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Ecological resilience of physical plant–soil feedback to chronic deer herbivory: Slow, partial, but functional recovery

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Abstract

Ecological resilience to ungulate overbrowsing is an important issue in forest ecosystems. After chronic herbivory, the recovery rate of understory vegetation and its related functions can be slow even with decreasing grazing intensity; thus, detecting elasticity during alternative successional trajectories is fundamental to understanding state perturbations. In this context, we focused on physical plant–soil feedback (functional interactions between plant growth and soil physical conditions) and evaluated elasticity and recovery processes according to deer density. The effects of 40 years of chronic herbivory by sika deer (average density 14.7 individuals km^{−2}) on the recovery of understory plant communities and associated changes in soil physical properties in headwater catchments were assessed. Using 8 years of catchment-wide exclusion (fenced) and reduction (only culled; average 4.3 individuals km^{−2}) treatments, plot sampling was conducted in 2010 (before treatment) and 2018 (after treatment). The recovery of vegetation and soil physical properties were evaluated, and functional plant–soil relationships and spatial variability were assessed to detect recovery processes during alternative successional trajectory. Woody species increased only under the exclusion treatment and the average soil bulk density was lower than that under reduction treatments. Soil bulk density was negatively correlated with root biomass in the fenced catchment, and root biomass was positively associated with woody species richness. Reduced soil bulk density (~0.5 g cm^{−3}) was observed with greater root biomass and woody species richness on upper hillslopes in the deer-excluded catchment where plant coverage was minimal. Successional failure under the reduction treatment suggested slow recovery with a depressed threshold according to deer density, indicating a clockwise hysteretic response to deer density. Unlike plant coverage during the earlier period of overbrowsing, woody species root development led the recovery of functional physical plant–soil feedback; however, this was probably limited by the higher soil erosion rate in riparian areas and an under-developed herb layer. Our results highlight an alternative recovery trajectory of physical plant–soil feedback driven by an alternative plant element

(woody roots) to recovery trajectory with increasing plant cover. However, riparian erosion and herb layer would still suppress recovery. Therefore, recovery might be slower at the landscape scale.

KEYWORDS

altered successional trajectory, disturbance legacy, elasticity, hydrogeomorphological process, riparian zone, root, soil erosion

INTRODUCTION

Understanding alterations in ecosystem states associated with disturbances are fundamental challenges in ecology and non-equilibrium ecosystem management. Ecological resilience, defined as the capacity of a system to maintain a state while undergoing change, is represented by the strength of disturbance required to shift to another stable state (Angeler & Allen, 2016; Hodgson et al., 2015; Holling, 1973). This concept includes changes of the state not only when the system faces disturbance (i.e., collapse or resistance) but also following disturbance, which is defined as recovery (or “engineering resilience”; Angeler & Allen, 2016; Hodgson et al., 2015; Suding et al., 2004). The threshold (“tipping point”) and trigger for state changes as well as the regime of exogenous disturbances are the key processes in ecological resilience (Gunderson, 2000; Standish et al., 2014; Suding & Hobbs, 2009). Currently, interference of disturbance legacy, defined as the effects of successful species traits, residual species and changes in physical conditions (Johnstone et al., 2016; Suding et al., 2004), is recognized as a key determinant of secondary successions (e.g., Bürgi et al., 2017; Webster et al., 2018). Given this clockwise hysteretic disturbance regime response with the depressed threshold, investigating recovery processes, elasticity (the rate of state recovery, Hodgson et al., 2015) and variability in the landscape can help improve the understanding of perturbations in ecological states and develop restoration programs in forest ecosystems.

Among various disturbances, herbivorous ungulates can cause substantial changes to landscapes such as forests and grassland (e.g., Suding et al., 2004; Takatsuki, 2009). After severe herbivory, plant species can recover slowly with threshold (or sudden) responses according to ungulate density (Côté et al., 2004; Tremblay et al., 2006). Thus, even when ungulate density is reduced, original plant communities and their functions can show low elasticity (Tanentzap et al., 2012). Regulating the influence of herbivores using enclosure or culling is easier than dealing with other disturbances; consequently, many studies have been conducted on plant communities and restoration programs have been developed accordingly (e.g., Öllerer et al., 2019).

Overpopulation of ungulate population is defined as the density during the period that understory vegetation cover and palatable species are not maintained (Mysterud, 2006). Once overpopulated ungulate density often remains above the carrying capacity (McCullough et al., 1997) and the duration of such excessive browsing (defined as over-browsing) can be a major determinant of the strength of the press disturbance. Based on the intensity (e.g., ungulate density) and duration, integrating the effect of press-disturbance strength on elasticity is currently a challenge for researchers seeking to understanding perturbation of this herbivore–plant system.

Elements of disturbance legacy, such as the domination of plant species that are unpalatable or tolerant to ungulates, degradation of seed banks and their sources, modification of soil properties and changes to forager behaviors and items, are thought to interfere with the recovery of plant communities and functions (e.g., Tanentzap et al., 2012). Repeated browsing reduces growth of plant populations and limits vertical plant distributions (Knight et al., 2009; Pisanu et al., 2012; Rooney & Waller, 2003). Thus longer-lived and taller species, including woody species, are particularly vulnerable to long-term repeated browsing (e.g., Gill & Morgan, 2010; Hidding et al., 2012) and the previously developed “recalcitrant” layer of unpalatable and tolerant herbs is known as a typical suppressing force for slow- or later-growing plant species and forest regeneration (Horsley et al., 2003; Husheer et al., 2003; Royo et al., 2010; Webster et al., 2005) with the exception of protection effects (e.g., Akashi et al., 2021; Maltoni et al., 2019). Furthermore, chronic herbivory strengthens such indirect effects (Nuttall et al., 2014; White, 2012; Wright et al., 2012) and probably depresses the threshold of browsing intensity or causes irreversible changes (de la Cretaz & Kelt, 2002; Tanentzap et al., 2009). Hence, after long-term chronic herbivory, elucidating the recovery processes that include woody species is vital in improving our understanding of ecological resilience in understory plant communities and their functions.

