RESEARCH ARTICLE

Applied Vegetation Science IAVS

Clear-cutting triggers regeneration of abandoned secondary forests but risks alternative successional trajectories with high deer density

Maki Suzuki[1] 🔾 | Tsutomu Karukome[2] | Koji Fujihira[2] | Mitsukazu Mitsugi[2] | Yoko Hisamoto[2]

[1]Graduate School of Frontier Sciences, The University of Tokyo, Kashiwa, Japan

[2]Graduate School of Agricultural and Life Sciences, The University of Tokyo Chiba Forest, The University of Tokyo, Kamogawa, Japan

Correspondence
Maki Suzuki, Room 568 Environmental building, GSFS, The University of Tokyo, Kashiwahoha 5-1-5 Kashiwa, Chiba, 277-8563 Japan.
Email: suzukima@edu.k.u-tokyo.ac.jp

Abstract

Questions: Does clear-cutting intended to boost regeneration of abandoned secondary forests lead to an irreversible shift to non-forest vegetation under high deer density?

Location: Warm-temperate forests in Boso Peninsula, Chiba Prefecture, Japan.

Methods: We designed a factorial experiment including two levels of forest canopy treatment (clear-cutting or intact canopy) and two levels of herbivory control (presence or absence of deer) using 24 plots of 10 m × 10 m. Vegetation dynamics occurring under each experimental treatment were tracked for 7.5 years.

Results: Ground vegetation under the closed canopy did not change significantly for 7.5 years both inside and outside the deer fences. However, plots were rapidly covered by early-seral plants till 1.5 years after the cutting event. The quick growth of ground vegetation after clear-cutting was supported by plants that are known to have soil seed banks, as suggested by their ubiquity immediately after clear-cutting. Species richness of ground vegetation was maximized at that time and gradually decreased afterward, suggesting biological filtering. This filtering process worked differently inside and outside the deer fences, resulting in different types of vegetation. The clear-cut-and-fence plots became dominated by tree recruits that will recover secondary forests in the future. Contrastingly, vegetation outside the fences lacked many species (e.g., common tree species) that were found inside the fences and became dominated by shrubs and plants unpalatable to deer. This post-cutting vegetation outside the fences was not similar to that inside the deer fences at any seral stage. This means that the vegetation outside the fences could be tracking an alternative successional trajectory rather than a case of arrested succession.

Conclusions: Here, abandoned secondary forests still seem to maintain a high regeneration potential that would be triggered by clear-cutting, but reducing herbivory pressure by deer is necessary to avoid the risk of alternative successional trajectories.

KEYWORDS
alternative successional trajectory, arrested succession, clear-cutting, fencing, resilience, secondary forests, sika deer, unpalatable species

1 | INTRODUCTION

Cervid populations are increasing and causing negative effects on forest regeneration in many developed countries. Through the loss of seedlings and saplings of trees (e.g., Gill, 1992; Akashi & Nakashizuka, 1999; Horsley et al., 2003; Husheer et al., 2003) and decline of soil seedbanks (Beauchamp et al., 2013; Shinoda & Akasaka, 2019), overpopulated cervids are suggested to potentially halt forest regeneration for decades (Tanentzap et al., 2009, 2011; Kelly, 2019). However, the temporal delay of regeneration does not necessarily mean permanent regeneration failure under the present disturbance regime. Many tree species are known to recruit when disturbances destroy the forest canopy; these species would not recruit under closed canopy even if deer are excluded, but they would do so if subjected to a combination of deer exclusion and destruction of the canopy layer, thereby driving the vegetation dynamics toward a forest ecosystem (Horsley et al., 2003). All forest systems have their own disturbance regime, or cycle of destruction and recovery that is inherent to the system (Attiwill, 1994); a forest can be considered resilient as long as the system maintains its regeneration potential under the disturbance regime (Ghazoul et al., 2015). From this perspective, forests' true resilience against deer impact should be judged based on whether the secondary succession in canopy gaps direct to forest regeneration after deer impact was reduced.

Gap creation by natural or anthropogenic disturbances generally facilitates the regeneration of ground vegetation, but when herbivory pressure is high, it does not necessarily lead to the automatic regeneration of forests (Gill, 1992; Russell et al., 2001; Young et al., 2001). In the simplest case, deer damage seedlings and saplings of major trees and allow their competitors (e.g., grasses, shrubs, and ferns) to cover the ground layer in the canopy gap (Horsley et al., 2003; Husheer et al., 2003; Tremblay et al., 2006). In this case, however, trees may recruit once herbivory pressure would be reduced. A more difficult case occurs when non-tree competitors establish a competitive advantage over trees while the latter is being suppressed by herbivores ("recalcitrant understory"; Royo & Carson, 2006). This situation tends to be observed where herbivory pressure remains high for a while after gap creation (Stromayer & Wallen, 1997, Horsley et al., 2003, Nuttle et al., 2014). Once it happens, the recruitment of trees would be inhibited even after herbivory is reduced, and thus forest would not grow for a considerable time while the herbivory pressure was retarded (Stromayer & Wallen 1976, Hidding et al., 2013; Nuttle et al., 2014). Both cases above are frequently referred to as "arrested succession" (AS; Gibson & Brown, 1992), implying inhibition of unidirectional change to the local climax by direct or indirect effects of herbivory (Young et al., 2001). To be precise, however, the two cases above have different meanings for forest restoration. In the first case, trees would recruit after herbivory pressure is reduced; but they would not in the second case. Meanwhile, the second case is rather an example of "alternative successional trajectory (AST)," or a case where recovery of a degraded system to its original state is prevented by some mechanism inherent to the system (Suding et al., 2004). The difference between AS and

AST is critical in predicting future regeneration of damaged forests, but it was not paid much attention in earlier studies (e.g., Tschöpe et al., 2011; Thrippleton et al., 2018; Ramirez et al., 2019).

This issue of AS and AST is of practical importance for secondary forests that have long been managed for human use. Recently, abandonment of these forests carries a conservational threat for some developed countries like England, Spain, Italy, the Czech Republic, and Japan (Rackham, 2008; Oono et al., 2020). The management activities stopped after the 1940s–1970s according to the drastic social changes (Oono et al., 2020); as the result, species groups that are dependent on anthropogenic disturbances have decreased (Keith et al., 2009; Hédl et al., 2010; Ito et al., 2012; Kopecký et al., 2013). A common countermeasure is to cut canopy trees to support recruitment of saplings, but this will not work under high herbivory pressure by deer. In such a situation, deer also decrease ground vegetation (Suzuki et al., 2008, 2013; Takatsuki, 2009; Ohashi et al., 2014) and invertebrates (Takada et al., 2008; Takagi & Miyashita, 2012; Suzuki & Ito, 2014; Iida et al., 2018), and in addition degrade physical properties of the soil (Wardle et al., 2001; Yanagi et al., 2008; Shelton et al., 2014; Suzuki & Ito, 2014). Whether these forests could recover or not depends on the management practices such as cutting trees and/or reducing herbivory.

