



Quantitative evaluation of forest communities and effects of oak wilt in a secondary forest in western Japan

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Received: 6 February 2023 / Revised: 13 July 2023 / Accepted: 1 September 2023 / Published online: 5 October 2023
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Abstract

In Japan, secondary forests associated with agriculture (satoyama) had been maintained traditionally by small-scale clearcutting and short-rotation coppice forestry. After forest management was discontinued due to modernization, shade-intolerant, deciduous trees such as *Q. serrata* and *Q. variabilis* have become dominant in many secondary forests of southwestern Japan. In recent years, however, tree death from Japanese oak wilt has become wide-spread. To identify forest communities that will be most affected by oak wilt, we investigated stand structure and species composition in a 64-ha unmanaged secondary forest in Kobe, Japan. We identified three forest communities using cluster analysis of 27 survey plots. We then analyzed and visualized vegetation similarity among the communities using non-metric multidimensional scaling (nMDS). In secondary forests, *Pinus densiflora*–*Rhododendron macrosepalum* and *Quercus serrata*–*Quercus variabilis* communities, which established after pine wilt were identified. We also found communities dominated by *Cryptomeria japonica*, a plantation species. We predicted that *Quercus serrata*–*Quercus variabilis* communities will experience significant vegetation change after oak wilt and become low-statured, evergreen-deciduous forests. These communities, therefore, should be prioritized for active management by small-scale clear cutting to prevent further spread of oak wilt and subsequent biodiversity decline.

Keywords Satoyama · Coppice management · Forest structure · Plagiosere · Community analysis

Introduction

In Japan, “satoyama” refers to secondary forests managed by short-rotation coppice forestry for obtaining firewood, charcoal and organic fertilizer (Takeuchi 2010). Loss of satoyama in the landscape due to modernization has heightened awareness of their cultural, recreational and educational value, as well as their role in species conservation and ecosystem integrity (Fukamachi and Sakuma 1998). Intermediate disturbances, such as cutting, mowing and removal of leaf litter, had prevented these forests from reaching climax state (Kobori and Primack 2003) and maintained species

diversity in the semi-natural landscape (Buckley 1992), representing coexistence of human activity and ecosystem integrity (Cetinkaya 2009; Takeuchi 2010).

In western Japan, secondary forests consisted of fast-growing, shade-intolerant, early successional species such as pines and deciduous oaks (e.g., *Pinus densiflora*, *Quercus serrata*) (Iida and Tanimoto 1992). These forests were managed under 10- to 30-year, short-rotation coppice forestry (Arioka 2004). However, during the 1950–1960s, social changes such as fossil fuels and chemical fertilizer replacing firewood, charcoal, and organic leaf litter, resulted in abandoning of satoyama forest management in many regions (Hong et al. 1995; Fukamachi et al. 2001; Ohwaki et al. 2013). In these unmanaged, secondary forests, early-successional trees grew tall and large (Kamada and Nakagoshi 1990), while shade-tolerant species invaded and succession progressed (Azuma et al. 2014; Hirayama et al. 2011; Okuda et al. 2007). In some regions, where seed sources for late-successional species were limited, diverted succession occurred as a result of

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invasion by exotic and ornamental species (Kameyama 1992; Tojima et al. 2004; Iwasaki and Ishii 2007). Such forests are species-poor compared to the original satoyama (Hattori and Ishida 2000).

In the past, pine wilt disease, caused by the pine wood nematode, *Bursaphelenchus xylophilus*, and vectored by the pine beetle, *Monochamus alternus*, spread in abandoned secondary forests (Kiyohara and Tokushige 1971; Morimoto and Iwasaki 1972), wiping out *P. densiflora* from vast areas across the landscape (Fujiwara 1996; Morishita and Ando 2002). Since the 1990s, oak wilt, caused by the fungus, *Raffaelea quercivora*, and vectored by the ambrosia beetle, *Platypus quercivorus*, has become a wide-spread problem (Kuroda and Yamada 1996; Kinuura 2008). This disease affects multiple species of oak such as *Quercus mongolica*, *Q. serrata*, *Quercus variabilis*, and agriculturally important trees such as Japanese chestnut (*Castanea crenata*) (Nishigaki et al. 1998; Shiomi and Ozaki 1997). The ambrosia beetles prefer to swarm large-diameter trees for mating and abandoned secondary forests, which include many such trees, are at high risk of being devastated by oak wilt (Kobayashi and Ueda 2005; Yamasaki and Sakimoto 2009). The spread of oak wilt could completely alter the structure and composition of secondary forests across the landscape (Nakajima and Ishida 2014; Nishikawa et al. 2020; Saito and Shibata 2012).

