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RESEARCH ARTICLE

Prescribed burning effectively maintains threatened species in semi-natural grasslands on lava flows

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Societal Impact Statement

Prescribed burning shows promise for managing certain grassland types, but relying solely on it often reduces plant diversity, including threatened species. In Japanese dry grasslands established on volcanic ejecta, we explored conditions under which burning maintains high diversity. Lava grasslands, especially those on young lava flows with hard, shallow, and acidic soil and high rock and stone cover, harbored the most diverse plants, including threatened species. Burning helps prevent forest encroachment, efficiently maintaining species-rich grasslands on lava flows. We recommend this approach to land managers for maintaining grasslands and conserving threatened plants, particularly in shallow, acidic soil conditions.

Summary

- Prescribed burning can be an effective and efficient method for managing large areas of grasslands, particularly in face of global increases in grassland abandonment. However, relying solely on regular burning often leads to declines in diversity of grassland plants including threatened species in Eurasian countries. Therefore, investigating conditions under which prescribed burning effectively conserves threatened species is highly important. We hypothesized that under specific soil physicochemical conditions, even burning-only management can maintain high threatened species diversity.
- To test the hypothesis, we compared soil physicochemical properties and vegetation among burning-managed grasslands on different volcanic bedrocks (young/old lava and scoria) in Nashigahara, Yamanashi, Japan. We quantitatively investigated how bedrock, soil, and vegetation properties affected diversity of plants, including threatened species.
- We found the highest plant diversity in young lava grasslands, which were characterized by hard and shallow soil and high rock and stone cover, than old lava and young/old scoria grasslands. Meanwhile, soil nutrients (N, P, K, Ca, and Mg) did not vary among bedrock types and had no significant effects on plant diversity. In

Airi A. Asada and Atushi Ushimaru contributed equally to this work.

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young lava grasslands, shallow soil, low soil pH, and resulting low vegetation height caused high threatened species diversity, supporting the hypothesis.

- Mature vegetation on lava flows often comprises forests worldwide. Nonetheless, our findings suggest that prescribed burning successfully suppresses tree dominance and promotes the establishment of highly species-rich grasslands on lava flows. We propose that prescribed burning can effectively conserve threatened species in semi-natural grasslands established under specific soil environments, such as those on lava flows.

KEYWORDS

endangered species, fire, meadows, red list index, soil nutrients, volcanic ejecta

1 | INTRODUCTION

Globally, semi-natural grasslands are maintained through human management practices such as grazing, mowing, and in certain cases prescribed burning, which have a significant impact on plant diversity and composition (Dengler et al., 2014; Koyama et al., 2017; Koyanagi et al., 2013; Nagata & Ushimaru, 2016; Pärtel et al., 2005). Grazing and mowing, however, are often labor-intensive and economically not profitable in marginal regions so that semi-natural grasslands have currently been decreasing worldwide due to abandonment or simplification of management, leading to a decrease in biodiversity (Daskalova & Kamp, 2023; Milberg & Tälle, 2023; Prangel et al., 2023).

Against a background of increasing global abandonment of grassland management, burning-only grassland management has garnered attention as a management option (Valkó et al., 2014; Valkó & Deák, 2021). Burning is the oldest among various grassland management practices and has been used since prehistoric times in many regions (Feurdean et al., 2018; Lewis & Maslin, 2018; Zaloumis & Bond, 2016). Prescribed burning for grassland management is considered to be effective and efficient in maintaining relatively large areas of grasslands with less frequency and labor than grazing or mowing, although it can be dangerous without appropriate knowledge of fire use (Tsuda et al., 2002; Valkó et al., 2014; Valkó & Deák, 2021; Yoder, 2004). Indeed, in Europe, Japan, and the United States, there is ongoing discussion about the potential of prescribed burning for maintaining semi-natural grasslands, restoring abandoned grasslands, and conserving biodiversity (Milberg et al., 2018; Tsuda, 2022; Valkó et al., 2016; Valkó & Deák, 2021) and there is an increasing trend of managing through prescribed burning alone for Japanese semi-natural grasslands (Tsuda, 2022).

