Anthropogenic disturbances alter responses of understory plants to deer density: A 9-year deer density control experiment

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ABSTRACT

The increasing deer population and their expanding distribution have altered the diversity and biomass of the plant community in the northern hemisphere. Furthermore, anthropogenic disturbances such as nitrogen deposition and logging threaten plant diversity in many parts of the forests. Therefore, it is necessary to investigate the effects of deer on plant communities under nitrogen deposition and logging conditions to understand and conserve plant diversity in forest ecosystems. We conducted a field experiment that controlled three levels of deer densities (exclosure: 0 deer/km^2, low: 10 deer/km^2, and high: 20 deer/km^2) and four anthropogenic disturbances (without anthropogenic disturbances [control], nitrogen addition, logging, and nitrogen addition and logging combined) in a cool temperate secondary forest in northern Japan for nine years. We surveyed the effects of deer density and anthropogenic disturbance treatments on species richness and vegetation cover of life forms (forbs, ferns, trees, graminoids, unpalatable species, vines, and shrubs) and all species of understory vascular plants. We estimated the constant effect (without the elapsed year) and the temporary effect (with the elapsed year) of deer density, anthropogenic disturbances, and their interactions on the species richness, vegetation cover, and Simpson's index as separate parameters in full models and selected the best model. The high deer density negatively affected the species richness of some life forms and all species and accelerated these effects over time for all species. The vegetation covers of most of the life forms were negatively affected by high deer density, and the effect was reduced over time. In contrast, the exclosure negatively affected the species richness of some life forms and positively affected the vegetation cover of most of the life forms and all species. The effect on the cover accelerated over time. Nitrogen addition accelerated the negative effect of high deer density on the species richness of shrubs. On the other hand, logging reduced the negative effect of high deer density on the species richness of all species. The cover of unpalatable species in the high deer density site with logging was approximately nine times higher than that in the high deer density site without anthropogenic disturbances in the last surveyed year. The high deer density and logging decreased the Simpson's diversity index score. These results indicate that the effects of deer density, anthropogenic disturbances, and their interactions vary with time. These interactions must be considered to manage deer's effect on forest ecosystems.

1. Introduction

The species diversity of understory plants, such as forbs, tends to be considerably higher than that of canopy tree species in most temperate deciduous forests; understory plants contribute to more than 80% of the total plant species richness (Gilliam, 2007). Understory plants compete with the seedlings and saplings of canopy tree species; the interactions

among the understory plants can affect forest dynamics through the recruitment process of canopy trees (Royo and Carson, 2006; Gilliam, 2007; Kuijper et al., 2010). Understory plants substantially contribute to forest ecosystem functions, such as nutrient and water cycling (Gilliam, 2007; Elliott et al., 2015; Stefanowicz et al., 2023). Understanding and conserving the biodiversity and function of forest ecosystems requires clarifying the mechanisms of maintenance and conservation of

understory plant diversity.

Ungulates are a significant driver of plant diversity, and they constrain the structure of plant communities in forest ecosystems. Substantial vegetation change as a result of ungulate browsing can become a biodiversity conservation issue (Hester et al., 2000; Rooney and Waller, 2003; Côté et al., 2004). The deer population in most of the northern hemisphere has increased and expanded its distribution (Côté et al., 2004).

Human activities lead to biodiversity decline due to altered abiotic conditions and biological interactions (Suding et al., 2005; Gilliam, 2006; Bobbink et al., 2010; Gibson et al., 2011). Interference with the nitrogen cycle, one of the most significant human activity loads, could have disastrous consequences for humanity (Rockstrom et al., 2009). Forest ecosystems near human activity areas are exposed to nitrogen deposition, which lowers plant diversity (Gilliam, 2006; Bobbink et al., 2010). Gaps created by logging also significantly affect plant diversity (Roberts and Gilliam, 1995; Gibson et al., 2011), and most forest ecosystems have experienced logging (Morales-Hidalgo et al., 2015; FAO, 2020).

Therefore, to understand understory plant diversity maintenance mechanisms and conserve them in forest ecosystems in large areas of the northern hemisphere, it is necessary to reveal the influence of deer under the effects of nitrogen deposition and logging, which are major anthropogenic disturbances. The anthropogenic disturbances may alter the influence of deer on the plant community in forest ecosystems. For instance, nitrogen deposition can affect the sensitivity of plants to herbivores (Bobbink et al., 2010) because of changing foliar quality, including secondary defense compounds (Throop and Lerdau, 2004). Moreover, the creation of canopy gaps facilitates the resistance and tolerance of plants to herbivores because the increased resource availability, such as light radiation, enhances chemical and physical defensive traits against herbivores (Coley et al., 1985; Bryant et al., 1987; Nabeshima et al., 2001; Nakamura et al., 2008; Takafumi et al., 2010; Piper et al., 2018) and compensation growth (Rosenthal and Kotanen, 1994; Wise and Abrahamson, 2007; Cronin et al., 2010). A field experiment manipulating white-tailed deer (*Odocoileus virginianus*) density and logging treatment showed that the survival rate of balsam fir (*Abies balsamea*) under high deer density was higher in clear-cuts than in control areas (Hidding et al., 2012). Previous studies have shown that logging modifies the effect of deer on vegetation (Horsley et al., 2003; Tremblay et al., 2006, 2007; Hidding et al., 2012; Burton et al., 2021; Royo and Carson, 2022). However, no studies have focused on the effect of combined nitrogen deposition and logging on the relationships between deer and vegetation, even though these anthropogenic disturbances broadly occur in forest ecosystems worldwide.

Deer density and a plant community's structure were reported as nonlinear relationships (Persson et al., 2005; Tremblay et al., 2006; Suzuki et al., 2008; Koda and Fujita, 2011). The comparison of vegetation between only two levels of deer density cannot illustrate the nonlinear relationship (Hester et al., 2000). However, most previous studies evaluating the relationship between deer herbivory and vegetation set the deer density at two levels using deer exclosure (e.g., Royo et al., 2010; Beguin et al., 2011; Suzuki and Ito, 2014). Some studies analyzed vegetation under more than two levels of density using a natural deer density gradient among forests (e.g., Suzuki et al., 2008; Koda and Fujita, 2011). These studies have difficulty ascertaining the relationships between deer density and plant community owing to the difference in flora, browsing history and climate condition between forests. Therefore, field experiments that directly manipulate deer densities are needed to examine the relationships between deer density and vegetation (Hobbs, 1996; Hester et al., 2000; Rooney and Waller, 2003; Côté et al., 2004).