Some researchers recommend re-implementing small-scale clear-cutting and short-rotation coppice management to prevent the spread of oak wilt (e.g., Kuroda 2010). However, this could be difficult because many private forest owners no longer manage their forests and there is no economic incentive for continuing coppice forestry. Local governments, therefore, must prioritize areas for subsidized management. Predicting effects of oak wilt on forest structure and species composition is important for selecting priority areas for clear-cut management. Previous studies report various pathways for vegetation succession of secondary forests after oak wilt. In a cool-temperate, secondary forest in Toyama Prefecture, death of large canopy trees due to oak wilt resulted in more open conditions contributing to regeneration of diverse woody species in the lower-canopy (Nakajima and Ishida 2014). In a warm-temperate secondary forest in Kyoto Pref., advance regeneration of shade-tolerant evergreen trees prevented understory regeneration and resulted in low diversity (Ito et al. 2009). Because vegetation succession of secondary forests in Japan depends on various circumstances including landscape-level patterns of seed dispersal and disease outbreaks (Kawata et al. 2023), we must accumulate empirical data and develop methodology for predicting succession and preventing the spread of oak wilt. To predict effects of oak wilt on vegetation succession and identify communities that should be prioritized for prevention, we analyzed structure and composition of a

secondary forest in western Japan, where oak wilt is currently spreading.

Methods

Study site and vegetation survey

The study site is a 64-ha municipal forest in Kita Ward, Kobe City, Hyogo Prefecture, Japan (34° 75' N, 135° 10' E, 240–280 m ASL, Fig. 1). Mean annual temperature and precipitation from 1991 to 2020 at the Kobe Meteorological Station (34° 41' N, 135° 4' E, 5.3 m ASL) were 17.0 °C and 1277.8 mm, respectively (Japan Meteorological Agency). This area lies in the humid, warm-temperate climatic region according to Koeppen's climate classification. The vegetation is mostly unmanaged secondary forest. According to the vegetation map of the Ministry of the Environment based on the vegetation survey conducted in 2021 (Biodiversity Center of Japan, <http://gis.biodic.go.jp/>), this area is documented as mostly comprising *Q. serrata*–*Q. variabilis* communities with *Pinus densiflora*–*Rhododendron macrosepalum* communities occurring on ridges. Local villagers claim that coppice management was discontinued about 60 years ago.

We chose this study site because oak wilt is currently spreading rapidly and the city is planning to implement prevention measures against oak wilt, which calls for quantitative assessment of areas to be prioritized for clear-cutting. Tree death by oak wilt has been reported in the area since 2019 and is spreading rapidly (Hyogo Prefecture 2021). We conducted an aerial survey using drones and found that as many as 30 trees ha⁻¹ have died due to oak wilt (Fig. S1).

To document the vegetation, we established 27 study plots, ranging from 100 (10 m × 10 m square) to 400 m² (20 m × 20 m square) along forest roads in summer of 2021 (Fig. 1). The plots were selected purposively by to include the various communities found on the vegetation map. For logistic and safety reasons, the plots were established within feasible access from forest roads. Plot sizes were varied depending on the stand structure and geographical features of the location. Small plots (100 m²) were established where it was steep and dangerous to work, and tree height was low (e.g., ridges). The total area surveyed was 3050 m². In the study plots, we identified species and measured diameter at breast height (DBH, 1.3 m above average ground level) of all trees larger than 5 cm DBH. Tree height (*H*) was measured using a telescoping pole and laser clinometer (Truepulse 360, Lazer Technology).

