

# Region-wide mass mortality of Japanese oak due to ambrosia beetle infestation: Mortality factors and change in oak abundance

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## ABSTRACT

Insect and pathogen disturbances can result in a decline in the abundance of host tree species, leading to changes in tree species composition at a regional scale. *Quercus crispula* and *Q. serrata* are dominant oak species in Japanese secondary forests, which are mostly composed of abandoned coppice. In recent decades, these two oak species have suffered mass mortality from Japanese oak wilt disease (JOW), which is caused by the ambrosia beetle *Platypus quercivorus*. This study analyzed factors affecting oak mortality during a JOW epidemic, and quantified the impact of the epidemic on forests at a regional scale in Toyama Prefecture, central Japan using data from 101 plots in the National Forest Inventory. Plot measurements before the epidemic (1999–2003) and re-measurements after the epidemic (2012–2014) were used for analysis. Before the epidemic, *Q. crispula* was the most dominant species in the natural forests and was distributed at a wider elevation range than *Q. serrata* (the third most dominant species). The mortality rate during the epidemic was 68% for *Q. crispula* and 21% for *Q. serrata*. The mortality of both species positively related with plot-level oak volume, suggesting that stand development after abandonment of coppice forests was an important factor in the epidemic. The mortality of *Q. crispula* related inversely with elevation and was especially low above 1000 m, probably because of the low reproductive success of *P. quercivorus* at high elevation, suggesting that global warming was a factor increasing the mortality from JOW. The total volume of *Q. crispula* in the study region decreased by 56% during the epidemic, while that of *Q. serrata* increased by 13%. After the epidemic, the dominance of *Q. crispula* in the natural forests decreased below that of *Fagus crenata* and *Q. serrata*. There were few regenerating *Q. crispula* and *Q. serrata* in the canopy gaps formed by dead oak because of their low numbers of saplings. Regenerating trees comprised various shade-tolerant canopy tree species and shrub species, and forests will change toward multispecies mixed, uneven-aged forests. This study comprehensively quantified forest change due to a JOW epidemic at a region-wide scale, and revealed that the epidemic was caused by multiple interactions among coppice abandonment, global warming, ambrosia beetles, and oak trees.

## 1. Introduction

Insect and pathogen disturbances can result in a decline in the abundance of host tree species through mortality, leading to changes in forest structure and species composition at a regional scale, especially if the hosts are regionally dominant species (Lovett et al., 2006; Kurz et al., 2008; Gandhi and Herms, 2010; Kautz et al., 2017). Insect and pathogen-caused mortality of host species varies among forests; factors vary and can include climate conditions, topographic location, tree size, and density of host trees (Negrón et al., 2009; Kärvelö et al., 2014; Sproull et al., 2015; Shearman et al., 2015; Crocker et al., 2016). Forest recovery following insect and pathogen disturbances is affected by this heterogeneous mortality of host trees and the species/size composition of remaining trees (Flower and Gonzalez-Meler, 2015; Axelson et al.,

2018). Therefore, region-wide impacts of insect and pathogen disturbance on forests should be evaluated with the heterogeneity of mortality among forests in a region. Such comprehensive quantification of disturbance impacts will be useful for policy making and forest management.

A National Forest Inventory (NFI) is a useful source of data for analyzing region-wide impacts of disturbance because most NFIs consist of permanent plots located systematically on a national-scale grid (Lawrence et al., 2010). Many studies using NFI data have been conducted worldwide to analyze factors affecting mortality and to detect change in abundance of specific species and/or species composition at a regional scale (McShea et al., 2007; Fei et al., 2011; Rigling et al., 2013; Hanberry, 2013; Morin and Liebhold, 2015; Shearman et al., 2015; Crocker et al., 2016; Moreno-Fernández et al., 2016; Tyler et al., 2018),

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although few such studies have used Japanese NFI data (Nakajima, 2017).

In Japan, *Platypus quercivorus*, an ambrosia beetle and vector of the pathogenic fungus *Raffaella quercivora*, causes mortality in Fagaceae species (including genera of *Quercus*, *Castanea*, *Castanopsis*, and *Lithocarpus*), and mainly in the deciduous oaks *Quercus crispula* and *Q. serrata* (Ito and Yamada, 1998; Kubono and Ito, 2002; Kobayashi and Ueda, 2005; Kinuura and Kobayashi, 2006; Hulcr and Dunn, 2011). This mortality is called Japanese oak wilt disease (JOW). Oak species dominate Japanese secondary forests (Miyawaki, 1984; Kamada and Nakagoshi, 1996); these were used formerly as coppice forests to produce charcoal and fuel wood, but were mostly abandoned in the 1960s owing to changes in socio-economic conditions (Hong et al., 1995; Fukamachi et al., 2001). JOW was first reported in the 1930s and then sporadically until 1980 (Ito and Yamada, 1998). Since the 1980s, JOW has been epidemic and has spread into regions in which it had not previously been reported (Ito and Yamada, 1998; Kamata et al., 2002; Shoda-Kagaya, et al., 2010). The JOW epidemic is thought to be connected to the growth of oaks after abandonment of coppice forests, because large oaks are favorable hosts for *P. quercivorus* (Kobayashi and Ueda, 2005). In addition, ongoing global warming is thought to be a factor expanding the epidemic area (Kamata et al., 2002). The volume of dead trees from JOW throughout Japan was presumed to peak in 2010 (Forest Agency, 2018), and the epidemic had ended in some regions in the 2010s (Nakajima and Ishida, 2014). It should, therefore, be possible to evaluate the region-wide impacts of JOW and factors influencing mortality throughout an entire epidemic, if re-measurement can be conducted for permanent plots that were established before the beginning of the epidemic.

Many studies have examined tree mortality from JOW and forest dynamics influenced by JOW (Shiomi and Osaki, 1997; Nishigaki et al., 1998; Kobayashi and Hagita, 2000; Kamata et al., 2002; Itô et al., 2009; Yamasaki and Sakimoto, 2009; Saito and Shibata, 2012; Itô, 2016; Watanabe et al., 2016; Matsuura and Nakajima, 2016; Hata et al., 2017). These studies revealed higher mortality of *Q. crispula* than of *Q. serrata*, high mortality in large oak trees, high mortality in oak-abundant stands, and change in species composition. However, these studies were conducted in one to several specific plots set after the incidence of mortality from JOW and/or set in oak-dominated forests. Therefore, disturbance impacts and factors affecting mortality at a regional scale could not be analyzed because of the small number of plots and the biased setting of plots toward stands with JOW and/or oak-dominated forests. In addition, although oak species are distributed in a wide elevation range and the reproductive success of JOW vector *P. quercivorus* is elevation dependent (Fukuzawa et al., 2019), no study examined mortality from JOW along the whole elevation gradient. Two studies did use many plots for analysis (Nakajima and Ishida, 2014; Oguro et al., 2015). Oguro et al. (2015) examined landscape and stand-level factors on oak mortality at a local level using several hundred plots but a plot survey was conducted only once, following the spread of JOW, and forest change was not examined. Nakajima and Ishida (2014) analyzed stand dynamics of 16 permanent plots that were set over a region before the JOW epidemic, but their plot arrangement in the region was uneven and did not cover the whole elevation range of oak distribution; they did not estimate change in oak abundance at regional scale; and they did not analyze mortality factors. Consequently, at a regional scale, no study has quantified the impact of JOW on forests and analyzed factors affecting mortality.