It is important to consider that the legacy of the influence of deer on the plant community remains over decades when conducting these field experiments (Nuttle et al., 2014). Once high deer densities thoroughly alter vegetation, regime shifts occur owing to seed limitation and shade

from the domination of resistant species, and the vegetation will not recover to its original state even if deer densities are reduced (Tanentzap et al., 2012; Harada et al., 2020; Suzuki et al., 2021; Royo and Carson, 2022). Therefore, researchers should start the field experiment at densities lower than those at which deer thoroughly alter vegetation to evaluate the historical role of more typical or natural levels of deer (Royo et al., 2010). However, few studies have begun field experiments before deer densities are high (but see Royo et al., 2010).

The relationship between deer density and plant communities is sometimes dynamic; plant communities change over time, even at the same deer density (Horsley et al., 2003; Tremblay et al., 2006; Bachand et al., 2015). For example, a study that manipulated deer density and logging intensity and monitored understory vegetation for ten years reported that the diversity of understory plants in thinning stands was negatively related to deer density three and five years after the manipulation (Horsley et al., 2003); however, the negative relationship was not detected after ten years in the experiment. The relation between deer density and understory plant biomass also varies over time. The aboveground biomass of *Epilobium angustifolium*, *Cornus canadensis,* and other shrub species decreased with deer density, and the trend was more pronounced three years after the deer density manipulation than after one year (Tremblay et al., 2006). Examining time as a factor will help us to understand the relationship between deer and vegetation and provide insight that will contribute to forest management.

The sensitivity of understory plants to deer herbivory would differ among life forms (e.g., forbs, ferns, graminoids, and shrubs). For example, deer can feed on tree species all year round, while forb species can avoid feeding pressure in winter owing to aboveground withering in cool-temperature forests. Furthermore, palatable and low-tolerant species would decrease, while unpalatable and highly tolerant species would increase through relaxing competition among plant species (Rooney and Waller, 2003; Côté et al., 2004). The effect of deer on the understory plants can change plant diversity and dynamics in the forests through the difference in sensitivity to the effect of deer and competition between plants.

We experimentally manipulated both deer (*Cervus nippon yesoensis*) density and anthropogenic disturbances in a forest, where the deer density has been very low for approximately 100 years. We set the density of deer at three levels, 0, 10, and 20 deer/km^2, and carried out nitrogen addition and selective logging as anthropogenic disturbances at each deer density level. We monitored the structure of the plant community, such as species diversity and vegetation cover of understory plants, for nine years. These treatments were aimed to clarify the responses of each life form and all species of understory vascular plants, that is, increases or extinction, to deer by considering the elapsed time. The main questions addressed in this study were 1) How do species diversity and vegetation cover of understory plants respond to deer density? 2) Do nitrogen addition and logging alter the influence of deer density on understory plants? 3) If deer density or a combination of deer density and nitrogen addition or logging alter understory plants, is it accelerated or reduced over time? To the best of our knowledge, this is the first study to comprehensively test the long-term chronological responses of plants to combined nitrogen fertilization and logging under various deer densities, starting with low deer density.

2. Materials and methods

2.1. Study site

Our field experiment was conducted in the Tomakomai Experimental Forest (TOEF), Hokkaido University (42°41′ N, 141°36′ E), Hokkaido, northern island (ca. 78,000 km^2) of Japan. The mean monthly temperature ranges from − 3.2 to 19.1 °C, and the annual average precipitation is 1450 mm. Snow cover reaches a depth of 50 cm from December − March. There was no extreme weather during the study period. Approximately 350 vascular plants have been recorded in the TOEF

(Kudo and Yoshimi, 1916). The dominant canopy tree species in the natural stands are *Quercus crispula*, *Acer mono*, *Sorbus alnifolia*, and *Tilia japonica* (Hiura, 2001). The understory species include *Dryopteris crassirhizoma*, *Maianthemum dilatatum*, and *Scisandra chinensis* (Hiura, 2001). The soil horizon has a 0–6 cm depth, and 2 m deep volcanogenic regosols were accumulated from the eruptions of Mt. Tarumae in 1669 and 1739 under the horizon (Shibata et al., 1998).

Sika deer (*Cervus nippon yesoensis*), hereafter deer, are the only large herbivores in Hokkaido. The social behavior of deer is that the dominant male establishes his harem in the rutting season, and single-sex groups tend to be established during the rest of the year. The year-round home range size of resident female deer is 50–250 ha (Igota et al., 2004; Takafumi et al., 2017) and that of seasonal migrants male deer is approximately 450–2,600 ha excluding rutting period (Agetsuma et al., 2011). The population density of deer in western Hokkaido, including the TOEF, and other regions of Hokkaido drastically decreased in the early 20th century (Iijima et al., 2023; Kaji et al., 2010). The deer density was very low until the 1980 s. The density recovered from the 1990 s to the early 2000 s and became relatively stable after 2004 at approximately 10 deer/km^2 in the TOEF (Agetsuma et al., 2007). Based on route census data, the estimated deer density in the TOEF from 2004 to 2012 fluctuated between 3.6 and 8.5 deer/km^2 and increased to 12.3 deer/km^2 in 2013 (TOEF unpublished data). These densities are lower than the 14 deer/km^2 density that is starting to significantly affect forests in Hokkaido (Kaji et al., 2006).

2.2. Experimental design

The species composition of understory plants in the TOEF was mainly constrained by disturbance histories, such as logging, plantation, and typhoons (Takafumi and Hiura, 2009). The field experiment area shared the same disturbance history. It was covered with deciduous broad-leaved forest that regenerated after being disturbed by a severe typhoon in 1954 and salvage logging after the typhoon. The area has a homogeneous topography; elevation ranges from 28.0 to 33.4 m, and slope angle ranges from 0.3 to 2.3°. Furthermore, insect communities in the field experiment area have low spatial heterogeneity (Iida et al., 2016). Preliminary analysis using non-metric multidimensional scaling (NMDS) showed that the species composition in the first year did not considerably differ between the treatments (Supplementary information S1). Therefore, the understory plant community could be assumed to have low spatial heterogeneity.