Prescribed burning is effective for maintaining herb-dominated grassland conditions, however, relying solely on prescribed burning for the management of semi-natural grasslands often leads to declines in plant diversity in Eurasian countries (Koyama et al., 2017; Nagata & Ushimaru, 2016; Valkó & Deák, 2021). Managing semi-natural grasslands only by prescribed burning increases vegetation height than when combined with other management practices, which leads to a

lower diversity of low-growing native plant species, especially those that are currently becoming endangered (Koyama et al., 2017; Nagata & Ushimaru, 2016). Therefore, the effectiveness of prescribed burning as the measure for maintaining and conserving plant diversity in semi-natural grasslands is uncertain when comparing with other management practices (Nagata & Ushimaru, 2016). However, such studies are limited globally, with a lack of experimental evidence and field data, leaving a gap in the discussion of the effectiveness of prescribed burning (Valkó et al., 2014; Valkó & Deák, 2021). Therefore, it is highly valuable to investigate under what environmental conditions prescribed burning does not have a negative impact on the species richness of grassland plants (Valkó & Deák, 2021).

Given that edaphic conditions often influence plant diversity and species composition in semi-natural grasslands (Goulnik et al., 2020; Plue & Baeten, 2021), our study focused on this aspect. Here, we hypothesized that in areas with specific soil physical and chemical conditions, even burning-only management can maintain the diversity of grassland plant species, including threatened species. Under warm and humid climate conditions in the Palaearctic region, forests are the dominant vegetation type (Dengler & Tischew, 2018; Ushimaru et al., 2018). However, even under such climatic conditions, specific soil environments such as rocky areas with little soil formation and oligotrophic areas make it difficult for taller herb and woody species to invade and/or dominate, which promotes the establishment of grasslands with lower vegetation height (Dengler & Tischew, 2018; Shipley et al., 2024; Squires & Feng, 2018). One type of grassland vegetation in such specific soil conditions is that establishes on volcanic ejecta. Particularly, on lava plateaus, the soil is typically shallow, and grasslands dominated by herbs with low vegetation cover are often observed (Hayakawa, 2002; Ushimaru et al., 2020). Based on these findings that grasslands with low vegetation height are often established in specific soil environments, it is considered that the diversity of grassland species, including threatened species, can be maintained by prescribed burning alone in the semi-natural grasslands established on specific volcanic ejecta.

In this study, we further divided the hypothesis into two specific hypotheses and tested them in the semi-natural grasslands at the foot of Mt. Fuji, where the bedrock is composed of volcanic ejecta. In this

area, the bedrock consists of lava or scoria formed by different eruptions of Mt. Fuji (Nakano et al., 2007). Semi-natural grasslands maintained through traditional burning practices are observed to be established on these bedrocks (Figure 1). The first specific hypothesis focuses on soil physical properties. Due to slower weathering than scoria, soil formation is slower on lava (Candra et al., 2023; Zehetner et al., 2022), and we expect that only shallow soils are formed on lava than scoria even if they are of the same age (Ohwaki et al., 2018). Previous studies have shown that areas with shallow soil and high rock and stone cover tend to harbor a relatively high abundance of grassland species listed on the red list (the shallow soil hypothesis, SsH; Magnes et al., 2021). Based on the SsH that less developed soils harbor a higher diversity of threatened species, we predict that the lava grasslands around Mt. Fuji would support greater plant diversity, including threatened species, than the scoria grasslands.

Meanwhile, the second specific hypothesis features soil chemical properties. Soils derived from scoria are known to be nutrient-poor than those derived from lava (Zehetner et al., 2022). Previous studies have revealed that threatened species tend to thrive under phosphorus-limited conditions (Wassen et al., 2005). If the oligotrophic nature of the soil is more crucial than its physical properties for maintaining the diversity of threatened plants (the oligotrophic soil hypothesis, OsH), then grasslands on scoria may exhibit higher plant diversity than those on lava. By testing SsH and OsH, we aimed to investigate how the differences in physicochemical properties of soils derived from different volcanic bedrocks affect the plant diversity and composition of the semi-natural grasslands, managed solely by prescribed burning.