This study analyzed the region-wide impact of a JOW epidemic on forests using NFI data in Toyama Prefecture, central Japan. In this region, *Q. crispula*, *Q. serrata*, and *Fagus crenata*, which are tall deciduous trees, dominate in secondary forests. Both *Q. crispula* and *Q. serrata*, suffering mortality from JOW, were target species for analysis. *F. crenata* was co-analyzed as a contrast species that did not suffer mortality from JOW, although there were reports of boring by *P. quercivorus* (Kobayashi and Ueda, 2005). The specific objectives were: (1) to

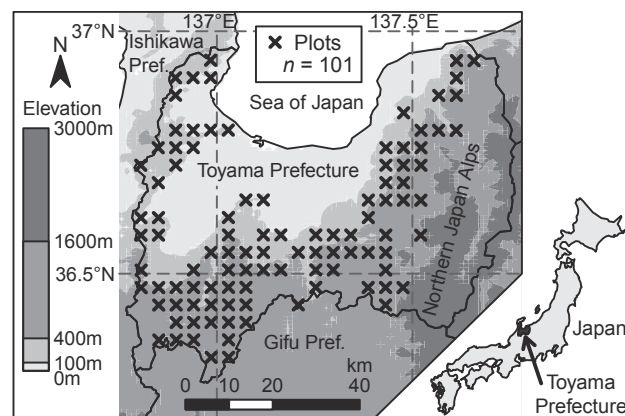


Fig. 1. Study region and plots.

quantify change in the regional abundance of oak species during the JOW epidemic; (2) to clarify factors affecting oak mortality during the epidemic; and (3) to reveal species likely replacing dead oak trees after the epidemic.

## 2. Materials and methods

### 2.1. Study region

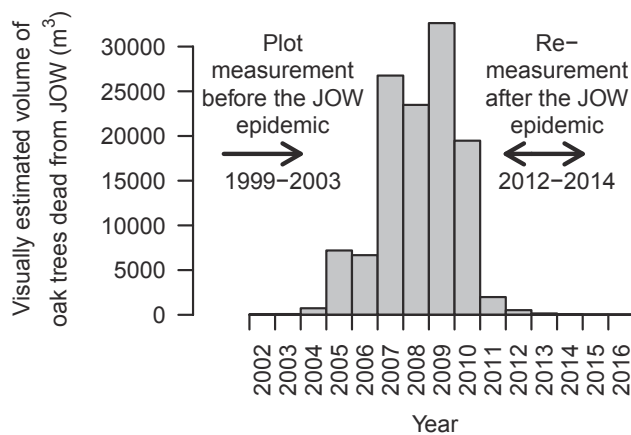
Japan consists of 47 Prefectures. Toyama Prefecture, the study region, occupies 4248 km<sup>2</sup> in central Japan (Fig. 1), and forests cover ca. 2800 km<sup>2</sup>. The Prefecture includes the Northern Japan Alps (ca. 3000 m in elevation) and most forests are in a steep, mountainous area. The proportions of secondary, primary, and plantation forests are 36%, 45%, and 19%, respectively (Nakajima and Kobayashi, 2014). A high proportion of natural forests (secondary and primary forests) is characteristic of Toyama Prefecture. Distribution of forests is regulated by elevation zone: the warm-temperate zone is 0–400 m, cool-temperate zone is 400–1600 m, and sub-boreal zone is 1600–2400 m (Nakajima and Kobayashi, 2014). Secondary forests are distributed in the warm-temperate zone (dominated by *Q. serrata*) and cool-temperate zone (dominated by *Q. crispula* and *F. crenata*), and most of these forests are abandoned coppice forests (Nakajima and Ishida, 2014). Primary forests are mainly distributed in the cool-temperate zone (dominated by *F. crenata*) and sub-boreal zone. Plantation forests are distributed in the warm- and cool-temperate zones and most planted trees are Japanese cedar (*Cryptomeria japonica*). The two oak species (*Q. crispula* and *Q. serrata*) that suffered mortality from JOW were mainly distributed in secondary forests, although they were also mixed in primary forests and sometimes invaded plantation forests (Hasegawa and Taira, 2000).

Japanese forests are classified by ownership into national forests and private forests (any forests other than those owned by the national government) (Hirata et al., 2010). In Toyama Prefecture, national forests (ca. 1000 km<sup>2</sup>) are mainly distributed in the sub-boreal zone and most (86%) are primary forests in national parks. Private forests (ca. 1800 km<sup>2</sup>) are mainly distributed in the warm- and cool-temperate zones and most are secondary forests; the proportions of secondary, primary, and plantation forests are 51%, 22%, and 27%, respectively (Nakajima and Kobayashi, 2014). This study analyzed the forest dynamics of NFI plots in private forests.

### 2.2. Data collection

#### 2.2.1. Period of plot measurement

In Toyama Prefecture, mortality from JOW was first reported in 2002 (Nishimura et al., 2007). Since then, in private forests, the Prefectural government has annually monitored crowns that are discolored to reddish-brown prior to autumn leaf-coloring, which is the feature of



**Fig. 2.** Visually estimated total volume of oak trees killed by Japanese oak wilt disease (JOW) in private forests of Toyama Prefecture, Japan (Toyama Prefecture, 2018). Plot measurement was conducted before the JOW epidemic in 1999–2003 and re-measurement was conducted after the JOW epidemic in 2012–2014.

mortality from JOW (Kobayashi and Ueda, 2005; Kondoh et al., 2015). The monitoring is conducted visually from roads and the volume of dead trees is estimated as the product of the number of discolored crowns and the uniform standard volume per crown. The estimated volume of dead trees is a useful indicator of a JOW epidemic, although the volume may have a large error because parts of forests are not visible from roads. The estimated volumes gradually increased, peaked in 2009, and then decreased (Fig. 2; Toyama Prefecture, 2018). The summed volume between 2004 and 2011 occupied 99.2% of the total (2002–2016) volume. Therefore, in this study, the epidemic period was regarded as the duration from 2004 to 2011; the first NFI (conducted from 1999 to 2003) was treated as the measurement before the JOW epidemic; and the re-measurement conducted from 2012 to 2014 was treated as measurement after the JOW epidemic. The forest dynamics during the JOW epidemic was defined as forest change between measurement before and after the JOW epidemic.