A historical change in physical conditions is also an essential aspect of ecological resilience; hence, physical plant–soil feedback can be a measure of ecological function important to recovery after chronic herbivory. In addition to deer trampling as direct impact on soil surface

(Pellerin et al., 2006; Ramirez, 2021), previous research has suggested that the loss of understory vegetation caused by deer browsing indirectly induces soil compaction and soil erosion (Evans, 1998; Suzuki & Ito, 2014; Yanagi et al., 2008). Moreover, soil erosion decreases when vegetation cover recovers rapidly (Ghahramani et al., 2011; Sakai et al., 2012; Wakahara et al., 2008). These findings emphasize the contribution of plant cover (i.e., leaves) and litter cover in preventing splash erosion by rain and indicate that a reversible response to the degradation phase exists (Figure 1a). However, a degraded ground surface can cause prolonged soil runoff with progressive

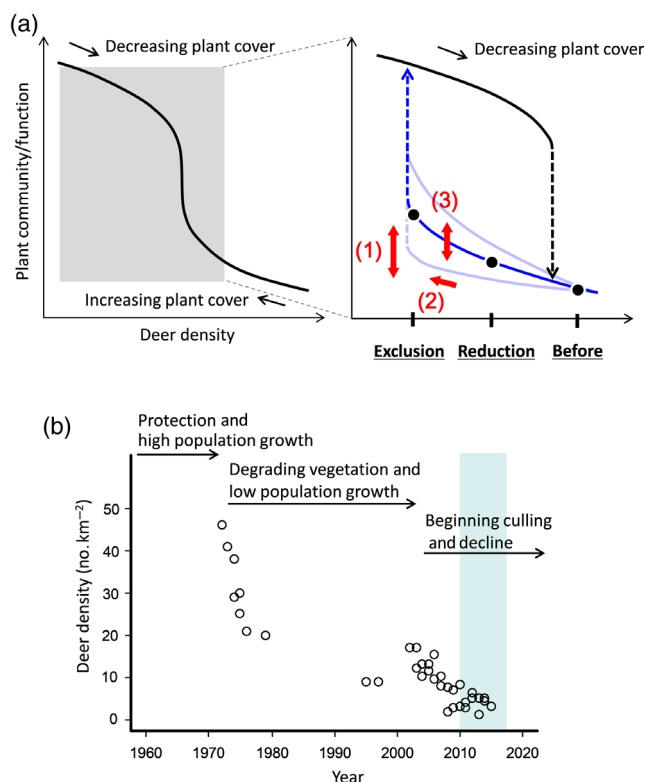


FIGURE 1 A conceptual model of the ecological resilience of physical plant-soil feedback according to deer herbivory intensity based on Côté et al. (2004) and Suding et al. (2004). (a) Reversible successional trajectory during early period after overbrowsing and (b) altered successional trajectory (blue line) during late period after chronic herbivory. To clarify the recovery processes after chronic herbivory, we (1) evaluated changes in the plant community and soil properties according to various deer densities (before, 14.7 individuals km⁻²; reduction treatment, 4.3 individuals km⁻²; exclusion treatment, 0 individuals km⁻²), (2) revisited functional vegetation elements to recover soil properties, and (3) disentangled spatial elastic variability related to positions on the hillslope. (b) Historical changes in the population density of sika deer in the Fudakake area of the Tanzawa Mountains based on Furubayashi and Yamane (1997), Yamane (1999), and Nagata and Iwaoka (2017). The shaded area indicates the observation period in which reduction (culling) and exclusion (fencing) treatments were applied.

erosion (splash to inter-rill, rill, and gully erosion; e.g., Page-Dumroese et al., 2006), whereas vegetation contributes in various ways to reducing the detachment of soil depending on the erosion process (Gyssels et al., 2005; Liu et al., 2018). Hence, for the recovery of the plant-soil feedback after chronic herbivory, alternative functional plant elements should be considered as potential drivers of recovery along with their relationships to woody species (Figure 1b). Furthermore, forest landscapes have topographic and environmental heterogeneities with hydrogeomorphological processes. The riparian area in a headwater catchment is particularly vulnerable to soil erosion because of its high water content (low infiltration capacity) and cascaded mass movement from upper hillslopes (e.g., Benda et al., 2005; Kuglerová et al., 2014); differences in elasticity depend on the location on a hillslope, which is a key variable in a forest landscape (Coomes et al., 2003).

Elasticity of plant-soil feedback after long-term chronic herbivory, particularly from the aspect of hydrogeomorphological processes, is relatively unknown. Hence, in the recovery process, detecting the threshold of herbivory intensity, the driver, and the variability are challenges for understanding and quantifying the elasticity. In this context, we focused on the ecological resilience of physical plant-soil feedback after chronic herbivory. Our main objective was to examine elasticity according to herbivory intensity and recovery processes considering the interference of disturbance legacies. This study was conducted in an area of the Tanzawa Mountains, central Japan, where sika deer *Cervus nippon* were overpopulated 50 years ago; thus the area suffered from chronic herbivory (e.g., Tamura, 2018). Using catchment-wide deer exclusion and reduction treatments over 8 years, we compared the effects of multiple deer densities (i.e., excluded, 0 individuals km⁻²; reduced, average 4.3 individuals km⁻²; and before treatment, average 14.7 individuals km⁻²) on plant communities and soil physical properties (Figure 1b). The sika deer density under reduction treatment was lower than that for recovering understory vegetation in the area where sika deer increased recently (5.5–7.1 individuals km⁻²; Suzuki et al., 2008). If disturbance legacy interfered strongly with recovery, the reduction treatment would fail to recover plant communities, particularly woody species, because of the depressed threshold. Moreover, if the plant-soil interactions were dependent on woody species, there would be a lack of effective positive feedback to soil physical properties under the reduction treatment. Based on this hypothetical scenario, we examined the following:

1. Changes to plant communities and soil physical properties according to deer density as a measure of recovery elasticity.
2. Functional vegetation elements to improve soil physical properties as a driver for recovering physical plant–soil feedback and the relationship to woody species.
3. Spatial variability of the elasticity in the functional plant–soil feedback related to the position on hillslope.

Based on these examinations for detecting signatures of the altered successional trajectory, we discuss the ecological resilience of a physical plant–soil system in a forest landscape after long-term ungulate herbivory.

METHODS

Study area

We conducted field sampling in two headwater catchments located in the Fudakake area in the eastern Tanzawa Mountains, Kanagawa prefecture, Japan (35°28' N, 139°12' E). In this region, two ungulate species, sika deer and Japanese serow *Capricornis crispus*, are distributed. The density of

Japanese serow is substantially lower than that of sika deer. Deer density and damage to understory vegetation in the Tanzawa Mountains are dependent on the activity in this region and the Fudakake area has a history of deer overbrowsing (Figure 2a). As a result of food shortages and related poaching activity after World War II, the deer population in the Tanzawa Mountains decreased largely in the 1950s; consequently, hunting was prohibited from 1955 to 1970. With this protection and an increase in forest planting, the deer population in this area increased rapidly in the 1960s to reach almost 50 individuals km⁻². During the 1970s, the deer population again decreased because forest growth reduced the number of early-successional blocks and exclosure fences enclosed plantation blocks (Furubayashi & Yamane, 1997). Subsequently, understory vegetation declined, but deer density was maintained at 9.0–21.0 individuals km⁻² (average 14.7 individuals km⁻² from the late 1970s to 2002; Nagata & Iwaoka, 2017; Yamane, 1999); thus this area has a history of 40 years of overbrowsing. Deer culling by the Kanagawa prefectural government began from 2003 to recover vegetation and related functions and to reduce damage to forestry and agriculture. Consequently, deer density in this area declined to 3.1–6.5 individuals km⁻²



FIGURE 2 Images of forest the understory during 2018: (a) a patch dominated by woody species on an upper hillslope in the deer-excluded catchment during 2018, (b) a patch dominated by unpalatable herbs on an upper hillslope of the deer-reduced catchment, and (c) on a lower hillslope. (d) Severely eroded hillslope and (e) the soil surface with developed soil pedestals.