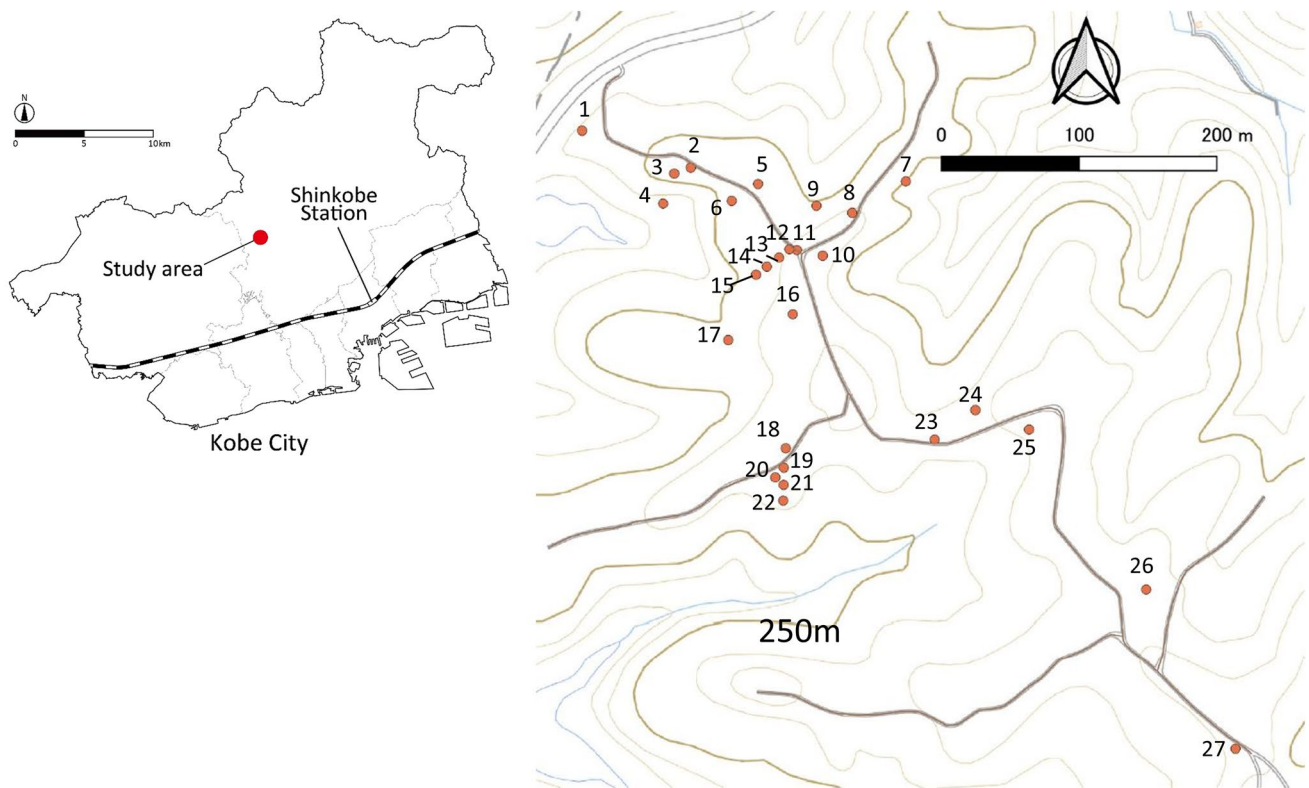


Fig. 1 Location of the study area in Kobe City, Hyogo Prefecture, Japan and the research plots therein

Data analysis

We calculated the basal area (BA, $\text{m}^2 \text{ha}^{-1}$) for each species based on the DBH of each tree. The relative BA of species in each plot was used to classify the plots into communities by cluster analysis using the “vegan” package in R (ver. 4.0.2, R Development Core Team). In this analysis, we calculated Bray–Curtis dissimilarity index based on relative BA of species in each plot and used the Ward method for clustering. The Ward method hierarchically combines cases (plots in this study) into clusters to maximize within-group homogeneity and between-group heterogeneity. Hierarchical cluster analysis and Ward’s method are commonly used to classify ecological communities including urban forest vegetation (e.g., Steenberg et al. 2015; Nitoslowski et al. 2017; Sasaki et al. 2018).