## 2.2.2. Measurement before the JOW epidemic

During the first NFI (1999–2003), 101 plots were established on a 4-km national grid in private forests of Toyama Prefecture (Fig. 1; Nakajima, 2016). The elevation of plots ranged from 20 to 1550 m, and they were in warm- and cool-temperate zones. According to the vegetation map of the Ministry of the Environment of Japan (2nd to 5th vegetation survey, [http://www.biodic.go.jp/index\\_e.html](http://www.biodic.go.jp/index_e.html)), plot centers were in primary forests (18 plots), secondary forests (53 plots), plantation forests (26 plots), and others (4 plots). The elevation of plots in primary forests ( $884 \pm 370$  m, mean  $\pm$  SD) was higher than in secondary ( $466 \pm 307$  m) and plantation forests ( $554 \pm 372$  m) ( $p < 0.05$ , Mann–Whitney  $U$  test with Bonferroni correction), but elevation ranges overlapped one another: 190–1550 m, 30–1400 m, and 80–1490 m for plots in primary, secondary, and plantation forests, respectively. Each plot consisted of three nested subplots, covering 0.01, 0.04, and 0.10 ha (Hirata et al., 2010); the plot shape was either a circle or a square (Nakajima, 2017). All stems, greater than or equal to 1-, 5-, and 18-cm diameter at breast height (DBH), were measured for each sub-plot. This DBH classification almost corresponds to the classification: understory, sub-canopy, and canopy trees. DBH measurement was conducted for all stems, and stem height was measured for some of the stems in each plot. All stems  $\geq 18$  cm DBH were labeled. Forest type classification between natural forests (secondary and primary forests) and plantation forests was recorded. These first NFI data were used as the data before the JOW epidemic (Fig. 2).

## 2.2.3. Re-measurement after the JOW epidemic

During the first NFI from 1999 to 2003, plots were established with the goal of re-measuring each plot every 5 years (Hirata et al., 2010); the second NFI was conducted from 2004 to 2008 and the third was conducted from 2009 to 2013. However, of the 101 plots established during the first NFI, almost half were not re-measured during the third NFI. Plots that were difficult to access were abandoned; plots with large location errors (distance between recorded and true coordinates) could not be found and alternative new plots were established; and the square-shaped plots were converted to circular plots (Nakajima, 2016, 2017). Therefore, the author revisited and restored the plots established by the first NFI (Nakajima, 2016) and re-measurement was conducted for the 101 plots from 2012 to 2014; these were used as re-measurement data after the JOW epidemic (Fig. 2). Intervals between measurement before and after the epidemic ranged from 11 to 13 years. During these intervals, clear-cut logging was conducted in three plots but the area of logging was restricted to a part of the plot; the proportion of logging area was 10%, 15%, and 40% of each plot area. In these areas, there was no canopy tree ( $\geq 18$  cm DBH) of any of the three Fagaceae species (*Q. crispula*, *Q. serrata*, or *F. crenata*). Therefore, the effect of clear-cut logging on analysis of this study was regarded as small and the data from these plots were included in the analysis.

To calculate mortality rate during the epidemic and analyze factors affecting mortality, stems of three Fagaceae species (*Q. crispula*, *Q. serrata*, and *F. crenata*) greater than or equal to 18 cm DBH before the epidemic were categorized into live or dead at re-measurement after the epidemic (stems less than 18 cm DBH were not targeted because they were not labeled). The number of stems was 375 stems in 41 plots for *Q. crispula*, 266 stems in 20 plots for *Q. serrata*, and 191 stems in 24 plots for *F. crenata*. Identification of each stem before the epidemic with a stem after the epidemic was conducted using labels preserved during the first to third NFIs. However, especially in the plots where the second and third NFIs were not conducted, there were some stems whose labels seemed to have disappeared. In these cases, the identification was conducted using the information of stem size (DBH), stem composition (size and number) of a multi-stemmed individual (individuals are often composed of some stems in secondary forests; Nagaike et al., 2003), the sub-plot where the stem was recorded, and the size and species of stems recorded around the target stem. After these procedures, stems before the epidemic that were not linked to any stems after the epidemic were categorized as dead.

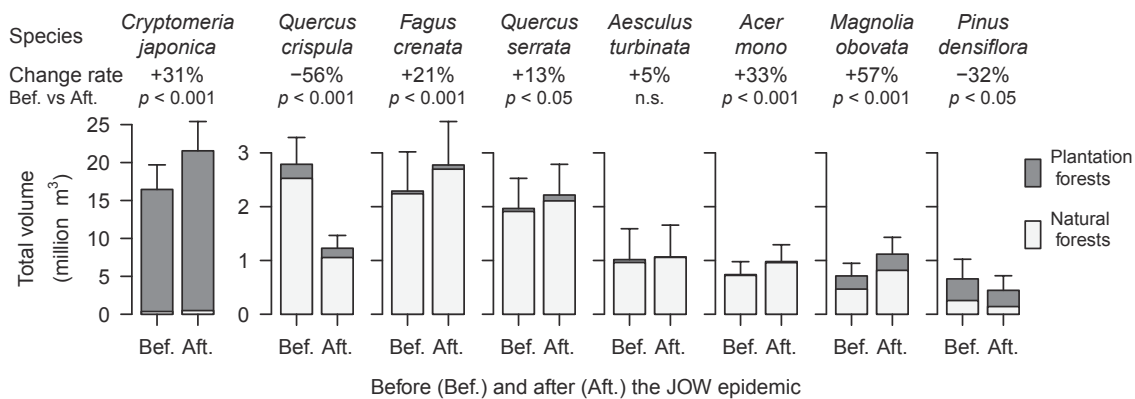
## 2.2.4. Gap successors

To examine trees likely to replace oaks that had died during the JOW epidemic, 2-m radius microplots were set in canopy gaps larger than 10 m<sup>2</sup> (Nakashizuka, 1984) generated by dead oak, during re-measurement after the epidemic. The height and species of the tallest regenerating tree in the microplot were recorded as gap successor (Yamamoto and Nishimura, 1999). A microplot was set beneath each dead oak stem  $\geq 18$  cm DBH. If there was more than one dead stem in a multi-stemmed oak, the microplot was set only beneath the stem with the largest DBH. The microplot was set at the approximate center of presumed crown projection area before gap creation. In this way, 194 microplots were established in 37 plots.

## 2.3. Data analysis

### 2.3.1. Volume and relative abundance

Stem volume was calculated from DBH and stem height using equations established by the Forest Agency (1970) of Japan. As stem height was measured for some of the stems in each plot, stem height was estimated from DBH using equations of relation between DBH and stem height in each plot derived from stem data with both DBH and stem height. Plot-level volume (m<sup>3</sup>/ha) of each species was calculated as the sum of living stem volume, and relative abundance was determined by the proportion of plot-level volume of a species to that of



**Fig. 3.** Estimated total volume of main species in the study region before and after the JOW epidemic. The top eight species in total volume before the epidemic are shown and placed from left to right. Note that the scales of the y-axis are different between *C. japonica* and the other species. Bars are standard error of mean. P-values are the result of comparison before and after the JOW epidemic with paired Wilcoxon test ( $\alpha = 0.05$ ). Change rate is the ratio of  $\Delta$  total volume to total volume before the JOW epidemic.

all species. The total volume of each species in the study region was estimated as the product of the average plot-level volume (including zero data) and study area; study area was simply determined by the range where the study 101 plots were established on a 4-km national grid (i.e.,  $101 \times 4 \times 4 = 1616 \text{ km}^2$ ). This area was smaller than that of private forests (ca.  $1800 \text{ km}^2$ ) because there were some grid points whose plots were not established because of difficult access. The volume change rate from before to after the JOW epidemic was determined by the ratio of  $\Delta$  total volume to total volume before the epidemic. The total volume of each species was compared between before and after the epidemic using Wilcoxon signed-rank test for paired plot-level volume before and after the epidemic. Regional relative abundance of each species was determined by the proportion of total volume of a species to that of all species. Total volume was composed of volume of natural and plantation forests, and thus regional relative abundance was determined for both natural and plantation forests.