While the effects of the differences in management practices and their resulting soil environments on grassland plant diversity have been extensively studied (Koyama et al., 2017; Koyanagi et al., 2013; Nagata & Ushimaru, 2016; Stohlgren et al., 1999), few studies have investigated the effects of bedrock types on plant diversity under the same management. In this study, we test the two contrasting predictions outlined by SsH and OsH. Our aim is to determine whether grasslands managed solely through prescribed burning can maintain high plant diversity on lava flows, where soil formation is restricted, or on scoria bedrocks characterized by oligotrophic soil conditions. To verify these predictions, we quantitatively investigated how soil properties affected the diversity of plants, including threatened species, focusing not only on the differences between lava and scoria bedrocks but also on the differences in their formation years.

2 | MATERIALS AND METHODS

2.1 | Study area

In this study, we conducted surveys on semi-natural grasslands located in Nashigahara (ca. 19 km²; Ohwaki et al., 2018), a training ground of the Japan Self-Defense Force, Yamanashi, Japan (35°24'00"-27°04'N, 138°47'14"-49°56' E) in 2022 (Figure S1). The study area comprises four types of grasslands: grasslands established

on lava flows about 1200 years ago (young lava grasslands), grasslands established on lava flows about 2300 years ago (old lava grasslands), grasslands established on scoria ejected by volcanic eruptions from ca. 2300 years ago to the present (young scoria grasslands), and grasslands established on scoria ejected by volcanic eruptions from ca. 4800 to 2300 years ago (old scoria grasslands) (Figures 1 and S1). It should be noted that the terms “young” and “old” express relative ages for each bedrock type in this study. Details of the climatic condition of this area are provided in Methods S1.

In the entire study area, grasslands had been traditionally maintained as meadows by local residents through typical Japanese meadow management practice combining both prescribed burning and mowing for making the thatched roof and green manure and collecting mountain vegetables since ancient times (Koyama, 2010; Ushimaru et al., 2018). Since becoming government-owned land in the Meiji period, it has been used as a military training ground for the imperial army, the US military, and the Ground Self-Defense Force, but currently, entry as common land is also allowed on certain days. For at least the past 50 years, the grasslands in the entire study area have been maintained only by prescribed burning once a year, in April, except for some roadside areas where mowing is performed at a regular interval.

2.2 | Study plots

In the study area, we set 50 large-plots (10 × 10 m, 100 m²) based on the standardized Eurasian Dry Grassland Group (EDGG) sampling methodology (Dengler et al., 2016) at 25 points in both the lava and scoria grasslands. Among them, 15 and 10 large-plots were placed in the young and old lava grasslands and 12 and 13 large-plots in the young and old scoria grasslands, respectively (Figure S1). Following the EDGG sampling methodology, within each large-plot, one 1 × 1 m (1 m²) plot was placed in the southeast and northwest corners. Hereafter, we call the 1-m² plot as plot. In total, we set 100 plots (2 per large-plot). The location information (latitude and longitude) of each plot was measured using a GPS device (eTrex 30x, Garmin Ltd.). We surveyed vegetation and environmental factors within these plots.

2.3 | Vegetation and environmental surveys

Vegetation surveys were conducted twice in each of the 100 study plots in June and September 2022. We recorded the presence/absence of all the vascular plant species in the plots using the shoot-presence method, even if their roots extended outside the survey area but a portion of their plant body (such as leaves) was within the plot (Dengler et al., 2016). For the identification of native grassland species, we referred “Wild Flowers of Japan” (Table S1; Satake et al., 1985). We counted richness of total and native grassland species for each plot. Additionally, we calculated the red list index (RLI) for each plot as an indicator of the diversity of endangered and threatened species within each plot. First, we calculated the red list index

