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Bark Stripping by Deer Disturbs Regeneration in a *Larix–Abies* Subalpine Forest

Takuo Nagaike

Yamanashi Forest Research Institute, Fujikawa, Yamanashi 400-0502, Japan; nagaike-zty@pref.yamanashi.lg.jp

Abstract: Deer can slow the natural succession of forests from light-demanding to shade-tolerant species or even keep forests in an early successional stage. This study examined the effects of bark stripping by deer (*Cervus nippon*) on the stand dynamics in a *Larix kaempferi–Abies veitchii* subalpine forest in central Japan. Bark stripping by *C. nippon* was concentrated on smaller *A. veitchii* individuals, and the number of stems with stripped bark increased over the study period (2007–2019). Unlike other tree species in the study plot, the main mortality factor of *A. veitchii* was bark stripping. In addition, the mortality factors of *A. veitchii* clearly differed among tree sizes: smaller *A. veitchii* trees (diameter at breast height ≤ 15 cm) died owing mainly to bark stripping, whereas larger individuals died owing mainly to uprooting, snapping, and standing dead trees. At this forest site, bark-stripping deer preferred the late-successional species (*A. veitchii*) to the early-successional species (*L. kaempferi*), and consequently, the progress of succession was disturbed.

Keywords: debarking; Mt. Fuji; mortality; regeneration; sika deer

1. Introduction

Forest ecology and succession are important concepts in the management and restoration of forests [1,2]. The species composition in a seral forest community is in the midst of changing from dominance of early-successional tree species to late-successional trees, and the course of succession is governed mainly by the light requirements of the trees that compose the forest [3,4]. However, such forest change can be disturbed and altered by drivers such as climate change and biological interactions [5]. For example, under the current influence of climate change, forest succession is also being affected by deer overabundance [5,6]. In addition, Nagaike [7,8] reported that forest stand dynamics were affected by bark stripping by deer as well as tree size and competition between tree species.

Deer populations are often overabundant (e.g., [9,10]) and can severely affect forest succession through browsing, bark stripping, and trampling (e.g., [11,12]). These deer's effects can also slow the natural succession of forests from light-demanding to shade-tolerant species or keep the forest in an early successional stage [6]. Because tree species that are more palatable for browsing and bark stripping fail to regenerate, their numbers decrease relative to those of less palatable species [13–16]. The disruption of succession, however, depends on which trees are browsed by deer. In a forest in France, Bernard et al. [16] reported that *Abies alba*, a late-successional tree that is highly palatable to *Cervus elaphus*, may not outcompete *Picea abies*, a non-preferred and early-successional tree species. Thus, deer effects on regeneration and the consequent seral community seem to depend on the relative palatability of the species in a forest [17].

In the subalpine zone of central Japan, disturbed sites, such as those occasionally formed by avalanches and lava flows, are invaded by *Larix kaempferi*, a deciduous conifer and early-successional species [18]. *Abies veitchii*, an evergreen conifer, is a secondary seral species that invades gradually and eventually replaces *L. kaempferi* [18,19]. These seral mixed *Larix–Abies* forests have a multilayered structure composed of different successional species [18].

Cervus nippon (sika deer) recently colonized Mt. Fuji [20] in central Japan, the nation's tallest mountain. The deer have caused severe bark stripping in both coniferous plantations [21] and natural forests [7,8,22]. If the late-successional species *A. veitchii* is preferred by *C. nippon*, then the normal course of succession in the region could be disturbed because the interaction between deer preference and successional stages of trees may affect the future forest species composition. To properly manage both deer populations and forests, it is important to understand how the successional stage is affected by deer. Few studies, however, have investigated the effects of bark stripping by deer on seral communities.

The aim of this study is to clarify the effects of bark stripping by *C. nippon* on the stand dynamics of a seral subalpine forest. First, which species and sizes of trees the deer preferred to strip bark from were identified. Second, the factors affecting the survival of the three dominant tree species were elucidated.

2. Materials and Methods

2.1. Study Site

The study was conducted in a subalpine zone at 1900 m a.s.l. on the northern slope of Mt. Fuji (35°22′ N, 138°41′ E). At the nearest meteorological station (Kawaguchiko; 860 m a.s.l.), the mean annual precipitation was approximately 1600 mm and the mean annual temperature was 10.6 °C. Snow cover at the site from December to April was usually about 50 cm.