We manipulated deer density, nitrogen addition, and logging. We set deer density at three levels: zero (0 deer/km^2, deer exclusion), low (approximately 10 deer/km^2, natural density in the study area), and high (approximately 20 deer/km^2) in the experimental area. The criteria for "high deer density" and "low deer density" were defined by reference to Kaji et al. (2006), which comprehensively discussed deer management in Hokkaido and indicated that the effect of deer is not significant below 14 deer/km^2 in forest lands. We fenced 18.0 ha areas with 2.3 m high metal nets and divided the inside area into a 1.5 ha area as an exclosure for the deer exclusion site and 16.5 ha as an enclosure for the high deer density site (see Minoshima et al., 2013; Iida et al., 2016). The area outside of the fence (12 ha), adjacent to the exclosure and the enclosure, was used for the low deer density site. Three females, one male, and one unknown sex were introduced into the enclosure in the spring of 2004, and all but the male deer died in the winter of 2005. Only male deer were introduced into the exclosure from 2005 onward. We maintained a stable deer density in the enclosure as much as possible by introducing wild deer inhabiting the TOEF when deer escaped or died. During most of the study period, we kept 3–5 male deer in the high deer density site, and although the density was 1–2 deer in a few months (3.3 deer/km^2 on average), the average deer density for the study period was 20 deer/km^2. Permission to capture and handle wildlife, including animal welfare and ethics, was obtained from the Hokkaido government.

We randomly established 16 research plots (20 × 20 m) in the high and low deer density sites and 8 plots in the deer exclusion site (a total of 40 plots). We established four anthropogenic disturbance treatments (without anthropogenic disturbances as the control, nitrogen addition, logging, and nitrogen addition plus logging); these treatments were assigned to the randomly selected plots. Replication of each disturbance treatment was done four times for the high and low deer density sites and twice for the deer exclusion site. In nitrogen addition plots, we scattered granular ammonium sulfate fertilizer at 10.5 Ng/m^2 in April of 2005–2013 after snow melt. The amount of nitrogen addition was similar to other nitrogen addition experiments (Chapin et al., 1995; Press et al., 1998; Strengbom et al., 2001; Klanderud and Totland, 2005). Nitrogen deposition in large areas of South and East Asia is predicted to exceed 5 Ng/m^2/yr in the future (Galloway et al., 2004). In logging plots, we selected individual trees to cut at 30% of the basal area of each plot in April 2005. These selective cutting reduced the biomass, but it did not significantly change the relative species composition of canopy and sapling trees of the plots before and after the logging. The mean basal area of canopy trees and the total number of trees per plot did not differ significantly among the deer density manipulation sites in 2008 (Minoshima et al., 2013). The logging ratio to the basal area was standard in Japanese forest management operations and did not exceed the maximum selective logging ratio regulated by the Japanese Forest Act (Ministry of Agriculture, Forestry and Fisheries, 2020).

Our experiment did not have replications for each deer density manipulation site. Thus, our experiment design can be defined as pseudoreplication (Hurlbert, 1984), and it may be difficult to fully detect whether deer density is the only factor leading to changes in understory plants. However, experiments involving unreplicated treatments may be the only or best option to study large-scale systems, and researchers can test the treatment effects by checking whether the time trajectories of the treatments and control start to diverge from the initiation of the experiment (Oksanen, 2001). In our study, the effects of the treatments could be tested by focusing on the changes in the understory plant community over time after the treatments. However, we could not completely avoid the possible influence of spatial bias in the plant community on the effects of treatments on the understory plants.

2.3. Vegetation survey

We set up four permanent quadrats (1 × 1 m) for vegetation surveys in each research plot. We surveyed understory plants, which were less than 1 m tall in the quadrats, between late July and middle August in 2005, 2006, 2007, 2009, and 2013. We identified most of the vascular plant species in the quadrats to the species level, although some plants were identified to the genus level. Some unknown plants were too small to identify, and the frequency of appearance was less than 0.4% compared to the total species records each year. In addition, in 2007, 2009, and 2013, the percentage cover of the entirety of the understory plants and each plant species were visually estimated in each quadrat by researchers. To maintain the accuracy of the visual evaluation, we brought transparent plastic sheets whose area was known as references in the survey.

2.4. Data analysis

The species richness in a plot was calculated by pooling the quadrats' survey records. The percentage of cover in a plot was calculated by averaging the percentage of cover in the quadrats. To evaluate the response of each life form (forbs, ferns, trees, graminoids, unpalatable species: based on Sukeno and Miyaki (2007), vines, and shrubs) concerning deer density and anthropogenic disturbance treatments, we calculated the species richness and cover of each life form in each plot. The definition of unpalatable species for deer followed Sukeno and Miyaki (2007), and the species were *Pachysandra terminalis*, *Senecio cannabifolius*, *Chloranthus serratus*, and *Arisaema peninsulae*. Simpson's diversity index (D) was calculated as follows using the relative cover p_s

of species s in each plot.

$$D = \frac{1}{\sum_s p_s^2} \tag{1}$$

To evaluate the effects of deer density, anthropogenic disturbances, and their interactions on species richness, vegetation cover, and the Simpson's index of each life form and all species, we used a Bayesian state-space model and estimated the constant effect (without the elapsed year) and the temporary effect (with the elapsed year) of the treatments and conducted model selection. These effects were estimated as separate parameters in the models to estimate the constant effect (without elapsed year) and the temporary effect (with elapsed year) of deer density, anthropogenic disturbances, and their interactions. The species richness was analyzed using the following equations:

$$S_{\mathrm{OBS}\,t,i} \sim Poisson(\lambda_{t,i}) \tag{2}$$

$$\ln(\lambda_{t,i}) = \ln(S_{\mathrm{EXP}\,t-1,\,i}) + \sum_{j=1}^{22}(\beta_{\mathrm{CON}j}\mathrm{T}_{i,j} + \beta_{\mathrm{TEMP}j}\mathrm{Y}_t\mathrm{T}_{i,j}) \tag{3}$$

