Effects of pine wilt disease invasion on soil properties and Masson pine forest communities in the Three Gorges reservoir region, China

Ruihe Gao*, Juan Shi*, Ruifen Huang, Zhuang Wang & Youqing Luo
Beijing Key Laboratory for Forest Pest Control, Beijing Forestry University, Beijing 100083, China

Keywords
Bursaphelenchus xylophilus, invasive alien species, Masson pine, pine wilt disease, soil property, three Gorges reservoir region.

Correspondence
Youqing Luo, Beijing Key Laboratory of Forest Pest Control, Forestry College, Beijing Forestry University, P.O. Box 113, 35 Qinghua East Road, Haidian District, Beijing 100083, China.
Tel:+86-10-62338042; Fax: +86-10-62336302; E-mail: youqingluo@126.com

Funding Information
This study was supported by Special Fund for Forest Scientific Research in the Public Welfare (201204501); National Natural Science Foundation of China (31170613) and Beijing Higher Education Young Elite Teacher Project (YETP0740).

Received: 15 May 2014; Revised: 15 October 2014; Accepted: 21 October 2014

Ecology and Evolution 2015; 5(8): 1702–1716
doi: 10.1002/ece3.1326
*The authors contributed equally to this manuscript.

Abstract
Pine wilt disease (PWD) has caused significant Masson pine mortality in the Three Gorges reservoir region in central China. In this study, five uniform Masson pine stand types infected by PWD were selected and surveyed on slopes and aspects with similar environmental conditions. In sites that had been infected, soil bulk density was reduced, and the difference among the groups was statistically significant (P < 0.05) at the 0–10 cm and 10–20 cm soil layers, but not at 20–40 cm. Other soil water-related physical properties, excluding noncapillary porosity, significantly differed among the groups in all soil layers. Additionally, the values of available phosphorus, sodium, potassium, calcium, and magnesium were higher in the invaded stands, but the total nitrogen and organic matter contents were lower. Masson pine does not become reestablished following PWD-induced mortality but is instead replaced by broad-leaved tree species. Among the 19 examined environmental variables, five were found to be significantly related with the ordination of plant community structure: Masson pine stumps (MPS), K⁺, capillary water holding capacity (CWHC), capillary porosity (CP), and soil water content (SWC). Among these factors, the plant community structure was principally related to MPS and K⁺. The findings of this study show that the outbreak of PWD has impacted Masson pine forest soil properties and altered forest community composition. The disease is negatively related with the presence of Masson pine and positively associated with that of broad-leaved tree species.

Introduction
With the rapid development of international trade, tourism, and transportation, invasive alien species have become increasingly common and pose a great threat to regional biodiversity, ecosystems, and human health (Shi et al. 2010). Invasive alien species have triggered dramatic declines in ecologically important forest tree species, resulting in enormous environmental impacts, the disruption of ecosystem processes, and decreased native species genetic diversity and abundance, as well as variation in population structure and forest community composition (Cohen and Carlton 1998; Curnutt 2000; Ellstrand and Schierenbeck 2000; Daehler and Carino 2001; Hejda et al. 2009; Gandhi and Herms 2010; Hulcr and Dunn 2011). Approximately 488 nonindigenous species are now established in China, including 171 animals, 265 plants, 26 fungi, 3 protists, 11 prokaryotes, and 12 viruses (Xu et al. 2012). The pine wood nematode Bursaphelenchus xylophilus (Steiner and Buhrer) Nickle (Nematoda:
Aphelenchoididae), which originated in North America and causes the destructive pine wilt disease (PWD) (Dropkin et al. 1981; Shi et al. 2007), is identified as the leading forest pest in China (Wan et al. 2005; Shi et al. 2006). Symptoms of PWD include the loss of green color in infected needles, turning them reddish brown while retaining them on the tree (Dropkin et al. 1981). *Bursaphelenchus xylophilus* can be transferred from infected pine trees to healthy ones via its vector, the pine sawyer beetle (*Monochamus alternatus* Hope (Fig. 1)). Once infected, Masson pines (*Pinus massoniana* Lamb.) die within 2–3 months (Hu et al. 2012), and no effective biological or chemical control policies currently exist for PWD in forest ecosystems.

The Three Gorges Project is one of the largest hydropower complex projects in the world. This multiobjective development project has great potential benefits for flood control, power generation, and navigation. The Three Gorges reservoir region is located at the north rim of the mid-subtropical region of central China, where the climate becomes more temperate. The varied topography of the Three Gorges reservoir region provides a sensitive ecological transition zone for its fauna and flora. Masson pine, which is an indispensable forest species in the Three Gorges reservoir region, is widely distributed across 19 southern provinces in China and accounts for approximately 10% of the national total area of forest resources (Chen et al. 1997). The pine is a pioneer tree species for afforestation in South China and plays an important role in wood production, C sequestration, and the provision of ecosystem services (Wilson 1993; Zhang et al. 2006b). Of even greater concern is the severe harm that may occur to these forests by the serious invasion of *B. xylophilus*. Therefore, PWD poses an extremely grave threat to the 5.69 × 10^5 ha^2 of Masson pine forest in the Three Gorges reservoir region, and related problems such as soil erosion, landslides, and high rates of sediment accumulation threaten the ecological security of the Three Gorges Dam.

In China, PWD was first detected in 1982 at Sun Yat-Sen’s Mausoleum in Nanjing. By the end of 2013, this disease had spread to 16 provinces and 178 counties (Fig. 2) (The bulletin of State Forestry Administration 2014). Unfortunately, PWD affects several economic and ecological processes on multiple scales; cutting down a tract of damaged pine trees causes a serious economic loss of forest resources, alters the forest microenvironment, modifies the composition of woodland plant and insect species, and alters the landscape structure (Shi et al. 2007, 2013; Gao et al. 2013). Recommendations for the control of this disease have focused on the direct control of pine bark beetles by felling, debarking, and immediately burning damaged pines (Suzuki 2002). Therefore, the invasion of *B. xylophilus* has caused considerable economic losses to the timber value and economic value of pine forests (Yu et al. 2011). Moreover, the risk of the spread of PWD is increasing due to the high frequency of trade in the global economy, the active domestic economy, and the implementation of several national basic construction projects (Xie et al. 2009; Shi et al. 2013).

Numerous studies are required to devise an effective control system for PWD in affected regions and to prevent its rapid spread. Previous studies of PWD have mainly focused on pine sawyer beetles, host plants, morphological analysis, and molecular biological examination of *B. xylophilus*, etc. (Mamiya 1988; Yoshimura et al. 1999; Gao et al. 2013; Shi et al. 2013). Other studies have examined the relationship between PWD and various environmental factors and soil properties, such as temperature (Mamiya 1988; Yoshimura et al. 1999), light conditions (Mabuhay and Nakagoshi 2012), soil water content (Suzuki and Kiyohara 1978; Miki et al. 2001; Akema and Futai 2005), and soil physicochemical properties (Kim et al. 2010; Mabuhay and Nakagoshi 2012). Environmental factors influence the spread of PWD (Mabuhay and Nakagoshi 2012), and soil conditions can be altered when drastic variations of forest structure occur due to the invasion of *B. xylophilus*. Research into the changes of soil properties is critical for understanding the ecological consequences of vegetation recovery (Makeschin 1994; Paniagua et al. 1999). Yet, how the effects of PWD on forest plant community structure and soil properties vary depending on the invasion of the disease remains relatively unexplored. Therefore, it is vital to examine the changes in soil conditions in forest stands that have suffered infection by PWD.