This study examines the resilience of secondary forests heavily damaged by sika deer using a field experiment system (Suzuki, 2013). The system was established approximately 10 years ago in secondary forests that developed after the cessation of fuelwood harvesting. In these abandoned forests, ground vegetation — including tree recruits — had almost vanished due to the combined effects of deer damage and light limitation. A 2 × 2 experimental treatment of [clear-cutting/no cutting] × [deer exclusion/no exclusion] applied in these forests resulted in regrowth of ground vegetation only in plots with clear-cutting (Suzuki, 2013; Suzuki & Ito, 2014). This result suggests the high regeneration potential of these forests under their disturbance regime. However, these earlier studies reported only the situation right after the treatment, and thus they could not determine the resilience of the forests. Especially, it should be distinguished whether the vegetation established after clear-cutting would become a mature forest in the future, or would have fallen into the AS or AST. For this purpose, we compared the 7.5-years trajectories of floristic changes in the above experimental plots. We first tried to examine whether the forests were recovering in each plot. Then we compared the developmental process of community structure between two clear-cutting treatments (deer exclusion/no exclusion) to reveal how vegetation dynamics were affected by herbivory continued after clear-cutting. Based on the results, we finally judged whether the floristic development in canopy gaps expresses AS or AST, or neither of them.

2 | METHODS

2.1 | Study sites

This study took place in The University of Tokyo Chiba Forest (UTCBF: 35.8–35.11° N, 140.7–140.9° E, 50–300 m above sea level)

located in the Boso Peninsula 50 km southeast of Tokyo. This region has a humid warm-temperate climate: the annual mean air temperature is 15°C (−4°C~+35°C), and the mean annual precipitation is less than 2500 mm. Three study sites, each 2–5 km apart, were established in UTCBF in 2007. See Suzuki (2013) for detailed conditions of the sites.

These forests had been utilized for fuelwood sampling with intervals of 30–40 years — almost all woody species used to be cut to make firewood and charcoal. Fuelwood sampling ended in the 1950s, in the era of a nationwide energy revolution; these woodlands were abandoned and gradually maturing after that. The study sites' vegetation was a cover of deciduous trees and evergreen shrubs in the mid-1980s (Miyawaki, 1986); now, these forests are dominated by evergreen trees such as *Quercus glauca*, *Quercus acuta*, *Quercus salicina*, and *Castanopsis sieboldii*. These species are accompanied by evergreen (e.g., *Eurya japonica*, *Cleyera japonica*, *Myrsine seguinii*, *Camellia japonica*, *Cinnamomum yabunikkei*, *Ilex integra*, *Dendropanax trifidus*) and a few deciduous species at sub-canopy layers. Evergreen shrubs (e.g., *Aucuba japonica*, *Maesa japonica*) and ground plants (e.g., *Arachniodes sporadosora* and *Arachniodes aristata*, *Rubus buergeri*, *Ardisia japonica*, *Trachelospermum asiaticum*) were common and abundant in the forests until the 1980s (Kabaya, 1988). However, now they have vanished as a result of herbivory except for some species not eaten by deer (Suzuki, 2013).

Sika deer have been distributed in Boso Peninsula from prehistoric times (Nishimoto, 2010) and are a native species (Asada & Ochiai, 2009). Hunting pressure and habitat loss shrank their population gradually. High pressure during the modernization era (19th to early 20th century) once led to the extinction of the population. After WWII, conservation efforts and social changes helped in the recovery of the sika deer population. Since then, deer in the Boso Peninsula gradually increased their population size with an expanding distributional range; they became overabundant after the 1990s when culling activities were restarted (Chiba Prefecture, 2004). The latest estimation of deer density around the study sites was 10–15 deer km^{-2} (Hisamoto et al., 2019), still exceeding a level at which damages on natural vegetation is concerned (Suzuki et al., 2008), but being far less than the maximum record in 1996 (ca. 40 deer km^{-2}: Chiba Prefecture, 2004). They have a significant impact on natural vegetation (Suzuki et al., 2008; Suzuki et al., 2013), above-ground invertebrates (Miyashita et al., 2004; Takada et al., 2008), and topsoil characteristics (Yanagi et al., 2008) in this peninsula. Recently, wild boar (*Sus scrofa*, native) and Reeves's muntjac (*Muntiacus reevesi*, introduced) are also increasing their population in the Boso Peninsula. However, in this study, their potential impact on forest vegetation was assumed to be much less than that of deer, following the existing reports from other countries (e.g., Barrios-Garcia & Ballari, 2012).

2.2 | Experimental treatments

Eight plots of 10 m × 10 m were established in 2007 at each of the three study sites (Appendix S1). All the eight plots were placed next to each other in one site, whereas in the other two sites, two groups of four plots each were set approximately 10 m apart. In February or March 2008, all trees in an area of approximately 20 × 20 m, which covered four plots in each site, were removed by clear-cutting. The woody debris produced by the clear-cutting was removed from the plots. In each study site, two out of four plots were surrounded by fences to exclude deer (EC plots = exclosure and clear-cutting) soon after the clear-cutting, while two other plots were left with deer existence (C plots = clear-cutting). Among the other four plots under a closed canopy, two plots were also surrounded with deer fences in February or March 2008 (E plots = exclosure), while the other two were left in natural conditions as control plots, where both deer and a tree canopy exist (Ctrl plots). The fences that surrounded E and EC plots were 1.5-m high and made of polyethylene netting and grass-fiber poles.

2.3 | Records of vegetation change

The first census (vegetation survey) was carried out in late summer 2007, about half a year before the experimental treatment (0.5 years before treatment). In each plot, five 1-m^2 quadrats, each being 1 m apart, were set up in the slope's direction. For each quadrat, total foliar cover (0–100%) of the ground vegetation (0–2 m high: within reach of deer) was estimated visually, and the maximum heights of the tallest woody and non-woody plants were measured. The foliar cover of each species was also estimated visually for each quadrat. The number of plant species recorded in all the five quadrats represented the species richness of the plot. This parameter — measured in an area of 5 m^2 — accounted for approximately 75.7% of the species richness recorded using a quadrat of 5 m × 5 m per plot in 2017 (data not shown). This series of the census was also conducted in the late summer of 2008, 2009, 2012, and 2015 (0.5, 1.5, 4.5, and 7.5 years after treatment respectively). Species nomenclature follows Yonekura and Kajita (2003). Species were classified by their growth forms (trees, shrubs, climbing plants, non-woody plants [ferns, grasses, and herbs]), phenology types (evergreen or summer green), and seed bank availability, based on the description of a flora list (Makino, 1940). Woody species not clearly determined in that list were classified as trees or shrubs according to their height at the adult stage exceeding 5 m or not. Based on previous studies, the palatability of species to sika deer was also noted (Kabaya, 1992, 2001; Hashimoto & Fujiki, 2014).