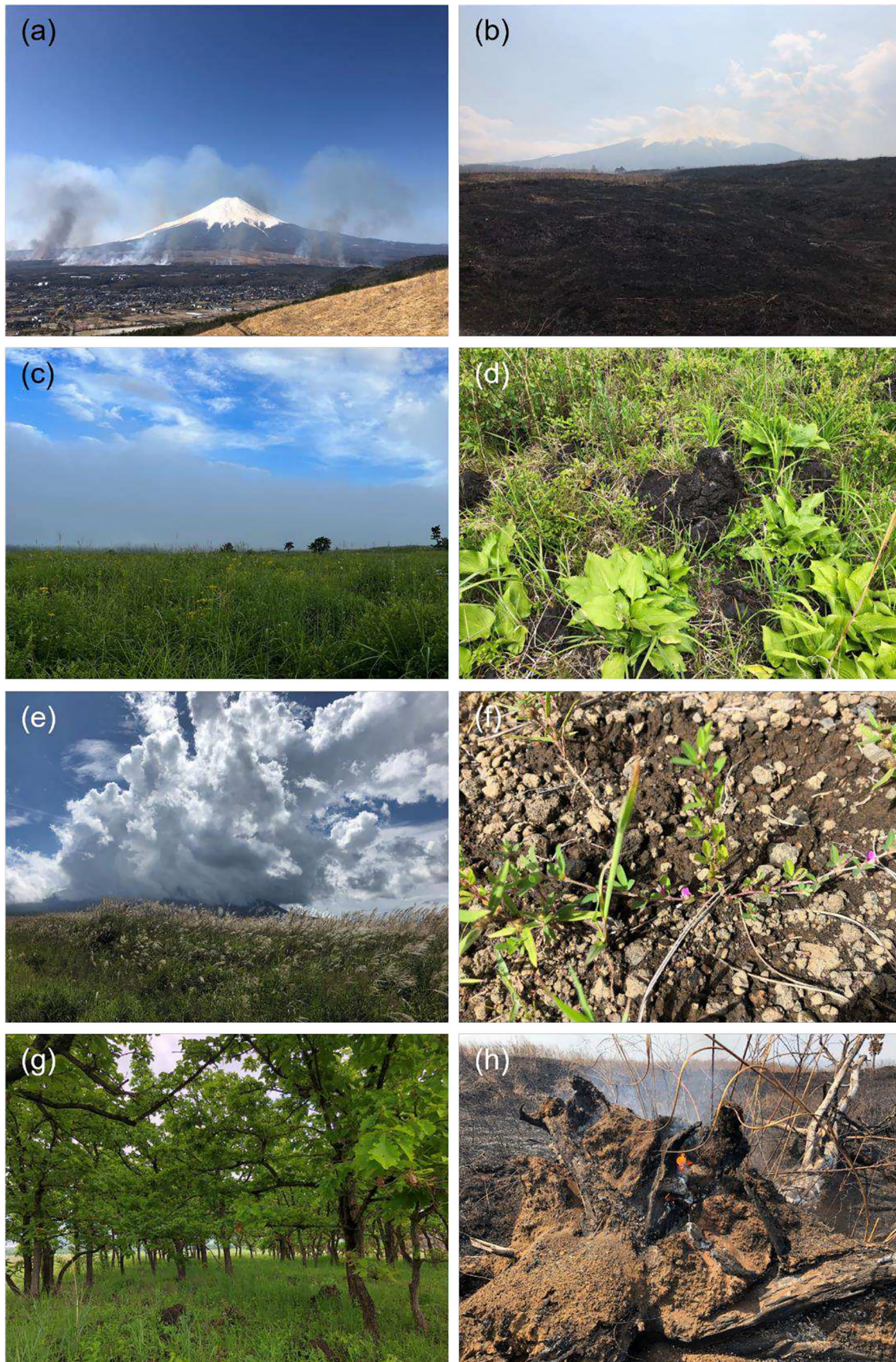


FIGURE 1 Landscape photographs of the study area: prescribed burning practice (a) and grasslands just after burning in April (b). (c) and (d) are a young lava grassland; (e) and (f) are a young scoria grassland. Woody species are more dominant on the lava grasslands (g), and prescribed burning is effective in removing trees and shrubs (h). Photos: Airi A. Asada (a–d, g, h) and Atushi Ushimaru (e, f).

for species i (RLI_i) based on the rank of the species listed on the red lists of the 47 Japanese prefectures as follows:

$$RLI_i = \frac{\sum_{j=1}^{47} R_{ij}}{4D_i},$$

where R_{ij} is the red list rank for species i in prefecture j (extinct = 4, critically endangered/endangered = 3, vulnerable = 2, near threatened = 1, others = 0) and D_i is the number of prefectures where the species i is distributed.