Biological disturbances due to exotic pathogens and insects can result in the selective loss and replacement of

![Figure 1. Pine sawyer beetle (*Monochamus alternatus* Hope) is one of the most important vector of pine wood nematode in China.](image-url)
particular tree species, causing significant changes to ecosystem composition and processes (Castello et al. 1995; Spiegel and Leege 2013). These disturbance effects can be seen at the forest and ecosystem levels; initial changes in tree species composition then affect ecosystem characteristics such as forest structure, productivity, nutrient cycling, soil organic production and turnover, hydrology, and the food web (Lovett et al. 2006). The rapid tree death caused by PWD is likely to cause serious biological disturbances in areas where pine trees were once abundant, because the mortality of pine trees may significantly impact plant population structure, canopy creation, and forest community composition. Several stand-level characteristics change during forest vegetation succession after PWD infection, including light and soil conditions, tree population structure, and the forest community.

The objective of the current study was to investigate the dynamic changes of soil properties and the composition and distribution of plant community structure in various Masson pine forest stands damaged by PWD. We addressed the following questions for damaged Masson pine forest sites in the Three Gorges reservoir region: (1) What are the effects of Masson pine mortality on soil properties? (2) What are the effects of Masson pine mortality on forest composition and community structure? (3) What is the relative importance of different environmental variables in structuring plant populations after infection by the pine wood nematode?

Materials and Methods

Study sites

The study sites were located in the Yiling District (latitude 30°32’–31°28’N, longitude 110°51’–111°39’E), an eastern part of the Three Gorges reservoir region containing the demarcation point of the upper and middle reaches of the Yangtze River (Fig. 3). This area has an eastern mid-subtropical monsoon climate, with a mean annual precipitation and mean annual temperature of 997–1370 mm and 16.6°C, respectively. Masson pine trees are distributed widely in this region at an altitude of 45–1500 m, reaching from the bank of the Yangtze River to the top of the mountain. *Bursaphelenchus xylophilus* attacked the Masson pines in the Yiling District in 2006; PWD has since spread rapidly, reaching its peak in 2012.

Fifteen Masson pine plots were established with loamy sand soil, the same bedrock type, and same-facing slopes and aspects to minimize spatial variations in the soil properties (Kim et al. 2010). The plots were divided into five stand types: ST1 was an uninfected control, while ST2, ST3, ST4, and ST5 had all been infected by PWD and contained 2.67, 4.33, 6.67, and 8.50 Masson pine stumps per 100 m², respectively. Three permanent 30 m × 30 m Masson pine forest plots were established on separate sites for each of the stand types in this study (Table 1). Selective cutting of infected and dead pine trees
was conducted every winter after the appearance of PWD in the infected Masson pine forest plots.

Field surveys

Field surveys were conducted in 12 infested plots and three control plots to collect tree data for all trees with a diameter at breast height (DBH) ≥ 2.5 cm, including species name, tree height, DBH, and status (live or dead). In addition, environmental factors such as altitude and slope were recorded. As infected Masson pine trees had been cut down in the infected plots, the quantity of cut stumps was measured to calculate the damage rate.

Soil sample collection and processing

Soil samples were collected for physical and chemical analyses by digging soil pits at five randomly selected points in each plot. Using the cutting ring method (ring = 100 cm³), soil samples were collected at 0–10 cm, 10–20 cm, and 20–40 cm in depth and then taken to the laboratory to be measured for water-related physical properties. Soil particle size distribution was determined through a hydrometer method. Soil bulk density (BD, g/cm³) samples were dried at 105°C to measure bulk density. The soil water content (SWC, %) was measured from the mass loss after oven drying the samples at 105°C for 48 h to a constant weight. The natural state of the soils, along with the cutting rings, was weighed (m₁, g) after soaking for 12 h in water to estimate the maximum water holding capacity (MWHC, %). The cutting rings were then placed on dry sand for 2 h, allowing the nonpore water to be completely drained, then weighed (m₂, g) and used to calculate the capillary water holding capacity (CWHC, %). Finally, the soil was sampled from the cutting rings and dried in an aluminum box to a constant weight (m₀, g). The equations of maximum water holding capacity, capillary water holding capacity, capillary porosity (CP, %), noncapillary porosity (NP, %), and total porosity (TP, %) were as follow (Zhang and Xu 1986; Zhang et al. 2006a):

\[
MWHC = \frac{m_1 - m_0}{m_0} \times 100\% \quad (1)
\]

\[
CWHC = \frac{m_2 - m_0}{m_0} \times 100\% \quad (2)
\]

\[
CP = CWHC \times BD \quad (3)
\]

\[
NP = (MWHC - CWHC) \times BD \quad (4)
\]

\[
TP = CP + NP \quad (5)
\]

For chemical analyses, soil samples were collected from 0–40 cm in depth and then mixed and homoge-
nized; rocks, litter, and other large particles were removed manually. The soil was then air-dried, ground, and passed through a 2 mm sieve. Subsamples of soil were stored at 4°C until use. The soil pH level was tested in a 1:5 mixture of soil:DI water using a glass electrode. Soil organic matter (%) was analyzed using the potassium dichromate oxidation method. Total nitrogen (%) was determined using the Kjeldahl nitrogen method. Available phosphorus (%) was monitored with a UV-Vis spectrophotometer (UV-2550, Shimadzu, Kyoto, Japan). Subsamples of soil were analyzed for potassium (%), sodium (%), calcium (%), and magnesium (%) using an atomic absorption spectrophotometer (SpectrAA220, Varian, Australia).

Importance values

Relative density, relative frequency, and relative dominance were summed using the basal area of trees ≥ 2.5 cm in DBH to calculate the importance value (IV) for each woody species in the five stand types. The following formula was used to calculate the IV for each tree layer (Spiegel and Leege 2013):

\[
IV(\%) = \frac{(\text{Relative density} + \text{Relative frequency} + \text{Relative dominance})}{3}
\]

where relative density = (absolute density for species \(i\) \(\times\) of density for all species) \(\times\) 100; relative frequency = (absolute frequency for species \(i\) \(\times\) of freq. for all species) \(\times\) 100; relative dominance = (absolute dominance for species \(i\) \(\times\) of dom. for all species) \(\times\) 100.

Data analysis

Analysis of covariance (ANCOVA) was conducted among the means of the soil chemical and physical parameters in the different stand types. The least significant difference (LSD) test at the \(P < 0.05\) level was used to compare the means of the soil parameters when the results of the ANOVA were significant at the \(P < 0.05\) level. All of the statistical analyses were performed using SPSS 18.0 for Windows, SPSS Inc., Chicago, IL, USA.

The variation in plant or animal populations along a series of environmental variables can be analyzed through the method of ordination (Lepš and Šmilauer 2003). Redundancy analysis (RDA) is a constrained linear form of principal component analysis based on Euclidean distance (Legendre and Legendre 2012). This method provides a direct multivariate statistical tool for identifying the particular factors that influence the composition of community structure among large sets of environmental variables. Relatively few studies have used RDA to relate environmental variables to the distribution of plant or insect community structure in pine forests damaged by PWD. Gao et al. (2013) used woodland environmental variables to analyze the distribution of parasitic insects under different environmental gradients in a Masson pine forest damaged by PWD at Zhoushan Island, Zhejiang Province, in eastern China.

The ordination of the plant community structure among the different stand types was determined using CANOCO 5.0 (Microcomputer Power, Ithaca, NY) according to Ter Braak and Šmilauer (2012). The plant species data (quantity of each tree species, IV > 1.00)
were subjected to logarithm transitions and used as individual response variables. The largest gradient length obtained using detrended correspondence analysis (DCA) was 1.45; therefore, RDA was the most appropriate analytical method (Legend/C20 S and Legend/C20 Smilauer 2003). Based on the field survey and biological measurements, a total of 19 environmental variables were employed in the analysis of plant community structure, including the quantity of Masson pine stumps, slope, altitude, canopy closure, and soil physical and chemical properties (from 0 to 40 cm in depth) of each study site. Based on a Monte Carlo permutation test with 499 iterations, the forward selection procedure was used to determine the most significant environmental variables (P < 0.05) for the ordination of plant community structure, and the selected significant variables were used in the RDA (You et al. 2014).

