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Long-Term Deer Exclusion Releases Dwarf Bamboo, Reducing Vascular Plant Diversity

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ABSTRACT

Aims: Overgrazing by excessive deer populations harms native plant communities across most north temperate and boreal regions. In regions where deer impact is particularly severe, fencing is sometimes employed as a conservation measure to safeguard rare and threatened species and ecosystems. Here we examine how forest vascular plant communities have been affected by 21 years of sika deer exclusion by fencing of a 900 ha area.

Location: Nikko National Park, Tochigi prefecture, Japan.

Methods: We surveyed vascular plant cover in 240 plots and measured forest density on both sides of the fence in stands dominated by larch (*Larix kaempferi*) and oak (*Quercus crispula*).

Results: Vascular plant species richness was found to be lower in forest areas protected by the fence. At the same time, dwarf bamboo, often the most abundant understory component in Japanese open forests, was taller and denser inside the fence where deer had been excluded. In addition, the lack of natural tree regeneration inside the fence, likely due to strong dwarf bamboo competition, was also notable. This suggests that deer exclusion has benefitted dwarf bamboo while inhibiting the competition of other species, thereby lowering vascular plant richness. Vascular plant communities outside the fence instead seem to be strongly shaped by abundant sika deer; several species found there are known to be unpalatable or grazing tolerant, and there were few tree seedlings.

Conclusion: These results show that fencing to protect forest flora against overgrazing may have unintended consequences where there is a risk that competitive species can dominate understory plant communities. Instead of fencing, improved game management to maintain moderate deer populations may be a better strategy for large-scale conservation of forest flora and for promoting natural tree regeneration.

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1 | Introduction

Overabundant ungulate populations are altering the composition and structure of forest vegetation across most north temperate and boreal regions (Rooney and Waller 2003; Miyaki and Kaji 2009; Kishimoto et al. 2010; Petersson, Bergstedt, et al. 2019; Reed et al. 2022). Intense deer grazing can even lead to landslides by removing understory vegetation and loosening root systems' hold on soil (Wakahara et al. 2008). Deer's selective foraging also affects floral diversity by changing competitive relations among vascular plant species (Côté et al. 2004). Plant community impacts of deer overgrazing can be long lasting or even irreversible when species are eliminated from the seed bank (DiTommaso et al. 2014; Nuttle et al. 2014; Tamura 2016).

The area of Japan inhibited by sika deer (*Cervus nippon*) has increased from 25% to 70% between 1978 and 2018, and the estimated deer population in Japan outside of Hokkaido has grown from 250,000 in 1989 to 2,180,000 in 2020 (MOE 2021; Anonymus 2022). Several factors are likely behind this rapid growth. When the Japanese gray wolf (*Canis lupus hodophilax*) went extinct in 1905 because of hunting, sika deer's only natural predator disappeared (Walker 2005). During that time and throughout the first half of the 20th century, sika deer numbers in Japan were particularly low (Uno et al. 2022). In an attempt to increase the deer population, hunting female sika deer was banned from 1963 (Oka et al. 2022). At the same time, rapid urbanization led to extensive abandoned croplands and orchards which provided newly suitable deer habitat. When the doe-hunting ban was lifted nationwide in 2007, deer populations had reached levels causing significant damage to agriculture and forestry (Oka et al. 2022). More recently, climate change has made heavy snowfall and periodically occurring extremely low winter temperatures less common, resulting in increased fawn survival, sparking further population expansion (Ueno et al. 2018).

In temperate-forested areas of Japan, sika deer's staple food is several species of dwarf bamboo of the genera *Neosasamorpha*, *Pleioblastus*, *Pseudosasa*, *Sasa*, and *Sasamorpha* (Campos-Arceiz and Takatsuki 2005; Murata et al. 2009; Kobayashi 2015; Kagamiuchi and Takatsuki 2020; Takatsuki 2022). They are widely distributed in the temperate zone of eastern Asia, where they often form the understory of open to semi-open forests (Kobayashi 2015). Following disturbances, for example, forest cutting and fire, dwarf bamboo can form dense clonal patches covering large areas (Oshima 1961). If undisturbed, pure stands of dwarf bamboo can persist indefinitely, especially in open forests and alpine environments (Oshima 1961). Here, they dominate understory plant communities and may even exclude other understory species (Fukamachi et al. 1996; Itô and Hino 2005; Kudo et al. 2011; Černý et al. 2013). In areas with winter snow cover, sika deer continue feeding on dwarf bamboo as long as it remains accessible. However, when snow gets too deep (about 100 cm), sika deer increasingly forage on bark, damaging and sometimes killing trees (Minamino and Akashi 2011). During summer and in areas without snow cover, the foraging habits of sika deer vary more. While summer bark stripping has also been observed (Yokoyama et al. 1996), their diet often includes a variety of understory plants in addition to dwarf bamboo, as well as twigs and tree leaves (Yokoyama et al. 1996; Miyaki and Kaji 2004; Iijima and Nagaike 2015). The dense populations of sika deer today have led to reported changes in plant communities across different regions of Japan (Yokoyama and Shibata 1998; Kato and Okuyama 2004; Murata et al. 2009; Uno et al. 2019). Concerns have also been raised regarding the potential long-term impacts of intense deer grazing, which could have profound and irreversible effects on the flora (Takatsuki 2009).

Forest understory communities are highly influenced by site conditions and the characteristics of the overstory trees (Barbier et al. 2008; Petersson, Holmström, et al. 2019). Overstory tree species and tree densities impact available light transmitted to forest-floor communities (Lariviere et al. 2021; Petersson et al. 2021). Litter from trees forms the soil layer, which in turn affects nutrient availability and soil moisture, further influencing understory community composition (Xiong and Nilsson 1999).

In this study, we aim to examine the combined effects of sika deer grazing, overstory tree species, and stand densities in an area of Nikko National Park, Tochigi Prefecture, Japan. For the first time, in this article we examine how sika deer exclusion affects understory vascular plant communities over a large area consisting of different forest types. By comparing the vegetation within and outside a ~900 ha deer exclosure that has been fenced for 21 years, along with information on tree species and stand density, we seek to address the following research questions:

i. How is the forest vascular plant flora affected by sika deer exclusion?
ii. How has deer exclusion affected species richness and community composition of forest vascular plants?
iii. How do overstory tree species and forest density affect vascular plant species richness inside and outside the fence?

2 | Methods

2.1 | Study Area

The study was conducted in 2022 in Nikko National Park in Tochigi Prefecture, Japan (36.77° N, 139.43° E, elevation 1380–1470 m) in a broad high-altitude valley in a mountainous area (Figure 1). The average temperature in this area was 7.1°C, and precipitation averaged at 2102 mm between 2002 and 2011 (Tadakara et al. 2014). The bedrock is siliceous, primarily composed of various forms of granite and rhyolite (Yamamoto et al. 2000). It is covered by haplic andosol and podzol (Oyama et al. 1969; Yamamoto et al. 2000). Lake Chuzenji and Mount Nantai are prominent landmarks within this area, which is a popular destination for tourists because of the scenic landscape of forests, lakes, waterfalls, wetlands, and mountains. Above Lake Chuzenji lies the Senjogahara plateau and marshlands, formed by an eruption of Mount Nantai about 20,000 years ago.

