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Large, retained trees of *Cryptomeria japonica* functioned as refugia for canopy woody plants after logging 350 years ago in Yakushima, Japan

H. Roaki Ishii[a,1,*], Takuya Minamino[a,1], Wakana Azuma[a,b], Kana Hotta[a], Akira Nakanishi[b]

[a] *Department of Plant Science, Graduate School of Agricultural Science, Kobe University, Kobe 657-8501, Japan*
[b] *Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan*

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ABSTRACT

Trees retained during green-tree retention forestry are expected to function as biological legacies that promote biodiversity and enhance ecosystem functions in plantation forests. Investigating how historically retained trees function as biological legacies could help predict the long-term ecological potential of current retention practices. Here, we investigated whether large, retained trees of *Cryptomeria japonica* D. Don (> 1000 years old) functioned as refugia for persistence of canopy woody plants after logging in a 350-year-old secondary forest in Yakushima, southern Japan. We climbed five each of retained and regenerated trees in a 1-ha research plot, measured trunk and crown structures, and tagged and measured every woody plant stem found on each tree. Compared to regenerated trees, retained trees had twice the surface area available for canopy plant colonization. Moreover, retained trees hosted disproportionately greater abundance of canopy woody plants. Together, the five retained trees hosted 22 species of woody plants comprising 1188 individuals, whereas regenerated trees hosted only 8 species (37 individuals). Combined with our ground-based measurement, canopy woody species contributed 16% of all woody plant species in the plot. Among the five retained trees, woody plant abundance increased markedly with increasing age of trunk breaks. This was because numerous epicormic branches had sprouted below trunk breaks creating large surface area upon which arboreal soil accumulated and woody plants established. Canopy woody plants on retained trees showed wide vertical distribution corresponding to complex crown structure, whereas those on regenerated trees occurred almost exclusively on the lower trunk. Maximum stem size of canopy woody plants was constrained by the volume of arboreal soil upon which they grew. Based on their size structures, we inferred that three species endemic to Yakushima (*Vaccinium yakushimense* Makino., *Viburnum urceolatum* Sieb. et Zucc., and *Rhododendron yakushimanum* Nakai), maintain stable populations in the retained trees by sprouting. Several other species scarcely found on the ground were also regenerating in the canopy. Our results demonstrate that retained trees of *Cryptomeria* functioned as refugia allowing canopy woody plants to persist after logging and give support to the importance of conserving large trees for enhancing biodiversity in forests where canopy plants contribute to species diversity.

1. Introduction

Biological legacies are organisms, organic matter, and structural features (e.g., standing trees, snags, logs, organic soil, etc.) that persist through a disturbance carrying over biological attributes to the recovering ecosystem (Franklin et al., 2002). The concept of biological legacies has been applied to silviculture in the form of retention forestry to promote biodiversity and enhance ecosystem functions in plantation forests after logging (Rosenvald and Lohmus, 2008; Gustafsson et al., 2012). Retention forestry involves strategic maintenance of trees as biological legacies. Historically, trees have been retained purposively as seed trees and shade trees to enhance regeneration after logging (Kohm and Franklin, 1997), or haphazardly left standing because they were too damaged or deformed to be useful (e.g., Takashima et al., 2017). Investigating how historically retained trees function as biological legacies can help predict the long-term potential of current retention forestry practices for conservation of biodiversity and ecosystem integrity (Root et al., 2007).

On Yakushima, a mountainous island in southern Japan, large *Cryptomeria japonica* D. Don. trees, which were too deformed to be used for timber, were left standing during a period of intensive logging in the Edo Era (1600–1800s, Takashima et al., 2017). There is speculation

* Corresponding author at: Science and Technology Building 2-411, Kobe University, Kobe 657-8501, Japan.
E-mail address: hishii@alumni.washington.edu (H.R. Ishii).
[1] These authors share first authorship.

