few years before and after the *B. xylophilus* invasion. Zhoushan Forestry Institute had conducted plant community analyses of pine forests in 1992, before the *B. xylophilus* invasion. We selected 24 typical land samples, based on distribution area, and sites, that were close to the 1992 land samples, and conducted vegetation surveys between July and September 2010 to determine the plant community structure. This study targeted pure *P. massoniana* or *P. thunbergii* forests, mixed forests of *P. thunbergii* and *P. massoniana*, and mixed forests of either *P. massoniana* or *P. thunbergii* and broadleaf trees. We revisited the forest land samples studied by the Zhoushan Forestry Institute in 1992 and compared the new data of 2010 with historical data. Land samples containing pine trees after a *B. xylophilus* invasion were selected for this investigation, which consisted of an analysis of the forest community structure after 18 years of natural restoration by considering the characteristics of local plant species.

In the early stages of this study, we also found that Zhoushan City had adopted physical control measures for pine wilt disease, including the cutting and removal of damaged trees, before and after 1995. After repeated cutting and removal of the trees at different stages, they were allowed to regenerate naturally. At present, the restored secondary forests in areas where trees had been cleared due to a *B. xylophilus* invasion have a high plant density, many small-diameter trees, and a low regeneration capacity. These results indicate that after a *B. xylophilus* invasion, the qualities of *P. massoniana* and *P. thunbergii* are significantly different within different communities. Regardless of the outcome of restoration, to promote the rapid recovery of damaged pine forests caused by an invasion, the key factors that affect the restoration direction and tree growth within all types of plant communities must first be identified. These factors (e.g., soil and light) are the main controlling factors that affect the direction of pine forest system regeneration and restoration after an invasion by *B. xylophilus*. Therefore, based on the analysis of the restoration trends in *P. massoniana* and *P. thunbergii* communities after *B. xylophilus* invasions, this article targets the biological characteristics of the restoration types and regeneration species to further analyze the ‘driving factors’ that lead to various types of restoration. Considering those factors together with the actual conditions of the study region, we propose specific system recovery and transformation strategies.

Materials and Methods

Overview of the Study Region. The Zhoushan Islands are located in the southern part of the mouth of the Yangtze River, between the East China Sea and the outer edge of Hangzhou Bay, at 29° 32′–31° 04′ N, 121° 31′–123° 25′ E. The islands comprise a total land area of 1,440.2 km², made up of 1,390 islands. The majority of the hills on the islands lie at altitudes of <250 m, and they encompass an area on the northern edge of the subtropical monsoon climate zone that is subject to marine influence. Zhoushan Island is the largest of these islands and is also China’s fourth largest island with an area of 502 km². Its highest peak is Huangyangjian, which has an elevation of 503.6 m. The annual average temperature is 16.5°C. The average temperature in the hottest month (August) is 27.3°C, and the average accumulated temperature ≥10°C is 5,120.8°C. The frost-free period is 251 d, the average annual precipitation is 1,351.3 mm, the average annual evaporation amount is 1,470.4 mm, and the average annual relative humidity is 79%. The mountain soils within this area are red soil and skeletal soil (Wang et al. 2011).

Data Collection. According to the 1992 Zhoushan Island vegetation survey data provided by the Zhoushan Forestry Institute, before the damage, most of the pine forests could be classified as one of four types: pure *P. massoniana* forest, pure *P. thunbergii* forest, mixed *P. massoniana* and broadleaf (generally *Liquidambar formosana* and *Quercus fabri*) forest, and mixed *P. thunbergii* and broadleaf forest. The regeneration layer of the tree species in these forests consists mostly of *Q. fabri*. Based on the existing vegetation and topography of the islands, avoiding the local residential areas, and the distribution area and site, 24 20 m × 20 m typical land samples (summarized in Table 1) in communities that were near to the land samples studied before the invasion (1992) were chosen for analysis. From July to September 2010, the individual species name, diameter at breast height (DBH), tree height, and crown width of the trees with DBH ≥1 cm were recorded. At the same time, 11 environmental factors were measured: seven terrain factors (elevation, slope steepness, slope aspect [AS], slope position [SP], bare rock ratio (BRR), distance from the coast in kilometers, and relative humidity of air in the forest) and four soil factors (soil depth [SD], soil humus depth [HD], soil pH, and soil moisture [SM]).