2.4 | Statistical analyses

Basic characters of ground vegetation (total foliar cover, maximum heights of woody and non-woody species, and species richness) were compared among treatments (EC, E, C, and Ctrl) using generalized linear mixed model (GLMM) or generalized linear model (GLM, for species richness) approaches. Total foliar cover or maximum heights in the sampling year fit a GLMM, using treatments as the

fixed factor and plots as the random factor, respectively. (Although our experiment has a nested design, models with nested random factors were not used because they tended to cause overfitting; Appendix S2.) Total foliar cover (%) for each plot was regarded as the number of points covered by foliage per 100 sampling points, and it was assumed to follow a binomial distribution with logit link. Maximum heights of woody and non-woody species (cm) were assumed to follow a log-normal and normal distribution, respectively. Species richness was calculated for each plot as the number of species in the five 1-m^2 quadrats and was fitted to a Poisson GLM with log link. The effect of study site on species richness was added as a fixed factor because its proper estimation as random factor was technically unfeasible. For each model, if the treatment effect was considered significant using deviance analysis, the difference between each pair of treatments was ascertained in a post-hoc test using the Tukey–Kramer method.

As described in the *Results*, many species were observed in C and EC plots and developed plant communities with time. The gradual development of species composition was expressed using the communities' nestedness analysis (Ulrich et al., 2009). Nestedness analysis is often applied to biogeographical patterns and species interaction networks, but it can also be used for other purposes, such as to examine changes in species composition along a succession trajectory (e.g., Kopecký et al., 2013). Forty-one highly abundant species, which accounted for 90% of the foliar cover recorded in all sample quadrats, were used in the present study for matrix-based analyses. A community matrix was created to summarize the presence (1)/absence (0) of the 41 species in each plot in each year (2 treatments × 2 replications × 3 sites × 4 census years [2008, 2009, 2012, and 2015] = 48 "samples"). Samples and species of this matrix were reordered to have the lowest matrix temperature with an iterative procedure. Nestedness metrics — NODF, N_{col}, and N_{row} (Almeida-Neto 2008) — would take the value of 0 if species compositions were completely nested, whereas they would equal 100 in case of perfectly random associations. The significance of these metrics was tested using a permutation test, which randomly swaps the matrix cells and calculates the metric value 999 times to examine whether metrics lower than the actual values were frequently produced by chance.

The combination of reordered matrix and nestedness metrics expresses vegetation dynamics, which allowed the evaluation of whether the situation was AS or AST. If plant communities of C plots were nested in those of EC plots, this would indicate that the herbivory pressure removed some species from EC plots. If some species were excluded as time goes on, a plant community in any year would be nested in that of an earlier year. Such a pattern would not be found in the case of AS; AS vegetations do not change with time, and thus are similar to each other across different census years. If vegetation in C and/or EC plots would be composed of a species set different from those of common secondary forests, a case of AST would be suggested.

In addition, an evaluation of whether the vegetation dynamics in C plots could be regarded as AS or AST was conducted using a permutation multivariate analysis of variance (perMANOVA). This analysis was applied to a species abundance matrix, whose cell values represented the total foliar cover of the 41 species in each plot for each year. If the vegetation in a C plot was "arrested" at some point of the succession trajectory, it would not change from 2008 to 2015, and also, the vegetation in C plots in 2015 would be very similar to that in EC plots in 2008. Test results deviating from these expectations would suggest an AST case, or a change in vegetation trajectory caused by deer. The proximity of the species compositions of C and EC plots across different years was also visualized by non-metric multidimensional scaling (NMDS) with 100 trials based on the Bray–Cartis dissimilarity.

We also analyzed the pattern of the order of appearance of species in the matrix. Ubiquitous species that commonly appeared in many sites in many census years would be ordered to the left part of the matrix, while temporal ones would be ordered to the right part. We checked whether the growth form, palatability to deer, and existence of a seed bank affected the order of appearance of species in the matrix by Wilcoxon's rank-sum test.

The above analyses were carried out in R 3.6.0 (R core team, 2019) using the packages *lme4* (Bates et al., 2015) and *vegan* (Oksanen et al., 2019).

## 3 | RESULTS

3.1 | Development of ground vegetation

Ground vegetation (<2 m high) of EC and C plots started to develop right after the clear-cutting, while no change was observed in the E and Ctrl plots (Figures 1, 2). No significant growth was observed in ground vegetation under the closed canopy 7.5 years after the treatment (Figure 1d). The difference increased yearly between the plots with and without clear-cutting, being always significant for both cover and height of vegetation, except for the first 0.5 years (Figure 2).

In EC plots, the foliar cover of regrown plants reached its maximum 1.5 years after the experimental treatments (Figure 2a). Rapidly growing woody species had grown up to 2 m in height and reconstructed a canopy layer until 4.5 years after the treatment (Figure 2b). Being shaded by these rapidly grown trees, the foliar cover of the ground layer gradually decreased afterward (Figure 2c).

Foliar cover in C plots increased more slowly than that in EC plots did, taking 4.5 years for the ground vegetation reach its maximum (Figure 2a). The developed foliage of C plots was predominantly composed of shrubs and non-woody species (Figure 1c); woody plants in C plots did not exceed 2 m in height even after 7.5 years had passed (Figure 2b). Foliar cover of the ground layer in C plots was dominated by unpalatable plants including shrubs (e.g., *Maesa japonica*, *Damnacanthus indicus*), ferns (*Arachniodes rhomboidea*), and climbing plants (e.g., *Trachelospermum asiaticum*) accompanied by herbivory-resilient plants (i.e., plants that can tolerate herbivory pressure as a result of their high growth rate) like grasses (e.g., *Miscanthus sinensis*