Then, we calculated the RLI for each plot:

$$RLI = \sum_{i=1}^N (p_i RLI_i),$$

where N is the total number of species confirmed in this study (= 179 species) and p_i is the presence or absence (1/0) of the species i within each plot. It should be noted that RLI_i indicates the endangered status of the species i within Japan. RLI used in this study was slightly modified from the RLI used in Uchida, Hiraiwa, & Ushimaru (2016). We divided RLI_i by 4, which represents the highest red list rank, to constrain its values within the range of 0–1.

We measured factors influencing vegetation, as recommended by the EDGG sampling methodology, including soil physical (water content [SWC], hardness [SH], and depth [SD]) and chemical properties [total extractable nitrogen (N), plant-available phosphorus (P), exchangeable potassium (K), exchangeable calcium (Ca), and exchangeable magnesium (Mg) contents and pH], rock and stone cover (RSC), vegetation height (VH), and vegetation cover (VC) (details are shown in Methods S2).

2.4 | Statistical analyses

Species distribution and vegetation properties often exhibit spatial autocorrelation, which can influence the analysis results (Dormann et al., 2007). In this study, spatial autocovariates were calculated based on the latitude and longitude of each plot, for the soil, vegetation, and/or diversity variables used as response variables in generalized linear models (GLMs) and structural equation modeling (SEM). By incorporating these spatial autocovariates as explanatory variables, the effects of spatial autocorrelation were considered in the analyses. The spatial autocovariates can also account for the effect of replicating two plots within a large-plot.

To examine whether plant diversity, soil physicochemical properties (SWC, SH, SD, N, P, K, Ca, Mg, pH, and RSC), and vegetation properties (VH and VC) differ among the four bedrock types, we conducted GLM analyses. Total or native grassland species richness (Poisson distribution and a log link function), RLI, each soil property, or each vegetation property (Gaussian distribution and an identity link function) for each plot was used as the response variable, while bedrock type and spatial autocovariate were included as the explanatory

variables in each model. To test for the significance of each explanatory variable in the GLMs, the Wald test and post hoc comparisons using the Tukey method were conducted after each GLM analysis.

To assess the direct effects of bedrock properties (bedrock type and the maximum elapsed years since bedrock formation, hereafter bedrock age) and the indirect effects mediated by soil properties and vegetation properties influenced by bedrock properties on plant diversity, as well as the effects of soil properties on vegetation properties, we conducted path analysis using SEM. In this analysis, the bedrock age for each grassland type was determined based on the earliest year of formation: 1200 and 2300 years for the young and old lava grasslands and 2300 and 4800 years for the young and old scoria grasslands, respectively. Path analysis is a statistical analysis method to examine potential causal relationships between variables based on covariance or correlation matrices. The full model, including all assumed paths, was designed based on the hypotheses presented in Figure S2.

To investigate the influence of soil physicochemical properties and vegetation properties on species composition, the dissimilarity of species composition between each pair of plots was calculated using the Jaccard index calculated using presence-absence data of each species. Based on the dissimilarity values between plot pairs, multidimensional scaling (MDS) analysis was conducted to visualize the species composition of each plot on a two-dimensional plane. Furthermore, to examine if there were differences in species composition centroids among bedrock types, permutational multivariate analysis of variance (PERMANOVA) was conducted. Prior to this analysis, we tested for significant differences in species composition variance among bedrock types. Additionally, to explore the relationships between species composition of each plot as depicted in the MDS plot and environmental factors or plant diversity indices, vector fitting analysis was performed.