Data Analysis. Using key values, such as the dominance index of the tree species in the land samples, the importance value (IV) can be calculated according to the following formula (Fang et al. 2009): IV = (relative abundance + relative frequency + relative breast height basal area)/300

Data from the 42 major tree species in the land samples with the greatest IVs were used to establish a species matrix. Following the method of Song et al. (2010), we assigned AS values on a scale of 1–8, 1 = north slope, 2 = northeast slope, 3 = northwest slope, 4 = east slope, 5 = west slope, 6 = southeast slope, 7 = southwest slope, and 8 = south slope, where higher values correspond to more sunlight and hotter and drier conditions. The SP values are as follows: 0 = low-lying land, 1 = at the bottom of a slope, 2 = below the middle of the slope, 3 = in the middle of the slope, 4 = above the middle of the slope, 5 = the top of the slope, and 6 = at the peak.

The 11 environmental factors described above were used to establish an environmental matrix, using the two-way indicator analysis method (Bowman and Fensham 1991, Vermeerscha et al. 2003, Zhang 2011) and canonical correspondence analysis (CCA) (Chen 1992, Jiang et al. 1994, Gao and Zhang 2010, Liu et al. 2010) to classify the number of communities.

In ecological studies, with several samples, biserial correlation analysis is often used for studying the correlation between the presence of a species and environmental factors (Broegden 1949). For each sample, the existence of tree species (present as 1, absent as 0) and the values of the environmental factors are recorded. Then, the double series correlation coefficients are used to describe the correlation between the species and environmental factors. At this time, the environmental factors are divided into two groups based on the presence of species. The biserial correlation coefficients are calculated as follows:

$$r_p = \frac{|M_p - M_q|}{S_x} \sqrt{p \times q}$$

where r_p is the biserial correlation coefficient, M_p and M_q are the average values of the two groups p and q , S_x is the standard deviation, and p and q represent the ratio of the number of observations of the two groups. A t -test can be used to test the significance of the coefficient.

The CANOCO for Windows 4.5 software was used for the CCA (Leps and Smilauer 2003, Peres-Neto et al. 2006). The remaining data analysis was performed using the R software ‘vegan’ package.

Results

Quantitative Classification of the Communities. To determine the tree species classification on Zhoushan Island based on the IV matrix of

Table 1. Land sample characteristics

Land sample No.	Forest origin	Elevation (m)	Slope steepness (°)	AS (°)	SP	Crown density	Plant density (DBH ≥ 1 cm, plants/ha)
S1	<i>Pinus massoniana</i> and broadleaf trees	53	14	144	Below middle	0.79	7,900
S2	<i>P. massoniana</i> and broadleaf trees	81	20	150	Middle	0.75	6,400
S3	<i>P. massoniana</i> and broadleaf trees	80	21	23	Middle	0.71	8,775
S4	Pure <i>P. massoniana</i>	54	26	40	Middle	0.84	12,450
S5	Pure <i>P. massoniana</i>	57	24	303	Middle	0.72	11,800
S6	Pure <i>P. massoniana</i>	64	26	266	Middle	0.57	3,075
S7	Pure <i>P. massoniana</i>	138	18	358	Below the peak	0.41	9,150
S8	Pure <i>P. massoniana</i>	109	12	91	Below	0.89	7,400
S9	Pure <i>P. massoniana</i>	92	14	87	Middle	0.63	13,650
S10	Pure <i>P. massoniana</i>	113	10	205	Middle	0.62	3,875
S11	Pure <i>P. massoniana</i>	45	20	295	Below middle	0.85	12,425
S12	Pure <i>P. massoniana</i>	69	20	164	Middle	0.87	11,775
S13	Pure <i>P. massoniana</i>	71	18	273	Middle	0.83	12,775
S14	Pure <i>P. massoniana</i>	84	22	119	Middle	0.82	13,400
S15	Pure <i>P. massoniana</i>	27	19	78	Below middle	0.74	13,800
S16	Pure <i>P. massoniana</i>	144	32	234	Middle	0.79	7,200
S17	Pure <i>P. massoniana</i>	154	29	234	Above middle	0.76	10,300
S18	Pure <i>P. thunbergii</i>	78	12	241	Middle	0.31	650
S19	Pure <i>P. thunbergii</i>	92	23	23	Middle	0.96	5,325
S20	Pure <i>P. thunbergii</i>	99	36	36	Middle	0.94	5,600
S21	Pure <i>P. thunbergii</i>	87	42	14	Above middle	0.63	8,750
S22	Pure <i>P. thunbergii</i>	65	39	14	Below middle	0.68	2,350
S23	Pure <i>P. thunbergii</i>	77	30	32	Middle	0.58	6,750
S24	Pure <i>P. massoniana</i>	80	37	110	Above middle	0.69	6,425