We then compared canopy structure and species diversity among the communities identified by cluster analysis. Tree-height distributions were visually compared and upper- ($H \geq 13.3$ m), mid- ($9.3 \leq H < 13.3$ m) and lower-canopy ($H < 9.3$ m) trees were defined. Significant differences among communities in the modes of distribution for each canopy-height class were compared using Kolmogorov–Smirnov test. To compare species diversity among the communities, we calculated the Shannon–Wiener diversity index:

$$H' = - \sum_{i=1}^S P_i \times \log P_i$$

where S is number of species, P_i is the relative number of individuals of species i .

To compare species composition among the communities, we calculated Chao–Jaccard similarity index based on abundance (number of trees ha^{-1}). Together with the results of BA-based similarity, vegetation similarities were visualized using non-metric multidimensional scaling (nMDS) ordination using the function “metaMDS” of the package “vegan” in R software (Oksanen et al. 2020). The nMDS is a distance-based ordination technique where relationships among biological communities are drawn on a two-dimensional plane to display graphically similarities among ecological communities. It is suited for ecological analyses because it is nonparametric and can be used to relativize distance measures based on a wide variety of ecological data (McCune et al. 2002). Distance between plots on the nMDS ordination plane represents their relative similarities. We used type-2 permutational multivariate analysis of variance (PERMANOVA) using distance matrices of abundance (Chao–Jaccard index) and BA (Bray–Curtis index) to test significant differences among communities and change over time in species composition and stand structure, respectively. PERMANOVA (9999 permutations) was conducted

using the function “adonis2” of the “vegan” package in R. Multiple comparisons were conducted using the “pairwiseAdonis2” package (Hervé 2016). Finally, to predict effects of oak wilt on community structure, we conducted BA-based similarity analysis (Bray–Curtis index) excluding *Q. serrata* and *Q. variabilis* and compared it with the current stand structure in each plot. Although our plot sizes were small, because we have multiple plots and data from all plots within a community type were pooled to calculate H' , the sizes of individual plots should not affect our analyses.

Results

Identification of forest communities

The 27 research plots were divided into three groups according to cluster analysis based on BA composition (Fig. 2). The three communities were named: MIXED, PINUS and QUERCUS communities. The MIXED community was distinguished from the PINUS and QUERCUS communities, which were more similar to each other.

The MIXED community was dominated by *C. japonica* and *Q. serrata* in BA, while *C. japonica* was the most numerous species (Figs. 3, 4, 5, Table S1). *C. japonica* was the most numerous in all canopy layers, while *Q. serrata* was mostly found in the upper-canopy layer (Fig. 6). Core

Fig. 2 Results of cluster analysis indicated that, based on their species composition, the study plots can be divided into three community types: MIXED, QUERCUS and PINUS

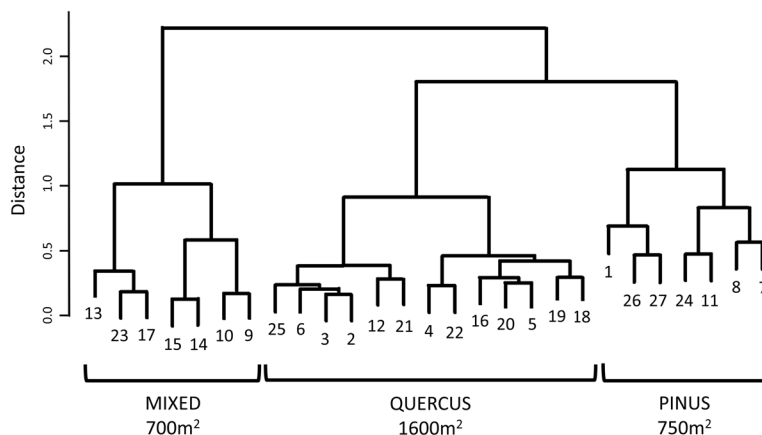


Fig. 3 Stand structures of the three community types in a secondary forest in Kobe City, Japan