To identify species contributing to the compositional differences among bedrock types, indicator species analysis was conducted, calculating indicator values for each species (Dufrêne & Legendre, 1997). The indicator values range from 0 to 1, with higher values indicating a stronger association with a specific bedrock type. In this analysis, a significance level of 0.05 was set to extract indicator species.

In this study, the statistical analyses were conducted using the statistical software R version 4.2.2 (R Core Team, 2022), its packages “lavaan”, “multcomp”, “vegan”, and “labdsv” and their functions “glt”, “glm”, “sem”, “betadisper”, “metaMDS”, “envfit”, and “indval.”

3 | RESULTS

In total, 179 species were recorded, including 126 native perennial, 20 annual and biennial, 28 woody, and five exotic species (Table S1). The number of native grassland species was 149. Forty-six species had RLI_i values exceeding 0.1 (Table S1). Additionally, seven nationally endangered species were identified within the plots (Figure S3).

3.1 | Differences in plant diversity, soil, and vegetation properties among bedrock types

Both total and native grassland species richness were the highest in the young lava grasslands, followed by the old lava, old scoria, and young scoria grasslands (Figure 2a,b; Table S2). Significant differences were found between young lava and young/old scoria grasslands, as well as between young scoria and young/old lava grasslands (Figure 2a,b). RLI was highest in the young lava grasslands, significantly exceeding those of the young and old scoria grasslands, whereas that of the old lava grasslands exhibited an intermediate value (Figure 2c).

Regarding N, P, K, Ca, Mg, and SWC, no significant differences were found among bedrock types, while other soil properties significantly varied among them (Figures 3a–g and S4; Table S2). The young lava grasslands exhibited significantly lower pH and SD than the young/old scoria grasslands, respectively, and the old lava grasslands had intermediate values (Figure 3c,f). SH was significantly higher in the young lava grasslands than the old lava and young scoria grasslands, while the old scoria grasslands exhibited intermediate values (Figure 3e). The young lava had significantly higher RSC than other bedrock types (Figure 3g).

The young lava grasslands exhibited significantly lower VH than the young and old scoria grasslands, while the old lava grasslands had intermediate values (Figure 3h; Table S2). No significant differences in VC were found among the bedrock types (Figure 3i; Table S2).

3.2 | Path analysis using SEM

SWC was higher in lava grasslands than scoria grasslands, and SWC increased with the bedrock age (Figure 4; Figure S5). SD was shallower in lava grasslands than in scoria grasslands, and plots with higher RSC had shallower SD, while RSC decreased with the bedrock age (Figure 4; Figure S5). Additionally, positive and negative correlations were found between SWC and SH and between SH and SD,

respectively (Figure 4; Figure S5). VH was lower in lava grasslands than scoria grasslands, and it increased with increasing pH and decreased with increasing SH and SD (Figure 4; Figures S5 and S6a–c). VC decreased with increasing SH and RSC (Figure 4; Figures S5 and S6d,e).

Total plant species richness increased with increasing SWC and decreasing SD and VH (Figures S5 and S7). Moreover, total plant species richness exhibited a significant spatial autocorrelation effect (Figure S5). Thus, the greater total species richness in lava grasslands than scoria grasslands was attributed to the higher SWC, shallower SD, and lower VH (Figure S5).

For native grassland species richness, relationships similar to total plant species richness were observed, and it increased with decreasing RSC (Figure 4a; Figure S8). As bedrock aged, RSC decreased, indirectly positively affecting native grassland species richness (Figure 4a). Native grassland species richness also exhibited a significant spatial autocorrelation effect (Figure 4a).

Regarding the RLI, while a positive effect from SWC was not observed, SD, RSC, and VH similarly influenced as they did for native grassland species richness (Figure 4b; Figure S9). Furthermore, RLI decreased with increasing the bedrock age (Figure 4b). A significant spatial autocorrelation effect was also observed for RLI (Figure 4b).