Various types of forests in different successional stages exist on Mt. Fuji due to volcanic activity [18]. Most of the mountain is covered by old-growth forests, typically dominated by *Abies mariesii*, *A. veitchii*, and *Tsuga diversifolia* [19,23,24]. In areas covered by lava flows about 800 years ago, forests are dominated by *L. kaempferi* [19]. Nakamura [18] roughly estimated the life span of *L. kaempferi* on Mt. Fuji as 150 years, that of *Abies* spp. as 200 years, and that of *T. diversifolia* as 300 years. The understory of subalpine coniferous forests in Japan is classified as herbaceous, dwarf bamboo, or moss type [24], and the study forest is the moss type.

The estimated density of *C. nippon* in this area increased sharply from 1.4/km^2 in 2005 to 55.1/km^2 in 2012 [20]. The acceptable density of *C. nippon* in the natural vegetation zone by the Ministry of the Environment, Japan is 3–5/km^2, indicating that the density in the study area was highly overpopulated. Culling to control the *C. nippon* population has been performed at lower elevations (below 1500 m a.s.l.), not in the study area. In the study area, coniferous tree species have been stripped but not heavily browsed by *C. nippon* [7,8,21,22] in contrast to other regions, where heavy browsing was reported (e.g., [13,24–26]).

2.2. Field Study

In 2007, a 50 m × 120 m (0.6 ha) plot was set in the old-growth subalpine coniferous forest. The canopy layer was composed of only three coniferous species: *A. veitchii*, *L. kaempferi*, and *T. diversifolia*. The plot was divided into 240 cells of 5 m × 5 m. All trees in the cells that were ≥2 m in height were tagged and identified by species, and their diameter at breast height (DBH, at height of 1.3 m) was measured. These trees and new recruits were counted and measured in 2013 and 2019.

In each census, the degree of bark stripping visible on each tree was recorded as the maximum proportion of the tree circumference that had been stripped, in increments of 10%. This proportion is referred to as the bark stripping ratio (SR). A 100% SR indicated that deer had stripped all of the bark from the circumference. At each census, a cause of death was assigned to each dead tree: uprooted, snapped, standing dead, toppled by other trees [27], or bark stripped. No death of *A. veitchii* caused by bark beetle (*Curculionidae*) was observed in this plot [28].

2.3. Analysis

Bark-stripped trees were limited to those with DBH ≤ 15 cm (see Results), so the cause of death was classified according to size (i.e., DBH ≤ 15 cm or >15 cm). Because most

trees suffered repeated stripping [7,29], the maximum bark stripping ratio (MSR) of each tree during each census period (2007–2013 and 2013–2019) was determined. To analyze the effects of canopy condition and tree competition (i.e., shading and crowding) on the survival of the focal trees, the total cumulative basal area in the cell where a focal sapling was located was used as a competition index (CI), following Nagaike [7].

Recursive partitioning and regression tree analysis were used to identify the degree to which the size of the focal trees, MSR, and CI affected the survival of focal trees. This analysis uses a binary recursive partitioning approach to split the data set into subsets based on explanatory variables chosen to minimize the deviance in the response variables in each of the resulting subsets [30]. Here, the survival of each focal sapling in each study period is the response variable. As explanatory variables, DBH in the first year (i.e., 2007 for 2007–2013 and 2013 for 2013–2019) and the CI and MSR in the last year (i.e., 2013 for 2007–2013 and 2019 for 2013–2019) were used. Since allowing the regression tree to grow unpruned would result in an overfitted model, as noise is fitted along with data [31], a complexity parameter was used for pruning splits in each analysis.

All statistical analyses were performed in R v. 3.5.2 software [32], and the regression tree analysis was performed in the "rpart" package [30].