The Senjogahara marshland flora includes an abundant cover of *Spiraea salicifolia*. The marshland is shifting from wetland to forest due to both natural succession and previous artificial drainage. Hence, the border zone between the previously drained marshland is dominated by semi-open stands of the early-successional tree species *Malus toringo*. Most forest around Senjogahara consists of one-layered stands of Japanese larch (*Larix kaempferi*, below referred to as "larch") and Mongolian oak (*Quercus crispula*, syn. *Quercus mongolica* var. *crispula*, below called "oak"). The stands probably grew after large areas of old forests were harvested after World War II. Today, only a few remnant larch and oak trees from an older tree generation remain among the otherwise even-aged stands (Figure 2). Other commonly occurring tree species in the area are *Abies homolepis*, *A. firma*, *Acer* spp., *Betula* spp., *Fagus crenata*, *Fraxinus mandshurica*, *Kalopanax septemlobus* subsp. *septemlobus*, *Pterocarya rhoifolia*, *Sambucus racemosa* subsp. *sieboldiana*, and *Ulmus davidiana var. japonica*.

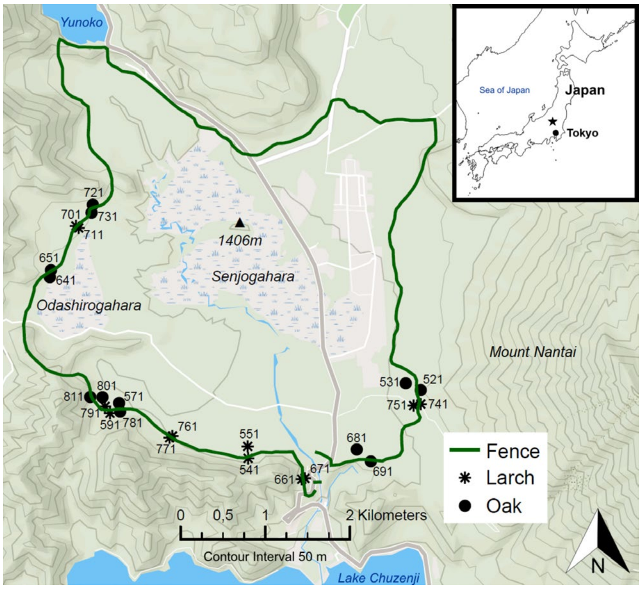

FIGURE 1 | Study area is situated in Nikko National Park (★), Japan. Pairs of plots were placed on each side of the fence in 12 stands of larch and oak. Three-digit stand numbers can be used for comparing vascular plant species richness and cover in different stands (see Appendix S2, Figure S1). *Source:* OpenStreetMap.

2.2 | Deer Fence

To protect the rare flora of Senjogahara marshland and to promote forest regeneration in the surrounding areas, a fence was installed in 2001 (Bansho and Amemiya 2010). The fence encloses an area of 900 ha, including Senjogahara marshland, the smaller Odashirogahara marshland, and contiguous areas of forest (Figure 1). The fence aimed to completely exclude sika deer from the inside area. However, especially during winter, deer occasionally get inside the fence (Bansho and Amemiya 2010). After targeted efforts to remove intruding deer started in 2005, the number of deer present inside the fence has decreased (Bansho and Amemiya 2010). However, deer are still occasionally seen inside the fence (personal observations), but they are actively removed during winter as harmful wildlife control, and consequently, deer herbivory is low.

2.3 | Stand Selection

We identified 24 forest stands suitable for the study, 12 each of larch and oak, in the southern portion of the fenced area (Figure 1). The stands were selected so that a replicate with the same dominant tree species was situated as close as possible on the opposite side of the fence. If no stand replicate could be found within 300 m, the stand was not used. We also ensured that the selected forest stand pairs were located on similar ecosites, with comparable tree ages, stand densities, topography, and soil properties.

Only larch or oak stands in the south-western area were included in the study. Some of the eastern and western parts of the fenced area are dominated by other deciduous trees, so they could not be used. The northeastern section of the fence is dominated by larch and oak stands; however, we could not see any signs of deer grazing outside the fence in this area. The reason why deer were not foraging here is unclear. It is possibly due to the steep alluvial fan topography and the Sakasa River and Misawa gorge, which may restrict access to the area outside the fence.

FIGURE 2 | Deer fence in an oak-dominated area. The area to the left is inside the fence, here dominated by dwarf bamboo. To the right, the area outside the fence has an understory dominated by the unpalatable *Aster leiophyllus* var. *leiophyllus*. Near the center of the picture, an older remnant oak can be seen. The picture was taken in the southeast part of the fenced area (Figure 1). Photo: Lisa Petersson.

2.4 | Plot Inventory

The vascular plant inventory was conducted between 21 July and 20 September 2022. Ten circular plots per stand were established, for a total of 240 circular plots (120 inside and 120 outside the fence). Each plot covered an area of $10\,\text{m}^2$ and was centered on either a larch or oak tree. Because the plots were established around trees (rather than in the spaces between them), the results primarily reflect the vegetation directly beneath the canopies rather than other nontree areas of the stand. Starting from the stand reference tree in the stand center, nine other live trees >10 cm in diameter at 130 cm above ground were selected as additional plot centers. These were chosen so that two or three plots were located toward each cardinal direction (Figure 3). The minimum distance between plot center trees was 5 m, and plots were placed at the first possible acceptable position according to cardinal direction and minimum distance between plot centers. Occasionally, solitary or small groups of trees such as *Abies*, *Acer*, *Betula*, or *Kalopanax* were found inside the stands. To avoid potential influences from canopy trees other than larch and oak, plots were only placed a minimum of 10 m from trees of other species with stem diameter >30 cm.

In every plot, the height of understory dwarf bamboo was determined from the average of the measured height from five random points per plot. We also measured the diameters and recorded the species of all surrounding trees within a 7-m radius from the plot center. Additionally, we noted the compass bearing and distance to the plot center for each measured tree. All species of understory vascular plants, including trees and shrubs <1.3 m tall, were recorded. The cover of the different species was measured using a modified version of Braun–Blanquet's cover classes with seven different cover categories (Table 1). In this modified version, there was more emphasis on differences in cover between small cover classes. Note that when adding different species growing nested together in the same plot, total cover may exceed 100%.

