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Relative importance of multiple scale factors to oak tree mortality due to Japanese oak wilt disease

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ABSTRACT

Although landscape structure is known to affect the transmission and occurrence of tree diseases, relatively little is known about the scale dependency of these relationships. Japanese oak wilt (*Raffaelea quercivora*) is a vector-borne disease transmitted by the flying ambrosia beetle, *Platypus quercivorus*, and causes mass mortality in the fagaceous species of Japan. In this study, we examined the impact of stand and landscape factors on the mortality of *Quercus crispula* and *Quercus serrata* trees at a radius of up to 1000 m, to evaluate the relative importance of these factors that operate at different spatial scales. Of the factors considered, stand-level density, i.e., the total basal area of the host species within a 10 m radius, had the highest importance values for mortality. However, other stand-level factors such as the density of non-host species and individual tree size did not have substantial effects on mortality. In addition, landscape factors assessed within a 1000 m radius of target trees had a greater impact on mortality than those assessed within a 100 m radius. These patterns might be a reflection of the transmission mode of the disease. Because the spatial scale at which a disease responds differs among diseases, studies examining the relationship between landscape factors and diseases must take multiple spatial scales into consideration.

1. Introduction

Infectious diseases affecting woody plants seriously damage forest ecosystems around the world (Gibbs and Wainhouse, 1986; Loo, 2009). The impact of infectious diseases is not limited to effects had on individual trees and the population dynamics of a host plant, but also affects community and ecosystem processes such as the species composition of a community, nutrient cycling, and water cycling (Ellison et al., 2005; Rhoades, 2007; Elliott and Swank, 2008; Loo, 2009). Since the resources available for diseases control are often limited, the ability to predict occurrences, infection processes, and disease impacts is essential for effective forest management.

Several forest diseases, including the devastating Dutch elm and pine wilt diseases, are vectored by insects (Gibbs and Wainhouse, 1986; Loo, 2009; Park et al., 2013). Therefore, factors affecting the movement patterns of insect vectors also affect the transmission and occurrence of such diseases. For example, the characteristics of host trees and their surrounding environment, such as the size of individuals (Yamasaki and Sakimoto, 2009; Park et al., 2013) and local host density (Yamasaki and Sakimoto, 2009; Solheim et al., 2011; Yamasaki et al., 2014), can affect the occurrence of diseases vectored by insects.

Disease occurrence is also affected by landscape structure, i.e., the large-scale configuration of host habitat and the spatial patterns associated with host species (Holdenrieder et al., 2004; Meentemeyer et al., 2012). Although studies of plant diseases in a landscape context are less common than similar investigations of animal diseases (Meentemeyer et al., 2012), landscape structure can affect the transmission of tree diseases. For instance, the occurrence of Scleroderris canker (*Gremmeniella abientina*) is facilitated by topology that creates suitable microclimate conditions for the disease (Nevalainen, 2002). In addition, the probability of sudden oak death (SOD) (*Phytophthora ramorum*) occurrence is higher at forest edges, because the reservoir hosts of the disease are commonly present in such areas (Kelly and Meentemeyer, 2002). Furthermore, the connectivity of host habitats is known to affect the transmission of several tree diseases (Holdenrieder et al., 2004; Ellis et al., 2010). Because of the spatial nature of forest disease processes, understanding the relationship between landscape structure and the occurrence of forest diseases is essential for the identification of forest areas with a high risk of disease occurrence. However, to the best of our knowledge, no existing studies have

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elucidated the relationship between landscape structure and the occurrence of a forest disease vectored by insects.

In addition, some studies have demonstrated the spatial scale-dependency of landscape patterns on disease occurrence. For example, Condeso and Meentemeyer (2007) and Dillon et al. (2014) found that the relationship between the surrounding forest area and the severity of SOD differed among the spatial scales at which the landscape metric was calculated. In addition, Nevalainen (2002) found that the relationship between the topographical features of a landscape, such as relative elevation and surface features, and the severity of Scleroderris canker outbreaks, differed among spatial scales. However, despite the possible scale dependency of the relationship between landscape structure and the severity of forest diseases, few studies have employed multi-scale approaches (Meentemeyer et al., 2012).

Japanese oak wilt disease is an infectious fungal disease that causes mass mortality of fagaceous species in Japan (Kamata, 2008). This disease is caused by the fungus *Raffaelea quercivora* and is transmitted by the bark beetle *Platypus quercivorus* (Kinuura, 2002; Kubono and Ito, 2002; Kinuura and Kobayashi, 2006). Transmission of the disease occurs as follows: first, a male *P. quercivorus* beetle selects a healthy host tree and bores an entry hole (Yamasaki et al., 2014). Next, the male emits the aggregation pheromone quercivorol [(1*S*, 4*R*)-*p*-menth-2-en-1-ol] (Kashiwagi et al., 2006); consequently, both males and females of the species aggregate on the tree (Ueda and Kobayashi, 2001). Females possess a specialized organ called the mycangia (mycetangia), with which they transport *R. quercivora* to a new host (Kinuura, 2002). Female beetles bore galleries into the sapwood, where they spread the symbiotic fungus (Yamasaki et al., 2014). After infection, *R. quercivora* prevents the rise of sap through the tree's vascular tissue. When the rise of sap stops completely, the tree dies (Kuroda and Yamada, 1996; Kuroda, 2001). Because the beetles prefer trees with large diameters, such trees tend to suffer higher mortality rates, and forests with large old trees are at the greatest risk of attack by this disease (Kobayashi and Shibata, 2001; Kobayashi and Ueda, 2001, 2005).