3. Results

3.1. Stand Structure

By stem density, the plot was dominated by *A. veitchii*, followed by *L. kaempferi* and *T. diversifolia*. (Figure 1). The stem density of the three species declined slightly during the study period. By basal area, *L. kaempferi* was dominant, indicating that large trees of *L. kaempferi* were major components of the plot (Figure 1). While coverage of *A. veitchii* by basal area declined from 23.1% in 2007 to 14.6% in 2019, that of *L. kaempferi* increased from 73.3% to 81.1%, respectively.
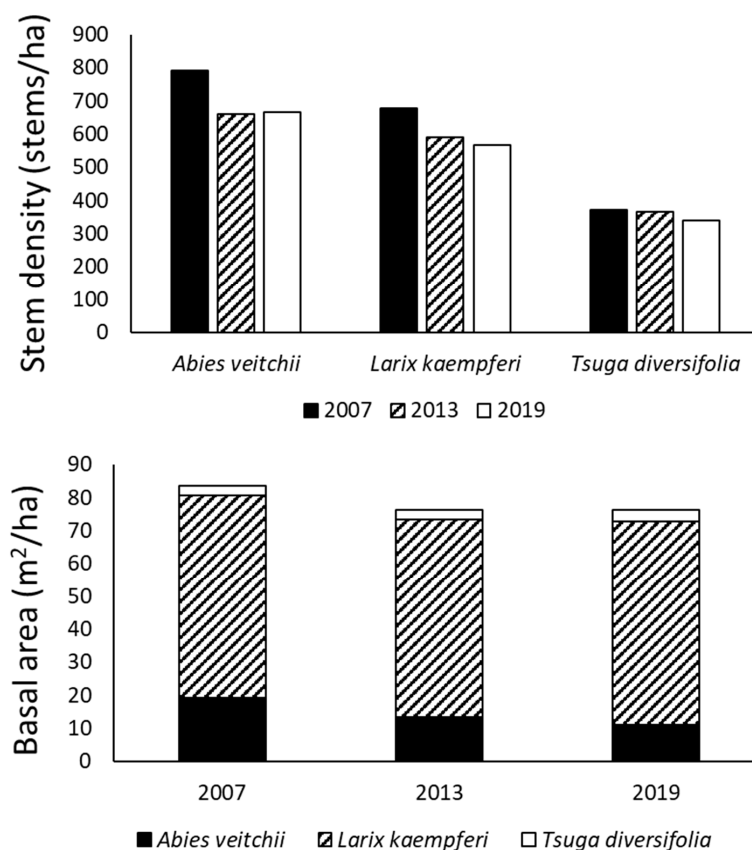

Figure 1. Changes of stem density and basal area of the three dominant species in the study plot between 2007 and 2019.