Certain plants could not be identified to species and were instead recorded at the genus or family level and occasionally at higher taxonomic or functional group levels (e.g., fern, herb, vine; see the species list in, Appendix S1). For convenience, we grouped together all species of dwarf bamboos *Sasa kurilensis*, *S. nipponica*, *S. palmata*, and *Sasamorpha borealis* that often formed extensive areas where different species grew intermixed. These were collectively recorded as the *Sasa* spp. group in the species list. Since we rarely encountered flowering specimens of other graminoids, it was not possible to differentiate between species, and they had to be pooled as *Carex*, *Juncus*, *Luzula*, and Poaceae. Other nonflowering plants recorded at the genus level included *Rosa*, *Rubus*, and *Viola* (excluding *Viola tokubuchiana* var. *tokubuchiana*). Additionally, due to challenges in identifying small tree seedlings in the field, we recorded all species of *Acer* together except for *A. rufinerve*, which was recorded separately. Trees of *Betula platyphylla var. japonica* and *B. ermanii* were grouped as *Betula*, and all trees and shrubs of *Euonymus* were grouped together, namely *E. alatus*, *E. macropterus*, and *E. sieboldianus*, while treating the vine *E. fortunei* as a separate entity. Nomenclature follows the Wamei checklist version 1.10 (Yamanouchi et al. 2022).

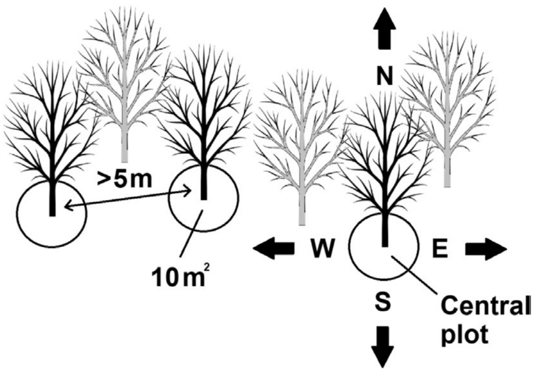

FIGURE 3 | Plot selection layout. First, a stand reference tree was identified in the center of each stand. From the stand reference tree, two or three additional plots were selected in each of four cardinal directions, for a total of 10 plots per stand. All plots were established with a minimum distance of 5 m between plot-center trees.

2.5 | Tree Influence Index

To examine how vascular plant species richness may be affected by different stand densities, we computed a tree influence index (TI). The index incorporates tree diameter, cardinal direction, and distance from the sample plot center to surrounding trees as

$$\mathrm{TI} = \sum_i \frac{\left(\left(-\cos\left(\left(\theta_i - 180\right)/180\right) + 1\right) \times 0.4 + 0.2\right)\left(C_i/2\pi\right)^2}{D_i^2}$$

where Θ_i is the compass direction from the plot center to the tree, C_i is the circumference of the tree and D_i is the distance from the plot center tree. All trees and shrubs >1.3 m height (i) within a distance of 7 m (extended to 10 m when less than four trees occurred) from the plot center were included in the calculation of the TI index. This index is a sum of the total tree basal area ($C_i^2/4\pi$) in the vicinity of the plot center weighted by two factors. The first factor is distance (D_i) to the tree whose influence we treat as diminishing with the square of distance, analogous to many physical laws. The second is the compass bearing (Θ) to the tree. The term

TABLE 1 | Braun–Blanquet classes used for measuring vascular plant cover.

Braun–Blanquet scale	Cover range (%)	Used in calculations (%)
r	< 0.1	0.05
+	> 0.1–1	0.55
1	> 1–5	3
2	> 5–25	15
3	> 25–50	37.5
4	> 50–75	62.5
5	> 75–100	87.5 or 100[a]

[a] For dwarf bamboo, which was highly abundant, 100% cover was used for Category 5. Using either number led to similar results.

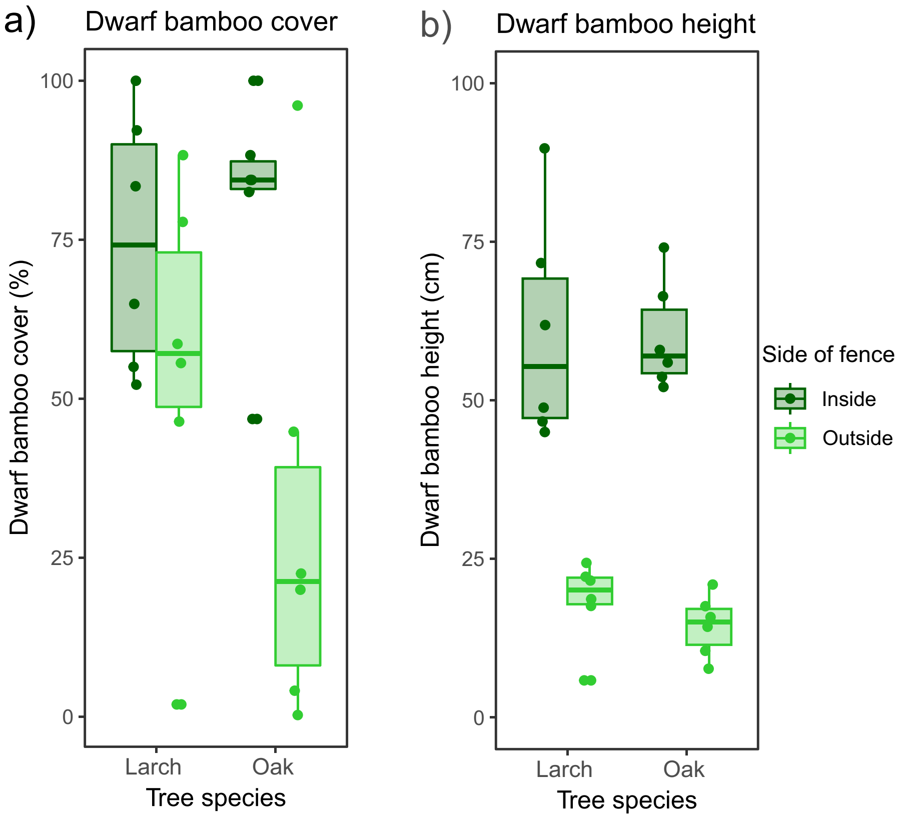

FIGURE 4 | Stand average (a) cover and (b) height of dwarf bamboo measured in 12 larch and 12 oak stands inside and outside the deer fence. The boxes denote the interquartile range (between the 25th and 75th percentiles), with the center line marking the median (50th percentile). Whiskers extend to data points within 1.5 times the interquartile range.

$((-cos((\theta_i-180)/180)+1)\times 0.4+0.2)$ transforms this bearing into a factor that scales from 1 for a tree due south of the center to 0.2 for a tree due north, and 0.6 for trees due east or west. This transformation aims to represent the relative contribution of trees in different directions to shading. The TI values ranged from 25.67 to 916.64 across the various plots, with an average of 291.51 ± SD 162.11. Prior to performing regression analyses, the values were normalized through scaling by centering using the scale() function in R.

3 | Statistical Methods

3.1 | Dwarf Bamboo and Vascular Plant Cover and Height

Differences in dwarf bamboo cover and height, and the total cover of vascular plants inside and outside the fence were compared at the stand level using paired *t*-tests. Stands near one another, but on opposite sides of the fence (Figure 1) were specified as pairs in the analysis. In the first test, all stands were tested together. In the second test, the same variables were tested separately for larch and oak stands.

3.2 | Species Richness Models

Plot-level species richness was tested using a generalized linear mixed model (GLMM) with a Poisson distribution using the R package "lme4" (Kuznetsova et al. 2017). To account for the hierarchical structure of the data, two random effects were specified in the model. First, since each stand consisted of 10 plots, the variable stand was also specified as a random effect in the analysis. Second, considering the proximity between stands on opposite sides of the fence, paired stands were specified as a random effect.