(average 4.3 individuals km^{-2}) from 2010 to 2018 (Nagata & Iwaoka, 2017).

A catchment-wide deer exclosure (7 ha) using wire fence (2 m in height) was established in winter 2010 after our 2010 sampling. Overall, our sampling area covered 12 ha (471–670 m above sea level), in which the average annual precipitation was ~ 3000 mm and snow cover was often observed from January to March. The average hill-slope gradient of the area was 36° , with steeper gradients located at the lower hillslopes along streams (e.g., Figure 2b). Forests in the catchments were composed of plantation coniferous trees, including Japanese cedar *Cryptomeria japonica* and Japanese cypress *Chamaecyparis obtusa*, and natural deciduous trees. The soil type of the area was mainly cambisol.

Sampling

We conducted field sampling from August to September in 2010 and 2018. Plots (50×50 cm) were scattered within or around the two catchments as follows: 42 and 16 plots in the excluded and reduced catchments, respectively, in 2010; 20 and 18 in the excluded and reduced catchments, respectively, in 2018. The locations of the plots were selected for the existence of typical variations in vegetation. Since our experiment was conducted based on a simple Before-After Control-Impact design, the plot samplings in the single pair of control-impact sites include a risk of spatially dependent effects even in similar sizes and locations. Thus, to ensure independency among plots, the plot locations of each period and treatment were distributed in different hillslopes (i.e., different orientations and curvatures) and vegetation patches for avoiding effects of synchronized hillslope processes and autocorrelations of plant distributions. To cover variations of vegetation development using the Braun-Blanquet cover-abundance scale (Braun-Blanquet, 1964), understory cover was classified into six classes at the field as follows: class 1, only a little litter coverage ($<40\%$); class 2, intermediate litter coverage (40% – 80%) with no vegetation; class 3, large litter coverage ($>80\%$) with no vegetation; class 4, a little vegetation coverage ($<40\%$); class 5, intermediate vegetation coverage (40% – 80%); and class 6, large vegetation coverage ($>80\%$). Samples were collected according to these classes. Class 1, 2, and 3 were covered only with litter; thus, they were termed “unvegetated plots.” Class 4, 5, and 6 were termed “vegetated plots.” To compare the effects of their positions on hillslopes, plots that were laterally within 10 m of a valley bottom were defined as lower hillslopes (i.e., the riparian area) and plots that were further from the valley bottom were defined as upper hillslopes. Average canopy

openness, taken by fish-eye camera above each plots, was 9.1% (range 1.5%–25.2%).

To assess the plant mass at each plot, the total cover ratio (plant and litter coverage on the ground surface), aboveground plant biomass and belowground plant (roots) biomass were sampled. First, we took a picture from a height of 1 m in the field and then extracted and quantified the total coverage of plant and litter within a plot using Adobe Photoshop 5.0 at the laboratory. After this picture was taken, all understory plants above the ground were collected. After the samples were identified, they were dried at 80°C for 24 h, and the dry masses were used to measure the aboveground biomass. Root biomass was sampled with soil using a cylindrical sampler (diameter 113 mm, depth 40 mm, 400 cm^3 ; see below), and roots were collected and weighed after being dried in the same manner as the aboveground biomass. Plant species were collected around the plot (2×2 m) because plant individuals outside the plot often add the cover and biomass within the 50-cm^2 plot. We identified the collected plants to the species or genus level at the laboratory before drying.

As soil surface properties, we measured the litter thickness and mass, height of the soil pedestal, and soil bulk density. The litter thickness above the soil surface and the height of the soil pedestal were measured at three points in each plot, and the average values were used for statistical analyses. Litter on the ground in the plot was collected and weighed after drying with the same method used for plant biomass. The cylindrical sampler was pounded into the surface soil to collect the soil samples. The soil samples from the cylindrical sampler were weighed after drying at 105°C for 12 h. As a soil physical property, soil bulk density was used to quantify the degradation in the soil's physical condition due to compaction and erosion. Additionally, the height of the soil pedestal was considered indicative of the early stages of soil detachment with splash and inter-rill erosion.

The sampling of plant species, aboveground biomass, litter thickness, height of the soil pedestal, and soil bulk density were conducted in both 2010 and 2018, whereas the total cover ratio, root biomass, and litter mass were sampled only in 2018 to examine the relative importance of components among aboveground plants, belowground plants, and litter.

Statistical analyses

To evaluate catchment-wide successional differences, we first compared the total plant species between exclusion and reduction treatments with a before-and-after comparison. As

our sampling included different sample sizes (number of plots) between treatments and between periods, the species richness per plot number (effective number of species, i.e., Hill number) was compared using rarefied (interpolated) and extrapolated species accumulation curves. We compared sample-based rarefaction and extrapolation curves using the presence or absence of plant species (incidence data) in all sampled plots. Using the R package iNEXT (Chao et al., 2014; Hsieh et al., 2016), species richness was extrapolated to 50 samples (endpoint = 50) and 95% confidence intervals (CIs) were calculated. This process was completed for total, herbaceous, and woody plant species richness. To examine changes in species composition, we compared the frequency of the 15 most abundant species and the share of herbaceous–woody and unpalatable/tolerant–palatable/intolerant species within total species richness. Species that were unpalatable to deer or tolerant to deer browsing were classified using a list from the Kanagawa Natural Environment Conservation Center (2016).

To evaluate changes in plant communities and soil conditions at the plot scale, plant species richness and soil (and surface) physical properties per plot were compared between treatments and between periods. Using samples of vegetated plots, the total, herbaceous and woody plant species richness were compared. Based on variables sampled from 2010 to 2018, the litter thickness, height of the soil pedestal, and soil bulk density were also compared. To assess the effects of vegetation, this comparison was conducted according to vegetated and unvegetated plots. This series of comparisons between periods and between treatments were analyzed using generalized linear mixed models (GLMMs). Sampling periods and interactions between periods and treatments were used as explanatory variables to assess changes in plant species richness and soil physical properties. Further, in addition to plot locations, we statistically considered the spatially dependent effects of using random effects for treatments and periods to avoid detecting unexpected effects of space and time between treatments and between periods except the fixed effects.

To assess the functional plant–soil relationship, we examined the effects of plant mass variables on soil bulk density in 2018 using a GLM. For each treatment, the plant and litter mass variables (total cover ratio, above-ground biomass, root biomass, and litter mass) were used as explanatory variables in a simple GLM with soil bulk density as the response variable. Furthermore, the relationship between functional plant mass and species composition (i.e., total, herbaceous, and woody species richness) was examined in relation to compositional change.