The DBH distribution of *L. kaempferi* was unimodal, and the median value was about 30 cm (Figure 2). *Abies veitchii* had a bimodal DBH distribution with more individuals in the smaller size classes (≤10 cm), whereas *T. diversifolia* was distributed only in smaller size classes (≤20 cm). The number of smaller *A. veitchii* trees was relatively consistent across the three census points, whereas the number of larger trees decreased.
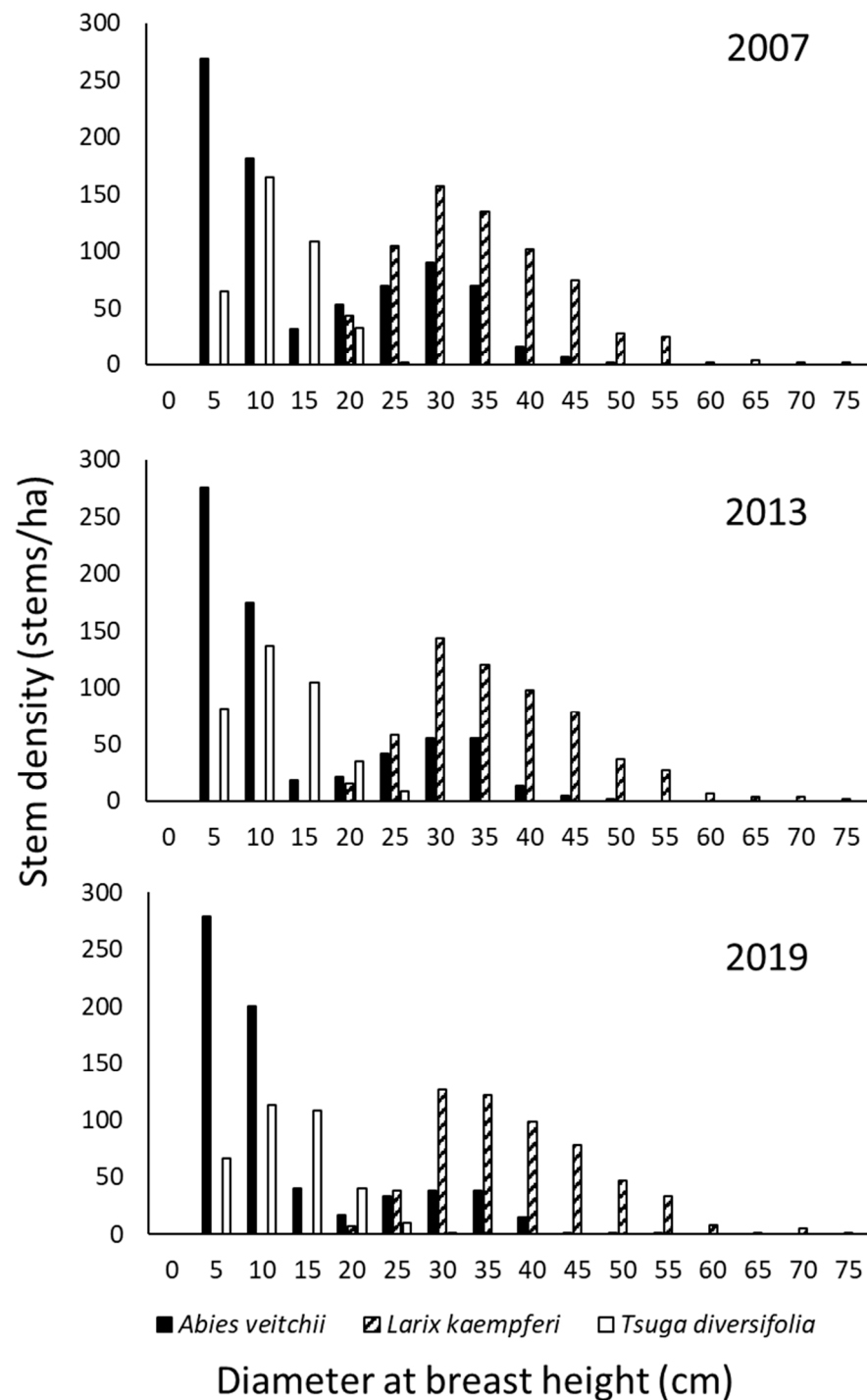
Figure 2. Changes of the stem density distribution of different diameter at breast height classes between 2007 and 2019.

3.2. Effects of Bark Stripping by Cervus nippon

Bark stripping by *C. nippon* was concentrated in smaller *A. veitchii* (Figure 3) and was not observed in individuals with DBH > 15 cm. Moreover, the number of bark-stripped stems increased over the course of the study period.
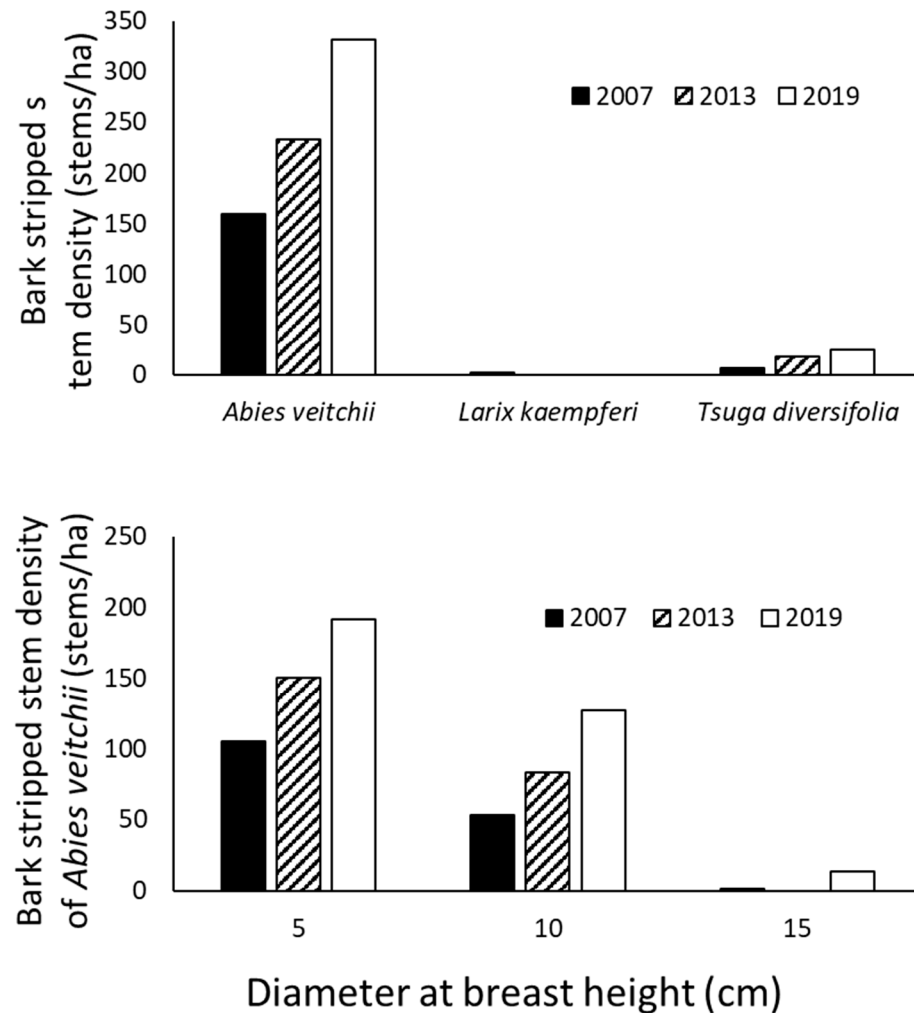