woody plants with DBH values ≥ 1 cm in all of the land samples, two-way indicator species analysis (TWINSPAN) was used for the hierarchical classification of the 24 land samples. Values of 0, 0.1, 0.2, 0.4, 0.6, and 1.0 were selected as the cutting levels of the species. TWINSPAN resulted in the division of the 24 land samples into nine groups (Fig. 1). In the second level, the present forest was divided into coniferous and broadleaf forests. The third level reflects the overall characteristics of the secondary forest formed on Zhoushan Island after damage by *B. xylophilus*. But according to the actual vegetation data obtained by the typical investigated community conditions, and taking into account the continuity of space, group 8 was merged with group 7. Considering the recovery characteristics after pine wood nematode interference, a fourth level was chosen to divide the 24 typical land samples into seven groups, as follows.

1. Pure *P. massoniana* forests (land samples 5 and 6). This type of community originally consisted of *P. massoniana* forests and transformed into secondary pine forests after being damaged by *B. xylophilus*. It is mostly distributed in the relatively poor soil in the mountain or hilltop areas along the coast. The average DBH of *P. massoniana* in these forests is 5.6 cm, and broadleaf trees, such as *Q. fabri*, *P. thunbergii*, and *Platycarya strobilacea*, are sparsely scattered. The young trees and seedlings of *P. massoniana* form the majority of the newer layer. *Loropetalum chinensis* is very dense in the understory. Overall, this group is a type of typical subtropical pine forest with *P. massoniana* as the pioneer species.
2. *P. massoniana* and *Q. fabri* forests (land samples 4, 11, and 13). This type of community originated from pure *P. massoniana* forests that received less damage from *B. xylophilus*. After selectively cutting and removing damaged trees, the original *P. massoniana* forests were partially preserved, but no seedlings were distributed. The average DBH of *P. massoniana* in this type of forest is 8.7 cm. This type of forest is mostly located on the lower slopes at lower altitudes and has a thicker soil layer, allowing the understory *Q. fabri* seedlings to grow rapidly and potentially become the primary species of the canopy. However, *P. massoniana* still has a dominant position. The shrubs in this forest type are mainly *L. chinensis* and *Rhododendron simsii*. This type of forest is the main pine forest type on Zhoushan Island.

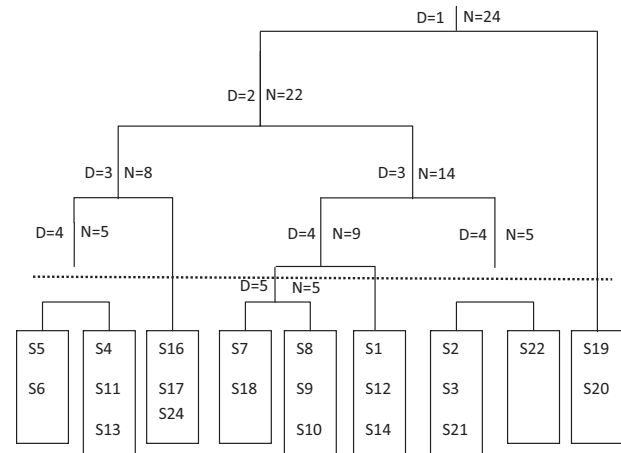


Fig. 1. Tree diagram of TWINSPAN classification of land samples. D represents the level of classification; N represents the number of land samples.

3. Miscellaneous hardwood and *P. massoniana* forests (land samples 16, 17, and 24). This type of community originated as pure *P. massoniana* forests, but *P. massoniana* has lost the dominant position in the canopy and has been replaced by the local broadleaf trees, such as *L. formosana*, *Ilex purpurea*, and *Albizia julibrissin*, as well as dominant shrubs. This type of forest is mainly distributed in the mountain areas far from the coast. It receives ample sunlight and has a thick humus soil layer.
4. *Q. fabri* and miscellaneous wood forests (land samples 7, 8, 9, 10, and 18). This type of community originated as pure *P. massoniana* forests or pure *P. thunbergii* forests. When *P. massoniana* or *P. thunbergii* became sparse, *Q. fabri* became the dominant species in the community and formed broadleaf mixed forests with dominant accompanying species, such as *A. julibrissin*, *Ficus erecta* var. *beecheana*, and *P. chinensis*. The shrubs in the understory are mostly *R. simsii* and *L. chinensis*.
5. *Q. fabri* and *L. formosana* forests (land samples 1, 12, 14, and 15). This type of community no longer includes coniferous tree species