Although, *P. quercivorus* is known to attack more than 50 tree species in Japan, dieback has been recorded to occur in only 15 species (Yamada, 2008). In addition, it is known that the mortality of fagaceous trees due to Japanese oak wilt differs among species, with both *Quercus crispula* and *Quercus serrata*, but especially *Q. crispula*, suffering the highest mortality rates (Yamada, 2008). Among the fagaceous species found in our study area, *Fagus crenata* is the only one for which dieback was not recorded (Kobayashi and Ueda, 2005).

Several measures have been adopted in order to protect trees from Japanese oak wilt, including the application of fungicides and the use of traps baited with aggregate pheromones (Saito, 2002; Kobayashi, 2008). However, these methods have not been very successful at protecting host trees from the disease. Thus, multi-scale forest management strategies that could reduce the probability of disease occurrence and tree mortality are required. However, although many studies have focused on the biology of *R. quercivora* and *P. quercivorus* (Kamata, 2008), few studies (Sato et al., 2004; Nobori et al., 2007) have investigated the effects of landscape structure on mortality due to oak wilt disease. Moreover, no study has investigated the relative impacts of stand conditions and landscape structure at different spatial scales on mortality due to Japanese oak wilt disease. If relevant landscape factors and their spatial scales of operation could be elucidated, such information could be utilized for the development of a disease-occurrence warning system, or to develop efficacious forest management strategies aimed at controlling this disease.

In this study, we investigated factors affecting the mortality of *Q. crispula* and *Q. serrata* due to Japanese oak wilt disease. First, we established statistical models that explain the relationship between multiple scale factors and *Q. crispula* and *Q. serrata* mortalities. To elucidate scale dependency, the landscape factors were calculated at two spatial scales. To test for differences in the patterns of host selection by *P. quercivorus* between the two host species, the relationship between multiple scale factors and host mortality were evaluated, as (1) two species together (suggesting whole impact of the disease in a forest), (2) *Q. crispula* alone, and (3) *Q. serrata* alone. We also integrated the results into a geographic information system (GIS), in order to predict the fragility (i.e., the probability of being killed by the disease) of *Q. crispula* and *Q. serrata* in the study region.

2. Materials and methods

2.1. Study location

This study was conducted in suburban areas of Tsuruoka City, Yamagata Prefecture, in the northern part of Honshu Island, Japan (E 139.82°, N 38.60°). We investigated the southern part of the city, where natural forest and plantations are the dominant land-use types. The initial occurrences of Japanese oak wilt in Tsuruoka were occasional: in 1959, Japanese oak wilt disease was first recorded in Tsuruoka, and was next recorded in 1977 and 1979 (Sato and Arai, 1993). After these initial occurrences, the presence of the disease was recorded every year since 1989 (Saito and Shibata, 2012) and has occurred in every part of the city since 2003. Because of the long period of time that has passed since the beginning of current outbreak, and because the disease has spread throughout the city, the occurrence of dieback in this area might reflect the risk of disease occurrence, due to both stand and landscape-level effects.

2.2. Field observations at the stand level

From June to early July of 2009, we traveled all forest roads that could be accessed by car in the former Asahi Village, Kushibiki Town, and Nurumi Town areas of Tsuruoka City (Fig. 1). These forest roads were selected to cover the variation in land-use types and vegetation, and because of their accessibility. Land-use types found in the study region include secondary forest dominated by *Q. crispula*, beech forest, coniferous plantations of *Cryptomeria japonica*, *Pinus densiflora,* and *Larix kaempferi*, rice fields, and residential areas.

Every 200 m along the forest roads, we searched for the nearest *Q. crispula* or *Q. serrata* individual and recorded its location using a Global Positioning System (GPS) device. We established a circular plot with a 10 m radius around each tree, and within that area identified all trees with a diameter at breast height (DBH) of >10 cm. *Q. crispula* stems with a diameter of <10 cm are rarely attacked by *P. quercivorus* (Nishimura et al., 2005). The DBH of each tree in each plot was measured, and trees were grouped into three classes according to size: 10–30 cm, 30–50 cm, and >50 cm. For all *Q. crispula* and *Q. serrata* individuals in the plot, we also recorded viability status (dead or alive). Overall, a total of 365 plots were surveyed, containing a total of 4482 trees, including 1089 *Q. crispula* and 846 *Q. serrata* trees.

Because previous studies (Nishigaki et al., 1998; Yamasaki and Sakimoto, 2009) showed that the size of an individual tree is positively related to the occurrence of dieback, the basal areas (BA) of individual trees were calculated using their DBH measurements and used for the analyses. The stand-level density of host trees is known to influence the occurrence of Japanese oak wilt (Yamasaki and Sakimoto, 2009; Yamasaki et al., 2014). In addition, the existence of non-host trees could potentially affect disease