Figure 3. Density of bark-stripped stems of the three dominant species and of *Abies veitchii* among various diameters at breast-height classes.

The mortality factors of *A. veitchii* were dominated by bark stripping (43% in 2007–2013, 38% in 2013–2019) and differed from those of the other species. In addition, they clearly differed between the size classes, with smaller trees (DBH $\leq$ 15 cm) dying mostly by bark stripping and no larger trees dying by that means (Figure 4). Among larger *A. veitchii* trees, most were standing dead in 2007–2013, and percentages were equivalent among standing dead, uprooting, and snapped in 2013–2019. *L. kaempferi*, composed mainly of canopy trees, were standing dead.
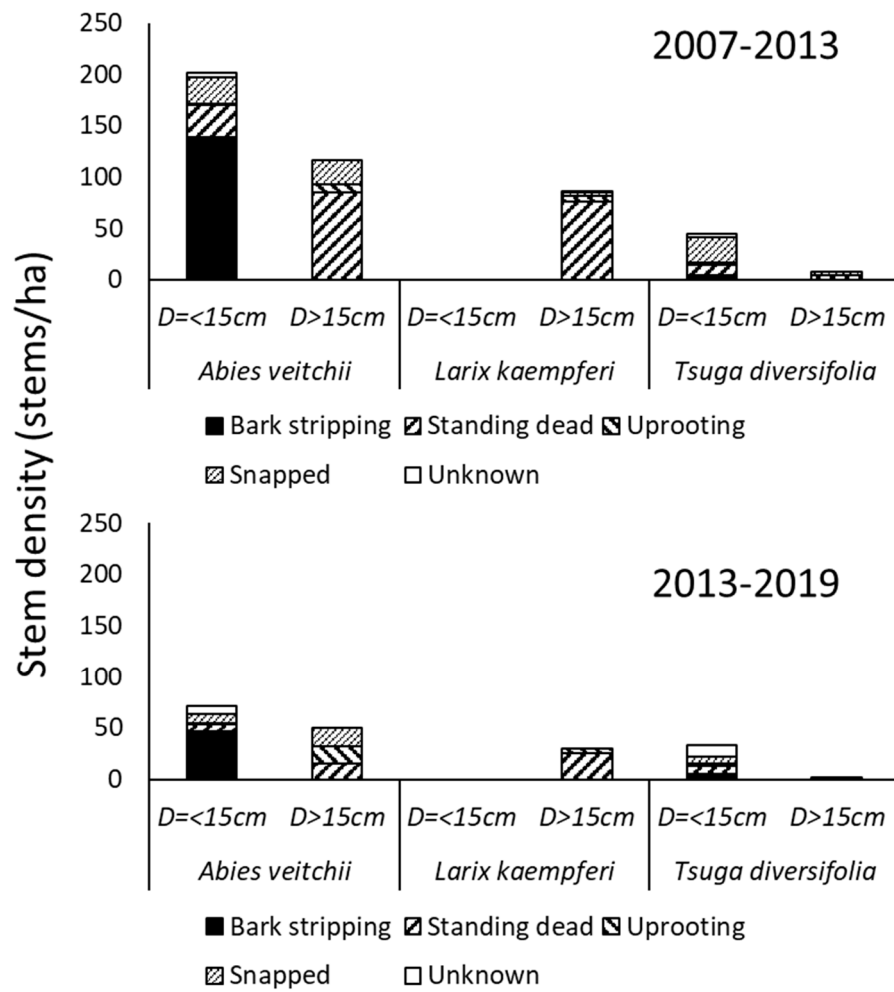
Figure 4. Causes of death of stems of the three dominant species in 2007–2013 and 2013–2019.