### 2.3.2. Mortality rate

Mortality rates during the JOW epidemic were calculated for each of *Q. crispula*, *Q. serrata*, and *F. crenata* from the number of dead stems during the epidemic ( $N_d$ ) of stems  $\geq 18 \text{ cm}$  DBH before the epidemic ( $N_0$ ) as  $N_d / N_0$ . Mortality rates were calculated at both region-wide and plot-level. Region-wide mortality rates were calculated from pooled data across all plots and compared among the three species using pairwise chi-square tests with Bonferroni correction. Plot-level mortality rates were used to examine the relation with elevation.

### 2.3.3. Factors affecting oak mortality

To clarify factors affecting mortality during the JOW epidemic, generalized linear mixed models (GLMMs) with binomial distribution and logit link function were developed for each of *Q. crispula* and *Q. serrata*. The stems  $\geq 18 \text{ cm}$  DBH before the epidemic were used for this analysis (see Section 2.2.3), and plot was used as random effect. The explanatory variables were five plot-level variables (target species volume before the epidemic, non-target species volume before the epidemic, elevation, slope inclination, and slope aspect) and one stem-level variable, DBH before the epidemic. For each of *Q. crispula* and *Q. serrata* mortality, three models that differed in target species (conspecific species, two oak species, and all susceptible host species) in volume calculation of host species were developed because there were some plots where both *Q. crispula* and *Q. serrata* existed and where susceptible host species of JOW other than *Q. crispula* and *Q. serrata* existed. The 'conspecific species' model used conspecific volume: for example, *Q. crispula* volume was used as the target species volume for the *Q. crispula* mortality model. The 'two oak species' model used sum

volume of *Q. crispula* and *Q. serrata*. The 'all susceptible host species' model used the sum volume of *Q. crispula*, *Q. serrata*, *Q. variabilis*, *Q. acutissima*, *Q. salicina*, *Q. acuta*, *Castanea crenata*, and *Castanopsis sieboldii*, whose mortality from JOW was reported somewhere in Japan (Kobayashi and Ueda, 2005). When all plot data before the epidemic were pooled, *Q. crispula*, *Q. serrata*, *C. crenata*, *Q. salicina*, *Q. acuta*, *Q. variabilis*, *Q. acutissima*, and *C. sieboldii* accounted for 52.2%, 36.8%, 4.9%, 3.2%, 1.2%, 0.9%, 0.7%, and 0.1% of the sum volume of these susceptible host species, respectively. Slope aspect was cosine transformed to represent 'northness' because *P. quercivorus* adults have a positive phototaxis (Igeta et al., 2003) and thus their host tree selection may be affected by the light environment. GLMMs were developed for all possible combinations of explanatory variables including null model (i.e., 64 candidate models were developed), and the model with the lowest Akaike information criterion (AIC) was selected as the best model. GLMMs were developed using R 3.4.3 (R Core Team, 2017) and the 'glmer' function in lme4 package (Bates et al., 2015).

### 2.3.4. Number of stems

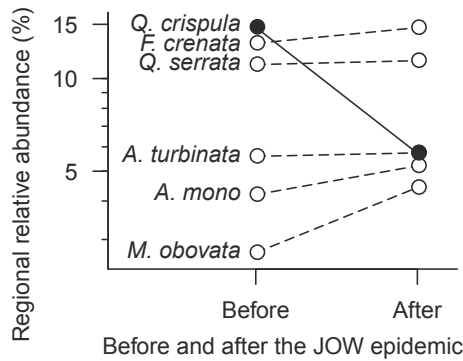
To examine the abundance of saplings that had a chance of replacing dead oak trees, the frequency distribution of stems among three developing stages at regional level was examined for *Q. crispula*, *Q. serrata*, and *F. crenata*. The developing stages were defined as sapling, sub-canopy tree, and canopy tree. These three stages were simply distinguished by DBH classes 1–5, 5–18, and  $\geq 18 \text{ cm}$ , respectively, corresponding to measurements of stem sizes in each of three nested subplots. The total stem number in the study region was estimated using the same method as for estimation of total volume.

## 3. Results

### 3.1. Forests before the JOW epidemic

Before the JOW epidemic, the top four species in total volume were *C. japonica*, *Q. crispula*, *F. crenata*, and *Q. serrata*, and they appeared in 52, 44, 27, and 27 plots, respectively (Fig. 3; Appendix A1). Of these species, *C. japonica* overwhelmingly dominated (87%) plantation forests (Appendix A1), while *Q. crispula*, *F. crenata*, and *Q. serrata* were the top three dominant species in natural forests (Fig. 4); the sum of these three species occupied 39% of natural forests. The elevation range where *Q. crispula*, *Q. serrata*, and *F. crenata* dominated was approximately between 400 and 800 m, below 400 m, and above 800 m, respectively (Fig. 5). Among these three species, *Q. crispula* appeared in the widest elevation range (200–1550 m). This elevation range included the low elevation zone dominated by secondary forests and the high elevation zone dominated by primary forests, implying the existence of





**Fig. 4.** Change of regional relative abundance in natural forests from before to after the JOW epidemic. Regional relative abundance was determined by the proportion of total volume of a species to that of all species. Species that had relative abundance above 4% before or after the JOW epidemic are indicated. The values are log-transformed. Solid circle and solid line represent decrease; open circle and dotted line represent increase. The full species names are shown in Fig. 3.

elevation-dependent size change in DBH. However, there was no significant correlation between elevation and *Q. crispula* DBH ( $r = -0.06$ ,  $p = 0.133$ ).

### 3.2. Volume change and mortality during the JOW epidemic

Region-wide mortality rates during the JOW epidemic were high in *Q. crispula* (68%), intermediate in *Q. serrata* (21%), and low in *F. crenata* (6%) (Table 1). The number of plots where there was no record of stems before the epidemic, but where there were recruiting stems during the epidemic, was 3, 3, and 2 plots for *Q. crispula*, *Q. serrata*, and *F. crenata*, respectively. Including these plots, the plots were divided by whether plot-level volume of a species decreased or increased during the epidemic (Fig. 6). The proportion of decreased plots was high (72%, 34/47) for *Q. crispula*, while the proportions for *Q. serrata* and *F. crenata* were relatively low at 20% (6/30) and 10% (3/29), respectively.

Of the top eight species in total volume before the JOW epidemic, statistical increase during the epidemic was detected for *C. japonica* (+31%), *F. crenata* (+21%), *Q. serrata* (+13%), *Acer mono* (+33%), and *Magnolia obovata* (+57%), while statistical decrease was detected for *Q. crispula* (−56%) and *Pinus densiflora* (−32%) (Fig. 3). Regional relative abundance of *Q. crispula* in natural forests decreased markedly from 14.7% to 5.7%, while that of *F. crenata* and *Q. serrata* increased from 13.0% to 14.6% and 11.1% to 11.4%, respectively (Fig. 4).