Given the strong correlation between dwarf bamboo height and the side of the fence (i.e., dwarf bamboo was consistently taller inside the fence than outside; Figure 4b), separate GLMM models were constructed to assess both the effects of fencing and dwarf bamboo height and cover. The first model aimed to evaluate the influence of three variables: side of fence (binary), canopy tree species (binary), and tree influence index (TI—continuous). In the first full model, species richness was examined for interactions between tree species, fence side (inside or outside), and TI. However, as there were no interactions between side of fence and tree species ($p=0.127$), side of fence and TI ($p=0.094$) tree species and TI ($p=0.975$), nor among all three variables together ($p=0.235$), these interaction terms were subsequently excluded from the final model.

In the second model, we instead aimed to test dwarf bamboo height as an explanatory variable for species richness together with the other variables. Just as in the previous model, there were no interactions between variable pairs: dwarf bamboo height and tree species ($p=0.948$), dwarf bamboo height and TI ($p=0.704$), and tree species and TI ($p=0.924$), nor among all three variables together ($p=0.216$), so the model was run without these interaction terms. Marginal and conditional R^2 were

TABLE 2 | Differences in dwarf bamboo cover, dwarf bamboo height, and total vascular plant cover inside and outside the fence.

Variables tested	Side of fence (inside vs. outside): mean diff.	CI (95%)	*t*	df	*p*
Dwarf bamboo cover (%)					
All stands	34.82	10.96–58.68	3.21	11	0.0083
Larch	19.85	−20.60 to 60.29	1.26	5	0.2628
Oak	49.79	15.34–84.24	3.72	5	0.0138
Dwarf bamboo height (cm)					
All stands	43.91	34.72–53.09	10.52	11	< 0.0001
Larch	42.25	21.56–62.95	5.25	5	0.0033
Oak	45.57	37.16–53.97	13.94	5	< 0.0001
Total vascular plant cover (%)					
All stands	21.60	−10.72 to 53.92	1.47	11	0.1694
Larch	−13.81	−45.99–18.35	−1.10	5	0.3198
Oak	57.01	13.20–100.82	3.35	5	0.0204

Note: In the analysis, stand-level averages are tested using paired *t*-tests.

calculated using the r2_nakagawa() function from the R package "performance" (Lüdecke et al. 2021). The final models were checked for overdispersion.

The different models were compared using the Akaike information criterion (AIC; Appendix S3). In addition to the full models, the two models with the lowest AIC values were selected: one using side of fence as a predictor and the other using dwarf bamboo height as a predictor.

3.3 | Multivariate Analysis

Species community composition was analyzed with nonmetric multidimensional scaling (NMDS) in the R package "vegan" (Oksanen et al. 2022), using the Bray–Curtis dissimilarity index. Average cover of the different species at the stand level was used for the analysis. Prior to testing, species only occurring in one plot of the entire survey were removed from the dataset. In total, 31 species were recorded only once, leaving 86 species for the analysis.

Using a two-dimensional solution for the NMDS resulted in a stress value of 0.196. To examine the stands' and species' associations, we made scatterplots of the first two NMDS axes of the vegetation plots, indicating paired stands to compare community similarity across the fence. To test for differences in community composition across the fence and between canopy tree species, permutational multivariate analysis of variance (PERMANOVA) was conducted using the R function adonis2() (Oksanen et al. 2022), using 999 permutations. Since there was no significant interaction between the side of the fence and tree species ($p = 0.495$), the final model was run without the interaction term.

To assess whether deer exclusion or physical proximity between paired plots had a greater impact on understory vegetation community composition, we compared the distances among the NMDS site scores. As a measure of deer impacts, we used the distance between paired plots on opposite sides of the fence, separately for plots with oak and larch canopies. For a background measure of community variability among plots on a particular side of the fence, we computed the mean distance from each plot to all other inside or outside plots in NMDS space for oak and larch canopy plots. Differences in the mean NMDS distances among the computed inside, across, and outside fence plots were tested using independent sample *t*-tests.

Finally, we used a species indicator analysis (multilevel pattern analysis) to examine if some species were more associated with one side of the fence. The analysis was conducted using the multipatt() function of the R package "Indicspecies" (De Caceres and Legendre 2009). Species (excluding singletons) were analyzed for group associations (side of fence) with 9999 iterations.

4 | Results

4.1 | Dwarf Bamboo Cover and Height

Dwarf bamboo had significantly higher cover inside the fence compared to outside (Table 2). Inside the fence, cover averaged 77.8% ± 18.4% (all values reported as mean ± SD) compared to 43.0% ± 33.6% outside the fence (Figure 4a). When testing dwarf bamboo cover separately for larch stands, there was no significant difference between inside (74.6% ± 20.1%) and outside (54.8% ± 30.1%) the fence (Table 2). However, in oak stands, the cover inside the fence (81.1% ± 17.9%) was significantly greater than that outside (31.3% ± 35.5%; Table 2; Figure 4a).

Dwarf bamboo was also significantly taller inside the fence (60.3 ± 15.0 cm) compared to outside (16.4 ± 6.7 cm; Table 2; Figure 4b). This difference remained consistent when testing

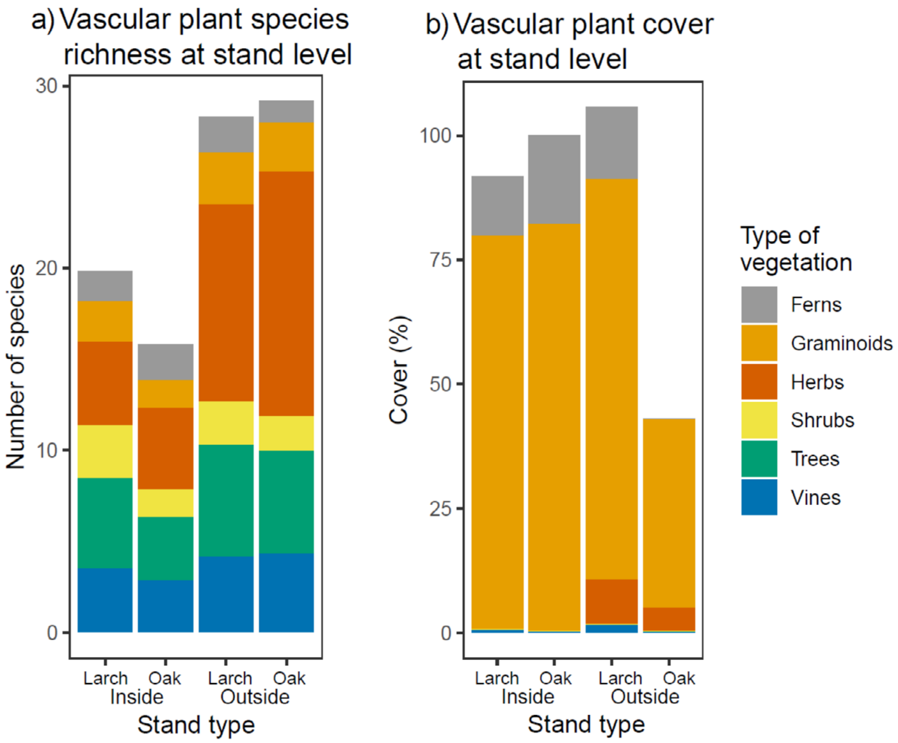

FIGURE 5 | (a) Species richness and (b) cover of different categories of understory vegetation inside and outside the deer fence of 12 larch and 12 oak-dominated stands. Species richness estimates are conservative because graminoids and some tree and shrub species were only identified at genus level.

larch (60.6 ± 17.6 cm inside; 18.4 ± 6.6 cm outside) and oak stands separately (60.0 ± 8.5 cm inside; 14.4 ± 4.8 cm outside; Table 2).