### Results

**Dynamic changes in soil water-related physical properties and chemical properties**

The soil water-related physical properties varied greatly across the stand types (Table 2). At sites with more broad-leaved tree species, there was a nonsignificant trend toward decreased bulk density. Compared with the control stands (ST1), the value of soil bulk density at the infected stands (ST2, ST3, ST4, and ST5) was lower, and the differences between the groups were statistically significant (P < 0.05) at the 0–10 cm and 10–20 cm soil layers. At sites with *B. xylophilus* infestations, total porosity and capillary porosity were higher in all soil layers (P < 0.05). However, no significant differences were observed for soil noncapillary porosity (P > 0.05). The results also showed that maximum water holding capacity, capillary water holding capacity, and soil water content were higher at the infected sites than at the control sites, and these differences between stand types were significant for all soil layers (P < 0.05).

By contrast, the soil chemical properties were not significantly different among the different stand types (P > 0.05, Table 3). The soil pH was slightly acidic and showed little fluctuation (range from 4.78 to 6.89), with no significant differences observed between the groups. In the infected stands, the levels of available phosphorus, sodium, potassium, calcium, and magnesium were slightly higher than in the control stand. However, the opposite trend was observed for total nitrogen and organic matter.

**Effects of Masson pine mortality on forest composition and community structure**

A total of 37 tree species (DBH ≥ 2.5 cm) in 30 families and 33 genera were identified in the 15 study plots (Table 4). The species with the greatest number of individuals were *P. massoniana*, *Quercus aliena* Blume., *Cinnamomum camphora* (L.) Presl., and *Quercus variabilis* Blume. Only *P. massoniana* and *Q. aliena* were encountered in all sampled plots. Despite the wide variation in the stand composition of the pine ecosystem, *P. massoniana* had the highest IV (49.63%) almost 5.9 times that of the second highest IV (8.41%) observed for *C. camphora* and ranked as the dominant tree species in the study area. *Pinus massoniana* possessed the highest IV at the tree layer, followed by *C. camphora*, *Q. aliena*, *Q. variabilis*, and *Loropetalum chinensis* (R. Br.) Oliver. The remaining...
Table 2. Soil water-related physical properties after different periods of infection by pine wood nematode.

| Soil layer (cm) | Stand type | Bulk density (g/cm³) | Maximum water holding capacity (%) | Capillary water holding capacity (%) | Noncapillary porosity (%) | Capillary porosity (%) | Total soil porosity (%) | Soil water content (%) |
|----------------|------------|---------------------|-----------------------------------|-------------------------------------|--------------------------|-----------------------|------------------------|------------------------|
| 0–10 cm        | ST1        | 1.50 ± 0.10a        | 25.25 ± 2.68a                     | 20.17 ± 1.48a                       | 3.42 ± 1.52a             | 13.53 ± 1.51a         | 16.95 ± 2.44a          | 14.19 ± 2.57a          |
|                | ST2        | 1.49 ± 0.022a       | 30.13 ± 3.34ab                    | 24.90 ± 2.10a                       | 3.49 ± 1.64a             | 16.61 ± 1.66ab        | 20.10 ± 2.46ab         | 16.66 ± 1.49b          |
|                | ST3        | 1.33 ± 0.156b       | 32.85 ± 5.81b                     | 24.97 ± 3.50a                       | 6.88 ± 2.58              | 19.57 ± 4.60b         | 26.46 ± 7.15b          | 14.09 ± 3.36a          |
|                | ST4        | 1.28 ± 0.093b       | 40.27 ± 7.94c                     | 34.84 ± 7.36b                       | 4.29 ± 3.02a             | 27.67 ± 7.58c         | 31.96 ± 8.26c          | 29.63 ± 9.74b          |
|                | ST5        | 1.39 ± 0.122ab      | 33.38 ± 4.27b                     | 23.85 ± 2.98a                       | 6.98 ± 4.13a             | 17.31 ± 3.28ab        | 24.29 ± 4.97b          | 17.75 ± 2.75a          |
|                |            |                     | F-value: 4.247**                   | 7.103**                             | 10.852**                 | 2.508                 | 9.064**                | 6.442**                |
|                |            |                     | P-value: 0.009                     | 0.001                                | 0.068                    | 0.000                 | 0.01                   | 0.000                  |
| 10–20 cm       | ST1        | 1.61 ± 0.078a       | 25.31 ± 3.82a                     | 21.32 ± 3.66a                       | 2.50 ± 1.64a             | 15.88 ± 3.0a          | 16.39 ± 3.93a          | 16.72 ± 2.54a          |
|                | ST2        | 1.43 ± 0.102ab      | 30.89 ± 4.26ab                    | 23.88 ± 1.76ab                      | 5.06 ± 3.43a             | 16.85 ± 2.21ac        | 21.91 ± 4.75ab         | 18.85 ± 3.64a          |
|                | ST3        | 1.49 ± 0.156ab      | 27.52 ± 5.19a                     | 20.91 ± 4.38a                       | 4.56 ± 2.24a             | 14.29 ± 4.38a         | 18.85 ± 5.64a          | 14.36 ± 3.66a          |
|                | ST4        | 1.37 ± 0.126b       | 36.64 ± 6.94b                     | 34.56 ± 7.13c                       | 3.45 ± 0.60a             | 25.74 ± 7.17bc        | 30.92 ± 8.42b          | 24.21 ± 6.35c          |
|                | ST5        | 1.42 ± 0.074b       | 34.26 ± 4.14b                     | 29.31 ± 5.78bc                      | 3.47 ± 1.99a             | 20.77 ± 4.87c         | 24.24 ± 4.04a          | 11.32± 11.23**         |
|                |            |                     | F-value: 3.935*                    | 5.523**                             | 8.539**                  | 2.755                 | 7.253**                | 4.394**                |
|                |            |                     | P-value: 0.013                     | 0.003                                | 0.050                    | 0.001                 | 0.008                  | 0.000                  |
| 20–40 cm       | ST1        | 1.55 ± 0.071a       | 28.05 ± 4.11a                     | 22.24 ± 5.78a                       | 3.79 ± 3.04a             | 14.4 ± 3.99a          | 18.19 ± 3.24a          | 18.35 ± 5.51a          |
|                | ST2        | 1.43 ± 0.023a       | 28.33 ± 1.05a                     | 21.38 ± 3.32a                       | 4.89 ± 2.69a             | 14.93 ± 2.20a         | 19.82 ± 1.06a          | 17.72 ± 2.76a          |
|                | ST3        | 1.52 ± 0.243a       | 28.81 ± 7.92a                     | 23.13 ± 6.58a                       | 4.01 ± 2.55a             | 16.04 ± 6.08a         | 20.05 ± 7.97a          | 14.70 ± 5.30a          |
|                | ST4        | 1.37 ± 0.107a       | 37.01 ± 5.45b                     | 32.77 ± 3.03b                       | 2.53 ± 3.64a             | 24.83 ± 3.29b         | 27.36 ± 6.15b          | 30.52 ± 3.73b          |
|                | ST5        | 1.37 ± 0.076a       | 35.93 ± 4.34b                     | 31.81 ± 3.65b                       | 2.75 ± 0.90a             | 23.73 ± 4.78b         | 26.12 ± 4.13b          | 26.41 ± 1.79b          |
|                |            |                     | F-value: 2.538                     | 4.398**                             | 9.325**                  | 0.747                 | 9.065**                | 3.966**                |
|                |            |                     | P-value: 0.065                     | 0.008                                | 0.569                    | 0.000                 | 0.013                  | 0.000                  |

Values are mean ± SD. For each column, values with different letters are significantly different at P = 0.05.