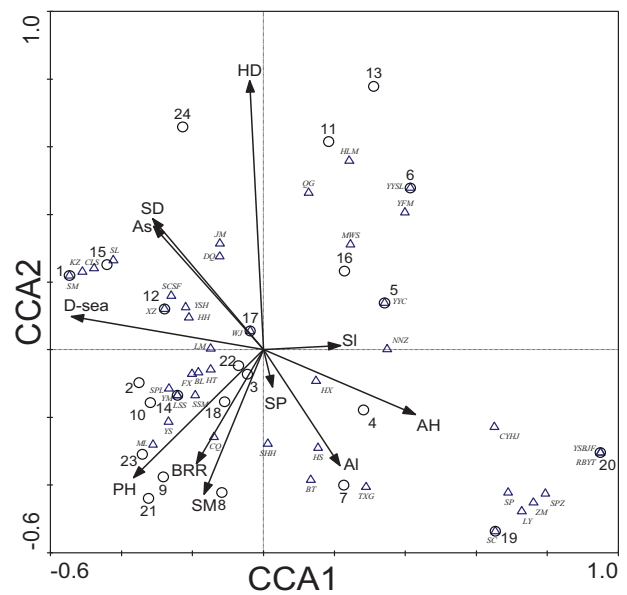
and evolved from the original pine forest after the repeated clearance of damaged trees. Because the local common species *L. formosana* and *Q. fabri* grew more quickly, they have become the main species of the canopy and were sometimes mixed with deciduous broadleaf species such as *Cyclobalanopsis glauca*, *Symplocos setchuenensis*, and *Styrax confusus*. The tree layer in this community also includes scattered evergreen species, such as *Castanopsis sclerophylla* and *I. purpurea*. It is a type of transition forest between deciduous broadleaf forests and evergreen broadleaf forests.

6. *Quercus variabilis* and *L. formosana* forest (land samples 2, 3, 21, 22, and 23). The original forests associated with this type of community included *P. massoniana*–broadleaf mixed forests or *P. thunbergii*–broadleaf mixed forests. After the conifers were damaged and removed, the original mixed broadleaf tree species, such as *Q. variabilis*, *L. formosana*, and *Q. acutissima*, rapidly grew into large trees with heights of 8–12 m. The major accompanying species are *Q. fabri*, *A. julibrissin*, and *Dalbergia hupeana*. The shrubs in the understory are mostly *Symplocos paniculata*, *R. simsi*, and *L. chinensis*.

7. *Celtis sinensis* and *A. julibrissin* forest (land samples 19 and 20). The original forest of this community was pure *P. thunbergii* forest and was mostly located along the coast of the northern island, which has characteristics such as poor light, high relative humidity, and an abundance of shrubs and grasses. After *P. thunbergii* were damaged and removed, the original forest evolved into a deciduous broadleaf forest with *C. sinensis*, *A. julibrissin*, and *F. erecta* var. *beecheiana* as the main tree species and broadleaf trees, such as *Ulmus parvifolia*, *Cudrania tricuspidata*, and *Zanthoxylum ailanthoides*, as the accompanying species. The shrubs in the understory are mostly *Elaeagnus umbellata* and *Camellia japonica*.

Community Ordination and Environmental Interpretation. To study the correlation between the spatial distribution of species and environmental factors, a 24 × 42 species matrix and a 24 × 11 environmental matrix were used for CCA ordination (Fig. 2). This diagram directly reflects the impact of all of the environmental factors on species distribution and the correlation among the environmental factors, which are represented in the figure as line segments with arrows. The quadrant of the arrow's location indicates the positive or negative correlation between the environmental factors and the ordination axis. The length of the connecting line represents the degree of correlation between the environmental factor and the species distribution; the longer the connecting line, the greater the correlation. The angle between the connecting line and the ordination axis represents the correlation between that environmental factor and the ordination axis; the smaller the angle, the greater the correlation. The closer a species is to the land sample, the greater weight the species has in that quadrant (Lai and Mi 2010). It can be observed from the figure that HD has the longest line segment and forms the smallest angle with the second axis, indicating that HD is the most important factor affecting species distribution. Other factors as SD, AS, distance to sea in kilometers (D-sea), soil pH (PH), and air humidity (AH) have the next greatest impact on species distribution, followed by the altitude (AI) and SM. The slope (SI) and SP have minimal impact. The relative strength of these factors is related to the fact that the majority of Zhoushan Island is made up of low hills. In addition, the colinearities of two pairs of factors, namely the SD and AS and the BRR and SM, were found to be more significant.