$S_{\mathrm{OBS}\,t,i}$ is observed species richness in plot i in year t, t is from 2005 to 2013. $S_{\mathrm{EXP}t-1,i}$ is the expectation of the species richness in year t-1 in plot i from the model and is equal to $\lambda_{t-1,i}$. $\beta_{\mathrm{CON}j}$ and $\beta_{\mathrm{TEMP}j}$ are the constant effect and the temporary effect of the treatments j on dependent variables, respectively. If only $\beta_{\mathrm{CON}j}$ is selected by the model selection described below, it means that treatment j has the constant effect on the response variables. If only β_{TEMP} is selected, it means that the effect of the treatment is accelerated or reduced over time. If both $\beta_{\mathrm{CON}j}$ and $\beta_{\mathrm{TEMP}j}$ are selected, the effect is specified by the composite of $\beta_{\mathrm{CON}j}$ and $\beta_{\mathrm{TEMP}j}$, and the effect varies over time. Prior distributions of $\beta_{\mathrm{CON}j}$ and $\beta_{\mathrm{TEMP}j}$ were Normal(0, 1000). $\mathrm{T}_{i,j}$ indicates whether each treatment j (deer density, nitrogen addition, logging, and their interactions) is conducted in plot i ($\mathrm{T}_{i,j} = 1$ if treatment j is conducted in a plot i and 0 otherwise). The maximum of j is 11, which is assumed from the treatments and their interactions. Specifically, four from high deer density, deer exclusion, nitrogen addition, and logging; four from the interaction of high deer density or deer exclusion and nitrogen addition or logging; one from the interaction of nitrogen addition and logging; and two from triple interaction of high deer density or deer exclusion and nitrogen addition and logging were included in the full model. For each of the 11 treatments, the constant and temporary effects were estimated, resulting in 22 coefficients of parameters estimated by the full model. Y_t indicates the number of years since the start of the survey, with the first year as 1, which is the number of years since 2005 for species richness. The species richness in the first year $S_{\mathrm{OBS}\,1,i}$ were determined as follows:

$$S_{\mathrm{OBS}\,1,i} \sim Poisson(\lambda_{1,i}) \tag{4}$$

$$\lambda_{1,i} \sim \mathrm{Uniform}(1, 100) \tag{5}$$

The prior distribution of $\lambda_{1,i}$ was a uniform distribution in the range of 1–100. The distribution was vague prior distribution since the minimum and maximum species richness in the plots during the study periods were 19 and 55, respectively. Vegetation cover and Simpson's diversity index were analyzed using the following equations.

$$V_{\mathrm{OBS}\,t,i} \sim Beta(a_{t,i},\, b_{t,i}) \tag{6}$$

$$a_{t,i} = \mu_{t,i}\theta \tag{7}$$

$$b_{t,i} = (1 - \mu_{t,i})\theta \tag{8}$$

$$\mathrm{logit}(\mu_{t,i}) = \mathrm{logit}(V_{\mathrm{EXP};\,t-1,\,i}) + \sum_{j=1}^{11}(\beta_{\mathrm{CON}j}\mathrm{T}_{i,j} + \beta_{\mathrm{TEMP}j}\mathrm{Y}_t\mathrm{T}_{i,j}) \tag{9}$$

$V_{\mathrm{OBS}\,t,i}$ is observed vegetation cover or Simpson's diversity index in

plot i in year t and assumed beta distribution. t in Eq. (6)–(9) is from 2007 to 2013. $V_{\mathrm{EXP}t-1,i}$ is the expectation of vegetation cover or Simpson's index in year t-1 in plot i from the model and is equal to $\frac{a_{t-1,\,i}}{a_{t-1,\,i}+b_{t-1,\,i}}$. Definition of $\beta_{\mathrm{CON}j}$, $\beta_{\mathrm{TEMP}j}$, $\mathrm{T}_{i,j}$ and Y_t in Eq. (9) are the same as in Eq. (3). The parameter θ is the precision parameter for beta distribution. The prior distribution of θ is half $-$Cauchy distribution (0, 2.5), which is a vague prior distribution. The vegetation cover or Simpson's diversity index in the first year $V_{\mathrm{OBS}\,1,i}$ was determined as follows:

$$V_{\mathrm{OBS}\,1,i} \sim Beta(a_{1,i},\, b_{1,i}) \tag{10}$$

$$a_{1,i} \sim half - Cauchy(0, 2.5) \tag{11}$$

$$b_{1,i} \sim half - Cauchy(0, 2.5) \tag{12}$$

In the analysis for vegetation cover of each life form, if the vegetation cover of each life form in a plot in a survey year was zero, a very small value of 10^{-4} was added to stabilize convergence. Because the vegetation survey was not conducted every year during the study period, there were missing values in the data set, and the time interval between the vegetation surveys was not constant. The state space model can estimate missing values and fit to time series data obtained at unequal intervals because the state at the point in a time corresponding to the missing data is compensated by the predictive distribution based on the data and the model (Clark and Bjørnstad, 2004). We introduced not applicable (NA) into $S_{\mathrm{OBS}\,2008,\,2010-2012;\,i}$ in Eq. (2) and $V_{\mathrm{OBS}\,2008,\,2010-2012;\,i}$ in Eq. (10) because the vegetation survey was not conducted in 2008 and from 2010 to 2012.

Model selections were performed based on the minimum leave-one-out cross-validation (LOO) index (Vehtari et al., 2017). LOO is a measure of a model's predictive accuracy based on log-likelihoods from posterior simulations of the parameter values to estimate point-wise predictive accuracy of the model to the data (Vehtari et al., 2017). LOO is similar to Akaike's Information Criterion (AIC), the Watanabe–Akaike information criterion (WAIC), and the Deviance Information Criterion (DIC); however, a robust index, rather than these indexes, makes no assumptions about the shape of the posterior distribution (Vehtari et al., 2017). The lower LOO model has better predictive accuracy than other models. The best models were selected from 256 candidate models. The set of candidate models was built with all possible combinations of parameters, but the interaction terms were considered only when the main effects were included in the model. For instance, when both β_{CON} and β_{TEMP} for the high deer density and only β_{CON} for the logging were included in a model, interaction term for high deer density plus logging included only β_{CON}. We estimated all the parameters using Markov chain Monte Carlo (MCMC) simulations with JAGS 4.3.0 (Plummer, 2003), runjags ver. 2.2.0–2 (Denwood, 2016), vegan ver. 2.6–4 (Oksanen et al., 2022), and loo ver. 2.5.1 (Vehtari et al., 2022) packages in R 4.1.3. (R Core Team, 2022) (Supplementary information S2). The convergence of the MCMC (three chains, ten thinning intervals, 1000 iterations) was evaluated by the autorun.jags function (100,000 samples to assess the convergence) in library runjags, based on Gelman–Rubin convergence diagnostic.