3.3 | Comparison of species composition among bedrock types

Species composition variance did not vary among four bedrock types ($p = 0.053$). We found a significant compositional difference among bedrock types (PERMANOVA, no. of permutations = 999, $p = 0.001$). While the centroids of lava and scoria grasslands were widely separated, the centroids of young and old lava grasslands, as well as young and old scoria grasslands, were closer to each other (Figure 5).

The vector fitting analysis revealed significant associations between species composition differences among plots and several variables: N, pH, SH, SD, RSC, VH, VC, total and native grassland

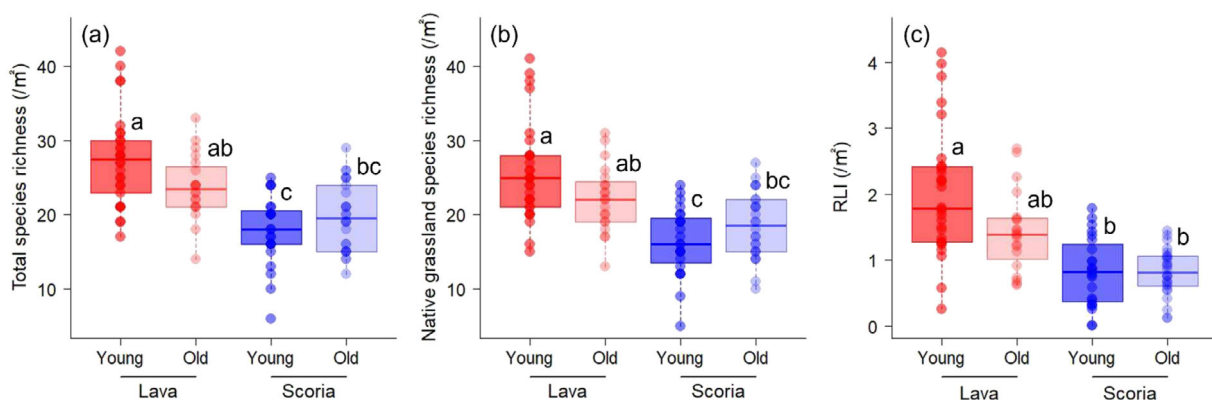


FIGURE 2 The results for comparisons of plant diversity indices among bedrock types: (a) total and (b) native grassland species richness and (c) red list index, RLI. The colors indicate bedrock types: young lava, dark red; old lava, light red; young scoria, dark blue; old scoria, light blue. Different letters indicate significant differences in each plant diversity index between bedrock types.