4.2 | Species Richness and Cover of Different Species Groups

A total of 117 species or species groups were recorded in the plots: 11 ferns, 5 graminoids, 60 herbs, 13 shrubs, 17 trees, and 11 vines (Appendix S1: Table S1). However, graminoids (grasses and sedges, including dwarf bamboos) were not identified to species level, and some species of trees and shrubs were recorded together (see Methods section) so the total number of species is conservatively estimated. The total number of plant species was 82 inside the fence and 92 outside. Species richness averaged 5.0 ± 3.2 species per plot and 17.8 ± 8.4 species per stand inside the fence and 10.4 ± 3.5 species per plot and 28.6 ± 5.1 species per stand outside the fence (Figure 5a).

Total cover of vascular plants was highest in larch stands outside the fence and lowest in oak stands outside the fence (Figure 5b). However, total vascular plant cover did not differ significantly when comparing all stands inside (95.9% ± 31.9%) and outside (74.3% ± 50.0%) the fence (Table 2). When larch-dominated stands on different sides of the fence were compared, there was no significant difference in total cover, but for oak stands, total cover was significantly different across the fence (Table 2).

For stand-wise compilation of species richness and species cover, see Appendix S2 and Figure S1a,b.

4.3 | Fencing, Dwarf Bamboo, and Forest-Density Effects on Species Richness

The GLMM analysis showed that plot-level species richness was higher outside the fence than inside (Figure 6; Table 3: Models 1 and 2). When dwarf bamboo height was used as a predictor instead of fencing, species richness responded negatively to taller dwarf bamboo (Figure 6, Table 3: Models 3 and 4). Using dwarf bamboo height as a predictor instead of the side of the fence also improved the model by lowering the AIC value. Adding the influence of forest density (as calculated by tree influence index—TI) led to further improvement of the models, as indicated by a lower AIC (see Appendix S3). The significant p value for TI indicates a negative effect on species richness when forest density increases. The lower AIC values (1164.0 and 1149.4) in Models 2 and 4 show that including TI and excluding tree species gives the best model fit.

4.4 | Community Composition of Vascular Plants

Community composition of vascular plants within NMDS space was significantly different inside and outside the fenced area (Table 4). This is also illustrated in Figure 7a, which shows the association of species with different stand types. However, there were no significant NMDS differences between communities beneath larch and oak trees (Table 4; Figure 7a). Figure 7b, which is based on the same calculation, instead shows the association between stands located on opposite sides of the fence. For understory vegetation beneath oak canopies, the NMDS-space distance across the fence between plot pairs was significantly greater than the mean NMDS distance

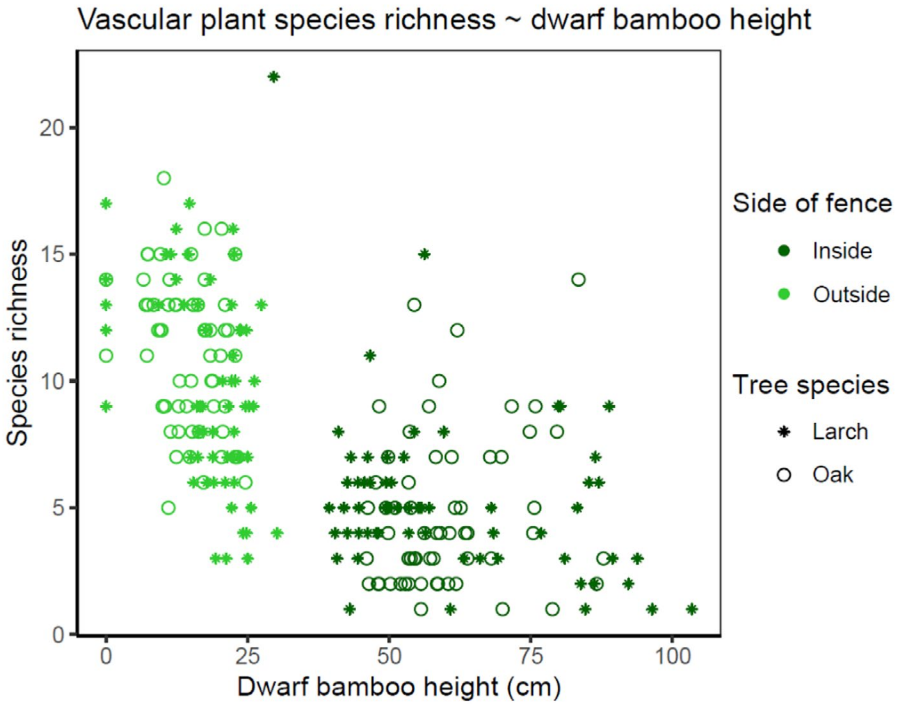

FIGURE 6 | Species richness of vascular plants in individual plots as a function of dwarf bamboo height. Ten plots were distributed in each of 12 larch and 12 oak stands inside and outside the deer fence for a total of 240 plots.

TABLE 3 | Results from GLMM models (full models and best-fit models).

Model	Combination of explanatory variables	Estimate	SE	z	p	AIC	Marginal R^2/conditional R^2
1	(Intercept)	1.546	0.117	13.22	<0.0001	1166.0	0.411/0.632
	Fence (outside = 1)	0.775	0.109	7.11	<0.0001		
	Tree species (oak = 1)	−0.004	0.144	−0.03	0.976		
	Tree influence index	−0.055	0.027	−2.04	0.041		
2	(Intercept)	1.544	0.093	16.63	<0.0001	1164.0	0.411/0.632
	Fence (outside = 1)	0.775	0.109	7.11	<0.0001		
	Tree influence index	−0.055	0.027	−2.06	0.039		
3	(Intercept)	2.555	0.126	20.21	<0.0001	1151.3	0.414/0.639
	Dwarf bamboo height	−0.016	0.002	−7.59	<0.0001		
	Tree species (oak = 1)	−0.037	0.142	−0.26	0.794		
	Tree influence index	−0.057	0.027	−2.08	0.037		
4	(Intercept)	2.536	0.103	24.55	<0.0001	1149.4	0.415/0.640
	Dwarf bamboo height	−0.016	0.002	−7.59	<0.0001		
	Tree influence index	−0.056	0.027	−2.07	0.039		

Note: In Model 1 (full model), side of fence (categorical 1/0) was used as a predictor for species richness together with canopy species (larch/oak) and rescaled tree influence index (ranging from −1.67 to 3.82). In Model 2 (the best-fit model when side of fence was used as a predictor), tree species was removed. In Model 3, side of fence was replaced by dwarf bamboo height (0–103.4 cm). In Model 4 (the best-fit model with dwarf bamboo height as a predictor), tree species was removed. Stand and stand pair (stands located on opposite sides of the fence) were used as random effect factors in all models.

among plots either inside or outside the fence (Figure 8; *t*-test, $p < 0.05$). For plots beneath larch canopies, cross-fence NMDS distances were significantly less than among plots outside the fence (Figure 8; *t*-test, $p < 0.05$), but indistinguishable from NMDS distances among plots outside the fence (Figure 8; *t*-test, $p > 0.05$).