Based on the functional relationships among plant species richness, plant mass, and soil bulk density, variability was assessed with the effects of treatments

considering interference of disturbance legacy derived from soil erosion rate and prior-developed layer. To assess the vulnerability of soil erosion based on the position on a hillslope, sampling plots were divided into lower and upper hillslope areas and these areas were compared. To assess effects of the rate at which vegetation cover develops, six cover classes were used. Differences in plant species richness were then determined using the locations according to treatment interaction. To identify partial effects of treatments depending on vegetation cover classes, pairwise Tukey's post hoc tests were conducted. The relationship between soil bulk density and plant mass per the location was also plotted to visualize the interaction between the position on the hillslope and the vegetation cover classes. For this comparison, random effects were included for the treatments.

For comparisons and regressions using GLMMs and GLMs, Poisson distribution with a log-link function was used for species richness, whereas gamma distribution with a log-link function was used for plant biomass and soil physical properties. GLMs were performed using the R package lme4 (Bates et al., 2015). A likelihood ratio test with a chi-square test statistic was used to evaluate the effectiveness of each model; these tests were conducted using the R package lsmeans (Lenth, 2016). All statistical analyses were conducted in R 3.5.2 (R Core Team, 2018).

RESULTS

Evaluating the recovery of plant communities and soil physical properties

In total, 151 understory plant species were sampled in 2010 and 2018 including 81 herbaceous species and 69 woody species (37 and 32 shrub and tree species, respectively). In terms of deer browsing, 16 unpalatable or tolerant species were found, 13 and 3 of which were herbaceous and were woody plants, respectively. The estimated total plant species richness of the 50 plots in the excluded catchment increased from 78.0 (95% CIs: 64.7–91.2) in 2010 to 111.0 (91.9–130.1) in 2018 (Figure 3b). Similarly, the total plant species richness in the reduced catchment increased from 52.6 (32.0–73.2) to 86.5 (67.2–105.7) over the 8 years (Figure 3a). When divided into herbaceous and woody species, the estimated herbaceous species in the reduced catchment increased from 28.0 (15.0–40.9) in 2010 to 62.9 (45.1–80.7) in 2018, whereas that in the excluded catchment showed a smaller increase from 48.9 (37.3–60.4) to 67.3 (49.9–84.7; Figure 3c,d). In contrast, the estimated woody species richness in the excluded catchment increased from 29.1 (23.0–35.1) in 2010 to 46.1 (32.9–59.4) in 2018, but that in

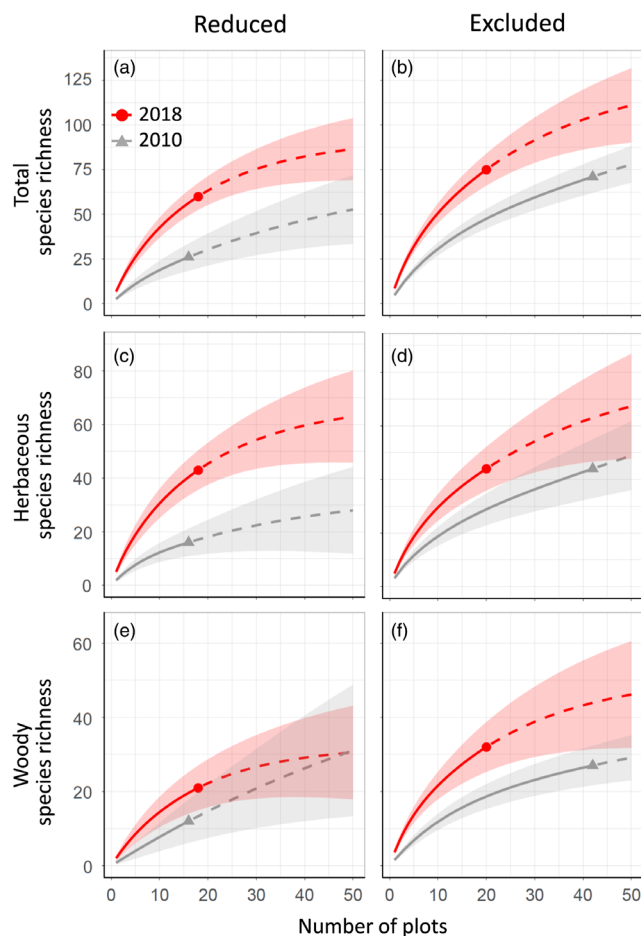


FIGURE 3 Changes in the effective number of species for total plant (a, b), herbaceous (c, d), and woody (e, f) species in the deer-excluded and reduced catchments from 2010 to 2018. Solid and broken lines indicate rarefied (interpolated) and extrapolated number of species, respectively, and the shaded areas indicate their 95% confidential intervals.

the reduced catchment did not increase (30.5 in 2010, 31.1 in 2018; Figure 3e,f).

Unpalatable herbaceous species, such as *Boenninghausenia japonica* and *Oplismenus undulatifolius*, occurred frequently in both periods and across treatments (Figure 4). However, palatable or intolerant woody species, mainly shrub species such as *Rubus palmatus* var. *coptophyllus*, *Berchemia racemosa*, and *Boehmeria spicata*, occurred frequently in the excluded catchment in 2018 (Figure 4d). In addition to the frequently occurring tree species *Zelkova serrata* (Figure 4d), other tree species that grow tall and form overstory, such as *Kalopanax septemlobus*, *Abies firma*, and *C. japonica*, were found only in the excluded catchment in 2018. In all species observed from 2010 to 2018, the share of palatable and intolerant herbaceous species decreased (from 0.58 to 0.49), whereas that of woody species increased (from 0.29 to 0.39) in the excluded catchment (Figure 4c,d). On the other hand, the share of palatable and intolerant

herbaceous species (from 0.38 to 0.42) and woody species (from 0.38 to 0.40) did not change across years in the reduced catchment (Figure 4a,b).

The total plant species richness per plot increased significantly over 8 years ($\chi^2 = 16.391$, $p < 0.001$), with an interaction effect of enclosure detected ($\chi^2 = 24.416$, $p < 0.001$; Appendix S1). Woody species also increased over this period, with an interaction effect of period and treatment (period, $\chi^2 = 18.258$, $p < 0.001$; period \times treatment, $\chi^2 = 14.188$, $p < 0.001$; Appendix S1), whereas herbaceous species showed no significant increase (period, $\chi^2 = 3.010$, $p = 0.083$; period \times treatment, $\chi^2 = 0.926$, $p = 0.336$; Appendix S1). In addition, the plant biomass did not change with period or treatment (period, $\chi^2 = 0.075$, $p = 0.784$; period \times treatment, $\chi^2 = 0.357$, $p = 0.550$; Appendix S1).