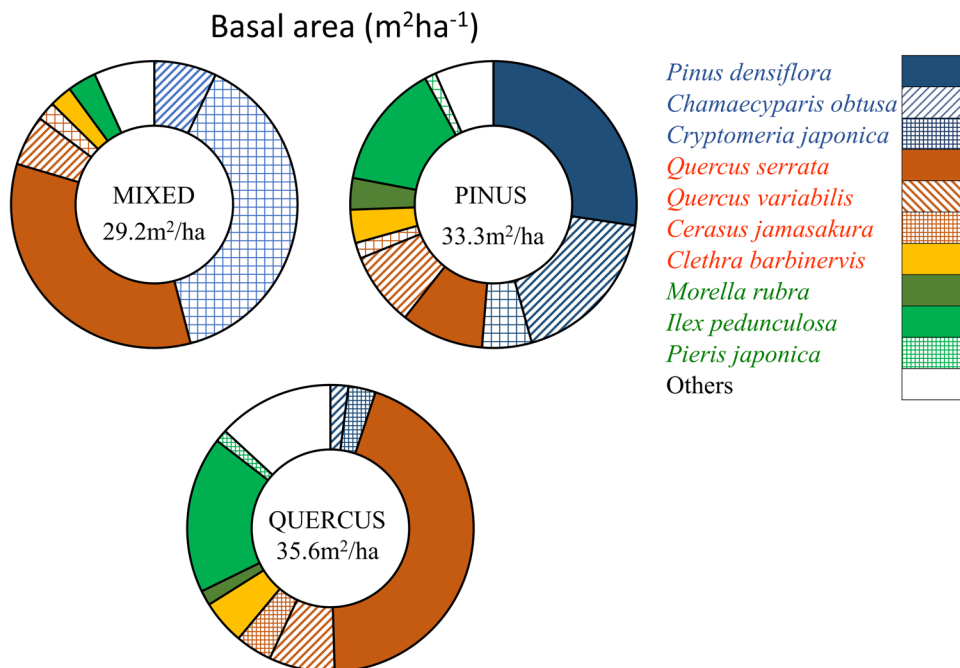


Fig. 4 Species compositions of the three community types in a secondary