3. Results

3.1. Species richness

In total, 142 understory plant species were recorded in all plots during the study period.

In the low deer density site without anthropogenic disturbances, the species richness of each life form and all species in the plots did not change significantly during the survey period (Fig. S1). However, in the high deer density site, the species richness of ferns and vines constantly decreased, species richness of all species decreased, and the decline of all species was accelerated over time (Fig. 1, Table 1). The exclosure
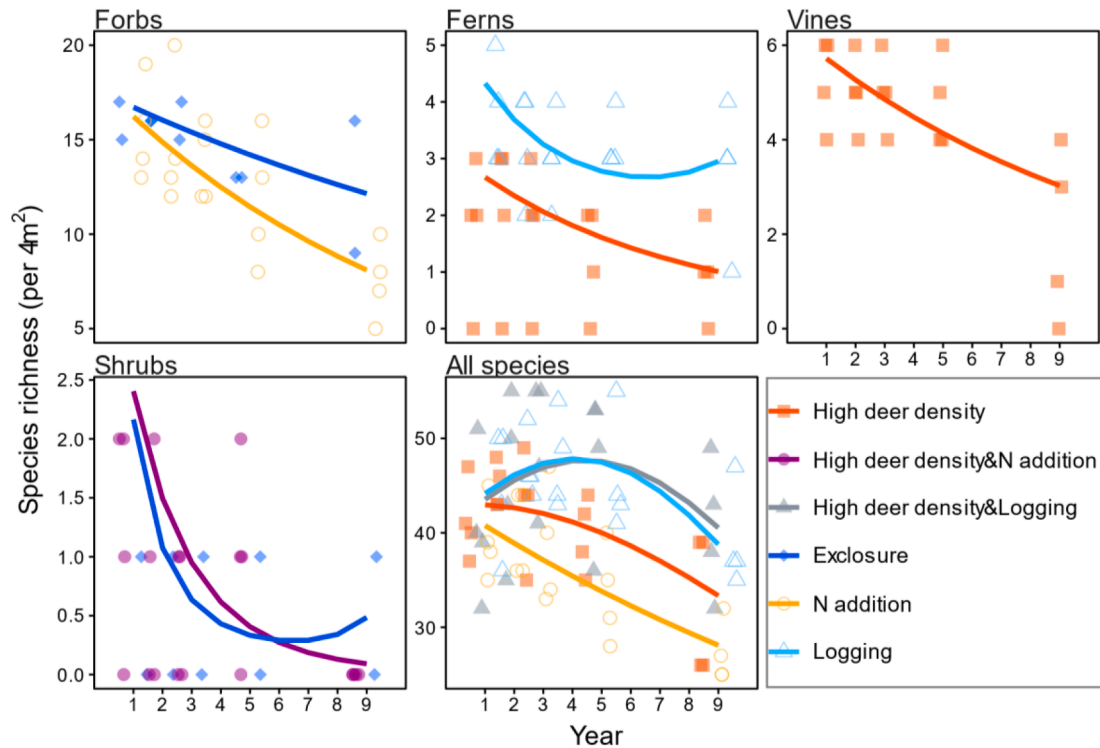
Fig. 1. Changes in observed values and predicted values from the best model for the species richness of each life form and all species of understory plants across years in deer density and anthropogenic disturbance treatments. X-axis indicates the elapsed years from starting the experiment. Lines represent the mean of the predicted values only for treatments selected in the best model and for which the estimated 95% confidence intervals for either or both the constant effect and the temporal effect do not contain zero (see Table 1). The points indicate the observed values in the plots, which are only the treatments that met the same criteria as the prediction lines. For instance, when the predicted lines of high deer density treatment are indicated, the observed values of plots in high deer density without anthropogenic disturbances are indicated as points. The fourth and sixth to eighth years were not surveyed.

negatively affected the species richness of forbs and shrubs. The species richness of forbs in the enclosure treatment without anthropogenic disturbances decreased from 16.0 ± 1.0 (SE) in the first year to 12.5 ± 3.5 (SE) in the last year.

The negative interaction of the high deer density and nitrogen addition was observed in the species richness of shrubs. The high deer density and nitrogen addition were included in the best model, and these factors had a negative effect on the species richness; however, the treatments were not statistically significant. The coefficient for the interaction of treatments was statistically significant and greater than that for the independent treatments. In contrast, the positive interaction of the high deer density and logging was observed in the species richness of all species, and the effect accelerated over time. The species richness of all species decreased with time in the high deer density site and responded concavely with time to the logging treatment. The species richness in the high deer density site with logging also responded concavely with time, and the slope was moderate compared to that of logging independently. The difference in the species richness in the high deer density site without anthropogenic disturbance and with logging became large over the years. The species richness in high deer density treatment was 41.2 ± 2.1 (SE) without anthropogenic disturbances, 40.5 ± 3.9 (SE) with logging in the first year, 32.5 ± 3.8 (SE) without anthropogenic disturbances, and 40.5 ± 3.6 (SE) with logging in the last year.

3.2. Vegetation cover and Simpson's index

The vegetation cover in the low deer density site without anthropogenic disturbances showed slight variation during the study period (Fig. S2). However, the high deer density negatively affected the cover of all life forms, except ferns and unpalatable species, and the negative

effect reduced over time (Fig. 2, Table 2). The decline of the cover of these life forms in the high deer density site was notable during the first five years of the study period. For instance, the cover of vines in the high deer density site without anthropogenic disturbances drastically decreased from 15.3 ± 2.6% (SE) in the third year to 3.0 ± 0.8% (SE) in the fifth year and then continued to decline modestly 0.9 ± 0.3% (SE) in the ninth year. The exclosure positively affected the vegetation cover of trees and all species; the positive effect on them accelerated over time. The cover of these life forms increased remarkably after the last half of the study period.

The effect of interaction between high deer density and nitrogen addition or logging on the vegetation cover was detected, and these interactions mostly varied over time. The high deer density site with nitrogen addition had a significant negative effect on the cover of forbs, and the decline of cover in the treatment was larger than that in the high deer density site without anthropogenic disturbances. In contrast, the interaction of high deer density and logging positively affected the cover of graminoids, unpalatable species, and shrubs. In particular, the cover of unpalatable species in the high deer density site with logging was higher than that in the high deer density site without anthropogenic disturbances, and the difference increased over time. The cover of unpalatable species in the high deer density site with logging increased remarkably from 6.3 ± 1.4% (SE) in the third year to 28.5 ± 5.9% (SE) in the ninth year (Fig. S2).