FIGURE 1 Image of vegetation change in experimental plots. (a) Appearance of an EC plot at 0.5 years from the treatment. This same plot in summer 2017 (9.5 years later) is shown in (b). (c) A C plot, occupied by a bush of a shrub species (*Maesa japonica*) in summer 2017. (d) An E plot (fenced plot) in summer 2017; trees in this photo are not recruits but have existed since before the experiment started
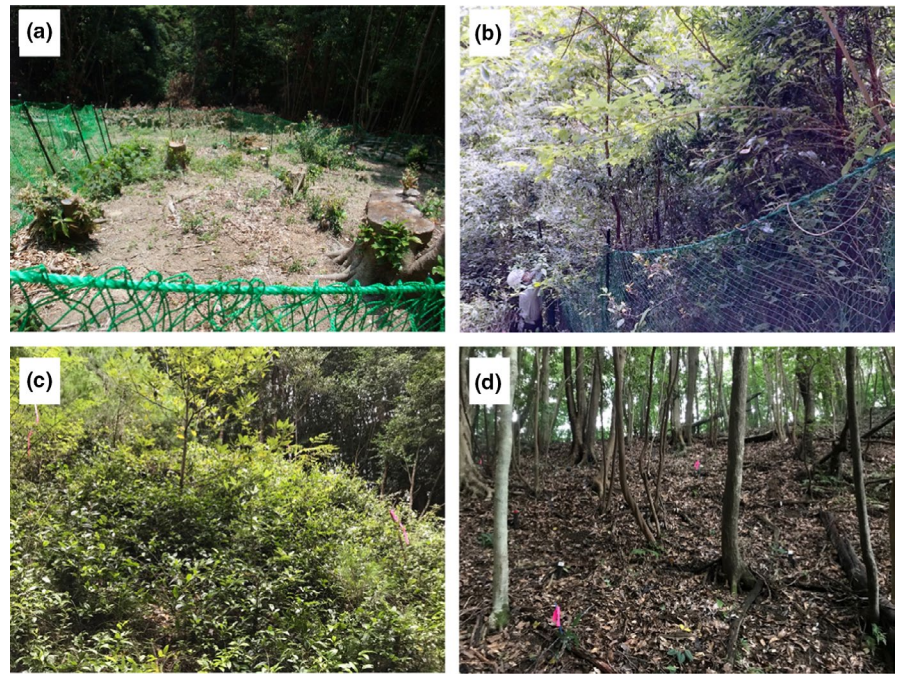
FIGURE 2 Change of foliar cover (<2 m) (a) and maximum heights (b, c) over the years after the treatments (symbols and error bars: mean plus one standard deviation). Significantly different values are indicated with different letters. Significant differences in the maximum height of non-woody species (c) at 0.5 elapsed years are shown in the inset as an enlarged view
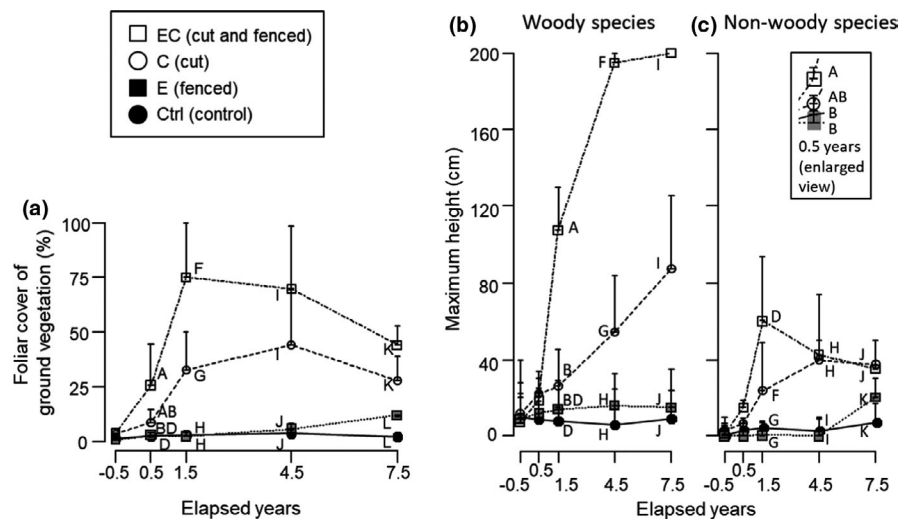

and *Carex* sp.) and shrubs (e.g., *Rubus microphyllus*). Except for unpalatable ones (*Pinus densiflora*, *Illicium anisatum*, *Osmanthus heterophyllus*, and *Neolitsea sericea*), trees did not grow taller than the shrub layer even if seedlings had germinated.

As these results change, EC plots and C plots became characterized by different functional types by 7.5 years after the treatment (Figure 3). At that time, trees in EC plots occupied approximately 50% of the ground cover, while those in C plots had a share of less than 20%. Instead, nearly half of the ground cover in C plots was occupied by unpalatable species, which had a very limited share in EC plots. The difference in the share of trees between EC and C plots was statistically significant (Wilcoxon's rank-sum test: $W = 34$, $p = 0.009$); also, the share of unpalatable species was significantly different between the two treatments ($W = 4$, $p = 0.026$).

3.2 | Development of plant community

Species richness in the E and Ctrl plots mostly did not change until 7.5 years after the treatment, but in EC and plots C increased right after the clear-cutting (Figure 4). The difference in species richness among the treatments was always significant between plots with and without clear-cutting. EC and C plots experienced a temporal increase of species richness from 0.5 to 1.5 years after the treatment, following a common developmental path of secondary succession. The difference between EC and C plots was maximized at this stage. Species richness of these plots gradually decreased as succession proceeded and species gradually dropped out.

This process of species sorting in EC and C plots was well expressed by the nested structure of the vegetation matrix (Figure 5). The temperature and fill of the reordered matrix were 29.0 ($z = -10.8$,
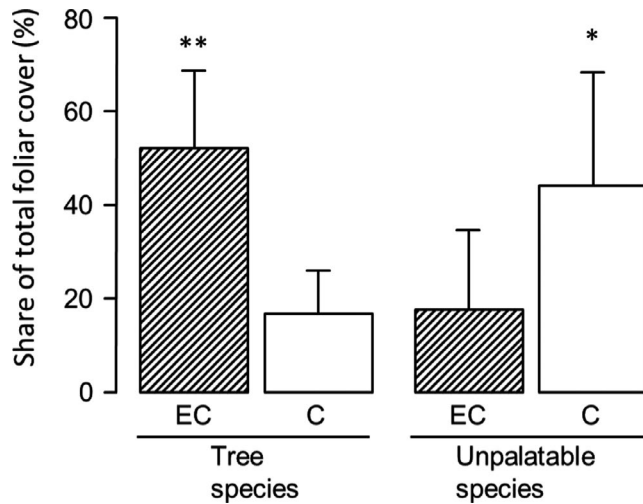
FIGURE 3 Share of trees and unpalatable plants in the foliar cover (percentage of total cover) of EC (exclosure and clear-cutting) and C (clear-cutting) plots in 2015. Error bars represent one standard deviation. Significantly greater values are indicated by asterisks (*, $p < 0.05$; **, $p < 0.01$)
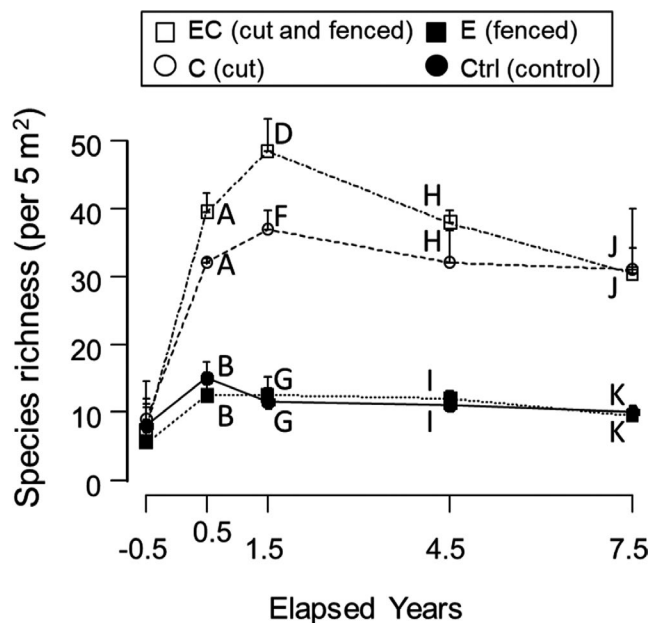
FIGURE 4 Changes in species richness after the treatments (symbols and error bars: mean plus one standard deviation)

$p = 0.001$) and 22.9%, respectively. Nestedness metrics NODF, N_{col}, and N_{row} were 40.2, 37.6, and 42.0 respectively, all being significantly greater than random ($p = 0.01$ for each), indicating nested structure for both sites and species. Communities of the EC plots in 2009 (1.5 years after the treatment) were placed at the top of this matrix, meaning that they covered the whole species pool of the study site (Appendix S3). Communities of EC plots in 2012 (4.5 years later) were located at the next-highest position, being followed by those in 2015 (7.5 years later). This arrangement of the

matrix, together with the change in species richness over the years (Figure 4), suggests the initial formation of a species assembly and a filtering process afterward.