The results showed that environmental factors explain 56.83% of the species data. This result, along with the results of the CCA, was used to conduct a Monte Carlo permutation test (999 times) to determine whether the explanatory level of the 11 environmental factors on the species distribution was significant. The results revealed a significance of 0.008, indicating that the ordination results were within the explanatory level. Furthermore, correlation coefficient and significance tests were conducted on the environmental factors on the first two axes of the ordination axes (CCA1, CCA2). The results (Table 2) showed



MWS	<i>Pinus massoniana</i>	LM	<i>Eurya japonica</i>
BL	<i>Quercus fabri</i>	CLS	<i>Evodia fargesii</i>
FX	<i>Liquidambar</i>	YFM	<i>Rhus chinensis</i>
SPL	<i>Quercus variabilis</i>	LSS	<i>Symplocos stellaris</i>
ML	<i>Quercus acutissima</i>	LY	<i>Ulmus parvifolia</i>
SHH	<i>Albizia kalkora</i>	HH	<i>Albizia julibrissin</i>
HS	<i>Pinus thunbergii</i>	SM	<i>Cunninghamia lanceolata</i>
SSM	<i>Styrax confusus</i>	YYC	<i>Euscaphis japonica</i>
SYHJ	<i>Zanthoxylum</i>	YYSL	<i>Photinia parvifolia</i>
SP	<i>Celtis sinensis</i>	HLM	<i>Pistacia chinensis</i>
CO	<i>Kalopanax septemlobus</i>	XZ	<i>Cinnamomum camphora</i>
HX	<i>Platycarva strobilacea</i>	ZM	<i>Cudrania tricuspidata</i>
BT	<i>Symplocos paniculata</i>	RBYT	<i>Mallotus japonicus</i> var.
HT	<i>Dalbergia hupeana</i>	KZ	<i>Castanopsis sclerophylla</i>
YS	<i>Diospyros morrisiana</i>	YSH	<i>Rhododendron simsii</i>
SL	<i>Lithocarpus glabra</i>	SC	<i>Camellia japonica</i>
DO	<i>Ilex purpurea</i>	SPZ	<i>Glochidion uberum</i>
JM	<i>Loropetalum chinensis</i>	NNZ	<i>Elaeagnus umbellata</i>
OG	<i>Cyclobalanopsis glauca</i>	YM	<i>Myrica rubra</i>
SCSF	<i>Symplocos</i>	TXG	<i>Ficus erecta</i> var.
YSBJF	<i>Alangium kurzii</i> var.	WJ	<i>Sapium sebiferum</i>

Fig. 2. CCA ordination map.

Table 2. Test of environmental factor significance

Environmental factor	CCA1	CCA2	r ²	Pr (>r)
SD	-0.723	0.691	0.333	0.025*
HD	-0.025	1.000	0.379	0.008**
PH	-0.782	-0.623	0.363	0.019*
SM	0.953	-0.302	0.137	0.184
AH	-0.476	-0.880	0.174	0.159
AI	0.626	-0.780	0.084	0.272
SI	0.997	0.073	0.097	0.629
AS	-0.741	0.671	0.338	0.024*
SP	0.264	-0.965	0.005	0.915
BRR	-0.602	-0.798	0.275	0.250
D-sea	-0.994	0.111	0.351	0.031*

**P < 0.01; *P < 0.05, the same below.

that HD is a very significant impact factor, while PH, SD, AS, and D-sea are significant impact factors. These results could be explained by the fact that the community is still in the initial stages of restoration of the pioneer species.

Impact of Environmental Variables on Species Distribution Patterns. To further study the impact of environmental factors on the spatial distribution of species populations, explanatory variables (soil and geological factors) were used for quantitative segmentation of environmental variables (Liu et al. 2006, Zhang et al. 2008). The total

eigenvalue of the corresponding species matrix analysis was 4.531. The canonical eigenvalue of the species under the constraints of the 11 environmental variables was 2.575; the individual explanatory power of the soil factors on the spatial distribution of the species was 18.54%, and the individual explanatory power of the geological factors on the spatial distribution of the species was 33.43%. The common explainable section of the interaction between the two was 4.95%, and the explainable section was 43.17%. The results are shown using a Venn diagram (Fig. 3).