Factors affecting the mortality of trees varied among species (Figure 5 for *L. kaempferi* and *A. veitchii*, and Figure S1 for *T. diversifolia*). Bark stripping was the most effective for *A. veitchii*, whereas those for other species were their size (i.e., smaller size) and competition.
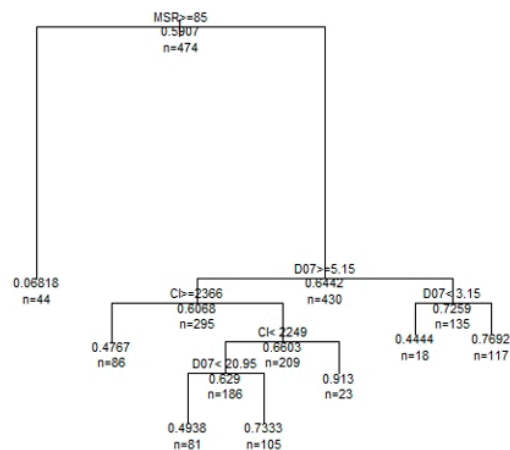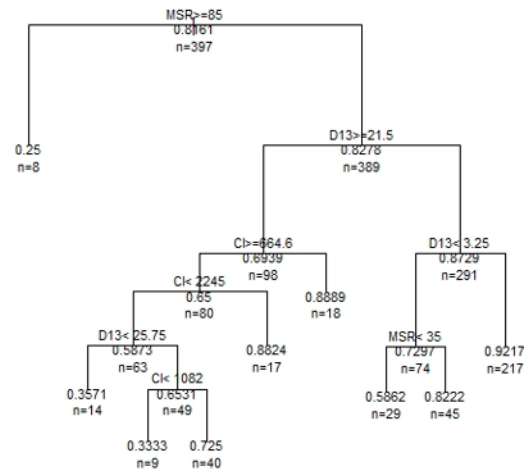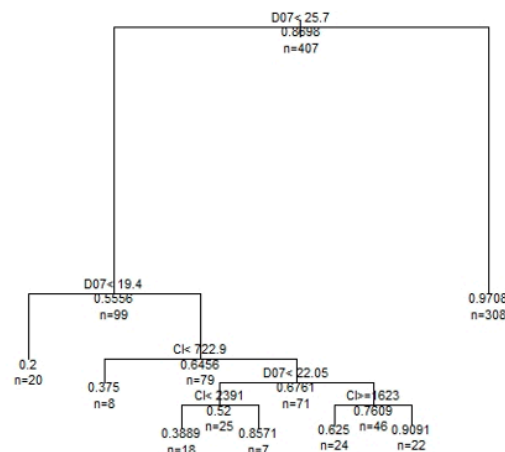

Figure 5. *Cont.*

Abies veitchii for 2013-2019

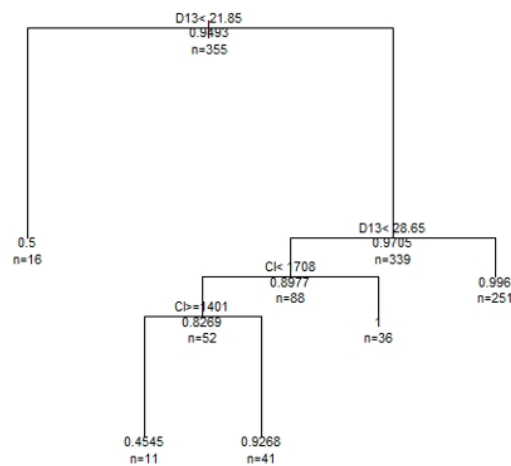## Larix kaempferi for 2007-2013

Larix kaempferi for 2013-2019

Figure 5. Factors affecting the mortality of trees for *A. veitchii* and *L. kaempferi* as assessed using regression tree analysis. D07 and D13, diameter at breast height in 2007 and 2013, respectively; CI, competition index (total cumulative basal area in cell of focal sapling); MSR, maximum bark stripping ratio.