*p < 0.05; **p < 0.01.
species included Koelreuteria paniculata Laxm., Broussonetia papyrifera (L.) Vent., Elaeocarpus sylvestris (Lour.) Poir., and nine other species that appeared in fewer plots and had lower IV.

Major community structural change occurred over the course of PWD infection and the human cutting of infected trees as B. xylophilus sharply decreased the prevalence of Masson pine in the forest canopy. Results for the IV of live stems (DBH ≥ 2.5 cm) at the tree layer indicated that P. massoniana was the most prevalent species at the control sites (ST1, IV = 67.23%), while after infection, this species showed a sharp decrease in IV (ST2–ST5, IV = 53.61–29.24%). The change in the IV of Masson pine between the control and infested stands shows that Masson pine forest communities have been significantly affected by the invasion of B. xylophilus. Pinus massoniana had the highest IV at the control sites, followed by Q. aliena, R. chinensis, and R. parvifolius (Table 5). As the intensity of PWD damage increased, the importance of P. massoniana decreased at the infection sites. Conversely, the IV of broad-leaved species such as Q. variabilis, L. chinensis, Q. aliena, and C. camphora were higher at infected sites than at control sites (Table 5). This result suggests that these species increased in dominance following the mortality of Masson pine trees.

**Ordination of plant community structure**

Based on Monte Carlo permutation with 499 iterations, five environmental variables were found to be significantly related (P < 0.05) with the ordination of plant community structure through the forward selection procedure in RDA: Masson pine stumps (MPS), K⁺, capillary water holding capacity (CWHC), capillary porosity (CP), and soil water content (SWC) (Lambda-B, Table 6).

As shown by the RDA results in Table 7 (first axis eigenvalue = 0.256 canonical, F-ratio = 1.721, P < 0.05, 499 permutations), nearly half of the variation in plant community structure can be explained through ordination by the five selective environmental variables (sum of the trace of Lambda-B, Table 6). In addition, the first two RDA axes explained 74.1% of the variance in the relationship between plant community structure and the five selective environmental variables; therefore, the analyzed relationships can be considered highly significant. Among the five factors identified in the RDA, the plant community structure was principally related to MPS (F-ratio = 2.95, P < 0.05) and K⁺ (F-ratio = 2.31, P < 0.05), while the other three variables did not significantly contribute to this distribution (Lambda-B, Table 6). Despite its comparatively high marginal effect, SWC (F-ratio = 0.70, P > 0.05) had no significant relationship with plant community structure.

The RDA ordination biplot, with plant community structure and environmental variables along the first two axes, is shown in Fig. 4. MPS, CP, and CWHC were positively associated with the growth of broad-leaved tree species C. camphora, R. chinensis, Cotinus coggygria Scop., Q. aliena, and Albizia kalkora (Roxb.) Prain, but were negatively associated with that of L. chinensis, R. typhina, and Symplocos sumuntia Buch. As revealed by the ordination graph, some species were clearly associated with higher soil water content, such as Litsea cubeba (Lour.) Pers., C. camphora, and R. chinensis. K⁺ was positively associated with the distribution of Q. variabilis and Trachycarpus fortunei (Hook.) H. Wendl. The RDA ordination graph indicates that MPS, K⁺, and SWC were negatively associated with the growth and spatial distribution of P. massoniana. Simultaneously, many plant species were apparently unassociated with any of the five dominant environmental variables (Fig. 3).

**Discussion**

In recent years, B. xylophilus has seriously invaded the Three Gorges reservoir region. Many studies have demonstrated that a large disturbance, especially by an invasive plant or animal, can alter the vegetation succession pattern, damage the native ecosystem, and homogenize local biodiversity (Fujihara 1997; Fujihara et al. 2002; Conner et al. 2005). The basic conditions of the pine forest, such as stand structure, microclimate, and soil moisture and nutrient conditions, different between the control stand and the stands that had been harvested after infection with PWD. To explore the influence of PWD on the ecosystem in the Three Gorges reservoir region, this study examined the soil water-related physical and chemical properties and the plant community structure of Masson pine forest stands after infection by PWD. We determined that the stand structure was significantly different after infection and that the disturbance associated with PWD stands was important for enhancing species diversity, especially the number of deciduous species (Sakamoto et al. 2003). The recovery of vegetation and emergence of abundant woody plants causes soil property changes, such as reduced soil bulk density, that seem to increase soil aggregate stability and saturated hydraulic conductivity (Li and Shao 2006). Our study was in accordance with these previous conclusions, indicating differences in the soil properties and the composition and distribution of the plant community in Masson pine forest stands after infection by PWD.

Soil water-related physical properties are key determinants of soil fertility and soil water conservation capacity. Soil bulk density is the ratio of soil mass to the bulk or macroscopic volume of soil particles and pore spaces in a
Table 3. Soil chemical properties after different periods of infection by pine wood nematode.

| Stand type | Total N (%) | Organic matter (%) | Soil pH (5:1) | Available P (mg/kg) | K⁺ (mg/kg) | Na⁺ (mg/kg) | Ca²⁺ (mg/kg) | Mg²⁺ (mg/kg) |
|------------|-------------|--------------------|--------------|--------------------|------------|-------------|--------------|-------------|
| ST 1       | Mean 0.13 ± 0.031a | 2.53 ± 0.427a | 5.15 ± 0.375a | 17.92 ± 0.699a | 163.11 ± 39.138a | 48.95 ± 7.641a | 1695.96 ± 820.095a | 21.71 ± 3.646a |
|            | Range 0.11–0.16 | 2.25–3.02 | 4.78–5.53 | 17.52–18.73 | 117.97–187.52 | 41.74–56.96 | 773.53–2342.65 | 17.59–23.04 |
| ST 2       | Mean 0.12 ± 0.004a | 2.67 ± 0.332a | 5.31 ± 0.112a | 15.34 ± 3.352a | 178.89 ± 0.944ab | 52.8 ± 5.119a | 1487.69 ± 550.722a | 22.01 ± 0.577a |
|            | Range 0.11–0.13 | 2.28–2.89 | 5.22–5.43 | 11.48–17.52 | 178.28–179.98 | 47.4–57.58 | 1081.62–2114.55 | 21.41–22.56 |
| ST 3       | Mean 0.14 ± 0.059a | 4.08 ± 1.827a | 5.80 ± 0.958a | 18.73 ± 5.539a | 173.42 ± 30.609ab | 44.86 ± 3.373a | 1903.18 ± 618.018a | 23.14 ± 1.141a |
|            | Range 0.11–0.21 | 2.66–6.14 | 5.08–6.89 | 13.89–24.77 | 142.02–203.17 | 42.41–48.71 | 1208.82–2574.26 | 22.07–24.34 |
| ST 4       | Mean 0.09 ± 0.016a | 2.39 ± 0.530a | 5.46 ± 0.285a | 15.91 ± 3.045a | 192.93 ± 9.793ab | 57.29 ± 7.740a | 2536.77 ± 802.410a | 23.27 ± 0.569a |
|            | Range 0.07–0.10 | 1.93–2.97 | 5.17–5.74 | 12.68–18.73 | 183.74–203.23 | 48.84–64.04 | 1627.21–3144.49 | 22.83–23.91 |
| ST 5       | Mean 0.12 ± 0.014a | 2.45 ± 0.544a | 5.14 ± 0.185a | 18.02 ± 0.699a | 209.41 ± 22.058b | 73.45 ± 41.151a | 2129.29 ± 674.501a | 23.86 ± 1.105a |
|            | Range 0.11–0.13 | 1.83–2.86 | 4.96–5.33 | 17.52–18.93 | 185.97–229.76 | 48.08–120.93 | 1682.35–2905.15 | 22.65–24.82 |

F-value 1.198 | 1.789 | 0.950 | 0.611 | 1.596 | 0.991 | 0.969 | 0.739
P-value 0.37 | 0.208 | 0.475 | 0.644 | 0.25 | 0.456 | 0.466 | 0.586

Values are mean ± SD. For each column, values with different letters are significantly different at P = 0.05.
soil bulk density at the 0–10 cm soil layer, which may occur due to the greater instability of the soil structure caused by the recovery of vegetation and emergence of abundant woody plants after cutting infected trees in the Masson pine ecosystem (Li and Shao 2006). In addition, the differences among the groups were statistically significant in all soil layers (P < 0.05) but were not significant at 20–40 cm (P > 0.05). These results indicate that outbreaks of PWD can significantly reduce soil bulk density at the 0–20 cm soil layer, which may occur due to the greater instability of the soil structure caused by the recovery of vegetation and emergence of abundant woody plants after cutting infected trees in the Masson pine ecosystem (Li and Shao 2006).