TABLE 4 | Permutational multivariate analysis of variance (PERMANOVA) of the vascular plant species matrix.

	df	Sum of squares	R^2	F	p
Tree species	1	0.179	0.051	1.371	0.219
Side of fence	1	0.598	0.170	4.589	0.001
Residual	21	2.738	0.779		
Total	23	3.515	1.000		

Note: The test was run with 999 iterations.

The indicator species analysis showed that in total, 13 species or species groups showed a significant ($p < 0.05$) association with one side of the fence (Table 5). One species was significantly more common inside the fence, and 12 were significantly more common outside.

5 | Discussion

The current abundance of deer in much of the northern hemisphere has led to a high grazing pressure severely affecting forest flora in several areas. This study aimed to examine the effects on the flora after 21 years of sika deer exclusion in Nikko National Park. The deer exclusion fence resulted in a significant increase in dwarf bamboo height inside the exclosure and a high cover, indicating its recovery in the protected areas. However, the cover of dwarf bamboo showed variation among stands outside the fence, possibly influenced by deer preferences, local topography, and snow cover duration.

Our study shows that the dominance of dwarf bamboo within the enclosure led to reduced vascular plant species richness. This finding for the first time considers this effect in different forest types and forest densities. We found no difference in species richness and in community composition of vascular plants between larch- and oak-dominated stands. Although we observed a weak effect of stand density on species richness, the primary factor influencing understory species communities appeared to be the exclusion of deer inside the fence and intense grazing outside the fence. The exclusion of deer has also resulted in the development of a different community composition inside the fence compared to the vegetation affected by grazing outside the fence. Below, we discuss these results in the context of forest flora conservation by fencing within forest ecosystems that are affected by intense deer grazing.

5.1 | Dwarf Bamboo

Our findings demonstrate a clear effect of the deer exclosure on dwarf bamboo abundance. This result aligns with previous studies, which highlight rapid recovery by dwarf bamboo in previously disturbed areas and its ability to rebound when protected from heavy deer grazing (Itô and Hino 2007; Shibata et al. 2008; Kisanuki et al. 2009; Kudo et al. 2017). In our study, the difference between sides of the fence was most notable in terms of dwarf bamboo height. The taller dwarf bamboo that was found inside the fence shows that deer exclusion by fencing has allowed greater dwarf bamboo growth. Deer grazing outside the fence, instead, has resulted in shorter dwarf bamboo.

There was also a large variation in ground cover among the different stands outside the fence (Appendix S2, Figure S1b). Notably, the cover of dwarf bamboo was similar between larch stands on different sides of the fence but was significantly higher inside the fence when compared among all stands together and in oak stands separately. The cover of dwarf bamboo was particularly low in one larch stand and in one oak stand outside the fence. In the larch stand, the dwarf bamboo layer was seemingly replaced by *Carex* and *Aster leiophyllus* var. *leiophyllus*. This change in dominance may have resulted from sika deer grazing and possibly other disturbances, affecting the prevalence of dwarf bamboo. It appears that *A. leiophyllus* var. *leiophyllus*, inedible to deer, thrives in stands outside the fence; hence, it is likely to be favored by the high deer grazing pressure in the area (Nomiya et al. 2003; Tamura 2019). Furthermore, not just dwarf bamboo cover but also the total vascular plant cover was particularly low in one oak stand in a steep area outside the fence. Here, the combination of a steep slope and deer grazing may have impacted soil stability (Ohashi et al. 2014), thus adversely affecting understory vegetation.

Variation in dwarf bamboo cover and total vascular plant cover between sites outside the fence may also be influenced by local topography, for example, by the influence on shading, soil water content, and snow cover longevity. Deer habitat selection, influenced by both the availability and quality of forage as well as cover for safety, may also affect temporal and spatial grazing patterns (Godvik et al. 2009). This may help explain the distinct differences in the cover of dwarf bamboo observed among stands outside the fence. Notably, given the consistent differences in dwarf bamboo height compared to the inconsistent cover results, dwarf bamboo height might serve as a more reliable indicator of deer grazing pressure than cover alone.

5.2 | Vascular Plant Species Richness in Relation to Dwarf Bamboo

The analysis revealed that vascular plant species richness was consistently higher outside the fence compared to inside, regardless of whether the stands were larch- or oak-dominated (Figure 6; Table 3). Furthermore, a negative relationship was observed between species richness and increasing dwarf bamboo height, and dwarf bamboo height was a better predictor for species richness than just the side of the fence (Figure 6; Table 3). The dominance of dwarf bamboo, leading to a reduction in vascular plant richness, has previously been documented in different areas of Japan (Fukamachi et al. 1996; Konno 2002; Itô and Hino 2005). The mechanisms involved in this exclusion of other plants often entail shading, litter fall, and reduced soil water content (Doležal et al. 2009). The response to these competitive abilities may differ among understory plant species. In particular, culm height seems to be an important predictor of herb species richness, as taller dwarf bamboo is more prone to shading out other vegetation (Kudo et al. 2011). In this study site, dwarf bamboo plants between 25 and 45 cm tall were quite rare (note gap in Figure 6), so it was not feasible to sample potentially