### 3.3. Factors affecting mortality during the JOW epidemic

For *Q. crispula*, all three models (which differed in target species in

**Table 1**

Region-wide mortality rates during the epidemic of Japanese oak wilt disease (JOW) calculated from pooled data across all plots. The rate is the proportion of the number of dead stems to stems  $\geq 18$  cm DBH before the JOW epidemic. Different letters indicate significant differences among species ( $p < 0.001$ ).

Species	Frequency of appearance <sup>a</sup>	No. of stems	Dead stems	Mortality
<i>Quercus crispula</i>	41	375	254	68% a
<i>Quercus serrata</i>	20	266	56	21% b
<i>Fagus crenata</i>	24	191	11	6% c

<sup>a</sup> Number of plots.

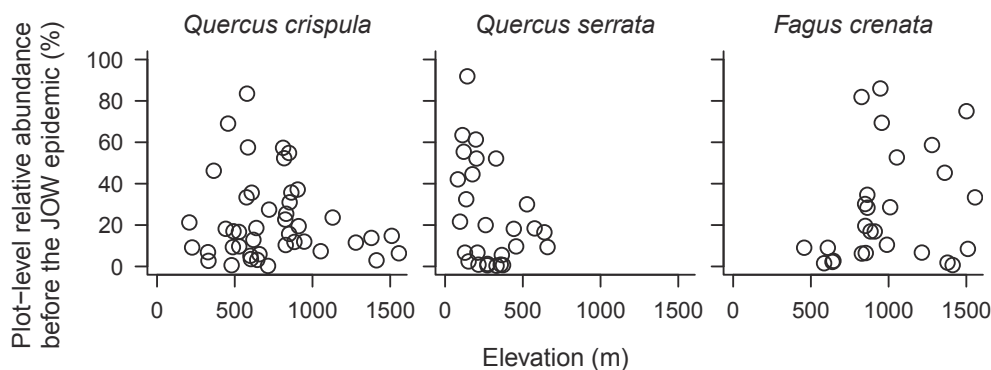
volume calculation of host species) revealed positive effects of target species volume and negative effects of elevation on mortality (Table 2; Appendix A2). Among these three models, the model with all susceptible host species as target species had the lowest AIC and the model with only *Q. crispula* as target species had the highest AIC, suggesting that adding more species to *Q. crispula* as target host species in volume calculation improved the model performance. The explanatory variables other than elevation and target species volume had no significant effect in all models. For *Q. serrata*, when all susceptible host species were used as target species in volume calculation of host species, the selected best model was the null model (i.e., inclusion of no explanatory variable) and model performance was worst among the three models that differed in target species in volume calculation. The other two models revealed positive effects of target species volume on mortality, and the model with two oak species as target species was a better model than the model with only *Q. serrata* as target species. The other explanatory variables had no significant effect in either model.

For *Q. crispula*, there was negative correlation between elevation and mortality rates (Fig. 7). The mortality rates of *Q. crispula* were especially low above 1000 m in elevation.

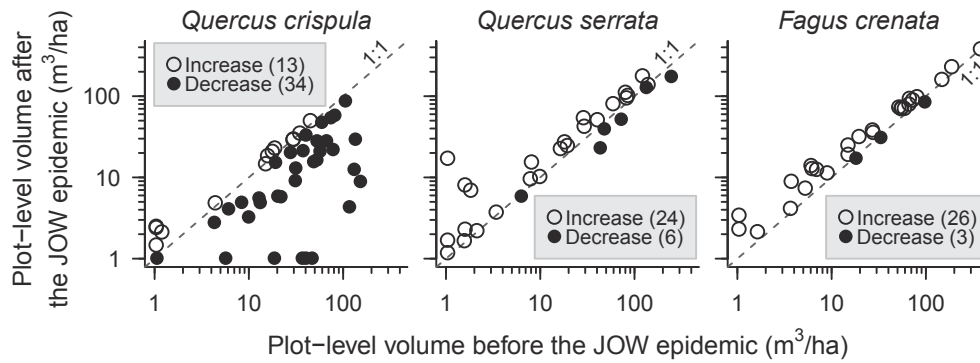
### 3.4. Sapling abundance and gap successors

Both before and after the JOW epidemic, the modal stage among three developing stages was sub-canopy tree or canopy tree for *Q. crispula* and *Q. serrata*, but was sapling for *F. crenata* (Fig. 8).

The number of gap successors was 130 for canopy tree species and 64 for shrub species (Table 3). Canopy tree species consisted of 24 species, dominated by *Acer sieboldianum*, *Carpinus japonica*, *Sorbus alnifolia*, *Ilex macropoda*, *Q. salicina*, *Prunus grayana*, and *Stewartia pseudocamellia*. Among these species, *A. sieboldianum* appeared in the widest elevation range (130–870 m). *Q. salicina* was the only evergreen species and appeared in the narrowest and lowest elevation range (190–430 m). The number of gap successors for *Q. crispula* and *Q. serrata* were only 2 and 1, respectively. There were 17 shrub species, dominated by *Hamamelis japonica* var. *obtusata* and *Acer japonicum*.



**Fig. 5.** Relation between elevation and plot-level relative abundance before the JOW epidemic. Relative abundance was determined by the proportion of plot-level volume of a species to that of all species.



**Fig. 6.** Relation between plot-level volume before and after the JOW epidemic. The values are log-transformed after adding 1 to avoid zero values. The plots are divided by whether plot-level volume increased or decreased during the JOW epidemic, and number of plots in each category is shown in parentheses.

**Table 2**

Summary of the best models for mortality of *Quercus crispula* and *Q. serrata* during the JOW epidemic. Further model details are shown in Appendix A2.

Dependent variable	Classification of models	AIC	Explanatory variable <sup>a</sup>					
	(Target species in volume calculation of host species)		Target species volume	Non-target species volume	Elevation	Slope inclination	Slope aspect	Stem DBH
Mortality of <i>Q. crispula</i> ( <i>Qc</i> )	All susceptible host spp. <sup>b</sup>	372.9	++	un	--	un	un	NS
	Two oak spp. ( <i>Qc</i> and <i>Qs</i> )	374.4	+	un	--	un	un	NS
	Conspecific sp. ( <i>Qc</i> )	375.6	+	un	--	un	un	NS
Mortality of <i>Q. serrata</i> ( <i>Qs</i> )	All susceptible host spp. <sup>b</sup>	268.3	un	un	un	un	un	un
	Two oak spp. ( <i>Qc</i> and <i>Qs</i> )	267.3	+	un	un	un	un	un
	Conspecific sp. ( <i>Qs</i> )	267.5	++	un	NS	un	un	un

<sup>a</sup> ‘+’ and ‘++’: positive coefficients ( $p < 0.05$  and  $p < 0.01$ , respectively); ‘--’: negative coefficient ( $p < 0.001$ ); ‘NS’: selected as an explanatory variable but the coefficient was not significant ( $p > 0.05$ ); ‘un’: not selected as an explanatory variable.

<sup>b</sup> All susceptible host species are *Q. crispula*, *Q. serrata*, *Q. variabilis*, *Q. acutissima*, *Q. salicina*, *Q. acuta*, *Castanea crenata*, and *Castanopsis sieboldii*.