Soil porosity, including capillary porosity (pore size < 0.1 mm) and noncapillary porosity (pore size ≥ 0.1 mm), refers to the amount of soil pores that can be filled by water or air and is closely related to soil physical behavior and root penetration (Pagliai and Vignozzi 2002; Sasal et al. 2006; Tangyan et al. 2009). This factor is the most critical determinant of the movement of water into the soil and is closely related to soil aeration and water permeability (Diaz and Nortcliff 1985; Berger and Hager 2000). In this study, the changes of soil structure were more significant for soil total porosity and capillary porosity than for noncapillary porosity. The value of soil noncapillary porosity fluctuated, but no obvious change was observed between control and infected stands. However, the values of soil total porosity and capillary porosity were higher in the infected sands, and differences in these factors were significant among the groups (P < 0.05). Greater porosity contributes to the effective infiltration of precipitation and the aeration of soil (Li and Shao 2006), benefitting the growth of plant root systems and plant community succession. Along with the greater total soil porosity at the infected sites, other soil water-related physical properties, including maximum water holding capacity, capillary water holding capacity, and soil water content, were also greater, and the differences between the stand types were significant in all soil layers (P < 0.05). The differences in soil water-related physical properties according to PWD damage may be attributed to the complex responses of PWD incidence to temperature and differences in the condition of organic matter (Yoshimura et al. 1999; Kim et al. 2010; Jeong et al. 2013).

Table 4. Important tree species with importance value (IV) over 0.50 in Masson pine forest.

| Species                  | Number of individuals | Number of plots | Total basal area (m²) | DBH (cm) | Height (m) | Crown breadth (m²) | Importance value (%) |
|--------------------------|-----------------------|-----------------|-----------------------|----------|------------|-------------------|----------------------|
| Pinus massoniana         | 1187                  | 15              | 22.82                 | 12.89 ± 8.90 | 10.41 ± 2.61 | 16.92 ± 16.61     | 49.63                |
| Cinnamomum camphora      | 160                   | 9               | 3.29                  | 13.89 ± 9.81 | 9.12 ± 2.37  | 28.82 ± 13.45     | 8.41                 |
| Quercus aliena           | 202                   | 15              | 0.75                  | 5.85 ± 3.59  | 5.35 ± 2.43  | 10.81 ± 10.22     | 7.39                 |
| Quercus variabilis       | 116                   | 13              | 0.54                  | 6.93 ± 3.33  | 5.57 ± 1.95  | 11.98 ± 8.38      | 5.3                  |
| Loropetalum chinensis    | 92                    | 12              | 0.22                  | 4.98 ± 2.39  | 5.69 ± 1.83  | 17.87 ± 10.51     | 4.31                 |
| Rhus chinensis           | 37                    | 7               | 0.19                  | 4.72 ± 3.14  | 4.25 ± 1.66  | 9.89 ± 13.94      | 2.31                 |
| Celtis bungeana          | 18                    | 8               | 0.03                  | 4.09 ± 1.43  | 4.36 ± 1.56  | 8.55 ± 5.06       | 2.02                 |
| Trachycarpus fortunei    | 13                    | 6               | 0.08                  | 8.64 ± 2.38  | 2.96 ± 1.13  | 12.69 ± 18.56     | 1.58                 |
| Cotinus coggygria        | 11                    | 6               | 0.02                  | 4.6 ± 1.35   | 3.69 ± 1.31  | 6.79 ± 4.26       | 1.47                 |
| Litsea cubeba            | 9                     | 6               | 0.02                  | 4.46 ± 1.65  | 3.56 ± 1.72  | 6.29 ± 2.98       | 1.44                 |
| Symlocos paniculata      | 11                    | 5               | 0.01                  | 3.61 ± 0.94  | 3.43 ± 0.84  | 6.65 ± 4.60       | 1.25                 |
| Rhus typhina             | 20                    | 4               | 0.03                  | 4.33 ± 1.35  | 5.61 ± 1.69  | 11.63 ± 7.99      | 1.12                 |
| Dalbergia hupeana        | 30                    | 3               | 0.05                  | 4.17 ± 1.50  | 3.66 ± 1.46  | 6.07 ± 6.76       | 1.19                 |
| Illex cornuta            | 6                     | 5               | 0.01                  | 3.43 ± 0.85  | 2.98 ± 0.71  | 3.65 ± 1.84       | 1.17                 |
| Albizia kalkora          | 10                    | 4               | 0.11                  | 7.99 ± 7.63  | 5.12 ± 3.41  | 9.16 ± 9.12       | 1.14                 |
| Symlocos caudata         | 9                     | 4               | 0.01                  | 4.16 ± 1.24  | 3.43 ± 1.35  | 12.38 ± 12.27     | 1.01                 |
| Aralia chinensis         | 6                     | 4               | 0.04                  | 7.43 ± 6.60  | 7.03 ± 3.10  | 18.96 ± 32.82     | 0.99                 |
| Rhamnus parvifolius      | 18                    | 3               | 0.02                  | 3.48 ± 0.63  | 3.26 ± 0.90  | 6.97 ± 6.82       | 0.96                 |
| Castanea mollissima      | 5                     | 3               | 0.01                  | 3.14 ± 0.79  | 4.62 ± 0.79  | 11.52 ± 9.08      | 0.73                 |
| Pistacia chinensis       | 5                     | 2               | 0.03                  | 8.18 ± 4.49  | 4.64 ± 1.67  | 15.18 ± 13.16     | 0.54                 |
| Deutzia grandiflora      | 5                     | 2               | 0.01                  | 3.86 ± 1.01  | 2.93 ± 1.11  | 4.66 ± 1.58       | 0.52                 |
| Camellia oleifera        | 5                     | 2               | 0.01                  | 3.61 ± 0.67  | 3.68 ± 1.60  | 5.62 ± 4.43       | 0.52                 |
| Melia azedarach          | 4                     | 2               | 0.01                  | 4.65 ± 0.66  | 5.63 ± 0.85  | 5.51 ± 2.21       | 0.5                  |
| Sapium sebiferum         | 4                     | 2               | 0.01                  | 7.16 ± 3.23  | 6.01 ± 2.22  | 5.67 ± 2.36       | 0.5                  |
| Sabina chinensis         | 4                     | 2               | 0.02                  | 6.62 ± 2.01  | 4.63 ± 1.08  | 5.73 ± 2.07       | 0.5                  |
| Remaining species(12)    | 19                    | 8               | 0.11                  | 4.82 ± 2.12  | 4.86 ± 1.63  | 13.23 ± 15.09     | 3.41                 |
After the invasion of *B. xylophilus*, the values of soil chemical properties differed among the stand types. Total nitrogen and organic matter were slightly higher in healthy forest than in the damaged stands (Table 3), despite their similarity in soil texture (Table 2). These results were supported by a study conducted by Mabushay and Nakagoshi (2012), who found that total nitrogen was higher in the top 5 cm of healthy sites undamaged by PWD than in that of infected sites. In addition, the levels of available phosphorus, sodium, potassium, calcium, and magnesium were generally slightly higher at the damaged sites than at the control sites. However, Kim et al. (2010) found that soil fertility was generally higher at undamaged sites than at damaged plots. The differences in these results may be due to the variation of soil properties with the observation period, forest conditions, and vegetation structure of the sites. Considered together, the differences of soil chemical properties were not statistically significant (*P* > 0.05), which may be due to the short-term stability of soil nutrient element composition. The changes of soil chemical properties as the extent of infection increases are not yet well understood and require further study.