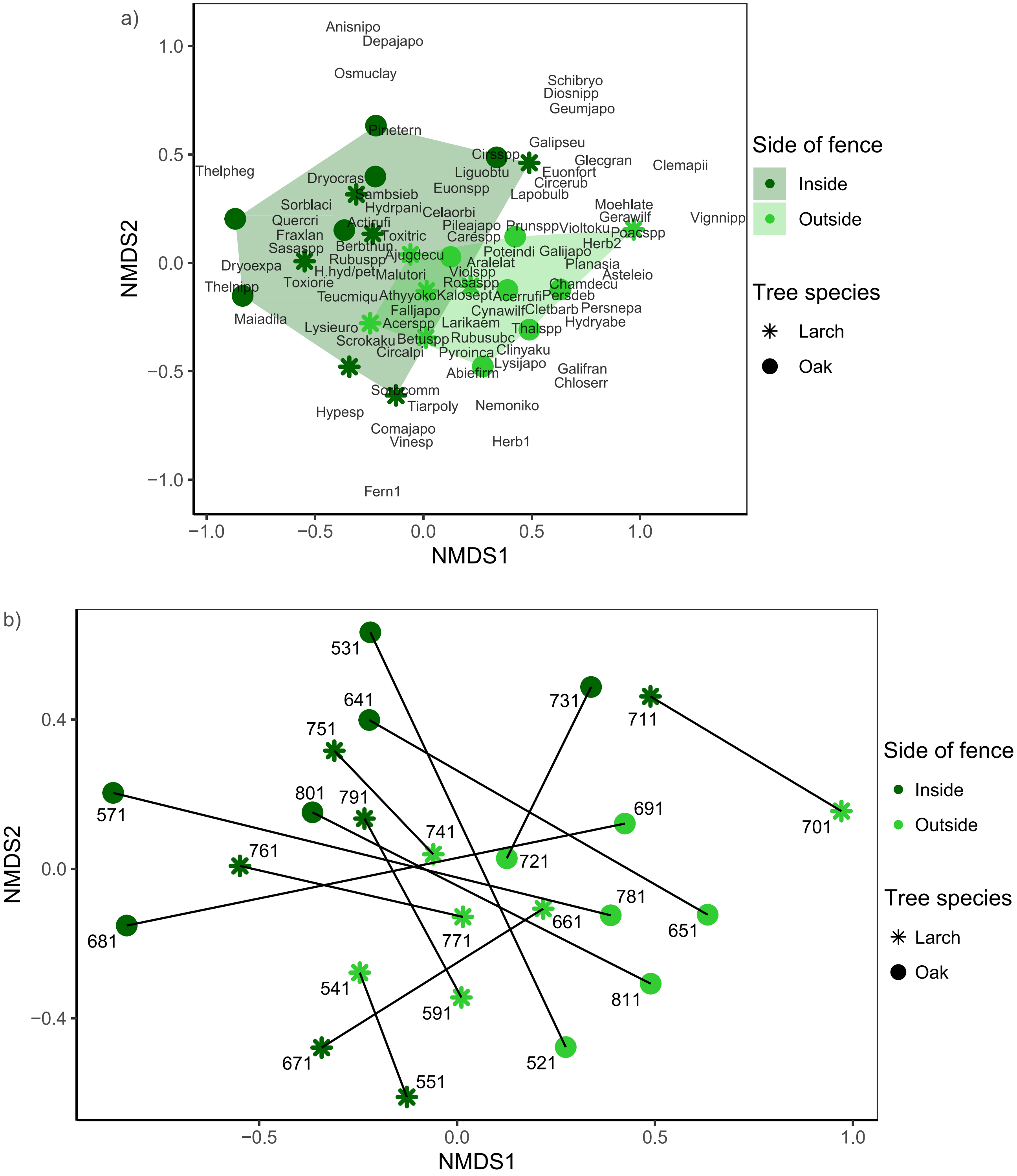

FIGURE 7 | NMDS ordination biplots showing vascular plant community composition in twelve larch stands and twelve oak stands. Stands were situated inside (dark green) and outside (light green) the deer fence. Plot (a) shows understory species associations with different stand types. Plot (b) shows similarities between paired stands, where a line connects paired stands on opposite sides of the fence. Numbers in the plot are the stand numbers used in the map in Figure 1.

different understory species communities growing among dwarf bamboo of these heights.

Besides the observed decrease in species richness inside the fence due to taller dwarf bamboo, the species richness models also revealed a species richness decline associated with higher stand density, although the effect was only weakly significant in the models. Notably, there was no effect of tree species on species richness. Possibly, the impact of tree species and tree density is outweighed here by the effects of intense grazing outside the fence and the exclusion of competitive dwarf bamboo inside the fence, which appears to be the primary influence on understory communities.

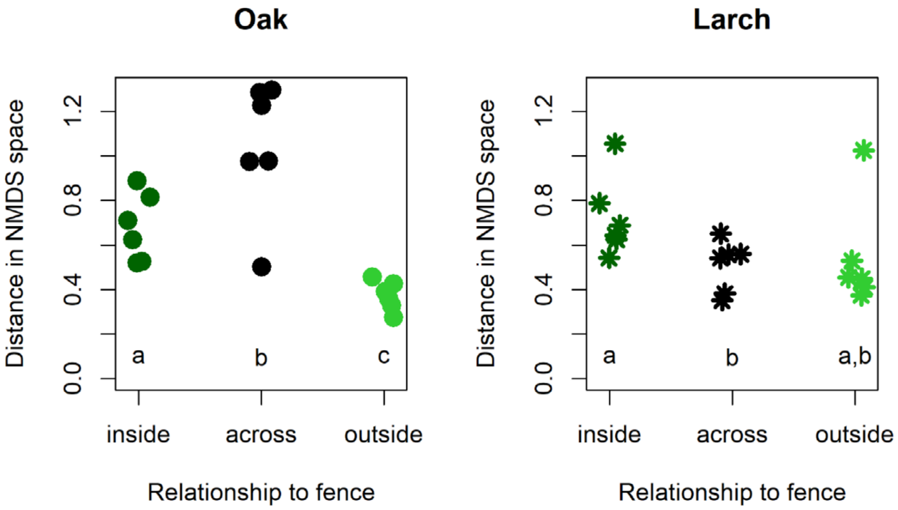

FIGURE 8 | Similarity of vegetation in plots beneath oak and larch canopies and how it was impacted by deer exclusion. Lower NMDS distances indicate greater similarities. For the inside and outside categories, the points show the average NMDS distance from each plot to all other plots of the same canopy tree type and side of the fence. For the across category, each value relates to a pair of plots of the same canopy composition, physically located nearby one another but on opposite sides of the fence. Different letters indicate statistically significant *t*-tests at $p < 0.05$.

TABLE 5 | Species or species groups showing a significant association with either side of the fence and their indicator value representing the strength of the association.

	Indicator value	*p*
Inside fence		
Dryopteris crassirhizoma	0.645	0.0385
Outside fence		
Aster leiophyllus var. *leiophyllus*	0.957	0.0001
Athyrium yokoscense	0.735	0.0156
Carex spp.	0.943	0.0079
Chamaele decumbens var. *decumbens*	0.697	0.0373
Clinopodium micranthum var. *micranthum*/*C. multicaule* var. *yakusimense*	0.707	0.0132
Cynanchum caudatum/*C. wilfordii*	0.764	0.0040
Kalopanax septemlobus subsp. *septemlobus*	0.870	0.0012
Persicaria debilis	0.726	0.0174
Poaceae spp.	0.762	0.0221
Potentilla indica	0.804	0.0049
Thalictrum spp.	0.748	0.0237
Viola spp.	0.921	0.0005

5.3 | Community Composition

Community composition analysis revealed noticeable differences between stands inside and outside the exclosure (Figure 7a; Table 4). Interestingly, there were no significant differences in community composition locations in NMDS space between the larch- and oak-dominated stands. NMDS distances between paired larch stands on opposite sides of the fence were not significantly different from the variation between stands outside the fence (Figure 8). This suggests that communities in the larch stands across the fence were more alike in comparison with the variation among larch plots outside the fence. For the paired oak stands, variation differed significantly between pairs and stands outside and inside the fence. This indicated that there was a larger variation between plant communities across the fence than when comparing communities outside or inside the fence with one another.