Changes in soil surface properties were partially detected among periods and treatments. There were no differences between periods in vegetated plots (litter thickness, $\chi^2 = 0.550$, $p = 0.413$; height of soil pedestal, $\chi^2 = 0.518$, $p = 0.474$; soil bulk density, $\chi^2 = 3.524$, $p = 0.060$; Appendix S2) or in unvegetated plots (litter thickness, $\chi^2 = 1.287$, $p = 0.257$; height of soil pedestal, $\chi^2 = 1.461$, $p = 0.277$; soil bulk density, $\chi^2 = 3.479$, $p = 0.064$; Appendix S2). Furthermore, treatment had no effect as an interaction with period for litter thickness (vegetated: $\chi^2 = 2.229$, $p = 0.136$; unvegetated: $\chi^2 = 0.117$, $p = 0.733$; Appendix S2) and height soil pedestal (vegetated: $\chi^2 = 0.869$, $p = 0.358$; unvegetated: $\chi^2 = 2.616$, $p = 0.106$; Appendix S2). However, treatment was effective for reducing soil bulk density only in vegetated plots (vegetated, $\chi^2 = 18.419$, $p < 0.001$; unvegetated, $\chi^2 = 0.380$, $p = 0.538$; Appendix S2). Although soil bulk density in both the excluded and reduced catchments tended to increase, the difference between the treatments was clearer after 8 years. Considered with increasing the height of soil pedestal and soil bulk density after 8 years, prolonged erosion processes still probably continued to degrade soil surface conditions, but the change in vegetated plots might be signature of a positive effect on the soil surface provided by the vegetation change.

Revisiting the functional vegetation elements to improve soil physical properties

The total cover ratio in both catchments was negatively but not significantly correlated with the soil bulk density (excluded catchment, coefficient \pm standard error = -0.0056 ± 0.0031 , $\chi^2 = 3.58$, $p = 0.058$; reduced catchment, -0.0043 ± 0.0033 , $\chi^2 = 3.41$, $p = 0.160$; Figure 5a). Furthermore, the aboveground plant biomass did not affect the soil bulk density (excluded catchment, -0.0009 ± 0.0017 ,

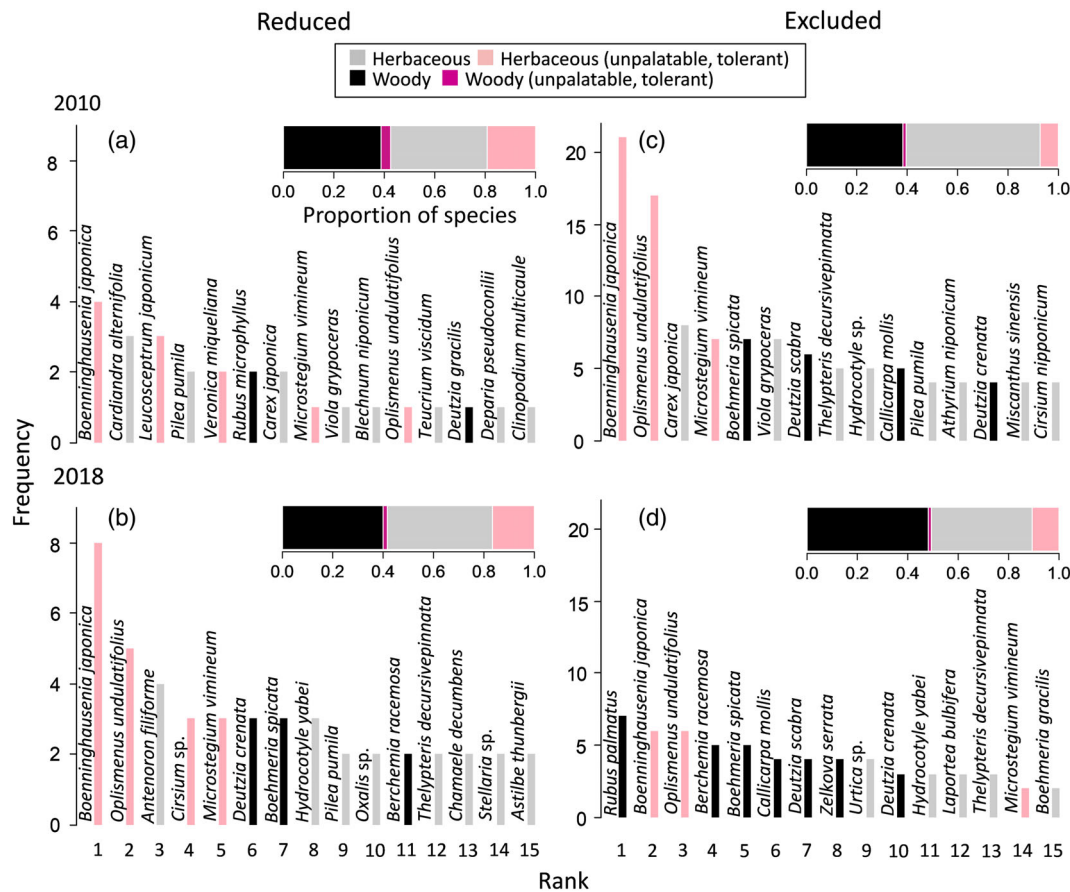


FIGURE 4 Frequency at which plant species occurred, considering the 15 most abundant species and shares of unpalatable/tolerant herbaceous, palatable/intolerant herbaceous, unpalatable/tolerant woody, and palatable/intolerant woody species richness in the deer-excluded and reduced catchment during 2010 (a and c, respectively) and 2018 (b and d, respectively).

$\chi^2 = 3.03$, $p = 0.594$; reduced catchment, -0.0006 ± 0.0034 , $\chi^2 = 3.41$, $p = 0.160$; Figure 5b). However, the litter weight was commonly and significantly correlated with the soil bulk density in both the excluded and reduced catchments (excluded catchment, -0.0004 ± 0.0002 , $\chi^2 = 4.84$, $p = 0.028$; reduced catchment, -0.0007 ± 0.0003 , $\chi^2 = 8.36$, $p = 0.004$; Figure 5c). Alternative to those aboveground plant conditions, the soil bulk density decreased significantly with increasing root biomass in the excluded catchment (-0.1550 ± 0.0710 , $\chi^2 = 5.73$, $p = 0.017$; Figure 5d; the estimated value decreased to 0.5 g cm^{-3} with greater root biomass), but not in the reduced catchment (-0.0982 ± 0.0578 , $\chi^2 = 3.14$, $p = 0.076$; Figure 5d). Plant and litter mass variables were not correlated with each other.