forest in Kobe City, Japan

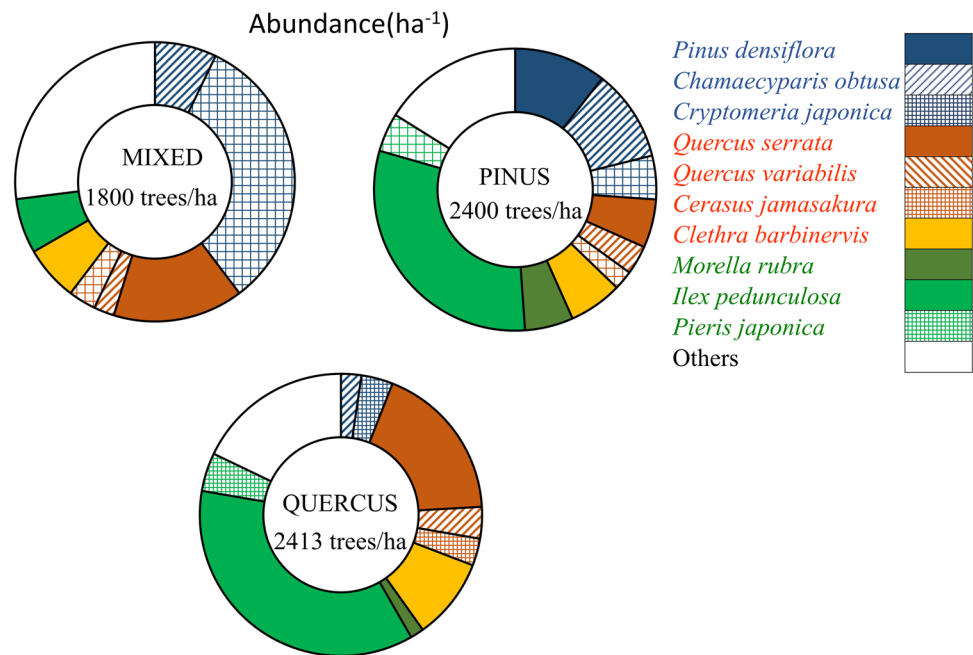
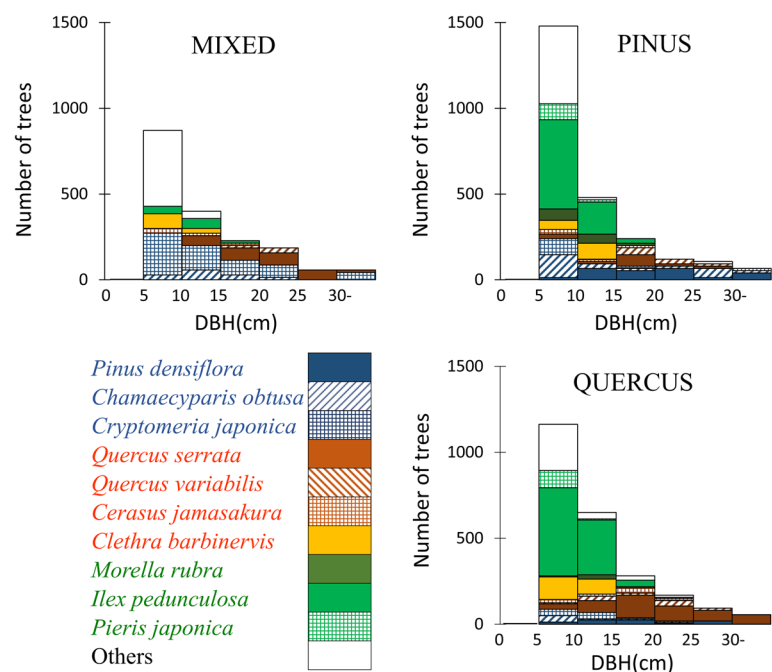