A total of 13 species were associated with the outside of the fence. Among them, the herbs *Aster leiophyllus* var. *leiophyllus* and *Viola* spp., along with the vines *Actinidia arguta*, *Cynanchum caudatum*, and *C. wilfordii*, were particularly abundant. Two abundant tree species associated with the outside of the fence were *Acer rufinerve* and *Kalopanax septemlobus* subsp. *septemlobus*. As *A. rufinerve* is unpalatable (Sakata et al. 2021) this was the only tree species that seemed to have the potential to form a new tree layer in the future. *K. septemlobus* subsp. *septemlobus* was only found as tiny seedlings. Because this species is favored by deer, it is not likely to grow large without protection from browsing (Takahashi and Kaji 2001). On both sides of the fence, abundant tree species included *Acer* spp., *Malus toringo*, and *Quercus crispula*. However, they were only present in the form of tiny seedlings, often concealed under the tall dwarf bamboo within the fenced area.

Other tree species that occurred in rather great abundances on both sides of the fence were different species of *Acer* spp., *Malus toringo*, and *Quercus crispula*. Common for these was that they all occurred as tiny seedlings, either hidden under the tall dwarf bamboo inside the fence or not yet found by sika deer outside the fence. In addition, young oaks could be found in the form of root collar suckers growing just beside the parent tree. Nevertheless, apart from inedible *Acer rufinerve*, we noticed a lack of successful tree regeneration on both sides of the fence. This absence of new tree seedling recruitment from species that currently occur only as large trees could pose long-term challenges for preserving the forest in the national park.

The lack of tree regeneration is not solely attributed to the high browsing pressure outside the fence. Interestingly, regeneration failure appears to be equally severe inside the fenced area, where young seedlings struggle to survive due to the competitive growth and dominance of the tall overshading layer of dwarf bamboo. These observations align with previous studies that have discussed the effect of fencing on tree regeneration (Itô and Hino 2007; Doležal et al. 2009; Murata et al. 2009; Simončič et al. 2019). On the contrary, Akashi et al. (2021) found that tall dwarf bamboo may protect tree seedlings by hiding them from deer. The hiding effect of dwarf bamboo is something that we could not evaluate in this study, since tall dwarf bamboo was only present in areas excluded from deer. More efforts to promote tree regeneration to secure the development of natural multilayered forests, instead of today's more or less one-layered forests, are needed in this area. One potential method to promote a more diverse forest flora and facilitate tree regeneration is the experimental removal of dwarf bamboo in selected areas. This has previously been successfully tested for restoring alpine forest flora (Kudo et al. 2017).

Only one species was significant as an indicator for the inside of the deer exclosure: the large cone-shaped fern species *Dryopteris crassirhizoma*. This species has overwintering leaves, which make it highly demanded by deer as winter forage. Yet, it has shown browsing resistance according to Inatomi et al. (2022). Notably, the overwintering leaves not only grant the fern a head start in spring but also provide essential shade, enabling it to dominate the neighboring area, facilitating new leaf development (Tani and Kudo 2005). This strategy may be particularly successful for enduring dwarf bamboo dominance, contributing to the success of *D. crassirhizoma* even among tall dwarf bamboo.

5.4 | Caveats and Potential for Future Studies

In this study, we investigated two contrasting habitats in terms of deer grazing: one experiencing exceptionally high grazing pressure and the other where deer are excluded. Our findings indicate that both extremes present challenges in supporting a diverse understory vascular plant community. However, an important aspect that remains unexplored in this study is the impact of intermediate levels of deer grazing on forest understory vegetation. This means we cannot draw any conclusions about which level of grazing pressure is optimal for promoting a rich understory flora.

An additional limitation of this study is the absence of historical data on the forest understory vegetation before the significant increase in deer populations during the 1980s. Long-term monitoring of the flora in this area, as well as in other regions with substantial deer populations, is essential for understanding the effects of deer densities over time. Including historical data on the forest flora would have allowed for a more direct evaluation of floral changes over the years. Addressing these caveats and conducting future studies encompassing a wider range of deer grazing pressures and incorporating historical data will contribute to a more comprehensive understanding of the intricate dynamics between deer foraging effects and the diversity of forest understory vegetation.

When surveying the understory vegetation, we concentrated the plots around trees. This approach may have resulted in slightly different results compared to distributing plots in the spaces between trees, as increased shading directly under the canopies might have influenced the vegetation. However, when comparing the flora further away from the trees, we did not observe any noticeable differences in species richness or community composition.

5.5 | Implications for Nature Conservation

Because our study was conducted 21 years after the fence was installed, succession may still be ongoing, with vegetation inside the fence still recovering from past intense deer foraging. We could clearly see that dwarf bamboo is the winner at this stage of succession. However, the longer-term ecological perspective may be that this dominance of dwarf bamboo over other understory species may change. Mass flowering of dwarf bamboo usually occurs every 60–100 years or sometimes longer (Makita 1998). Mass flowering and seeding are followed by extensive dieback. Monocarpic senescence can be found in different types of forest ecosystems (Tsvuura et al. 2011) and is an important disturbance in dwarf bamboo-dominated forest understories, which also helps in shaping the forest structure as synchronous senescence of dwarf bamboo is usually followed by seed germination from the seed bank (Taylor et al. 1995). The trigger for mass flowering and the length of intervals between flowering are still not understood (Cho et al. 2017). Taking this longer perspective into account, the current flora heavily suppressed by the dominance of dwarf bamboo may change rapidly when dwarf bamboo flowers. However, since the mass flowering and dieback of dwarf bamboo are so infrequent, conservation efforts may also be needed to ensure that forest species, especially annuals and species with limited seed banks, can manage long-term survival and reproduction. Other studies have shown that the removal of dwarf bamboo to reduce competition can be successful for improving vascular plant diversity (Kudo et al. 2017). More studies about dwarf bamboo removal for flora conservation purposes are recommended.

The problem with extensive grazing by sika deer is not just a local phenomenon in and around Nikko; sika deer damage to flora and forest regeneration has been reported across Japan, and other deer species cause problems for nature conservation in many areas of the northern hemisphere. Current deer-management efforts are clearly not enough for maintaining floral diversity and for enabling natural forest regeneration. Smaller populations of deer are needed before forest herb diversity is depleted, leading to irreversible effects, including local loss of vascular plant species with local adaptations. Improved game management and prioritization of areas for targeted conservation efforts are needed.

Author Contributions

Lisa Petersson, Carl Salk, Daniel Jensen, Göran Thor, and Tatsuhiro Ohkubo designed the research and wrote the article. Lisa Petersson and Daniel Jensen conducted the field inventory and measurements. Lisa Petersson, Carl Salk, and Daniel Jensen analyzed the data and drafted the figures.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data files are available from the Swedish National Data Service (SND) database: https://doi.org/10.5878/mxtb-y706.

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Supporting Information

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