The interaction of the high deer density site and logging had a negative effect on the Simpson's diversity index of understory plants, and the index constantly decreased over time (Table S3, Fig. S3).

Table 1

Effects of the deer density, nitrogen addition, logging treatments, and their interactions on the species richness of forbs, ferns, trees, graminoids, unpalatable species, vines, shrubs, and all species in the survey plots. The values indicate the estimated coefficients in the best model. * indicates that a parameter was selected in the best model and that the 95% confidence interval of the estimated coefficients did not contain 0. - indicates that a parameter was not selected in the best model.

Life forms	High deer density		Exclosure		Nitrogen addition		Logging		H×N		H×L		Ex×N		Ex×L		N×L		H×N×L		Ex×N×L	
	Const	Temp	Const	Temp	Const	Temp	Const	Temp	Const	Temp	Const	Temp	Const	Temp	Const	Temp	Const	Temp	Const	Temp	Const	Temp
Forbs	–	–	−0.04*	–	−0.09*	–	–	–	–	–	0.11	–	−0.04	–	0.04	–	–	–	–	–	–	–
Ferns	−0.13*	–	−0.06	–	–	−0.01	−0.19*	0.03	–	–	0.11	–	–	–	0.04	–	–	0.00	–	–	–	–
Trees	–	−0.01	–	0.00	–	0.01	0.00	−0.01	–	0.00	–	0.00	–	0.01	–	0.00	–	0.00	–	0.00	–	0.00
Graminoids	–	0.00	–	−0.02	−0.12	0.01	0.00	–	–	0.01	–	–	–	0.00	–	–	0.02	–	–	–	–	–
Unpalatable species	–	−0.01	−0.06	–	−0.13	0.00	−0.13	0.02	–	−0.02	–	0.00	–	–	0.04	–	–	0.00	–	0.01	–	–
Vines	−0.08*	–	–	−0.02	−0.10	0.01	–	–	0.08	–	–	–	–	0.02	–	–	–	–	–	–	–	–
Shrubs	−0.09	–	−0.84*	0.13	−0.02	–	−0.23	0.03	−0.36*	–	0.07	–	0.13	–	0.59	−0.09	0.05	–	0.24	–	−0.13	–
All species	–	−0.01*	−0.04	–	−0.05*	–	0.06*	−0.02*	–	–	–	0.01*	0.03	–	0.02	–	−0.01	–	–	–	−0.04	–

H: High deer density. Ex: Exclosure. N: Nitrogen addition. L: Logging. Const: Constant effect of each treatment. Temp: Temporary effect of each treatment.

4. Discussion

4.1. Relationships between deer density and understory plants

In this study, the species richness of life forms and all species showed a nonlinear decrease or increase with deer density. All significant responses of the species richness of life forms and all species were negatively correlated to either the high deer density or the exclosure (Fig. 1, Table 1). Previous studies using natural deer density gradients in a forest also indicated that species richness of understory plants tended to be in nonlinear relationships with deer densities (Suzuki et al., 2008; Hegland et al., 2013).

The species richness and vegetation cover for vines and all species in the high deer density site were lower than those in the low deer density site (Figs. S1 and S2). These results indicated a positive correlation between species richness and abundance (Gotelli and Colwell, 2001). Due to selective deer browsing, palatable plant species should be dispersed in high deer-density areas (Rooney and Waller, 2003; Côté et al., 2004). At the same time, unselective deer browsing and coincidental physical damage caused by deer trampling (Pellerin et al., 2006) might lead to a stochastic disappearance of low-abundance species and species less tolerant of these deer influences. These direct negative influences by deer would decrease the species richness of understory plants in the high deer density site.

In the deer exclusion site, the species richness of forbs and shrubs decreased, and the vegetation cover of some life forms and all species increased, especially the vegetation cover of tree species (Fig. 2). Deer exclusion decreases species diversity by the indirect negative effect of competitive exclusion among plants (Holmes et al., 2008; Hegland et al., 2013; Faison et al., 2016). This study also suggests that the increasing cover of understory plants would accelerate competition among them. In particular, tree species can grow taller than the other life forms, such as forbs and shrubs, and would induce species loss of other life forms through deep shading.

The cover of woody species (trees, vines, and shrubs) decreased in the high deer density site, and in particular, the cover of trees linearly decreased with deer density (Fig. S2). Browsing pressure throughout the year caused the substantial decrease of woody species in high deer density sites, whereas the other life forms are under the snow cover or the aboveground organs wither in winter. Food resources for deer are relatively low in winter in Hokkaido, and woody species are the main food resource for deer (Yokoyama et al., 2000). These different responses among life forms may lead to species composition differences among deer densities. Our results imply that a mosaic of deer density across a landscape would contribute to promoting plant diversity (Royo et al., 2010).