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that the largest trees may have been retained for ethical reasons because the Islanders considered them sacred (Ohsawa et al., 2006). Such trees may have functioned as biological legacies during subsequent natural regeneration of the forest. Large trees are important for biodiversity because they provide various ecological functions such as providing food and habitat for arboreal animals, hosting diverse epiphytes, etc. (Lindenmayer et al., 2012). Yakushima is famous for its giant *Cryptomeria* trees, which are important structural features characterizing primary mixed conifer-broadleaved forest. For example, in a survey of 37 of the largest and oldest *Cryptomeria* trees on Yakushima, as many as 13 species of woody plants occurred in the crown of a single large tree reflecting the importance of such trees in hosting diverse plant communities (Yoshida, 1999).

Globally, canopy plants (including vascular epiphytes), representing approximately 9% of vascular plant species (Zotz, 2013), are an important component of biological diversity of forest ecosystems. In tropical rainforests vascular epiphytes contribute as much as 25% (Nieder et al., 2001) to 50% (Kelly et al., 1994) of vascular plant species. Canopy plants are abundant in forests with high precipitation, such as neotropical cloud forests (e.g., Nadkarni et al., 2004; Gotsch et al., 2015) and temperate rain forests (e.g., McCune et al., 2000; Ellyson and Sillett, 2003; Williams and Sillett, 2007) and contribute to various ecological functions such as providing food and habitat for canopy fauna (Yanoviak et al., 2003; Ellwood and Foster, 2004; Scheffers et al., 2014) and constitute an important part of the nutrient and water cycles in the forest canopy (Bohlman et al., 1995; Hölscher et al., 2004; Köhler et al., 2007; Gotsch et al., 2016). In forests with diverse canopy flora, plant species diversity and ecosystem functions cannot be understood without consideration of the canopy plant community (Díaz et al., 2010).

Diversity and distribution of canopy plant communities are well documented for tropical and temperate rain forests of the Americas by directly accessing the canopy using rope-climbing techniques, observation towers, and canopy cranes (e.g. Pike et al., 1977; Nieder et al., 2000; Krömer et al., 2007; Sillett and Van Pelt, 2007; Gotsch et al., 2015). Population structure and dynamics of canopy plant communities, however, are less studied because it requires detailed measurement of plant abundance and sizes, which can be difficult to conduct with limited canopy access (Flores-Palacios and Garcia-Franco, 2001). Some plants are transient, ephemeral components of the canopy plant community (accidental epiphytes), while others are able to maintain stable populations (obligate and facultative epiphytes) (Benzing, 2004). In primary forests of Yakushima, *Vaccinium yakushimense* Makino., endemic to Yakushima, occurs almost exclusively on large trees and rocky outcrops and is rarely found on the forest floor (Tsutsumi, 2011). Consequently, in closed-canopy forests, *V. yakushimense* is an obligate epiphyte that can only regenerate in the canopy. Although rainforests of East Asia host rich and abundant canopy plant communities (Hsu et al., 2002; Chen et al., 2010; Nakanishi et al., 2016), past research on canopy plants in Japan, have been mostly limited to species inventories conducted from the ground using binoculars and telescoping pruners (e.g., Hattori et al., 2009). We are aware of only one study in Japan that observed canopy plants directly (Hirata et al., 2009). Because endemic species are ecologically important for biodiversity, direct, quantitative investigations in the canopy are needed to elucidate the demography and regeneration niche of unique canopy plants like *V. yakushimense*.