The communities of C plots were subsets of those of EC plots, possibly being filtered by herbivory pressure from the deer (Figure 5). Temporal diversification of the species assembly from 2008 to 2009 (0.5–1.5 elapsed years) was also observed in C plots, though inter-plot variation was large (Appendix S3). Communities of C plots in 2015 (7.5 years later) were located at lower positions in the matrix than those in 2012 (4.5 years later), suggesting a gradual progression of a species sorting. The structure of this community in 2015 was not like those of EC plots in any census year. Furthermore, in the NMDS biplot, communities in C plots and EC plots tended to be separate from each other in any census year (Figure 6). Thus, the communities in C plots did not seem to be "arrested" at the early stages of the succession found in plots EC. The perMANOVA results also suggested that vegetation dynamics in plots C were AST cases rather than AS cases: communities in C plots changed from 2008 to 2015 (Table 1a), and the communities in C plots in 2015 were not similar to those in EC plots in 2008 (Table 1b).
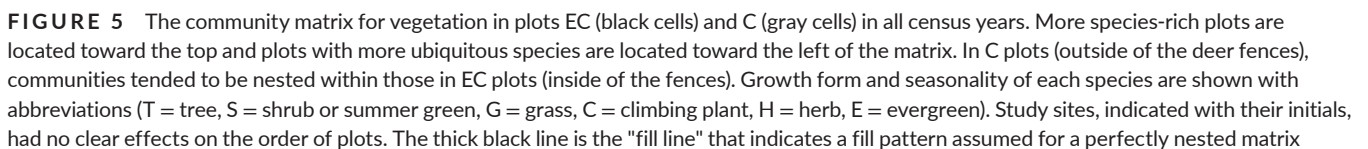
Plants with soil seed banks tended to be located at the left part of the matrix in Figure 5 ($W = 330$, $p < 0.001$), meaning that these species were ubiquitous and appeared irrespective of the deer impact and elapsed years. Shrubs also tended to appear in the left part of the matrix, although the trend was only marginally significant ($W = 240$, $p = 0.054$). Other growth forms, seasonality, and palatability to deer did not significantly affect the appearance order in the matrix.

4 | DISCUSSION

4.1 | The resilience of damaged secondary forests

The present results suggest that the secondary forests we studied had maintained regeneration potential. In EC plots, where herbivory was halted right after clear-cutting, tree species were successfully recruited, and the species composition was reconstructed following the usual secondary succession path. A species-rich association, temporally observed at an early stage, was gradually reduced, probably through abiotic and/or biotic processes (Purschke et al., 2013). These results suggest the regeneration potential of forests under the historical regime of anthropogenic disturbance. The role of natural disturbances on the regeneration of forests damaged by deer has often been pointed out (e.g., Nuttle et al., 2013); our results extend that theory to include anthropogenic disturbance.

A comparison with the Allegheny Plateau case study in the US reveals two key factors that played an important role in the high regeneration potential of EC plots. In some experimental plots established in the Allegheny Plateau, after the removal of white-tailed deer, tree regeneration after clear-cutting had been interrupted

FIGURE 5 The community matrix for vegetation in plots EC (black cells) and C (gray cells) in all census years. More species-rich plots are located toward the top and plots with more ubiquitous species are located toward the left of the matrix. In C plots (outside of the deer fences), communities tended to be nested within those in EC plots (inside of the fences). Growth form and seasonality of each species are shown with abbreviations (T = tree, S = shrub or summer green, G = grass, C = climbing plant, H = herb, E = evergreen). Study sites, indicated with their initials, had no clear effects on the order of plots. The thick black line is the "fill line" that indicates a fill pattern assumed for a perfectly nested matrix

by recalcitrant understorey layers for two decades (Nuttle et al., 2014). As an important initial condition in the Allegheny Plateau, ferns and black cherry, which are unpalatable to deer, had been abundant in the ground vegetation before clear-cutting; these unpalatable plants rapidly grew and smothered tree seedlings that otherwise would have driven forest succession. Although unpalatable species were also ubiquitous in our study sites (e.g., *Maesa japonica* and *Damnacanthus indicus*), their initial abundance before the experiment was low, possibly due to the light-limitated conditions typical of abandoned forests (Harada et al., 2020; Suzuki, 2013). Moreover, in the Allegheny Plateau, high deer density immediately after clear-cutting played a key role in the establishment of unpalatable vegetation (Horsley et al., 2003). Deer density in the area had been maintained at >10–12 deer km^{-2}, possibly providing further advantages to unpalatable plants (Nuttle et al., 2014). Similar conditions were found in our C plots, where the presence of deer favored the growth of unpalatable plants, as the animals removed saplings of palatable tree species. Such an advantage provided by deer was not available to the unpalatable plants in EC plots. In summary, the initial low density of unpalatable plants and

the rapid and complete removal of deer after clear-cutting are two factors that potentially contributed to the succesful forest regeneration observed in EC plots.

Seed banks and sprouts were important materials that enabled the rapid regeneration of woody species after clear-cutting (Suzuki, 2013). The existence of these rich regeneration sources is not accidental but may be attributable to the legacy of a past utilization. Canopy species of these forests that have survived repeated sampling of fuelwoods naturally show high sprouting potential. Additionally, the frequent cutting may have allowed fast-growing, short-lived species to leave their offspring in the soil as seed banks. Species with seed banks ubiquitously appeared in EC and C plots and remained for at least 7.5 years, as suggested by the vegetation matrix's biased appearance order. These regeneration materials might have supported the high regeneration potential even under herbivory pressure. If so, secondary forests of this type are generally expected to maintain high resilience against herbivory by deer. Dormant seeds of some early-seral trees potentially survive longer than 75 years (Sakai et al., 2005), but they may be gradually decreasing after cyclic harvesting was halted (Shinoda & Akasaka, 2019). Appropriate management is an urgent need for these forests to maintain their regeneration potential and their ecosystem services.
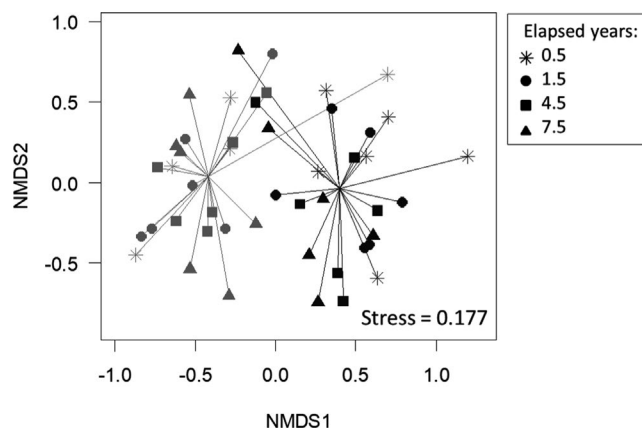
FIGURE 6 A non-metric multidimensional scaling (NMDS) biplot of plant communities in EC (black) and C (gray) plots in each census year. Communities found in same treatment are connected with lines