Analysis of the Effects of Environmental Factors on Species Distribution. To better explain the level of influence of environmental factors on the spatial distribution of the tree-layer woody plants on Zhoushan Island and to identify the factor that has the largest role in determining the different types of restorations, a biserial correlation analysis of species and environmental factors was conducted. According to the integrated consideration of the occurrence frequency and the IVs of species in the 24 land samples, 12 major tree species out of 42 species of woody plants were selected and analyzed in terms of the 11 environmental factors using biserial correlation analysis. The results (Table 3) show that the SP ($P=0.049$) and the spatial distribution of *P. thunbergii* had a significant negative correlation; SD ($P=0.018$), HD ($P=0.012$), and the spatial distribution of *F. erecta var. beecheyana* had a significant positive correlation; the impact of the AS on spatial distribution was significant ($P=0.007$); the AS ($P=0.050$) and the spatial distribution of *D. hupeana* had a significant positive correlation; PH ($P=0.044$) and the spatial distribution of *I. purpurea* had a significant positive correlation; BRR ($P=0.032$) and the spatial distribution of *L. chinensis* had a significant positive correlation; BRR ($P=0.032$) and the spatial distribution of *C. glauca* had a significant positive correlation; and PH ($P=0.039$) and the spatial distribution of *S. setchuenensis* had a significant positive correlation. Another five environmental factors, namely SM, AH, AI, SI, and D-sea, correlated with the spatial distribution of species, but the test results showed that these correlations were not significant.

From the biserial correlation analysis of the tree species and the environmental factors (Table 3), it can be seen that the spatial distribution characteristics of tree species such as *P. massoniana*, *Q. fabri*, and

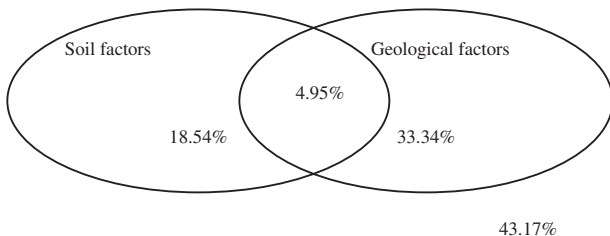


Fig. 3. Venn diagram of the quantitative segmentation of environmental variables.

L. formosana, which have pioneer characteristics, including attraction to sunlight and drought resistance, were negatively correlated with environmental factors such as SD, HD, and AI, while tree species that placed higher demands on the soil environment, such as *F. erecta var. beecheyana*, *A. julibrissin*, *P. thunbergii*, and *D. hupeana*, showed positive correlations with HD. Most of the tree species showed a negative correlation with D-sea, which may be related to the heavy winds along the coast and the relative infertility of the soil, which is not suitable for the growth of the majority of broadleaf tree species. Overall, the changing trends of current species distributions based on the environmental factors were related to the fact that the secondary communities were still in the pioneer stage of restoration.

Discussion and Conclusion

Because completion of the analysis phase of this study, the original pine forests on Zhoushan Island have been restored to the following seven types of secondary forest groups: pure *P. massoniana* forest, *P. massoniana* and *Q. fabri* forest, miscellaneous wood and *P. massoniana* forest, *Q. fabri* and miscellaneous wood forest, *Q. fabric*, and *L. formosana* forest, *Q. variabilis* and *L. formosana* forest, and *A. julibrissin* and *C. sinensis* forest. These results show that the recovery of the pine forest communities with different origins, in different geographic environments, and after sustaining different degrees of damage follows certain predictable paths. In the future, the pine restoration direction can be forecasted to some extent based on this information.

After being affected by *B. xylophilus*, the original pine forests on Zhoushan Island, which have undergone 18 years of natural recovery, have developed from pure conifer forests or conifer–broadleaf mixed forests into multiclass complex forest types, which at present includes pure conifer forests, conifer–broadleaf mixed forests, deciduous broadleaf mixed forests, and evergreen and deciduous broadleaf mixed forests. The community composition and structure tend to become more complicated and can mostly be considered as indicating progress or forward restoration (Lin, 1986). However, some of the land samples, such as S5 and S6, also show backward restoration. From the viewpoint of subtropical natural restoration progress, the *B. xylophilus* interference has accelerated the restoration progress of the Zhoushan Island vegetation communities from coniferous forests to evergreen broadleaf forests (communities of a typical subtropical climate), so the local plant communities have more complexity and stability. However, from another perspective, *B. xylophilus* is indeed a destructive pathogen. *B. xylophilus* invasion can lead to the collapse of fragile ecosystems, which might even restore ‘backwards’ to weeds and shrubs (Shi 2005).