The selective cutting of Masson pine trees infected by *B. xylophilus* opened canopy gaps in the forest, which has facilitated significant changes in forest composition and community structure (Spiegel and Leege 2013). The IVs indicate that the Masson pine ecosystem is dominated by relatively few species at the tree layer. *Pinus massoniana* is the dominant species, comprising 49.63% of the total IV. Another structural characteristic of the pine ecosystem is the relatively large IVs of broad-leaved tree species such as *Q. variabilis*, *L. chinensis*, *Q. aliena*, and *C. camphora*. At sites where *B. xylophilus* caused serious damage, Masson pine mortality was significant. These canopy gaps presumably generated the community composition shift observed in comparison with less-altered sites. These results suggest that Masson pine does not become reestablished following PWD-induced mortality but is instead replaced throughout the research area by broad-leaved tree species, which has implications for shifting forest composition and community structure. As the once extremely dominant Masson pine declines, this tree’s control

### Table 5. Importance values of Masson pine compared to other woody plant species in five Masson pine forest sites infected for different periods of time by pine wood nematode.

| Species                     | Importance value (%) |
|-----------------------------|----------------------|
| *Pinus massoniana*          | 67.23                |
| *Cinnamomum camphora*       | 53.61                |
| *Quercus aliena*            | 50.24                |
| *Quercus variabilis*        | 42.65                |
| *Loropetalum chinensis*     | 29.24                |
| *Rhus chinensis*            | 2.57                 |
| *Celtis bungeana*           | 2.02                 |
| *Trachycarpus fortunei*     | 1.88                 |
| *Cotinus coggyria*          | 1.72                 |
| *Litsea cubeba*             | 1.68                 |
| *Symplocos paniculata*      | 1.51                 |
| *Symplocos chinensis*       | 1.44                 |
| *Rhus typhina*              | 1.39                 |
| *Dalbergia hupeana*         | 1.28                 |
| *Ilex cornuta*              | 1.24                 |
| *Albizia kalkora*           | 1.22                 |
| *Symlocos caudata*          | 1.20                 |
| *Aralia chinensis*          | 1.18                 |
| *Rhamnus parvaolus*         | 1.16                 |
| *Castanea mollissima*       | 1.14                 |
| *Pistacia chinensis*        | 1.12                 |
| *Deutzia grandiflora*       | 1.10                 |
| *Camellia oleifera*         | 1.08                 |
| *Melia azedarach*           | 1.06                 |
| *Sapium sebiferum*          | 1.04                 |
| *Sabina chinensis*          | 1.02                 |
| Remaining species           | 0.98                 |

### Table 6. Marginal and conditional effects of environmental variables on plant community structure obtained from the summary of forward selection in redundancy analysis.

| Variables                             | Lambda-A1 | Lambda-B2 |
|---------------------------------------|-----------|-----------|
|                                      | Trace     | F-ratio   | P-value3 | Trace     | F-ratio   | P-value3 |
| Masson pine stumps (MPS)              | 0.18      | 2.95**    | 0.002    | 0.18      | 2.95**    | 0.002    |
| K*                                    | 0.17      | 2.57*     | 0.014    | 0.14      | 2.31*     | 0.026    |
| Capillary water holding capacity (CWHC)| 0.14      | 2.13*     | 0.042    | 0.08      | 1.56      | 0.148    |
| Capillary porosity (CP)               | 0.13      | 2.02*     | 0.049    | 0.05      | 0.82      | 0.622    |
| Soil water content (SWC)              | 0.16      | 2.49*     | 0.018    | 0.04      | 0.70      | 0.720    |

1Describes marginal effects, which show the variance explained when the variable is used as the only factor.
2Describes conditional effects, which show the additional variance each variable explains when it is included in the model.
3The Monte Carlo permutation with 499 iterations was performed at the 0.05 significance level.
* Significant at *P* < 0.05; ** Significant at *P* < 0.01.
of ecosystem structure and processes may wane (Ellison et al. 2005).

Among the 19 examined environmental variables, five were found to be significantly related ($P < 0.05$) with the distribution of plant community structure: MPS, $K^+$, CWHC, CP, and SWC (Table 6). The results of RDA ordination indicated that the plant community structure was significantly related to MPS and $K^+$, while the other three variables did not significantly contribute ($P > 0.05$) to this distribution. The RDA ordination graph indicates that MPS is positively related with the growth and spatial distribution. The RDA ordination graph also indicates that $R. chinensis$ and $Cinnamomum capillary$ porosity; SWC, soil water content. 1.

The practice of selectively cutting dead Masson pine trees is important for preventing the spread of PWD. As the degree of damage increases, PWD results in an increasing number of stumps due to this selective cutting. The invasion of $B. xylophilus$ has two general types of effects: economic and ecological. From an economic viewpoint, the loss of timber caused by PWD in China is estimated to be $5.0 \times 10^6$ m$^3$, with a direct economic loss of approximately renminbi (RMB) 2.5 billion yuan and indirect economic losses exceeding RMB 25 billion yuan (Zhang and Luo 2003). The outbreak of PWD also has multiple effects on tree growth rates, plant canopy structure, and arthropods at the stand level, which in turn may alter stand development patterns such as stand structure, composition, and productivity (Veblen et al. 1991; Li et al. 2012). In addition, this disturbance can affect ecological niches in the short term, as deciduous species benefit from the release of space and resources associated with the death of the canopy-dominating pine trees (Fujihara 1996). Previous studies have also concluded that the growth of some suppressed deciduous vegetation is accelerated after PWD infection, with the dominant vegetation changing from pine to deciduous oak (Fujihara 1997; Fujihara et al. 2002). Additional work has shown that mixed forests are more stable against pests than are pure forests (Humphrey et al. 1999; Hambäck et al. 2000; Jobidon et al. 2004; Li et al. 2012).

$Bursaphelenchus xylophilus$ epidemics have resulted in significant pine tree mortality across millions of hectares in central and southeastern China. Unfortunately, Masson pine is susceptible to attack by $B. xylophilus$ and the main measure used to control PWD to date has been the eradication of infected pines, which is costly and only partially effective (Shi et al. 2007; Yu et al. 2011). Therefore, the unchecked spread of PWD has raised fears that Masson pine will approach functional extinction across its range. This disturbance will cause remarkable changes in forest physical conditions and soil conditions, as well as soil microbiology (Fujihara et al. 2002; Johnston and Crossley 2002). Additionally, the effects of massive Masson pine mortality may proliferate through the wood web and

Table 7. Summary of statistical results of the redundancy analysis.

| Canonical axes | 1  | 2  | 3  | 4  | Total variance | F-ratio | P-value |
|----------------|----|----|----|----|----------------|---------|---------|
| Eigenvalues    | 0.260 | 0.105 | 0.086 | 0.022 | 1 | 1.721* | 0.018 |
| Species-environment correlations | 0.917 | 0.723 | 0.778 | 0.482 | | |
| Cumulative percentage of species variance (%) | 26.0 | 36.5 | 45.1 | 47.3 | | |
| Cumulative percentage of species-environment relation (%) | 53.2 | 74.6 | 92.2 | 96.7 | | |
| Sum of all eigenvalues | 1 | | | | | |
| Sum of all canonical eigenvalues | | | | | 0.489 | |

*Significant at $P < 0.05$. 