4.2. Anthropogenic disturbances alter the effect of deer on understory plants

There are many interactions between deer density and anthropogenic disturbances (Figs. 1 and 2; Tables 1 and 2). These interactions indicate that the deer density and anthropogenic disturbances combined have a significantly different effect on understory plants compared to the sum of the individual treatments alone. The remarkable negative interaction of high deer density and nitrogen addition was detected for the species richness of shrubs and the vegetation cover of forbs, although the cover may be more ecologically relevant for shrubs than species richness because of the limited species diversity of shrubs in our study area. These results suggested that the high deer density and nitrogen addition individually had a negative effect on and the combination of the treatments had a greater negative effect than independent treatments. Nitrogen addition alone strongly negatively affected the species richness and cover of understory plants (Figs. 1 and 2; Tables 1 and 2). Nitrogen addition generally depresses species diversity and biomass of understory vegetation (Gilliam, 2006). Furthermore, sulfur addition also
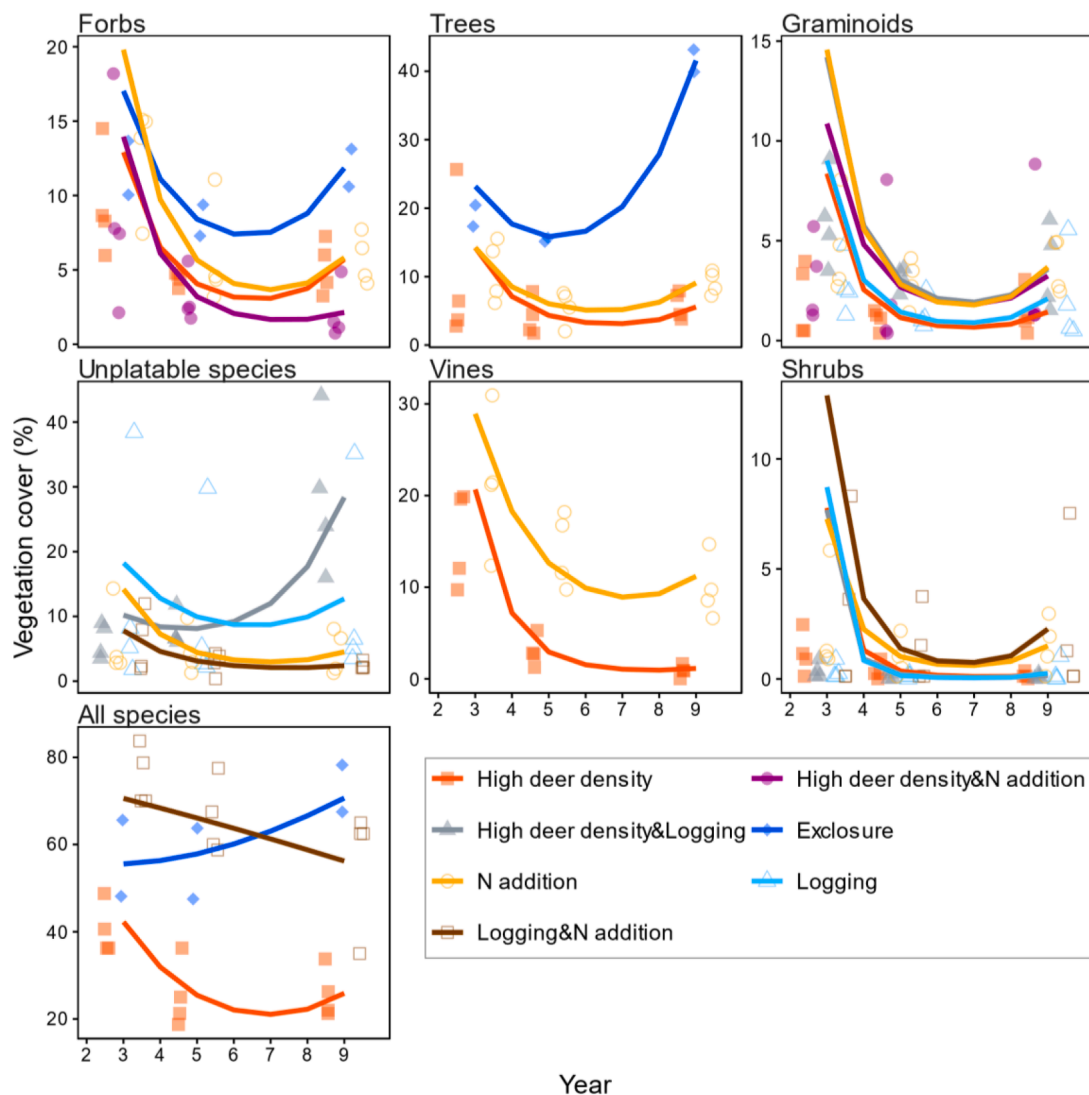
Fig. 2. Changes in observed values and predicted values from the best model for the vegetation cover of each life form and all species of understory plants across years in deer density and anthropogenic disturbance treatments. X-axis indicates the elapsed years from starting the experiment. Lines represent the mean of the predicted values only for treatments selected in the best model and for which the estimated 95% confidence intervals for either or both the constant effect and the temporal effect do not contain zero (see Table 2). The points indicate the observed values in the plots, which are only the treatments that met the same criteria as the prediction lines. For instance, when the predicted lines of high deer density treatment are indicated, the observed values of plots in high deer density without anthropogenic disturbances are indicated as points. The first two years, fourth, and sixth to eighth years were not surveyed.

decreases species richness and biomass due to decreased cation concentrations in soils (Jung et al., 2018). The ammonium sulfate used in this study contained nitrogen and sulfur; the sulfur may have influenced the plots that received nitrogen. The negative effect of nitrogen addition in our study may accelerate the negative effect of high deer density on these species' richness and vegetation cover due to the reduction in the resistance of understory plants to high deer density.

The interaction of high deer density and logging had a remarkable positive effect on the species richness of all species (Fig. 1, Table 1). The species richness in the high deer density site with logging was similar to control plots in the low deer density site without anthropogenic disturbances (Fig. S1). These results indicated that logging would moderate the negative effect of high deer density on species richness. This moderation effect is caused by increasing the tolerance of plants to herbivores under high resource availability for plants (Rosenthal and Kotanen, 1994; Wise and Abrahamson, 2007; Cronin et al., 2010) and accelerating the recruitment of early successional species under high light availability (e.g. Brunet et al., 1996).

In the high deer density with logging treatment, the cover of unpalatable species increased, and the cover was approximately nine times higher than that in the high deer density site without anthropogenic disturbances in the last survey year (3.2% without anthropogenic disturbances and 28.5% with logging, Fig. S2). These results were consistent with previous studies in which the cover of unpalatable species increased with deer density in clear-cut and thinning forest stands (Horsley et al., 2003; Suzuki et al., 2021); the negative effect of high deer density on the other life forms should relax competition between the unpalatable species and the other life forms. The increasing cover of unpalatable species may lead to a decreased Simpson's diversity index in the treatment. The different responses among each life form to the high deer density site with nitrogen addition or logging can further alter the species composition in the high deer density site.

Table 2

Effects of the deer density, nitrogen addition, logging, and their interactions on the vegetation cover of forbs, ferns, trees, graminoids, unpalatable species, vines, shrubs, and all species in the survey plots. The values indicate the estimated coefficients in the best model. * indicates that a parameter was selected in the best model and that the 95% confidence interval of the estimated coefficients did not contain 0. - indicates that a parameter was not selected in the best model.