Root biomass, as a functional vegetation element to decrease the soil bulk density in the excluded catchment, increased significantly with woody species richness (0.2153 ± 0.0625 , $\chi^2 = 12.614$, $p < 0.001$; Figure 5f) and total species richness (0.0939 ± 0.0459 , $\chi^2 = 4.25$, $p = 0.039$; Figure 5d), but not with herbaceous species richness (-0.0559 ± 0.08560 , $\chi^2 = 0.269$, $p = 0.604$; Figure 5e). In contrast, no significant relationships were

identified in the reduced catchment (total, 0.0774 ± 0.0801 , $\chi^2 = 0.462$, $p = 0.497$; herbaceous, 0.15853 ± 0.1045 , $\chi^2 = 0.159$, $p = 0.691$; woody, 0.0874 ± 0.1616 , $\chi^2 = 0.229$, $p = 0.633$, Figure 5d–f). These results indicate that recovering roots, including those of woody species, functionally contribute to decreasing the soil bulk density.

Disentangling the spatial variability of elasticity

A functional plant–soil relationship was partially discovered at plots located on the upper hillslope with less plant coverage. Woody species richness was significantly greater on the upper hillslope ($\chi^2 = 19.425$, $p < 0.001$), with an interaction effect of treatment detected ($\chi^2 = 44.072$, $p < 0.001$; Figure 6a). The functional relationship also depended on vegetation classes: woody species richness differed among classes ($\chi^2 = 23.914$, $p < 0.001$), again with an interaction effect of treatment ($\chi^2 = 48.614$, $p < 0.001$; Figure 6b). A post hoc test

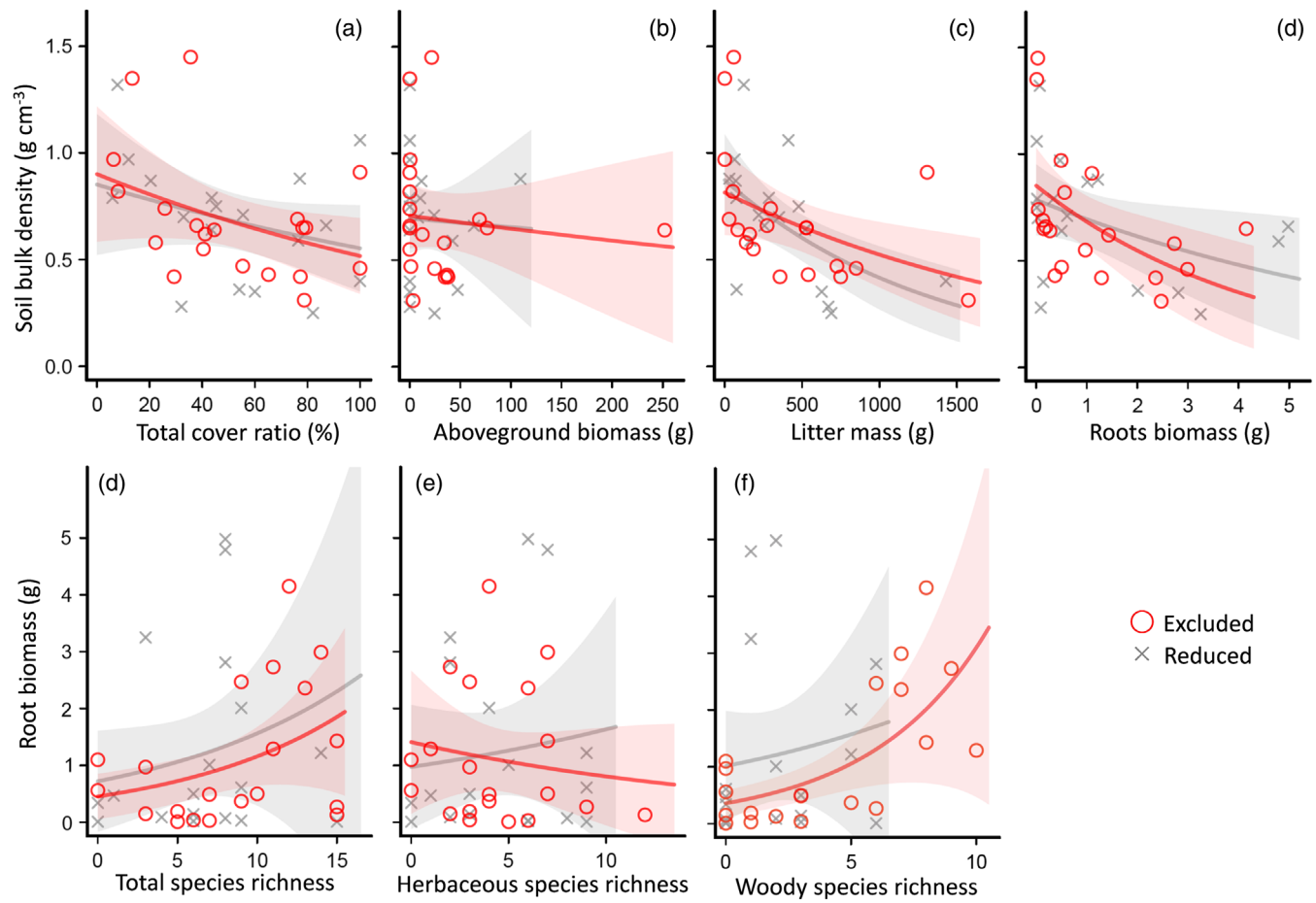


FIGURE 5 Relationships between the soil bulk density and plant and litter masses: (a) total (plant and litter) cover ratio, (b) aboveground biomass, (c) litter mass, and (d) belowground (root) biomass. Relationship between root biomass and plant species richness: (e) total plant species, (f) herbaceous species, and (g) woody species. All data are from the deer-excluded and reduced catchments in 2018. Lines indicate the regression curves obtained using generalized linear models and the shaded areas show the 95% confidence intervals (red, excluded catchment; gray, reduced catchment).

suggested that the difference was significant only in class 4 (<40% vegetation cover; $p < 0.001$), indicating that smaller plant coverage contributed to the development of woody vegetation. Thus decreasing soil bulk density with increasing root biomass was observed in class 4 on the upper hillslopes in the excluded catchment (Figure 6c,d). Although our samples based on existing variations in vegetation did not include the class 4 plots on the lower hillslopes, other vegetated classes (i.e., classes 5 and 6: 40%–80% and >80% vegetation cover, respectively) on the lower hillslopes showed greater soil bulk density and lower root biomass in the excluded catchment (Figure 6d). Accordingly, the lower hillslopes primarily exhibited greater soil bulk density, with limited recovery of the plant–soil interaction, although the canopy openness in the lower hillslopes (excluded catchment, average 12.2%, range 6.0%–17.9%; reduced catchment, 9.4%, 6.3%–14.5%) was not lower significantly than that in the upper hillslopes (fenced catchment, 14.4%, 6.4%–19.5%; unfenced catchment, 15.4%, 11.7%–18.8%).