Figure 4. First two canonical axes of the redundancy analysis (RDA) ordination biplot between plant community structure and dominant environmental variables. MPS, Masson pine stumps; $K^+$, the content of $K^+$ at 0–40 cm depth; CWHC, capillary water holding capacity; CP, capillary porosity; SWC, soil water content. 1. *Cinnamomum camphora*; 2. *Pinus massoniana*; 3. *Quercus aliena*; 4. *Quercus variabilis*; 5. *Loropetalum chinensis*; 6. *Rhus chinensis*; 7. *Celtis bungeana*; 8. *Trachycarpus fortunei*; 9. *Cotinus coggyria*; 10. *Litsea cubeba*; 11. *Symplocos paniculata*; 12. *Rhus typhina*; 13. *Dalbergia hupaeana*; 14. *Albizia kalkora*; 15. *Celtis bungeana*; 16. *Symplocos capillaris*.
affect community structure (Spiegel and Lege 2013). Of even greater concern is that creatures specifically dependent on Masson pine as a natural habitat or food source may experience significant population declines. Wild life habitat and bird nesting sites may also be reduced due to the mortality of Masson pine (Osborne 1985; Spiegel and Lege 2013).

In our study, stand types were not replicated because it is impossible to find replicate Masson pine stands with the same extent of PWD infection, stand composition, soil type, and environmental conditions in two different regions (Li et al. 2011). Our results suggest that in the infected sites, Masson pine mortality significantly altered soil water-related physical properties but not chemical properties. We surveyed sites at 1–7 years after PWD was detected, which was too soon for soil chemical properties to adequately respond to weathering processes, light conditions, and changes in forest composition where Masson pine has severely declined (Kim et al. 2010; Spiegel and Lege 2013). Finally, the data gathered from the control sites may be useful for pre- and postinfection analysis (Spiegel and Lege 2013), should these sites become infected by B. xylophilus in the future.

In summary, our research reveals differences in the soil properties and the composition and distribution of the plant community in Masson pine forest stands after infection by PWD. In general, soil water-related physical properties differed significantly between the stand types ($P < 0.05$), but soil chemical properties were not significantly different ($P > 0.05$). Masson pine does not reestablish following PWD-induced mortality but is instead replaced by broad-leaved tree species. In addition, plant community composition and structure are strongly related to MPS and $K^+$ in the infected plots. Given its formerly wide distribution, the extensive loss of Masson pine may have far reaching implications for the ecological security of the Three Gorges reservoir region in China. We hope to work with these sites over time to determine their long-term changes in soil properties and plant community composition and structure.

**Acknowledgments**

This work was supported by the Special Fund for Forest Scientific Research in the Public Welfare (201204501), and the National Natural Science Foundation of China (31170613), and Program for New Century Excellent Talents in University (NCET-10-0232).

**Conflict of Interest**

None declared.

**References**

Akema, T., and K. Futai. 2005. Ectomycorrhizal development in *Pinus thunbergii* stand in relation to location on a slope and effect on tree mortality from pine wilt disease. J. For. Res. 10:93–99.

Berger, T. W., and H. Hager. 2000. Physical top soil properties in pure stands of Norway spruce (*Picea abies*) and mixed species stands in Austria. For. Ecol. Manage. 136:159–172.

Black, G. R., and K. H. Hartge. 1986. Bulk density. Methods of soil analysis part I: physical and mineralogical methods. 2nd edn. American Society of Agronomy, Inc. Soil Science Society of America, Inc. Madison, WI.

Castello, J. D., D. J. Leopold, and P. J. Smallidge. 1995. Pathogens, patterns, and processes in forest ecosystems. Bioscience 45:16–24.

Chen, L., Q. Chen, and W. Liu. 1997. Forest diversity and its geographical distribution in China. Science Press, Beijing.

Cohen, A. N., and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279:555–558.

Conner, W. H., W. D. II Mixon, and G. W. Wood. 2005. Maritime forest habitat dynamics on Bulls Island, Cape Romain National Wildlife Refuge, SC, following Hurricane Hugo. For. Ecol. Manage. 212:127–134.

Curnutt, J. L. 2000. Host-area specific climatic-matching: similarity breeds exotics. Biol. Conserv. 94:341–351.

Daehler, C. C., and D. A. Carino. 2001. Hybridization between native and alien plants and its consequences. Biotic Homogenization, 81–102. Kluwer Academic, NY, USA.

Diaz, A., and S. Northciff. 1985. Effects of two land clearing methods on the physical properties of an Oxisol in the Brazilian Amazon. Tropical Agriculture 62:207–212.

Dropkin, V. H., A. S. Foudin, E. Kondo, M. Linit, M. Smith, and K. Robbins. 1981. Pinewood nematode: a threat to US forest? Plant Dis. 65:1022–1027.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, et al. 2003. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front. Ecol. Environ. 3:479–486.

Ellstrand, N. C., and K. A. Schierenbeck. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? Proc. Natl Acad. Sci. USA 97:7043–7050.

Fujihara, M. 1996. Development of secondary pine forests after pine wilt disease in western Japan. J. Veg. Sci. 7:729–738.

Fujihara, M. 1997. Structure of *Pinus ichuensis* forests affected by pine wilt disease in northern Taiwan. Nat. Hist. Res. Spec. Issue. 4:113–126.

Fujihara, M., Y. Hada, and G. Toyohara. 2002. Changes in the stand structure of a pine forest after rapid growth of *Quercus serrata* Thunb. For. Ecol. Manage. 170:55–65.

Gandhi, K. J., and D. A. Herms. 2010. Direct and indirect effects of alien insect herbivores on ecological processes and
interactions in forests of eastern North America. Biol. Invasions 12:389–405.

Gao, R. H., Z. Wang, J. Shi, and Y. Q. Luo. 2013. Characteristics of insect community and the spread of parasitic insects under environmental gradients in cut slash affected by pine wilt disease. Journal of Beijing Forestry University 35:84–90.

Hambäck, P. A., J. Ågren, and L. Ericson. 2000. Association resistance: insect damage to purple loosestrife reduced in thickets of sweet gale. Ecology 81:1784–1794.

Hejda, M., P. Pyšek, and V. Jarošík. 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. J. Ecol. 97:393–403.

Hu, G., X. H. Xu, Y. L. Wang, G. Lu, K. J. Feeley, and M. J. Yu. 2012. Regeneration of different plant functional types in a Masson pine forest following pine wilt disease. PLoS ONE 7:e36432. doi:10.1371/journal.pone.0036432.

Hulcr, J., and R. R. Dunn. 2011. The sudden emergence of pathogenicity in insect–fungus symbiosis threatens naive forest ecosystems. P. Roy. Soc B Biol. Sci. 278:2866–2873.

Humphrey, J., C. Hawes, A. Peace, R. Ferris-Kaan, and M. Jukes. 1999. Relationships between insect diversity and habitat characteristics in plantation forests. For. Ecol. Manage. 113:11–21.

Jeong, J., C. Kim, K. S. Lee, N. S. Bolan, and R. Naidu. 2013. Carbon storage and soil CO2 efflux rates at varying degrees of damage from pine wilt disease in red pine stands. Sci. Total Environ. 465:273–278.