Life forms	High deer density		Exclosure		Nitrogen addition		Logging		H × N		H × L		Ex × N		Ex × L		N × L		H × N × L		Ex × N × L	
	Const	Temp	Const	Temp	Const	Temp	Const	Temp	Const	Temp	Const	Temp	Const	Temp	Const	Temp	Const	Temp	Const	Temp	Const	Temp
Forbs	-0.97*	0.24*	-0.61*	0.16*	-1.07*	0.24*	–	–	0.88*	-0.24*	–	–	0.48	-0.13	–	–	–	–	–	–	–	–
Ferns	-0.04	–	–	–	-0.04	–	-0.03	0.01	-0.10	-0.10	-0.08	–	–	–	–	–	-0.04	-0.02	-0.17	–	–	–
Trees	-1.01*	0.24*	-0.51	0.19*	-0.76*	0.19*	–	-0.05	0.41	-0.39*	–	–	0.78	-0.23	–	-0.01	1.01	-0.28	-1.29	0.02	0.00	–
Graminoids	-1.52*	0.35*	–	–	-1.31*	0.31*	-1.50*	0.36*	1.66*	–	1.81*	-0.43*	–	–	–	–	1.00*	-0.26*	-0.21	0.35	–	–
Unpalatable species	0.00	–	–	–	-0.97*	0.22*	-0.69*	0.17*	0.06	-0.18	0.30*	–	–	–	–	–	2.77*	-0.64*	-2.22	–	–	–
Vines	-1.54*	0.29*	–	0.02	-0.76*	0.16*	–	–	0.89	–	–	–	–	0.00	–	–	–	–	–	0.50	–	–
Shrubs	-2.23*	0.46*	–	0.03	-1.50*	0.36*	-3.14*	0.73*	1.63	-0.44	2.73*	-0.62*	–	-0.03	–	-0.04	–	–	0.09	-0.03	–	–
All species	-0.59*	0.13*	–	0.03*	-0.01	–	0.02	–	-0.03	–	0.06	–	–	–	–	–	-0.12*	–	–	–	–	–

H: High deer density. Ex: Exclosure. N: Nitrogen addition. L: Logging. Const: Constant effect of each treatment. Temp: Temporary effect of each treatment.

4.3. Time-dependent effect of deer density and anthropogenic disturbances

In our results, the negative effect of high deer density on the species richness of all species increased over time (Table 1). On the other hand, the negative effect of the high deer density on the vegetation cover of most of the life forms and all species was substantial in the initial study period and became small over time (Table 2). These differences in time-series responses to the high deer density in the species richness and vegetation cover may be caused by the following mechanisms. Individual plant size rapidly declines in the high deer density site, but if the size is smaller than the height at which deer can easily forage, the change is relatively small. At this point, the individual plants are small but have not died, and local extinction of the species has not yet occurred. However, repeated foraging will lead to the disappearance of the individual plant, eventually reducing the species richness in an area through the loss of a local population. These mechanisms qualitatively predicted that increasing deer densities would first decrease the size of plant individuals and their population, especially palatable species, and then cause plant community changes (Mysterud, 2006). Our results provided quantitative support for this prediction.

The significant positive effects of exclosure on vegetation cover of forbs, trees, and all species accelerated over time. These results suggested that the freed-from-deer effect may have allowed the understory plants to retain and grow more plant biomass, resulting in an accelerated increase in individuals and population size over the years.

The logging effect on the species richness of all species temporally changed. There was a convex trend that was high in the middle of the study period. The canopy closing, subsequent logging treatment, and sapling growth after the treatment would lead to increased light resource for the forest floor for several years and then darken the forest floor. These changes in the light resource should promote the recruitment of plants such as pioneer species over several years and cause the recruitment species to disappear. The positive interaction between the high deer density and logging on the species richness of all species accelerated over time. Species declines due to high deer densities accelerated over time but logging treatments mitigated these declines. Therefore, the difference between species richness in the high deer density site and high deer density with logging may have increased over the years.

4.4. Management implications

Maintaining diversity in a region is one of the fundamental goals of ecosystem management (Christensen et al., 1996). Relationships between deer density and vegetation have often been discussed in ecosystem management aimed at managing deer effects on vegetation (Rooney and Waller, 2003; Côté et al., 2004), and a mosaic of deer densities across a landscape would maintain much of the plant diversity (Royo et al., 2010). This study showed that anthropogenic disturbances should also be considered as a crucial factor for managing deer effects on vegetation because anthropogenic disturbances can alter the effects of deer on vegetation. Nitrogen deposition may accelerate the negative effect of deer on vegetation and diversity. Nevertheless, it is not easy to eliminate the nitrogen load in ecosystem management. Furthermore, logging accelerated the changes in species composition of understory plants under high deer densities owing to increases in the biomass of unpalatable species, although it can mitigate the effect of deer on species richness or abundance of the understory vegetation. To maintain the species composition of understory plants in a region, extensive logging should be prevented in regions with high deer density.

In our study, understory plants were changed in the high or zero deer density treatments, anthropogenic disturbances, and their interaction. Many of these effects varied over the years after the experiment started. Some of the changes in the understory vegetation were intense in the beginning, and the trend eased with time, while some of the effects

became apparent over time. These results suggested that time was a crucial factor in the relationships between deer density and plant communities in forests. Therefore, it would also be incorrect to make future predictions of deer effects based on the results of short-term vegetation monitoring or deer density manipulation experiments. Long-term research is indispensable in revealing the relationships between deer density and vegetation.

The relationships between deer density and plant communities are altered by environmental characteristics in a region, such as plant productivity, flora, and browsing history (Hester et al., 2000; Côté et al., 2004). To establish a greater generality regarding the deer effects under anthropogenic disturbances from this study and apply it to ecosystem management, more long-term field experiments that set multiple levels of deer density with anthropogenic disturbances starting from low deer density in other regions are needed.

CRediT authorship contribution statement

HinoTakafumi: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Validation, Writing – original draft, writing – review & editing. **Naoki Agetsuma:** Conceptualization, Funding acquisition, Methodology, Resources, Validation, writing – review & editing. **Tsutom Hiura:** Conceptualization, Funding acquisition, Methodology, Resources, Validation, writing – review & editing.

Declaration of Competing Interest

Data availability

The data used for the analysis can be found online as supplementary materials.

Acknowledgments

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.120928.

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