On the upper hillslopes, soil bulk densities for class 4 in the excluded catchment were clearly lower than those in the reduced catchment with greater root biomasses (Figure 6c,d). Furthermore, the other vegetated classes in the excluded catchment also showed lower soil bulk densities with the tendency for more woody species than were found in the reduced catchment (Figure 6b,d). The partial contributions of woody species probably shaped the negative relationship between the soil bulk density and root biomass.

DISCUSSION

Hysteretic response of plant community recovery after chronic herbivory

The failure of forests to regenerate is a serious effect of ungulate overbrowsing; thus, growing seedlings and saplings of woody species is a key process to achieving

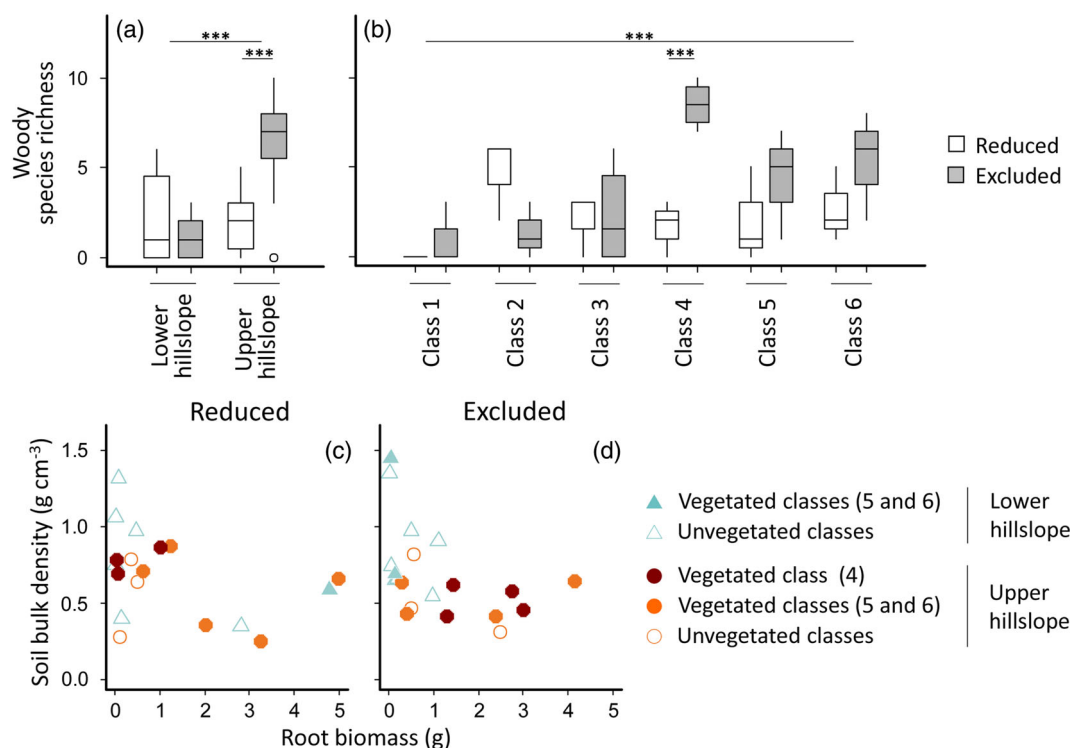


FIGURE 6 Boxplots of woody species richness according to (a) upper and lower hillslopes and (b) vegetation cover classes (4, <40%; 5, 40%–80%; 6, >80%) in both deer-excluded and reduced catchments during 2018. Relationships between the soil bulk density and root biomass, colored according to the position on the hillslope and cover classes, in (c) the reduced and (d) the excluded catchments during 2018. Asterisks indicate significant differences based on the location and location \times treatment comparisons obtained via generalized linear models (** $p < 0.001$).

recovery. According to our resampling results obtained over a period of 8 years, culling control was ineffective at improving the growth of woody species. The culling treatment studied here (average 4.3 individuals km⁻²) would be expected to promote forest regeneration in the early period after overbrowsing but not after chronic herbivory. In meta-analysis, general thresholds of ungulate density were calculated using metabolic weight density (MWD), with the threshold value for positive forest regeneration given as 115 kg km⁻² (Ramirez et al., 2018). This estimated value, including cases after long-term chronic herbivory, is equivalent to 3.4 sika deer (33.4 kg MWD per individual) per km²; thus, it could support our threshold value range. Such depressed threshold to recover woody species were found in white-tailed deer *Odocoileus virginianus* (21.6 kg MWD per individual); previous studies have suggested that the density of deer (white-tailed deer *Odocoileus virginianus*) must be <323.4 kg km⁻² (in eastern Canada; Tremblay et al., 2007), <125.0 kg km⁻² (in northern United States; Russell et al., 2017) and <172.7 kg km⁻² (in eastern United States; Schmit et al., 2020). However, after long-term overbrowsing over 40–50 years, stricter population controls have brought deer numbers down to 21.6–64.7 kg km⁻² (white-tailed

deer in northeastern United States; de la Cretaz & Kelly, 2002). Similarly, in cases of red deer *Cervus elaphus* (51.2 kg MWD) or multiple deer species including red deer (30.7 kg MWD in average; Ramirez et al., 2018), the density should be significantly lower than 102.4 kg km⁻² after overpopulation 40 years ago (red deer in New Zealand; Tanentzap et al., 2009) compared to other cases such as <319.9 kg km⁻² (multiple species in Poland; Borowski et al., 2021) and <429.4 kg km⁻² (multiple species in Britain; Gill & Morgan, 2010). Therefore, herb-dominated succession under culling demonstrated hysteretic recovery in woody species according to deer density.

In abiotic conditions that are habitable for plants, an alternate herb layer can be a major determinant of recovering declined woody species. In short vegetation, intensive foraging limits the growth of saplings (Opperman & Merenlender, 2000). As woody species grow above the herb layer, they are exposed to deer as they reach suitable height for foraging (Renaud et al., 2003). Although we did not examine the height distribution here, an expanded short herb layer of unpalatable plants (e.g., Figure 2d) and resultant changes in deer foraging behavior might still suppress elasticity under the reduction treatment. Below the earlier developed layer, shading or other competitive factors limit

the recruitment and growth of the later-growing species and induce succession along alternative trajectory (De Vriendt et al., 2021; Husheer et al., 2006; Royo & Stanovick, 2019). Likewise, a highly developed vegetation layer (e.g., class 5 and 6) would suppress the recovery of later-growing species, whereas the sparse cover of an herb layer could allow woody species to grow after substantially reducing deer herbivory. A slow and limited recovery of woody species along the successional trajectory might result from suppressions by these above- and below-herb layer factors as part of a disturbance legacy.