4.2 | AST caused by herbivory pressure after clear-cutting

Assuming the changes observed in EC plots as the typical pathway of plant succession, it was different from the situation in C plots, where AST (Suding et al., 2004) or "deflected succession" (Godwin, 1929) is suggested. Vegetation in C plots was occupied by plants unpalatable to deer instead of by trees abundant in EC plots, possibly because deer changed the results of plant–plant competition. Also, shrubs wsere abundant only in C plots though they were ubiquitous across the clear-cut plots. Some shrub species such as sagebrush achieve the initiative in plant–plant competition when deer are absent (Mainer & Hobbs, 2006), but others, like black cherry, rather become dominant under high herbivory pressure (Stromayer & Warren,

TABLE 1 PerMANOVA tables for the treatment effects on (a) vegetation change in C plots from 2008 to 2015 and (b) vegetation similarity between the EC plots in 2008 and C plots in 2015

(a) *n* = 11[†]	SS	df	F	R^2	p
Year (2008 or 2015)	0.78	1	3.02	0.25	0.002[**]
Residuals	2.32	9		0.75	
Total	3.10	10		1.00	

(b) *n* = 12					
Treatment (deer present or not)	1.10	1	3.62	0.27	0.003[**]
Residuals	3.04	10		0.73	
Total	4.14	11		1.00	

[†]One C plot had no vegetation in 2008 and was therefore removed from the analyses. [**], *p* < 0.01.

1997; Nuttle et al., 2014); the latter response group was common in our study site (e.g., *Rubus* spp. and *Maesa japonica*). The vegetation in C plots was moving toward a strange vegetation dominated by these shrubs and unpalatable plants. Such biased species composition was never found in EC plots at any stage of plant succession. Therefore, the vegetation in C plots has not been "arrested" at any stage of secondary succession heading to forests (Gibson & Brown, 1992; Young et al., 2001), but rather seemed to follow a pathway of deflected succession or AST. This means that C plots are gradually losing their potential to recover to normal forests after the deer population decreases.

It remains unclear how long the non-forest vegetation in C plots lasts after herbivores have been removed. Two possible causes are proposed for AST (Hidding et al., 2013): the priority effect (e.g., development of a recalcitrant understorey in the Allegheny Plateau) and extirpation of key drivers of vegetation dynamics. Our study site may have a priority effect: the shrub layer in C plots outcompeted trees as a recalcitrant understorey after deer were reduced. According to a meta-analysis in Europe, however, the risk of "permanently arrested" succession (a term seemingly equivalent to AST caused by the priority effect) tends to be high in xeric habitats with seasonal drought, where non-woody species had a competitive advantage over trees (Thrippleton et al., 2018). Such risk might be low for our study sites where warm and humid conditions benefit tree species over non-tree species.

On the other hand, our C plots have already lost many tree species that drove forest succession in EC plots due to post-cutting herbivory. In this situation, whether the vegetation in C plots could go back to a forest in the future depends on the introduction of trees from outside, for example, as anemochoric seeds. The true resilience of forests facing these risks needs to be examined by setting an exclosure around C plots and monitoring succession afterward, like the approaches taken by previous studies (e.g., Hidding et al., 2013).

5 | CONCLUSIONS

Clear-cutting abandoned secondary forests where deer occurred caused an AST case, as Suding et al., (2004) warned: some degraded systems cannot be recovered by causing a disturbance that the original systems have historically experienced, as a result of mechanisms inherent to the degraded system. In our case, deer herbivory was the mechanism that inhibited recovery of the secondary forests after a traditional disturbance (clear-cutting). In other words, if herbivory pressure were removed right after clear-cutting (as in EC plots), the system would successfully recover without falling into AST. Secondary forests on the Boso Peninsula damaged by deer have suffered long-lasting regeneration failure even after the herbivory pressure was retarded (Harada et al., 2020). Considering that firewood sampling was common in this region until several decades ago, cutting canopy trees and reducing deer density would be a possible solution to drive forest regeneration. Recently, traditional firewood harvesting in Japan has seen a growth in demand

as firewood is considered a souce of carbon-neutral energy (Oono et al., 2020) and because harvesting practices contribute to maintain the biodiversity of secondary forests (Ito et al., 2012). Installing deer fences soon after cutting firewood would help forest regeneration. One of our EC plots lost its surrounding fence by accident in 2019, but the vegetation there is still developing as a forest (as of April 2021). This suggests that a decade of deer exclusion was sufficient to allow the development of vegetation dynamics after a disturbance.

However, such a solution might not apply to other regions. Environmental productivity and herbivory pressure affect the successional trajectory after clear-cutting (e.g., Randall & Walters, 2011; Thrippleton et al., 2018; Ramirez et al., 2019). The succession trajectory also depends on members of the regional flora, especially of important groups such as unpalatable plants and early-seral trees. Combined effects of these factors would determine which successional pathway the forests follow. Conditions that trigger AS and AST after clear-cutting of abandoned forests should be revealed in future studies.

AUTHOR CONTRIBUTIONS
MS conceived of the research idea; all authors collected data; MS performed statistical analyses; MS, with many contributions from YH, wrote the paper; all authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT
The datasets and *R* codes are available as supporting information.

ORCID
Maki Suzuki https://orcid.org/0000-0003-4249-9789

REFERENCES

Akashi, N. & Nakashizuka, T. (1999) Effects of bark-stripping by sika deer (Cervus nippon) on population dynamics of a mixed forest in Japan. *Forest Ecology and Management*, 113, 75–82. https://doi.org/10.1016/S0378-1127(98)00415-0.

Asada, M. & Ochiai, K. (2009) Sika deer in an evergreen broad-leaved forest zone on the Boso Peninsula, Japan. In: McCullough, D.R. et al. (eds.), *Sika Deer: Biology and management of native and introduced populations.* Springer Japan, pp. 385-404.

Attiwill, P.M. (1994) The Disturbance of forest ecosystems - The ecological basis for conservative management. *Forest Ecology and Management*, 63, 247–300.

Barrios-Garcia, M.N. & Ballari, S.A. (2012) Impact of wild boar (Sus scrofa) in its introduced and native range: A review. *Biological Invasions*, 14, 2283–2300. https://doi.org/10.1007/s10530-012-0229-6.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Beauchamp, V.B., Ghuznavi, N., Koontz, S.M. & Roberts, R.P. (2013) Edges, exotics and deer: The seed bank of a suburban secondary successional temperate deciduous forest. *Applied Vegetation Science*, 16, 571–584. https://doi.org/10.1111/avsc.12036.

Chiba Prefecture (2004) *Science report on the management of sika deer on Boso Peninsula*. Chiba Prefecture, Chiba. 10pp, 63pp (in Japanese).

Ghazoul, J., Burivalova, Z., Garcia-Ulloa, J. & King, L.A. (2015) Conceptualizing forest degradation. *Trends in Ecology and Evolution*, 30, 622–632. https://doi.org/10.1016/j.tree.2015.08.001.

Gibson, C.W.D. & Brown, V.K. (1992) Grazing and vegetation change: Deflected or modified succession? *Journal of Applied Ecology*, 29, 120–131. https://doi.org/10.2307/2404355.