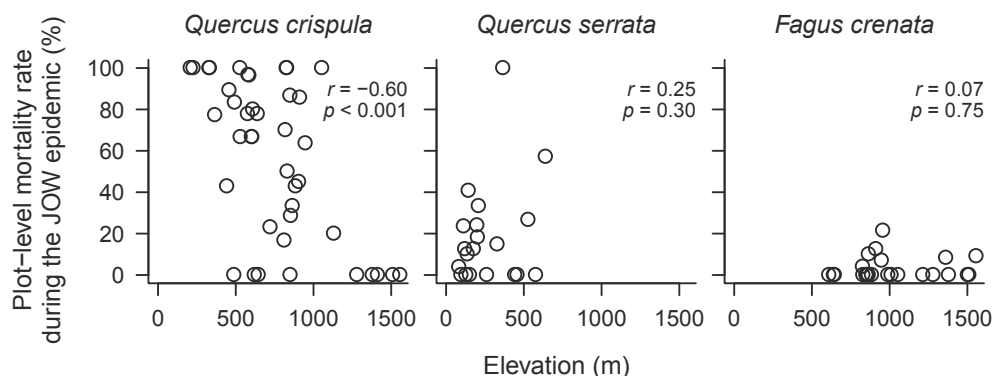
## 4. Discussion

### 4.1. Impact of JOW on forests

Most of the study region is represented by secondary forests, which are abandoned coppice forests dominated by *Q. crispula*, *Q. serrata*, and *F. crenata* (Nakajima and Kobayashi, 2014; Fig. 4). Among these three species, *Q. crispula* was distributed in the widest elevation range (Fig. 5) and so was the most dominant species in natural forests before the epidemic (Fig. 4). However, the total volume of *Q. crispula* in the study region decreased by 56% during the epidemic (Fig. 3) and its dominance declined below that of *F. crenata* and *Q. serrata* after the epidemic (Fig. 4). This remarkable decline was caused by high mortality of *Q. crispula* during the epidemic (Table 1). These results reveal that JOW had a huge negative impact on the regional abundance of *Q. crispula* and changed forest species composition at a regional scale. In the

elevation gradient, forests in the middle elevation zone (400–800 m) were most influenced by the JOW epidemic because *Q. crispula* dominated before the epidemic (Fig. 5) and mortality in this elevation zone was high (Fig. 7).

The mortality of *Q. serrata* during the epidemic was lower than that of *Q. crispula* (Table 1), consistent with previous studies that compared mortality from JOW between the two species at stand level (Shiomi and Osaki, 1997; Nishigaki et al., 1998; Kobayashi and Hagita, 2000; Kamata et al., 2002; Nishimura et al., 2007; Saito and Shibata, 2012; Matsuura and Nakajima, 2016). The present result that total volume of *Q. serrata* increased by 13% during the epidemic (Fig. 3) reveals that, at a regional scale, volume loss of *Q. serrata* from JOW could be compensated for in terms of volume increment by growth of surviving trees during the epidemic. In short, the impact of JOW on the regional abundance of *Q. serrata* was small. The increase in *Q. serrata* volume and the decrease in *Q. crispula* volume mean that the relative



**Fig. 7.** Relation between elevation and plot-level mortality rates during the JOW epidemic. Pearson's correlation coefficients are shown in the figure.

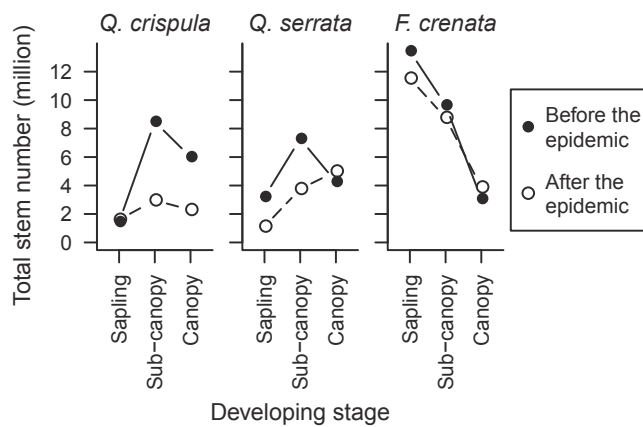


Fig. 8. Estimated total stem number of each of three developing stages (sapling, sub-canopy tree, and canopy tree) before and after the JOW epidemic.

importance of *Q. serrata* when oak wood is used has been enhanced in the study region, although its wood is recognized as being less versatile than that of *Q. crispula* (Hashizume, 1989).

The low mortality rate of *F. crenata* compared with *Q. crispula* and *Q. serrata* (Table 1) was because *F. crenata* does not die from JOW. As a result, *F. crenata* became the most dominant species in the natural forests after the epidemic (Fig. 4). The dominance of *F. crenata* in study region would have increased even if the JOW epidemic had not occurred. This is because the dominance of *F. crenata* in mixed secondary forests with deciduous oak species increases with secondary succession (Yoshida and Kamitani, 2000; Nakajima and Ishida, 2014) owing to the high shade tolerance of *F. crenata* compared with deciduous oak species (Masaki et al., 1992; Yoshida and Kamitani, 1997; Niinemets and Valladares, 2006; Takahashi and Goto, 2012).

During the JOW epidemic, a remarkable decline in *P. densiflora* was detected (Fig. 3), perhaps due to pine wilt disease induced by the pinewood nematode (*Bursaphelenchus xylophilus*) (Toyohara and Fujihara, 1998; Futai, 2013). In the study region, *P. densiflora* is mainly distributed below 400 m and is sometimes mixed with *Q. serrata* in secondary forests (Ishida, 1996). Therefore, the decline in *P. densiflora* contributed to enhancing the dominance of *Q. serrata* in this elevation zone.

#### 4.2. Factors affecting oak mortality

The mortality of *Q. crispula* was low at high elevation (Table 2; Fig. 7). This can be inferred from the elevation-dependent behavior of *P. quercivorus*, the vector of JOW. This beetle overwinters in the larval stage in wood (Kamata et al., 2002) but the larvae cannot overwinter in

high elevation zones because of the low temperature (Ohashi, 2015); this elevation zone is approximately above 1000 m in the study region (T. Matsuura, personal communication). Nevertheless, occasional deaths of *Q. crispula* from JOW above 1000 m have been reported (Ito and Ohashi, 2014). This would have been because the dead trees had been attacked by adult beetles, which flew in from the low elevation zone where the larvae could overwinter. Fukuzawa et al. (2019) examined flying adults at elevation gradients from 600 m to 1000 m and revealed that their numbers decreased with increasing elevation because of the increasing difficulty of overwintering and the decreasing host density (i.e., low dominance of *Q. crispula* in high elevation zones) (Fig. 5). Therefore, mortality from JOW is expected to decrease with increasing elevation and this would be the reason why *Q. crispula* had low mortality at high elevation, especially above 1000 m (Fig. 7).