Shifting drivers for recovering plant–soil feedback after long-term soil erosion

Long-term herbivory probably causes serious degradation of soil physical properties, due to not only decreasing understory vegetation but also deer trampling and the resultant soil compaction (Heckel et al., 2010; Sabo et al., 2017). However, major determinants of the soil bulk density in rainy and steep regions are mass movement and soil erosion (Nanko et al., 2017); thus, the recovery process examined in this study should also include a consideration of changes to soil erosion processes. The range of soil bulk densities observed included larger value (e.g., -1.55 g cm^{-3}) and wider distribution than those reported in other forests with similar soil type (i.e., cambisol) and in over-browsed ground floors (approximately -1.0 g cm^{-3} ; Suzuki & Ito, 2014). Furthermore, soil bulk densities in steep forested hillslopes were $0.62\text{--}1.11 \text{ g cm}^{-3}$ with various understory vegetation coverage including bare soil surfaces (Gomi et al., 2008); Shinohara et al. (2016) observed densities of $1.09\text{--}1.32 \text{ g cm}^{-3}$ after simulating intensive rainfall ($125\text{--}180 \text{ mm h}^{-1}$). Thus, the catchments studied here included areas that were severely eroded, suggesting that long-term chronic herbivory promotes such highly degraded soil surfaces. Negative relationships between litter biomass and soil bulk density were found commonly in the fenced and unfenced catchments. Greater litter biomass was potentially provided by Japanese cedar, which provided large and persistent amounts of litter on hillslopes for several years. Such accumulated litter cover could preserve soil physical properties against long-term erosion (Miura et al., 2003) and might contribute to protecting soil properties against chronic herbivory (Harada et al., 2020).

The contribution of vegetation to reducing soil erosion shifts depending on the soil erosion process in question. For example, the function of roots becomes effective during later erosion processes, such as rill and ephemeral gully erosion, with increasing contributions of overland

flow (Gyssels et al., 2005). Previously, recovering plant cover has been highlighted as a major driver of soil erosion reduction. Observations in a later-overpopulated area (i.e., a shorter period of chronic herbivory: about 10 years after overpopulation) in the Tanzawa Mountains also suggested the effectiveness of vegetation cover to control soil erosion (Ghahramani et al., 2011; Wakahara et al., 2008). The heights of the soil pedestals in vegetated plots were lower than the respective heights in unvegetated plots, but the erosion of hillslope was similar to that recorded in other areas ($1\text{--}3 \text{ cm}$; Miura et al., 2003). Given the weak relationship between surface cover (plant and litter) and soil bulk density, plants might be effective at but not sufficient for reducing soil detachment when erosion conditions are severe. Alternatively, our results highlight the function of roots, including those of woody species, in contrast to the surface coverage. This discrepancy with previous findings probably arose from flow-driven erosion processes caused by prolonged erosion, although our plots did not include typical rill and ephemeral gully.

To regulate flow-driven soil erosion, root morphology enhances the functional plant–soil interaction. Generally, herbaceous plants have fibrous and fine roots that are more effective in preventing soil erosion than the tap and coarse roots typically possessed by woody species (Gyssels et al., 2005); this is because surface-dense roots effectively prevent soil detachment (Burylo et al., 2012; De Baets et al., 2007; Vannoppen et al., 2017). However, as the soil condition in the present study had already been degraded severely, the function of roots might differ from such a degradation phase. During the recovery phase, plant recruitment requires an anchor by which plants can be fixed to the ground. At the seedling stage, woody plants, especially broadleaf tree species, develop vertical tap roots, followed by laterals (Reubens et al., 2007). Subsequently, the larger diameter of roots can strongly modify the surface to belowground conditions and thereby form obstacles for overland flow and increase infiltration capacity (Gyssels et al., 2005). Under the exclusion treatment in present study, the frequently observed tree species *Z. serrata* might function in this manner. On the other hand, frequently observed shrubs, such as *R. palmatus* var. *coptophyllus*, *B. racemosa*, and *B. spicata*, do not have tap roots; thus, stronger modification of the soil by coarse roots might be effective. In this processes, excluding deer trampling might support to recover those root–soil interactions through reducing direct damage on soil surface and seedling colonizations. Such recovery processes under the severe conditions might result in the limited elasticity of plant–soil feedback according to herbivory intensity. Further data on the effectiveness of roots (i.e., functional traits or

diversity) would support the quantification and evaluation of this plant function and of elasticity.

Spatially elastic variability of plant–soil feedback

A greater soil bulk density was found mainly in riparian areas and the position on a hillslope shaped the gradient of this variable in both the excluded and reduced catchments. The riparian zone included unvegetated and vegetated areas with few woody species and less root development. This indicates that the elasticity of plant–soil feedback would be low regardless of herbivory controls. Previously, Sakai et al. (2012, 2013) observed the recovery of riparian vegetation 3 and 4 years, respectively, after the establishment of a catchment-wide enclosure in central Japan, where understory vegetation declined from the 1990s. These observations indicated that the disturbance legacy related to prolonged erosion of the riparian area would be substantial and could restrict plant recruitment by disturbing colonization of seedlings and seedbank runoff. Thus, our observations provide evidence that long-term chronic herbivory forms a strong disturbance legacy and consequently causes resultant low elasticity in riparian areas.

Riparian areas are vulnerable to changing abiotic conditions that occur as hydrogeomorphological processes change; the recovery of critically degraded conditions is considerably slow and difficult. Previously, it was reported that recovering riparian vegetation could be difficult after long-term elk overpopulation in the northwestern United States because of the loss of riparian woody species and changing to abiotic conditions in larger streams with altered fluvial (inundation) processes (Beschta & Ripple, 2006, 2012). Our results, obtained from riparian areas of headwater streams, indicated that the recovery elasticity was reduced substantially by chronic deer overbrowsing with altering hillslope processes.

CONCLUSIONS

Changes to ecological states after ungulate overbrowsing are an important concern in forests. The ecological resilience of the physical plant–soil feedback is a key factor in recovery of hydrogeomorphological processes and resultant physical conditions. Based on our three examinations, our results suggested (1) 40 years of overbrowsing induced low elasticity in the reduced treatment, (2) a driver for recovering physical soil properties could shift to woody root development, and (3) such recovery

process was heterogeneous and ineffective in riparian areas. Therefore, the present results partly supported the hypothetical scenario in which woody species and the related functions recover with the lower range of herbivory intensity than that reported previously. This slow recovery would support an importance for determining management intensity of ungulate herbivory depending on the disturbance history in restoration programs. However, the spatially limited recovery during the earlier period of succession indicates that time to recover can vary according to the topography in a forest catchment and landscape. Such elastic heterogeneity may be considered to achieve desired recovery in management practices. Our results were obtained using sample replication in a pair of exclusion and reduction treatments of deer browsing. Examinations including replications of the treatments would clarify general pattern and process of the ecological resilience.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Ohira, 2022) are available in Dryad at <https://doi.org/10.5061/dryad.2rbnzs7nd>.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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