Gill, R.M.A. (1992) A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. *Forestry*, 65, 363–388. https://doi.org/10.1093/forestry/65.4.363-a.

Godwin, H. (1929) The sub-climax and deflected succession. *Journal of Ecology*, 17, 144–147.

Harada, K., Ann, J.A.M. & Suzuki, M. (2020) Legacy effects of sika deer overpopulation on ground vegetation and soil physical properties. *Forest Ecology and Management*, 474, 118346. http://www.ncbi.nlm.nih.gov/pubmed/118346.

Hashimoto, Y. & Fujiki, D. (2014) List of food plants and unpalatable plants of sika deer (Cervus nippon) in Japan. *Humans and Nature*, 25, 133–160 (in Japanese).

Hédl, R., Kopecký, M. & Komárek, J. (2010) Half a century of succession in a temperate oakwood: From species-rich community to mesic forest. *Diversity and Distributions*, 16, 267–276. https://doi.org/10.1111/j.1472-4642.2010.00637.x.

Hidding, B., Tremblay, J.P. & Côté, S.D. (2013) A large herbivore triggers alternative successional trajectories in the boreal forest. *Ecology*, 94, 2852–2860. https://doi.org/10.1890/12-2015.1.

Hismoto, Y., Satoru, O., Suzuki, M., Tsurumi, Y., Yonemichi, T. & Suzuki, M. (2019) Efficiency of estimating sika deer density using camera traps in the University of Tokyo Chiba Forest. *Miscellaneous Information of the University of Tokyo Forests*, 61, 65–74. https://doi.org/10.15083/00076485 (in Japanese).

Horsley, S.B., Stout, S.L. & deCalesta, D.S. (2003) White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications*, 13, 98–118.

Husheer, S.W., Coomes, D.A. & Robertson, A.W. (2003) Long-term influences of introduced deer on the composition and structure of New Zealand Nothofagus forests. *Forest Ecology and Management*, 181, 99–117. https://doi.org/10.1016/S0378-1127(03)00120-8Hobbs.

Iida, T., Soga, M. & Koike, S. (2018) Large herbivores affect forest ecosystem functions by altering the structure of dung beetle communities. *Acta Oecologica*, 88, 65–70. https://doi.org/10.1016/j.actao.2018.03.003.

Ito, H., Hino, T. & Sakuma, D. (2012) Species abundance in floor vegetation of managed coppice and abandoned forest. *Forest Ecology and Management*, 269, 99–105. https://doi.org/10.1016/j.foreco.2011.12.017.

Kabaya, H. (1988) *Changes of undergrowth of a broadleaved evergreen forest in relation to grazing effects by sika deer*. Bull Univ Tokyo for, 78, 67-82. (in Japanese with English abstract). http://hdl.handle.net/2261/23128

Kabaya, H. (1992) *List of food plants of sika deer (Cervus nippon) in the eastern part of Boso Mountains*, *Chiba Miscellaneous info* Univ Tokyo for, 29, 125-140. (in Japanese). https://doi.org/10.15083/00026288

Kabaya, H. (2001) Effects of large mammals on vegetation. Chibaken, S. & Kenkyu, Z. (eds.), *Natural history in Chiba Prefecture 5 vegetation*. Chiba Prefecture, Chiba. pp. 629-638. (in Japanese)

Keith, S.A., Newton, A.C., Morecroft, M.D., Bealey, C.E. & Bullock, J.M. (2009) Taxonomic homogenization of woodland plant communities over 70 years. *Proceedings of the Royal Society B: Biological Sciences*, 276, 3539–3544. https://doi.org/10.1098/rspb.2009.0938.

Kelly, J.F. (2019) Regional changes to forest understories since the mid-twentieth century: Effects of overabundant deer and other factors in northern New Jersey. *Forest Ecology and Management*, 444, 151–162. https://doi.org/10.1016/j.foreco.2019.04.050.

Kopecký, M., Hédl, R. & Szabó, P. (2013) Non-random extinctions dominate plant community changes in abandoned coppices. *Journal of Applied Ecology*, 50, 79–87. https://doi.org/10.1111/1365-2664.12010.

Makino, T. (1940) *Makino, Nihon shokubutsu zukan: An illustrated flora of Nippon, with the cultivated and naturalized plants*. Hokuryukan, Tokyo, pp., 1070.

Manier, D.J. & Thompson Hobbs, N. (2006) Large herbivores influence the composition and diversity of shrub-steppe communities in the Rocky Mountains, USA. *Oecologia*, 146, 641–651. https://doi.org/10.1007/s00442-005-0065-9.

Miyashita, T., Takada, M. & Shimazaki, A. (2004) Indirect effects of herbivory by deer reduce abundance and species richness of web spiders. *Ecoscience*, 11, 74–79.

Miyawaki, A. (1986) *Vegetation of Japan*. Kanto, Shibundo, Tokyo. 641 Pages. (in Japanese).

Nishimoto, T. (2010) Deer, Tokyo Nishimoto, T. & Niimi, M. (eds.), *Jiten Hito to dōbutsu no kōkogaku*. ISBN: 9784642080422. pp. 78-81. (in Japanese) Tokyo: Yoshikawa Kobunkan.

Nuttle, T., Ristau, T.E. & Royo, A.A. (2014) Long-term biological legacies of herbivore density in a landscape-scale experiment: Forest understoreys reflect past deer density treatments for at least 20 years. *Journal of Ecology*, 102, 221–228.

Nuttle, T., Royo, A.A., Adams, M.B. & Carson, W.P. (2013) Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. *Ecological Monographs*, 83, 3–17. https://doi.org/10.1890/11-2263.1.

Ohashi, H., Yoshikawa, M., Oono, K., Tanaka, N., Hatase, Y. & Murakami, Y. (2014) The impact of sika deer on vegetation in Japan: Setting management priorities on a national scale. *Environmental Management*, 54, 631–640. https://doi.org/10.1007/s00267-014-0326-7.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. et al. (2019) *vegan: Community Ecology Package*. R package version 2.5-6. https://CRAN.R-project.org/package=vegan.

Oono, A., Kamiyama, C. & Saito, O. (2020) Causes and consequences of reduced human intervention in formerly managed forests in Japan and other countries. *Sustainability Science*, 15, 1511–1529. https://doi.org/10.1007/s11625-020-00845-3.

Purschke, O., Schmid, B.C., Sykes, M.T., Poschlod, P., Michalski, S.G., Durka, W. et al. (2013) Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. *Journal of Ecology*, 101, 857–866. https://doi.org/10.1111/1365-2745.12098.

R Core Team (2019) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Rackham, O. (2008) Ancient woodlands: Modern threats. *New Phytologist*, 180, 571–586. http://www.jstor.org/stable/25150608.

Ramirez, J.I., Jansen, P.A., den Ouden, J., Goudzwaard, L. & Poorter, L. (2019) Long-term effects of wild ungulates on the structure, composition and succession of temperate forests. *Forest Ecology and Management*, 432, 478–488. https://doi.org/10.1016/j.foreco.2018.09.049.

Randall, J.A. & Walters, M.B. (2011) Deer density effects on vegetation in aspen forest understories over site productivity and stand age gradients. *Forest Ecology and Management*, 261, 408–415. https://doi.org/10.1016/j.foreco.2010.10.026.