Fig. 5 DBH distributions of the three community types in a secondary forest in Kobe City, Japan



samples collected from random individuals of *C. japonica* indicated that the upper-canopy trees were 50–70 years old. Compared to the other two communities, the MIXED forest had less trees in the mid- to lower-canopy layer (K–S test, $P < 0.01$).

The PINUS community was dominated by *P. densiflora* in BA, while *Ilex pedunculosa* was the most numerous species (Figs. 3, 4, 5, Table S2). Species composition of this community was similar to previously described *Pinus*

densiflora–*Rhododendron macrosepalum* communities. *Chamaecyparis obtusa* was most numerous in the upper-canopy layer. *P. densiflora* was the most numerous in the upper- to mid-canopy layers, while *I. pedunculosa* was the most numerous in the mid- to lower-canopy layer (Fig. 6).

The QUERCUS community was dominated by *Q. serrata* in BA, while *I. pedunculosa* was the most numerous (Figs. 3, 4, 5, Table S4). Species composition of the QUERCUS community was similar to previously described *Q. serrata*–*Q.*

Fig. 6 Height distributions of the three community types in a secondary forest in Kobe City, Japan

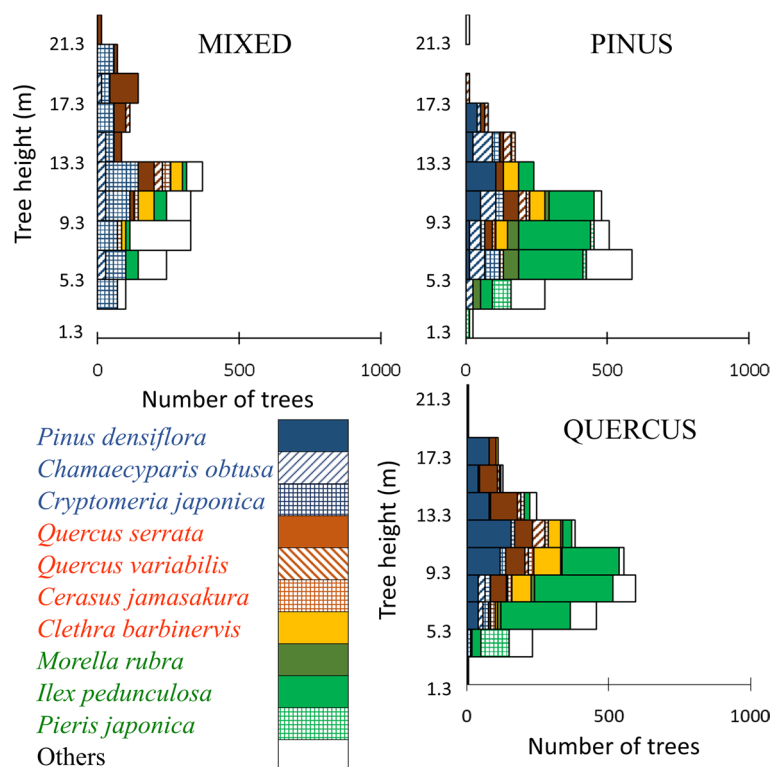


Table 1 Basal-area-based Bray–Curtis similarity index between pairs of communities at a secondary forest in Kobe City, Japan. Larger numbers indicate lower vegetation similarity

	MIXED	PINUS
PINUS	0.632**	
QUERCUS	0.491**	0.469**

** $P < 0.01$

variabilis communities. This community had diverse canopy structure, where upper-, mid- and lower-canopy layers were each dominated by different species: *Q. serrata*, *Clethra barbinervis*, and *I. pedunculosa*, respectively (Fig. 6).

Species diversity was highest for the PINUS community ($H' = 2.471$) followed by the MIXED community ($H' = 2.335$). The QUERCUS community had the lowest species diversity ($H' = 2.286$).

Analysis of vegetation similarity

Analysis of vegetation similarity indicated that the three communities differed from each other in stand structure (Table 1). On the BA-based nMDS plane, Axis 2, along which the MIXED and PINUS communities were distinguished from the QUERCUS community, was positively correlated with the BA of deciduous species and negatively correlated with that of the evergreen conifers (Fig. 7).

Abundance-based analysis of vegetation similarity indicated that the PINUS and QUERCUS communities were similar, while the MIXED community differed from

them (Table 2). On the abundance-based nMDS plane, the MIXED community was distinguished from the other two communities along Axis 1, which was positively correlated with abundance of *C. japonica* and negatively correlated with abundance of *I. pedunculosa* and *P. japonica*.

Comparison of stand structure between current and predicted vegetation indicated that stand structures of the MIXED and QUERCUS communities would change significantly if all individuals of *Q. serrata* and *Q. variabilis* were to die due to oak wilt ($F = 4.287$, $P = 0.026$ and $F = 11.524$, $P = 0.001$, respectively). On the other hand, stand structure of the PINUS would remain similar ($F = 0.557$, $P = 0.722$).

Discussion

Our results indicated the research area is a mosaic of three types of communities. In the MIXED community high density of *C. japonica* resulted in species-poor mid- to lower-canopy layers compared to the other communities. Plantation forests comprising even-aged monocultures have simplified forest structure and low species diversity compared to natural forests (Nagaike 2000). In *C. japonica* plantations, species diversity of the shrub layer declines markedly after canopy closure (Ishii et al. 2008; Seiwa et al. 2012). For example, in Kyushu, woody-species richness in *C. japonica* plantations was only half that of semi-natural broadleaved forests (Ito et al. 2003). We inferred that canopy structure

Fig. 7 Results of abundance- and basal-area-based nMDS analyses showing vegetation similarity among the three communities identified by cluster analysis (stress value < 0.01)