Our survey also found that many human factors have interfered with the natural recovery of damaged pine forests, such as the use of forest land to plant *Myrica rubra*, and a variety of electrical communication transmission equipment has been built on top of the mountain, which had a significant impact on the surrounding plant growth. In the 2010

Table 3. Double-series correlation coefficients between species and environmental factors

Tree specie	SD	HD	PH	SM	AH	AI	SI	AS	SP	BRR	Distance to sea in km D-sea
<i>Pinus massoniana</i>	-0.253	-0.505	0.101	0.083	0.047	-0.192	0.057	-0.048	0.025	0.262	-0.047
<i>Pinus thunbergii</i>	0.002	0.267	-0.088	0.188	0.133	-0.149	-0.047	0.196	-0.530*	-0.097	0.091
<i>Quercus fabri</i>	-0.401	-0.252	-0.196	-0.083	0.094	-0.103	0.351	-0.333	-0.133	0.212	-0.428
<i>Albizia julibrissin</i>	0.055	0.252	-0.333	-0.185	0.151	-0.337	-0.071	0.020	-0.064	-0.113	-0.094
<i>Liquidambar Formosana</i>	-0.224	-0.228	0.117	-0.541	-0.081	-0.112	-0.108	-0.169	0.287	0.050	-0.595
<i>Ficus erecta var. beecheyana</i>	0.428*	0.456*	-0.095	-0.355	-0.370	-0.401	-0.038	0.471**	0.001	-0.431	0.012
<i>Dalbergia hupeana</i>	-0.060	0.187	-0.489	-0.157	0.072	-0.049	-0.177	0.326*	-0.372	-0.091	-0.151
<i>Styrax confusus</i>	-0.210	-0.112	-0.469	-0.259	0.118	-0.045	-0.281	0.037	-0.256	0.052	-0.235
<i>Ilex purpurea</i>	0.074	-0.176	0.290*	-0.024	0.084	-0.153	-0.207	-0.506	-0.067	0.214	-0.339
<i>Loropetalum chinensis</i>	0.000	-0.365	0.222	-0.046	-0.194	0.056	-0.164	-0.301	0.046	0.303*	-0.216
<i>Cyclobalanopsis glauca</i>	0.035	-0.494	0.520*	-0.188	-0.302	0.200	0.115	-0.275	0.141	0.496*	-0.138
<i>S. setchuenensis</i>	-0.063	-0.226	0.366*	-0.241	-0.191	-0.247	-0.072	-0.436	0.030	0.208	-0.370

investigation of Zhoushan Island pine forests, researchers found that the secondary *P. massoniana* and *P. thunbergii* forests formed after the previous *B. xylophilus* invasion were already suffering from varying degrees of *B. xylophilus* damage, indicating that the secondary pine forests face a 'second round' of damage from *B. xylophilus* and that the recovery of pine forest vegetation communities faces a number of volatilities and uncertainties.

After the invasion of *B. xylophilus* and during the restoration of the pine forest, many of the forests sustained damage and degradation. Different degradation systems should be developed to target the formation of different communities after an invasion. Regarding the existing vegetation communities at various phases of degradation, different restoration strategies are required because of the differences in the species composition, structure, propagule bank, and soil matrix condition compared with the control community (Shen et al. 2005).

According to the results of this study, when targeting different communities for restoration, we must take measures based on the local conditions, propose different restoration strategies for pine forests with different degrees of damage, and reduce the negative impact brought by the invasion of *B. xylophilus* to the *P. massoniana* forest system.

Specifically, for the pine forests in areas with a thinner soil layer but thicker humus (which is related to the growth characteristics of *P. massoniana* and *P. thunbergii*), the restoration measures should be as follows: regularly cut off the damaged pine trees and *L. chinensis* in the forests and replant the forest gaps with barren-soil-resistant tree species, such as *Q. fabri*, which frequently accompany local pine trees (such as in groups 1 and 2).