Elevation-dependent tree mortalities have been reported worldwide and have been considered in association with ongoing climate change (Logan et al., 2003; Allen et al., 2010). The inverse dependence of *Q. crispula* mortality on elevation (Table 2; Fig. 7) suggests that global warming promoted the increased death of trees from JOW, as hypothesized by Kamata et al. (2002). This is because the elevation zone with high mortality from JOW would have been restricted to a lower zone if global warming had not progressed. In the study region, the JOW epidemic had ended (Fig. 2), but epidemics of JOW sometimes recur after about 10 years (Ito and Yamada, 1998). There is, therefore, concern that if global warming progresses then repeated epidemics may cause serious damage to *Q. crispula* in the elevation zone where mortality from JOW was low in the last epidemic.

There was no relation between mortality of *Q. serrata* and elevation (Table 2; Fig. 7). The elevation zone where *Q. serrata* appeared was below 650 m (Fig. 5). In this elevation zone, winter temperature does not prevent overwintering of *P. quercivorus* (Nishimura et al., 2007; T. Matsuura, personal communication). Therefore, JOW is not expected to generate elevation-dependent mortality for *Q. serrata*.

More *Q. crispula* and *Q. serrata* died in forests with a high volume of oak (sum volume of *Q. crispula* and *Q. serrata*) (Table 2), consistent with previous studies conducted at stand or local levels (Yamasaki and Sakimoto, 2009; Yamasaki et al., 2014; Oguro et al., 2015). The present study verified the dependence of mortality on stand-level oak abundance at a large geographical scale, taking elevation-dependent mortality into consideration. This result means that forests with large volumes of oak suffered exponentially increasing damage because oak abundance and its high mortality acted as a multiplier effect to increase volume loss from JOW. Similar results were reported for the interaction between the tree-killing bark beetle (*Ips typographus*) and its host tree (*Picea abies*) in Sweden (Kärveemo et al., 2014) and the interaction between the mountain pine beetle (*Dendroctonus ponderosae*) and its host tree (*Pinus ponderosa*) in the USA (Negrón et al., 2008). The dependency

Table 3  
Summary of gap successors.

Species type	Leaf habit	Species of gap successor	Number of gap successors	Frequency of appearance <sup>a</sup>	Elevation range <sup>b</sup> (m)	Stem height (mean ± SD) (m)
Canopy tree	Deciduous	<i>Acer sieboldianum</i>	32	11	130–870	7.9 ± 1.8
Shrub	Deciduous	<i>Hamamelis japonica</i> var. <i>obtusata</i>	18	8	320–810	3.9 ± 0.9
Canopy tree	Deciduous	<i>Carpinus japonica</i>	17	7	350–890	7.2 ± 2.5
Canopy tree	Deciduous	<i>Sorbus alnifolia</i>	16	7	350–650	7.8 ± 2.3
Shrub	Deciduous	<i>Acer japonicum</i>	9	6	320–940	5.7 ± 1.9
Canopy tree	Deciduous	<i>Ilex macropoda</i>	8	6	110–520	7.2 ± 2.3
Canopy tree	Evergreen	<i>Quercus salicina</i>	7	4	190–430	8.3 ± 1.6
Canopy tree	Deciduous	<i>Prunus grayana</i>	7	5	130–820	5.3 ± 0.9
Canopy tree	Deciduous	<i>Stewartia pseudo-camellia</i>	7	3	480–840	8.0 ± 0.7
Shrub	Deciduous	<i>Acer amoenum</i> var. <i>matsumurae</i>	7	3	520–810	5.4 ± 1.6
Canopy tree	Deciduous	<i>Fagus crenata</i>	6	3	450–900	8.5 ± 2.0
The other 16 canopy tree species			30			
The other 14 shrub species			30			

<sup>a</sup> Number of plots in which gap successors of each species appeared.

<sup>b</sup> Elevation of plots in which gap successors of each species appeared.

of oak mortality on stand-level oak abundance may be because *Platypus quercivorus* beetles target clumped host trees (Yamasaki and Sakimoto, 2009); subsequently, beetles are more attracted to groups of attacked trees where the aggregation pheromone works on a larger scale (Yamasaki et al., 2014).

Kobayashi and Ueda (2005) hypothesized that abandonment of oak-dominated coppice forests and subsequent growth in the size of oak generated a favorable environment for reproduction of *P. quercivorus* and thus for the latest JOW epidemic that occurred in various regions of Japan. The present study supports their hypothesis because the dependency of mortality on stand-level oak abundance (Table 2) means that more oak trees died in forests with higher oak dominance (i.e., used as coppice forests before abandonment) and more mature oak-dominated forests (i.e., the size of trees had increased with the passage of time from coppice abandonment).

The performance of mortality models differed according to target species in volume calculation of host species (Table 2). For mortality of both *Q. crispula* and *Q. serrata*, the model with two oak species (*Q. crispula* and *Q. serrata*) as target species had a higher performance than the model with only conspecific species. This suggested that the summed abundance of the two oak species was an important positive factor for mortality from JOW in mixed forests of the two oak species, which were distributed in elevations of 200–700 m (Fig. 5). The model with all susceptible host species as target species was better than the model with the two oak species for *Q. crispula* mortality, but was not true for *Q. serrata* mortality (Table 2). This inconsistency might be because vertical distribution and susceptibility to JOW differs among the host species. The main susceptible host species other than *Q. crispula* and *Q. serrata* were *Castanea crenata*, *Q. salicina*, and *Q. acuta*. Of these species, *Q. salicina* and *Q. acuta* are evergreen oaks, which are less susceptible to JOW than the deciduous oaks *Q. crispula* and *Q. serrata* (Ito and Yamada, 1998; Sueyoshi et al., 2018) and are distributed in the low elevation zone together with *Q. serrata* (Nakajima and Kobayashi, 2014). Therefore, more of these less-susceptible evergreen oaks were included in the *Q. serrata* mortality model as target host species than in the *Q. crispula* mortality model. This may mask the dependence of mortality on host abundance in the *Q. serrata* mortality model with all susceptible host species as target species.

Previous studies have revealed the target preference of *P. quercivorus* for thicker stems, and the higher mortality from JOW in these stems (Shiomi and Osaki, 1997; Nishigaki et al., 1998; Kobayashi and Ueda, 2001; Akaishi et al., 2006; Nishimura et al., 2007; Yamasaki and Sakimoto, 2009). However, in the present study, stem DBH did not affect the mortality of *Q. crispula* and *Q. serrata* (Table 2), although stand-level oak abundance was a significant variable. Similar results were revealed in a study by Oguro et al. (2015) which analyzed factors affecting the mortality of *Q. crispula* and *Q. serrata* due to JOW in many plots at local level (part of a municipality). They revealed that stand-level oak abundance was the most important factor, and that individual tree size did not have substantial effect on mortality. The inconsistency among studies with regard to significance of individual tree size on oak mortality may be because Oguro et al. (2015) and the present study used data from many plots spread over a geographical scale including plots with low oak dominance (Fig. 5), while other previous studies were conducted in a small number of plots and/or only in oak-dominated forests. Previous studies focused on differences in mortality among trees within plots but could not analyze differences in mortality among plots (Oguro et al., 2015). The present study supports the suggestion by Oguro et al. (2015) that, at a large geographical scale, the heterogeneity of mortality among individual oaks may be determined primarily by differences in forest composition such as host tree density.