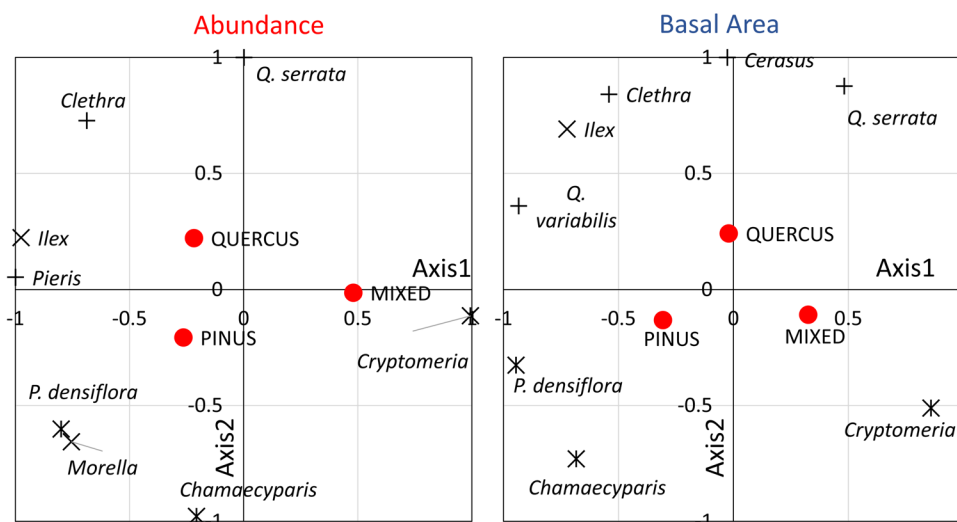


Table 2 Abundance-based Chao-Jaccard similarity index between pairs of communities at a secondary forest in Kobe City, Japan. Larger numbers indicate lower vegetation similarity

	MIXED	PINUS
PINUS	0.769*	
QUERCUS	0.736*	0.429

* $P < 0.05$

of the MIXED community is approaching that of a mono-layered plantation forest due to dominance by *C. japonica* in the upper canopy. Browsing of understory vegetation by deer is also serious problem for species diversity decline and stand regeneration in many parts of Japan (Nomiya et al. 2003; Ohashi 2022). Although the deer population in the study area is relatively low ($< 5 \text{ km}^{-2}$) compared to northern parts of Hyogo Pref. (Taguchi 2015) and effects on the vegetation seem limited so far, deer browsing could lead to further biodiversity decline in the future.

On the other hand, the PINUS and QUERCUS communities were characterized by changes observed in many unmanaged secondary forests in western Japan, namely dominance of evergreen species in the mid- to lower-canopy after occurrence of pine wilt. In a secondary forest in Kyoto Pref., *I. pedunculosa* increased in abundance and species diversity declined over ten years following pine wilt (Wu and Ando 2010). The PINUS community in our study corresponds to this pattern of succession. It should be noted that pine wilt still exists, thus structure and composition of the PINUS community is still in unstable dynamic condition even without oak wilt.

Dominance of evergreen trees in the mid- to lower-canopy could prevent establishment of upper-canopy trees for many years, hindering development of mature-forest canopy structure (Yamase 1998). In some cases, however, deciduous species may continue to dominate the stand

following successful recruitment of deciduous oaks, such as *Q. serrata*, immediately after pine wilt (e.g., Morishita and Ando 2002; Fujiwara 1996). The QUERCUS community in our study corresponds to this pattern of succession. This community had the lowest species diversity among the three community types, which may be explained by greater dominance of evergreen trees in the mid- to lower-canopy.

Our calculations and analyses using nMDS indicated that stand structures of the MIXED and QUERCUS communities will be affected by oak wilt. Large-diameter canopy trees of *Q. serrata* found in these two communities are most vulnerable to oak wilt and their death would lead to marked changes in stand structure. For the MIXED community, the loss of *Quercus* species from the canopy layer would result in a mono-layer canopy of *C. japonica*, similar to a plantation forest. For the QUERCUS community, loss of *Q. serrata* will result in a low-statured mixed forest dominated *I. pedunculosa* and *C. barbinervis*. In a secondary forest in Kyoto, *I. pedunculosa* dominated after oak wilt, preventing regeneration of canopy trees similar to dynamics observed after pine wilt (Ito et al. 2009). We predict that the QUERCUS community will follow a similar successional path after oak wilt. This community, therefore, should be prioritized when considering stands for clear-cutting to prevent oak wilt and subsequent biodiversity decline.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11355-023-00576-4>.

Acknowledgements We thank the Kobe City Office Environment Department and Hyogo Environmental Advancement Association for use of the data of tree surveys and aerial view of Japanese oak wilt. We gratefully acknowledge all members of our laboratory of Forest Resources, Kobe Univ. and Hyogo Forest Club for help with field

surveys. Finally, we declare that the experiments comply with the current laws of the country in Japan.

Author contributions TY conceived the study with supervision from HRI. TY led the field work with assistance from SO, TK, TR and supervision by HRI, DT, KKH. KKH and DT obtained the aerial photo data. TY analyzed the data with supervision from HRI. TY and HRI wrote the paper together and all authors approved.

Funding Open access funding provided by Kobe University.

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