Jobidon, R., G. Cyr, and N. Thiffault. 2004. Plant species diversity and composition along an experimental gradient of northern hardwood abundance in Picea mariana plantations. For. Ecol. Manage. 198:209–221.

Johnston, J. M., and D. A. Jr Crossley. 2002. Forest ecosystem recovery in the southeast US: soil ecology as an essential component of ecosystem management. For. Ecol. Manage. 155:187–203.

Kim, C., K. S. Jang, J. B. Kim, J. K. Byun, C. H. Lee, and K. S. Jeon. 2010. Relationship between soil properties and incidence of pine wilt disease and stand level. Landsc. Ecol. Eng. 6:119–124.

Legendre, P., and L. Legendre. 2012. Numerical ecology. Elsevier, Amsterdam, The Netherlands.

Lepš, J., and P. Smilauer. 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, CA.

Li, Y., and M. Shao. 2006. Change of soil physical properties under long-term natural vegetation restoration in the Loess Plateau of China. J. Arid Environ. 64:77–96.

Li, X., M. J. Yi, Y. Son, P. S. Park, K. H. Lee, Y. M. Son, et al. 2011. Biomass and carbon storage in an age-sequence of Korean pine (Pinus koraiensis) plantation forests in central Korea. J. Plant Biol. 54:33–42.

Li, J., J. Shi, Y. Q. Luo, and K. Heliovaara. 2012. Plant and insect diversity along an experimental gradient of larch-birch mixtures in Chinese boreal forest. Turk. J. Agric. For. 36:247–255.

Lovett, G. M., C. D. Canham, M. A. Arthur, K. C. Weathers, and R. D. Fitzhugh. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. Bioscience 56:395–405.

Mabuhay, J. A., and N. Nakagoshi. 2012. Response of soil microbial communities to changes in a forest ecosystem brought about by pine wilt disease. Landsc. Ecol. Eng. 8:189–196.

Makeschin, F. 1994. Effects of energy forestry on soils. Biomass Bioenergy 6:63–79.

Mamiya, Y. 1988. History of pine wilt disease in Japan. J. Nematol. 20:219–226.

Miki, N., K. Sakamoto, T. Nishimoto, K. Yoshikawa, and Y. Hada. 2001. Relationship between the incidence of pine wilt disease and the drainage area. J. For. Res. 6:181–186.

Osborne, P. E. 1985. Some effects of Dutch Elm disease on the birds of a Dorset dairy farm. J. Appl. Ecol. 22:681–691.

Pagliai, M., and N. Vignozzi. 2002. The soil pore system as an indicator of soil quality. Advances in GeoEcology 35:69–80.

Paniagua, A., J. Kammerbauer, M. Avedillo, and A. M. Andrews. 1999. Relationship of soil characteristics to vegetation successions on a sequence of degraded and rehabilitated soils in Honduras. Agr. Ecosyst. Environ. 72:215–225.

Sakamoto, K., N. Miki, T. Tsuzuki, T. Nishimoto, and K. Yoshikawa. 2003. Comparison of stand dynamics after dieback caused by pine wilt disease among pine forests with different management regimes in western Japan. J. For. Res. 8:303–309.

Sasai, M., A. Andriulo, and M. Taboada. 2006. Soil porosity characteristics and water movement under zero tillage in silty soils in Argentinian Pampas. Soil Till. Res. 87:9–18.

Shi, J., Y. Q. Luo, J. Song, X. Yan, P. Jiang, and Y. Wang. 2006. Impact of the invasion of pine wood nematode and the following different removal disturbance intensity on the plant diversity of Masson pine community. Chin. J. Appl. Ecol. 17:1157–1163.

Shi, J., Y. Q. Luo, J. Y. Song, H. W. Wu, L. Wang, and G. Z. Wang. 2007. Traits of Masson pine affecting attack of pine wood nematode. J. Integr. Plant Biol. 49:1763–1771.

Shi, J., Y. Q. Luo, F. Zhou, and P. He. 2010. The relationship between invasive alien species and main climatic zones. Biodivers. Conserv. 19:2485–2500.

Shi, J., F. Chen, Y. Q. Luo, Z. Wang, and B. Y. Xie. 2013. First isolation of pine wood nematode from Pinus tabuliformis forests in China. Forest Pathol. 43:59–66.

Spiegl, K. S., and L. M. Leeger. 2013. Impacts of laurel wilt disease on redbay (Persea borbonia (L.) Spreng.) population structure and forest communities in the coastal plain of Georgia, USA. Biol. Invasions 15:2467–2487.

Suzuki, K. 2002. Pine wilt disease—a threat to pine forest in Europe. dendrobiology 48:71–74.
Suzuki, K., and T. Kiyohara. 1978. Influence of water stress on development of pine wilting disease caused by Bursaphelenchus lignicolus. Eur. J. Forest Pathol. 8:97–107.

Tangyuan, N., H. Bin, J. Nianyuan, T. Shenzhong, and L. Zengjia. 2009. Effects of conservation tillage on soil porosity in maize-wheat cropping system. Plant Soil Environ. 55:327–333.

Ter Braak, C., and P. Šmilauer. 2012. Canoco reference manual and user’s guide: software for ordination (version 5.0). Microcomputer Power, Ithaca, NY, USA.

The bulletin of State Forestry Administration (2014) Bulletin No.2 of State Forestry Administration in 2014—The epidemic area of Pine Wilt Disease. Available via http://www.forestry.gov.cn/main/72/content-657815.html (accessed 14 February 2014).

Veblen, T. T., K. S. Hadley, M. S. Reid, and A. J. Rebertus. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. Ecology 72:213–231.

Wan, F. H., X. B. Zheng, and J. Y. Guo. 2005. Biology and management of invasive alien species in agriculture and forestry. Science publishing, Beijing.

Wilson, L. F. 1993. China’s Masson pine forests: cure or curse? J. Forestry 91:30–33.

Xie, B. Y., X. Y. Cheng, J. Shi, Q. W. Zhang, S. M. Dai, F. X. Cheng, et al. 2009. Mechanisms of invasive population establishment and spread of pinewood nematodes in China. Sci. China Ser. C. 52:587–594.

Xu, H., S. Qiang, P. Genovesi, H. Ding, J. Wu, L. Meng, et al. 2012. An inventory of invasive alien species in China. NeoBota. 15:1–26.

Yoshimura, A., K. Kawasaki, F. Takasu, K. Togashi, K. Futai, and N. Shigesada. 1999. Modeling the spread of pine wilt disease caused by nematodes with pine sawyers as vector. Ecology 80:1691–1702.

You, Y., J. Wang, X. Huang, Z. Tang, S. Liu, and O. J. Sun. 2014. Relating microbial community structure to functioning in forest soil organic carbon transformation and turnover, Ecol. Evol. 4:633–647.

Yu, M. J., X. H. Xu, and P. Ding. 2011. Economic loss versus ecological gain: the outbreaks of invaded pinewood nematode in China. Biol. Invasions 13:1283–1290.

Zhang, X. Y., and Y. Q. Luo. 2003. Major forest diseases and insect pests in China. China Forestry Press, Beijing.

Zhang, W. R., and B. T. Xu. 1986. The method of long-term research on forest soil. Chinese Forestry Press, Beijing.

Zhang, Y., S. Liu, and J. Ma. 2006a. Water-holding capacity of ground covers and soils in alpine and sub-alpine shrubs in western Sichuan, China. Acta Ecol. Sin. 26:2775–2781.

Zhang, Y., Z. M. Wei, M. L. Xi, and J. S. Shi. 2006b. Direct organogenesis and plantlet regeneration from mature zygotic embryos of masson pine (Pinus massoniana L.). Plant Cell Tiss. Org. 84:119–123.

1716 © 2015 The Authors. Ecology and Evolution published by John Wiley & Sons Ltd.