Because it can take many years for canopy plant communities to develop on trees, and because of their sensitivity to environmental change, canopy plants are often used as indicators of ecosystem integrity (McCune, 1993; Sillett, 1995; Köhler et al., 2007; Giordani et al., 2012). For example, epiphytic lichens and bryophytes in the crown of old-growth *Pseudotsuga menziesii* (Mirb.) Franco trees have a distinct vertical profile, which is not apparent in second-growth forests (McCune et al., 1997). In montane cloud forests of Costa Rica, biomass of epiphytic bryophytes and vascular plants on branches and trunks was 40 and 100 times greater in primary forest compared to secondary forest (Nadkarni et al., 2004). Trees retained after logging may function as refugia to "life-boat" species over the forest regeneration stage (Rosenvald and Lohmus, 2008). For example, in a northern hardwood forest in New York, USA, community compositions of epiphytic lichen were indistinguishable among single-tree retention, reserve shelterwood, and old-growth forests (Root et al., 2007). Although retention practices are old, green-tree retention for conservation purposes is still a relatively new forestry practice. Thus, only short-term effects (< 6 years) have been documented scientifically (e.g., Hazell and Gustafsson, 1999; Perhans et al., 2009; Lohmus and Lohmus, 2010; Lobel et al., 2012) and the long-term outcome is uncertain. Long-term persistence of canopy plants have only been inferred retrospectively from research on remnant trees following natural disturbance (e.g., Peck and McCune, 1997; Sillett and Goslin, 1999).

Secondary forests of Yakushima and the retained trees therein, present a unique opportunity to investigate the long-term outcome of green-tree retention. Here, we compared species diversity and population structure of canopy woody plants on retained trees with those of regenerated trees in a 350-year-old secondary forest dominated by

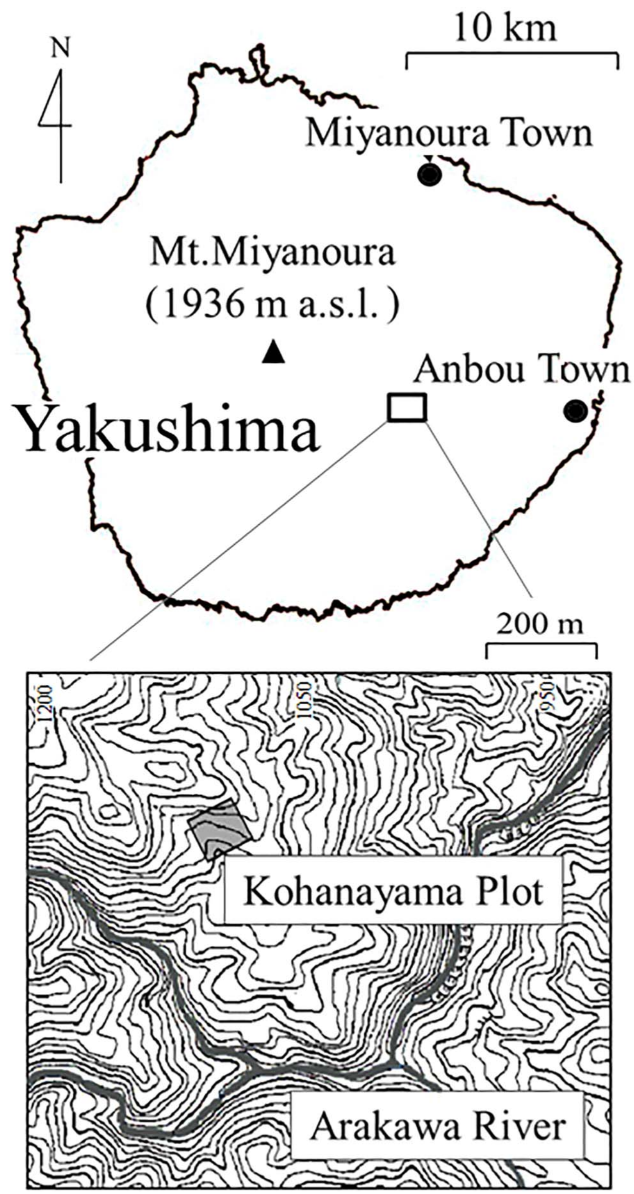

Fig. 1. Location of the study plot in Yakushima Island, Kagoshima, Japan. Contours are drawn at 10-m intervals.