There is another possible reason for no significance of stem DBH on oak mortality (Table 2). The present mortality analysis used the data of stems  $\geq 18$  cm DBH; that is, a larger lower limit of DBH than in previous studies and much greater than a lower threshold DBH (11.2 cm), above which *P. quercivorus* attacks occur with  $> 50\%$  probability

(Yamasaki and Futai, 2008). Therefore, the present data may not show size-dependent mortality because of lack of data of small stems that were expected to have low mortality from JOW.

#### 4.3. Regeneration of forests suffering mortality from JOW

It is widely recognized that *F. crenata* is shade tolerant, while *Q. crispula* and *Q. serrata* are less shade tolerant (Masaki et al., 1992; Yoshida and Kamitani, 1997; Niinemets and Valladares, 2006; Takahashi and Goto, 2012; Nakajima and Ishida, 2014). Therefore, seedlings of *F. crenata* can grow into saplings beneath a closed canopy, while this is not true for *Q. crispula* and *Q. serrata* (Kanazawa, 1982; Takenaka, 1986; Yamamoto, 1989). The present results confirmed this at a regional scale, because the sapling population of *F. crenata* was abundant, while that of *Q. crispula* and *Q. serrata* was scarce (Fig. 8). This trend was consistent from before to after the epidemic, implying that there was little recruitment of saplings from seedlings during the epidemic for the two oak species, although many canopy gaps were created by JOW. This would be because any existing oak seedlings in these canopy gaps were released from suppression by canopy oak trees, but most of them were not released from suppression by saplings or sub-canopy trees of shade-tolerant species such as *F. crenata* (which can grow even before canopy gap formation). Dense undergrowth such as *Sasa* spp. (dwarf bamboo) and *Camellia japonica* var. *decumbens* (evergreen shrub) may also have prevented regeneration (Masaki et al., 1999). These disadvantages of regeneration for oak species are the reason why there were few gap successors of *Q. crispula* and *Q. serrata* (Table 3). These results suggested that *Q. crispula* and *Q. serrata* rarely regenerate in the canopy gaps resulting from trees killed by JOW. Similar difficulties in oak regeneration in canopy gaps have also been reported in North American oak forests (Ehrenfeld, 1980; McCune and Cottam, 1985; Crow, 1988; Lorimer et al., 1994).

Shrub species accounted for 33% of gap successors (Table 3). These species inhibit the growth of canopy tree species below them and delay canopy restoration (Royo and Carson, 2006). Dominant gap successors of canopy tree species were *A. sieboldianum*, *Carpinus japonica*, *S. alni-folia*, *I. macropoda*, *Q. salicina*, *P. grayana*, and *S. pseudo-camellia* (Table 3). These species are expected to replace dead oak trees as canopy trees and will increase their dominance in forests that have experienced JOW. All these species, other than *Q. salicina*, are deciduous. They are shade tolerant (Yamamoto, 1989; Yoshida and Ohsawa, 1996; Gonzales and Nakashizuka, 2010), and thus able to survive and grow under a closed canopy before the canopy oak trees were killed by JOW. *A. sieboldianum* was the most dominant gap successor, consistent with the previous study conducted in the same region (Nakajima and Ishida, 2014), and gap successors of *A. sieboldianum* appeared in the widest elevation range (Table 3). This means that *A. sieboldianum* often existed in oak-dominated forests as saplings or sub-canopy trees, and tended to be gap successors in forests suffering from JOW. Replacement of *Acer* species after dieback of oak trees was also reported in North American oak forests suffering mortality from gypsy moth defoliation (Fajvan and Wood, 1996). Of the dominant gap successors, only *Q. salicina* was evergreen (Table 3). This evergreen oak is mainly distributed in southwestern Japan, and the study region is close to its most northern habitat (Matsui et al., 2018). In evergreen forests, *Q. salicina* is relatively less shade tolerant (Yamamoto, 1992; Manabe et al., 2000) and cannot grow into the sub-canopy layer beneath a closed canopy (Tanouchi et al., 1994). However, the gap successors of *Q. salicina* have been found to grow in deciduous oak forests where they had an advantageous capability of photosynthesis in winter while canopy trees were leafless (Miyazawa and Kikuzawa, 2005). Thus, *Q. salicina* would be gap successors. Regardless of the JOW epidemic, evergreen broad-leaved species have increased recently in secondary deciduous forests owing to succession after the cessation of coppicing and perhaps as a result of climate change (Hiroki, 2001; Suzuki et al., 2015).

Mortality from JOW was mostly below 100% even for *Q. crispula* at



stand level (Fig. 7). Therefore, in forests suffering from JOW, there were usually remnant trees in the canopy layer even if all canopy trees were *Q. crispula* and/or *Q. serrata*. The existence of the remnant oak trees and that of various species as gap successors suggests that forests suffering JOW (which were relatively monospecific and even-aged before the epidemic) will change toward becoming multispecies mixed, uneven-aged forests.

To redevelop oak-dominated forests that have suffered mass mortality from JOW, management of understory vegetation that suppresses oak seedlings (Crow, 1988; Lorimer et al., 1994) and/or artificial planting is essential, because natural regeneration of oaks in canopy gaps is difficult as this study suggests. In oak forests experiencing relatively low mortality from JOW during the latest epidemic, oak mortality in the next JOW epidemic may be reduced by thinning oak trees and promoting the growth of other species, because oak mortality was found to be low in forests with low volumes of oak (Table 2). Another possible strategy is clear-cutting and rejuvenation from oak sprouts (Kuroda et al., 2012; Nagashima et al., 2019) because *P. quercivorus* cannot propagate in thin oak stems. However, Dinh et al. (2019) suggested that oak sprouts alone were not enough to redevelop oak forests following the clear-cutting of aging abandoned coppice forests. Therefore, promoting oak seedling growth and/or planting oak trees will be also necessary for this strategy, if the objective is oak-dominated forests. With respect to the anticipated next JOW epidemic, the less-susceptible *Q. serrata* should be used when oak trees are planted, as long as the elevation of the location is in the *Q. serrata* distribution range. In addition, mixed planting of oak and non-host species for *P. quercivorus* will reduce mortality from JOW because of the relatively low oak dominance compared to single-species planting of oak.

## 5. Conclusions

*Q. crispula* was most dominant species in natural forests before the JOW epidemic, owing to the past land use for coppicing. However, its high mortality from JOW decreased its abundance dramatically and changed species composition at a regional scale. More oak trees died in forests having a high volume of oaks, suggesting that stand development after abandonment of coppice forests was an important factor in the epidemic. The mortality of *Q. crispula* was inversely related with elevation, suggesting that global warming was a factor increasing mortality from JOW. In forests suffering mortality from JOW, oak species rarely regenerated, and forests will change toward multispecies mixed, uneven-aged forests. This study has comprehensively quantified forest change due to a JOW epidemic on a region-wide scale, and revealed that the epidemic was caused by multiple interactions among coppice abandonment, global warming, ambrosia beetles, and oak trees. These findings and suggestions will be useful in informing management of forest resources in the study region, and countermeasures against epidemics of JOW in any region.

## Declaration of Competing Interest

The author declares that he has no conflict of interests.

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117468>.

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