4. Discussion

In the normal seral progression in subalpine forests on Mt. Fuji, *L. kaempferi* forests would be replaced by shade-tolerant genera, such as *Abies* and *Tsuga* [18]. With the over-abundant deer population, however, this succession has been disturbed by the larger mortality of *A. veitchii* saplings due to bark stripping. Other studies also reported that *C. nippon* prefer *Abies* spp. to *L. kaempferi* for bark stripping (Figure 3) [7,21] and prefer smaller *A. veitchii* regenerated in the forest understory (i.e., seedling or sapling bank) [33] for bark stripping (Figure 3) [7].

Regeneration of *Larix* spp. generally requires large-scale disturbance of the soil surface ([34,35], but see [36]). In *L. kaempferi* natural forests and plantations in central Japan, the regeneration of *L. kaempferi* without such disturbances is often limited by the lack of saplings [18]. In fact, seedlings and saplings of *L. kaempferi* were lacking in the study area (Figure 2). In contrast, evergreen conifers such as *Abies* and *Tsuga* can regenerate in the forest understory via the sapling bank [24,33,37]. These individuals await canopy disturbances that improve light condition and reduce competition [37,38] to grow from seedlings to saplings to trees. If there were no bark stripping by deer, more successful regeneration would occur. However, the main mortality factor for small *A. veitchii* was bark stripping, indicating that deer inhibited the species' regeneration and disturbed the normal course of succession.

The number of saplings of *A. veitchii* was relatively constant over the study period (Figure 2) despite them being severely damaged or killed by bark stripping (Figures 3 and 4). There are two possible explanations for this: (1) Highly advanced regeneration could compensate for the higher mortality due to bark stripping, and (2) improvement of light conditions in the understory following the death of canopy trees could maintain the sapling density of *A. veitchii*. Canopy gaps created by standing dead trees can also improve light conditions in the understory and reduce competition between strata [39]. With regards to mortality, most larger trees were standing dead during the entire study period, whereas for *A. veitchii*, the main class changed from standing dead in 2007–2013 to standing dead, uprooting, and snapping in 2013–2019 (Figure 4). Pioneer tree population could be maintained by canopy disturbance [40]. Thus, such severe canopy disturbance (i.e., uprooting and snapping) compared to standing dead might have maintained the regeneration of *A. veitchii* and mitigated the canopy competition from larger *L. kaempferi* trees. Chauchard et al. [41] reported that *A. alba* expansion into grasslands was not controlled by large herbivores, including *Capreolus capreolus* and *C. elaphus*, at moderate density because they had no fatal effects on the recruits. Without the mortality effects of deer on *A. veitchii*, the regeneration of the species would likely be improved and the normal course of succession in the forest may return.

The number of larger *A. veitchii* trees decreased over time, with standing dead as the main mortality class (Figures 2 and 4). Since *L. kaempferi* trees are larger than *A. veitchii* trees, they may compete more for light. However, MSR was the most important factor affecting the mortality of *A. veitchii*, mainly among the saplings (Figure 5). Thus, *L. kaempferi* will likely continue to dominate the forest.

5. Conclusions

In this study, a late-successional species (*A. veitchii*) was preferred by bark-stripping deer over an early-successional species (*L. kaempferi*), and consequently, the seral progression was disturbed. Under heavy pressure by deer, the combination of successional status and deer preference appear to be important for drivers of succession. Deer preference of bark stripping may shift in the future due to decreasing number and size of preferred species [8]. To ensure the original seral progression in the studied forest, deer management (e.g., culling) will be necessary [36].

Seasons in which the bark stripping occurred were not recorded. The bark stripping by deer was recorded in winter because of food shortage [25,42], while Ando et al. [43] clarified that the season was summer. Due to the season of bark stripping, deer management should

be changed. Studies clarifying the reason why *C. nippon* was bark-stripped in the area would be future challenges.

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