Royo, A.A. & Carson, W.P. (2006) On the formation of dense understory layers in forests worldwide: Consequences and implication for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research*, 36, 1345–1362. https://doi.org/10.1139/X06-025.

Russell, F.L., Zippin, D.B. & Fowler, N.L. (2001) Effects of white-tailed deer (Odocoileus virginianus) on plants, plant populations and communities: A review. *American Midland Naturalist*, 146, 1–26.

Sakai, A., Sato, S., Sakai, T., Kuramoto, S. & Tabuchi, R. (2005) A soil seed bank in a mature conifer plantation and establishment of seedlings after clear-cutting in southwest Japan. *Journal of Forest Research*, 10, 295–304. https://doi.org/10.1007/s10310-004-0138-3.

Shelton, A.L., Henning, J.A., Schultz, P. & Clay, K. (2014) Effects of abundant white-tailed deer on vegetation, animals, mycorrhizal fungi, and soils. *Forest Ecology and Management*, 320, 39–49. https://doi.org/10.1016/j.foreco.2014.02.02.

Shinoda, Y. & Akasaka, M. (2019) Species turnover differentiates diversity–disturbance relationships between aboveground vegetation and soil seedbank. *Plant Ecology*, 220, 595–603. https://doi.org/10.1007/s11258-019-00938-9.

Stromayer, K.A.K. & Warren, R.J. (1997) Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildlife Society bulletin*, 25, 227–234. http://www.jstor.org/stable/3783436

Suding, K.N., Gross, K.L. & Houseman, G.R. (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution*, 19, 46–53. https://doi.org/10.1016/j.tree.2003.10.005.

Suzuki, M. (2013) Succession of abandoned coppice woodlands weakens tolerance of ground-layer vegetation to ungulate herbivory: A test involving a field experiment. *Forest Ecology and Management*, 289, 318–324. https://doi.org/10.1016/j.foreco.2012.10.003.

Suzuki, M. & Ito, E. (2014) Combined effects of gap creation and deer exclusion on restoration of belowground systems of secondary woodlands: A field experiment in warm-temperate monsoon Asia. *Forest Ecology and Management*, 329, 227–236. https://doi.org/10.1016/j.foreco.2014.06.028.

Suzuki, M., Miyashita, T., Kabaya, H., Ochiai, K., Asada, M. & Tange, T. (2008) Deer density affects ground-layer vegetation differently in conifer plantations and hardwood forests on the Boso Peninsula, Japan. *Ecological Research*, 23, 151–158. https://doi.org/10.1007/s11284-007-0348-1.

Suzuki, M., Miyashita, T., Kabaya, H., Ochiai, K., Asada, M. & Kikvidze, Z. (2013) Deer herbivory as an important driver of divergence of ground vegetation communities in temperate forests. *Oikos*, 122, 104–110. https://doi.org/10.1111/j.1600-0706.2012.20431.x.

Takada, M., Baba, Y.G., Yanagi, Y., Terada, S. & Miyashita, T. (2008) Contrasting responses of web-building spiders to deer browsing among habitats and feeding guilds. *Environmental Entomology*, 37, 938–946. 1093/ee/37.4.938.

Takagi, S. & Miyashita, T. (2012) Variation in utilization of young leaves by a swallowtail butterfly across a deer density gradient. *Basic and Applied Ecology*, 13, 260–267. https://doi.org/10.1016/j.baae.2012.03.003.

Takatsuki, S. (2009) Effects of sika deer on vegetation in Japan: A review. *Biological Conservation*, 142, 1922–1929. https://doi.org/10.1016/j.biocon.2009.02.011.

Tanentzap, A.J., Bazely, D.R., Koh, S., Timciska, M., Haggith, E.G., Carleton, T.J. et al. (2011) Seeing the forest for the deer: Do reductions in deer-disturbance lead to forest recovery? *Biological Conservation*, 144, 376–382. https://doi.org/10.1016/j.biocon.2010.09.015.

Tanentzap, A.J., Burrows, L.E., Lee, W.G., Nugent, G., Maxwell, J.M. & Coomes, D.A. (2009) Landscape-level vegetation recovery from herbivory: Progress after four decades of invasive red deer control. *Journal of Applied Ecology*, 46, 1064–1072. https://doi.org/10.1111/j.1365-2664.2009.01683.x.

Thrippleton, T., Bugmann, H. & Snell, R.S. (2018) Herbaceous competition and browsing may induce arrested succession in central European forests. *Journal of Ecology*, 106, 1120–1132. https://doi.org/10.1111/1365-2745.12889.

Tremblay, J.P., Huot, J. & Potvin, F. (2006) Divergent nonlinear responses of the boreal forest field layer along an experimental gradient of deer densities. *Oecologia*, 150, 78–88. https://doi.org/10.1007/s00442-006-0504-2.

Tschöpe, O., Wallschläger, D., Burkart, M. & Tielbörger, K. (2011) Managing open habitats by wild ungulate browsing and grazing: A case-study in North-Eastern Germany. *Applied Vegetation Science*, 14, 200–209. https://doi.org/10.1111/j.1654-109X.2010.01119.x.

Ulrich, W., Almeida-Neto, M. & Gotelli, N.J. (2009) A consumer's guide to nestedness analysis. *Oikos*, 118, 3–17. https://doi.org/10.1111/j.1600-0706.2008.17053.x.

Wardle, D.A., Barker, G.M., Yeates, G.W., Bonner, K.I. & Ghani, A. (2001) Introduced browsing mammals in New Zealand natural forests: Aboveground and belowground consequences. *Ecological Monographs*, 71, 587–614.

Yanagi, Y., Takada, T. & Miyashita, T. (2008) Changes in the physical properties of forest soils in the Boso Peninsula due to sika deer revealed by surveys and a field experiment. Jpn. *J Conservation Biology*, 13, 65–74 (in Japanese, with English abstract). 10.18960/hozen.13.1_65.

Yonekura, K. & Kajita, T. (2003) *BG Plants Japanese name–scientific name index (YList)*. http://ylist.info/.

Young, T.P., Chase, J.M. & Huddleston, R.T. (2001) Community succession and assembly: Comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecological Restoration*, 19, 5–18. https://doi.org/10.3368/er.19.1.5.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Design of the experimental plots

Appendix S2. Comparison of generalized linear mixed models (GLMMs) with nested and non-nested random factors

Appendix S3. The community matrix for EC plots and C plots of each year

Appendix S4. Data: total foliar cover and the maximum heights

Appendix S5. Data: ratio of unpalatable species and tree species

Appendix S6. Data: species richness

Appendix S7. Data: plot–species matrix

Appendix S8. R code for generalized linear mixed model (GLMM) and post-hoc tests (Figure 2)

Appendix S9. R code for analyses in Figure 3

Appendix S10. R code for generalized linear mixed model (GLMM) and post-hoc tests on species richness (Figure 4)

Appendix S11. R code for non-metric multidimensional scaling (NMDS; Figure 6)

Appendix S12. R code for calculation of the nestedness indices

Appendix S13. R code for calculation of the nestedness indices

Appendix S14. Column names in the CSV files