Regarding the pine forests located in areas with a relatively thick soil layer, species such as *Q. fabri* and *L. formosana* should be replanted in the forest. The presence of these local broadleaf tree species along with *P. massoniana* gradually improves the forest soil environment. The changes in conifer–broadleaf mixed forests caused by human activities reduce the risk of destruction by *B. xylophilus* from generation to generation (such as in group 3).

For group 4 and 5 forests, the physical control measure of deforestation was taken after the infestation due to the severe damage present. High levels of germination in the existing forests resulted in a higher plant density in these forests. From the CCA ordination graph, we can see that these land samples, which are located mostly on the sunward side of low-altitude hills within islands, had a high soil pH and a thick soil layer. The recommended recovery measure for this type of pine forest is based on the appropriate thinning of trees to optimize the forest structure and the selective planting of proper tree species to match the land. Because those forests are far from the sea, their restoration could be focused on landscape ecology by planting evergreen tree types such as *Schima superba*, *C. sclerophylla*, and *I. purpurea*. Economically productive forests can also be developed in the forest areas that have a low average age, contain a higher proportion of shrubs, and are close to residential areas (such as S12 and S24). After thinning the forests, the main local economic tree species (Shen 2009), such as *M. rubra* and *Citrus reticulata*, could be planted.

For group 6 and 7 forests, the original communities were pine–broadleaf mixed forests with only a small proportion of pine trees. After the damaged pine trees were removed, the original broadleaf tree species mixed with the rest, such as *Q. variabilis* and *L. formosana*, and rapidly occupied the ecological position left by the removed pine trees, quickly growing into tall trees. The communities evolved into a stable forest structure constituting tall hardwood trees, dominant accompanying tree species, tree seedlings, and saplings. It is suggested that this type of pine forest does not require special recovery and reform measures. Closing the forest to harvesting and simply allowing the trees to grow while also monitoring pest infestation are necessary steps to enforce forest orientation recovery.

Another important aspect of this study was that CCA was conducted to analyze 11 environmental factors, and the results showed that the

explanatory level of the environmental factors regarding the spatial distribution of species was 56.83%, while the parts without explanation accounted for 43.17%. In addition to the unknown environmental factors that have not been considered, the spatial distribution of species in the natural recovery process of the secondary bare land is not only subject to environmental constraints, but also related to the original species in the communities, the surrounding species source, and human intervention. For example, we found that both sides of the village roads 1 km from S16 and S17 were planted with *L. formosana* and that the abundance of *L. formosana* on the mountain on both sides of the roads was significantly inversely proportional to the distance from the road.

Therefore, in terms of the CCA ordination results, the driving factors in the different restoration types of damaged pine forest recovery could be important for the recovery potential of the damaged pine forest vegetation in the future. With this knowledge, we will be able to help the damaged pine forests recover as soon as possible.

For the pine forests with better geographical locations (groups 1 and 2), the main environmental driving factors of restoration were the HD and SD. For the pine forests in other geographical locations (group 3), the main environmental driving factors of restoration were the original species of the communities, the surrounding species, and human intervention. The broadleaf forests with a thick soil layer, sufficient sun, and sufficient water (groups 4 and 5) faced fewer environmental constraints on plant growth and therefore a higher forest density. In these forests, the main environmental driving factors of restoration are competition for space and resources. For the broadleaf forest restored from the conifer–broadleaf mixed forest (group 6), the forest already had tall hardwood trees and a good soil environment. The main environmental driving factors of restoration in this case were the SD, PH, and BRR. Due to its higher northern mountainous terrain, the broadleaf forest located along the coast of the northern island (group 7) has a high canopy density that blocks the strong sea breeze that occurs throughout the year, causing a lack of sunlight and high AH; the main environmental driving factors for its restoration were AH and AI.

Furthermore, ecological issues, such as slow natural recovery of vegetation, large fluctuations of community structure, and forest landscape fragmentation, occurred. External factors, such as the large bridge built in December 2009 to connect Zhoushan Island to mainland China and the establishment of the Zhoushan Island District, approved in July 2011, will strengthen the domestic and international trade of Zhoushan Island. However, the current fragile and unstable ecosystem with its low resistance to potential invasive organisms is worrying. Therefore, the secondary forest that has been developing since the *B. xylophilus* invasion on Zhoushan Island urgently needs to be artificially cultivated and regenerated, and the local ecosystem should be stabilized by classified reformation according to local conditions based on the principle that protection and landscaping should be the major focuses in the management of Zhoushan Island forest resources.

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