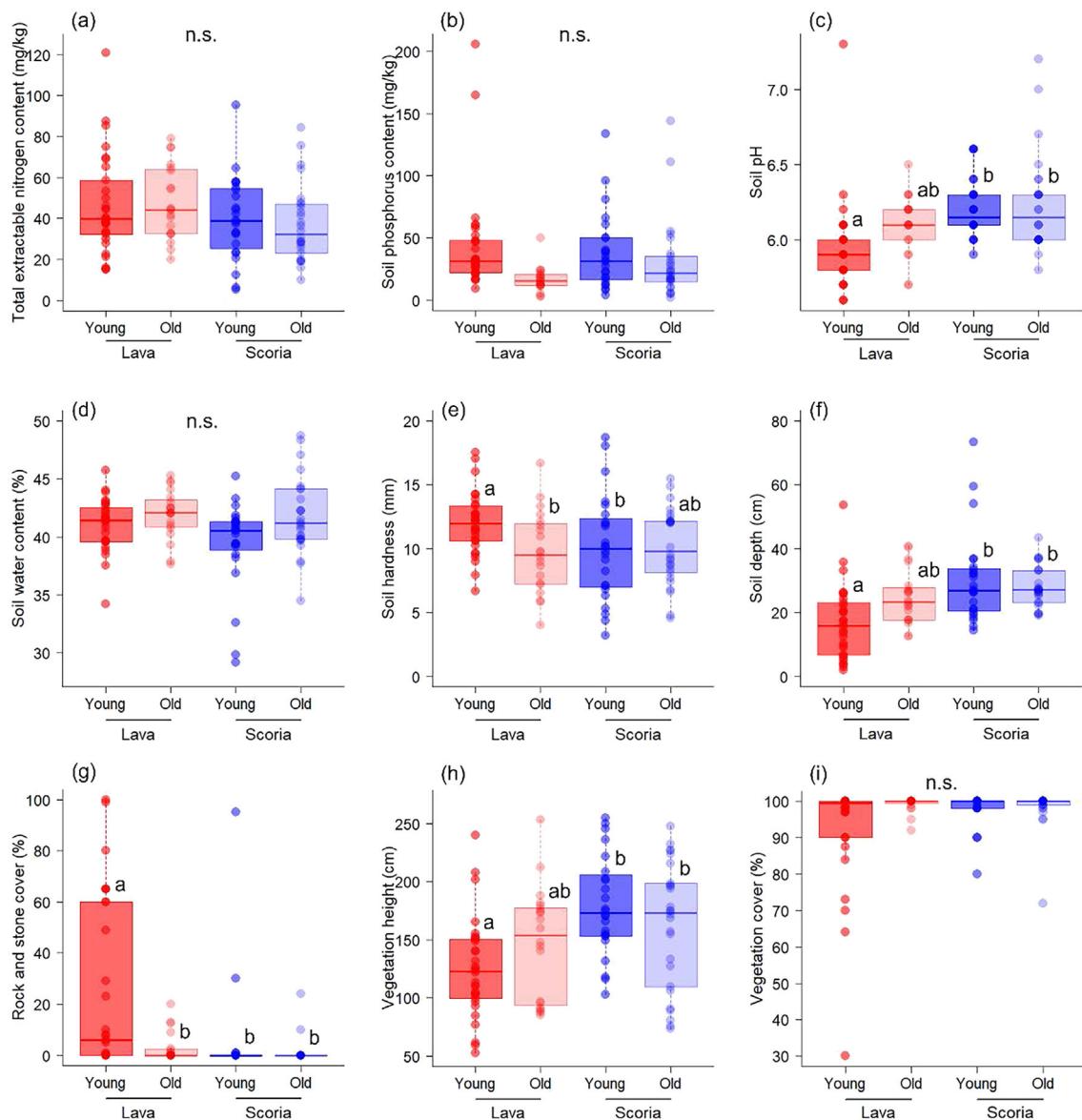


FIGURE 3 The results for comparisons of soil and vegetation properties among bedrock types: (a) total extractable nitrogen and (b) soil phosphorus contents, (c) soil pH, (d) soil water content, (e) soil hardness, (f) soil depth, (g) rock and stone cover, (h) vegetation height, and (i) vegetation cover. The colors indicate bedrock types: young lava, dark red; old lava, light red; young scoria, dark blue; old scoria, light blue. Different letters indicate significant differences in each soil or vegetation property between bedrock types. n.s. means no significant differences among bedrock types.

species richness, and RLI (Figure 5). The vector of pH and VH pointed towards the centroid direction of scoria grassland plots, suggesting that higher pH and taller VH contribute to the specificity of scoria grassland species composition (Figure 5a). Additionally, the vectors of SH and RSC, as well as SD and VC, indicated similar directions, revealing their correlated influences on species composition (Figure 5a). The vectors of total and native grassland species richness and RLI all pointed toward the centroid direction of lava grasslands, indicating that the high plant diversity in lava grasslands contributes to the specificity of its species composition (Figure 5b).

Indicator species analysis showed that 27, 7, 4, and 6 species were identified as indicator species for young and old lava and

young and old scoria grasslands, respectively, highlighting the presence of numerous indicator species in young lava grasslands (Table S3). Notably, the national red list species were identified as indicator species only in the young lava grasslands (*Platycodon grandiflorus* and *Vincetoxicum pycnostelma*). The average RLI_i for indicator species was 0.133 in young lava grasslands, while it was 0.085, 0.018, and 0.081 in old lava grasslands, young scoria grasslands, and old scoria grasslands, respectively, indicating that indicator species in young lava grasslands tend to be under higher risk of extinction within the country (Table S3). Meanwhile, young scoria grasslands had indicator species with lower extinction risk (Table S3).

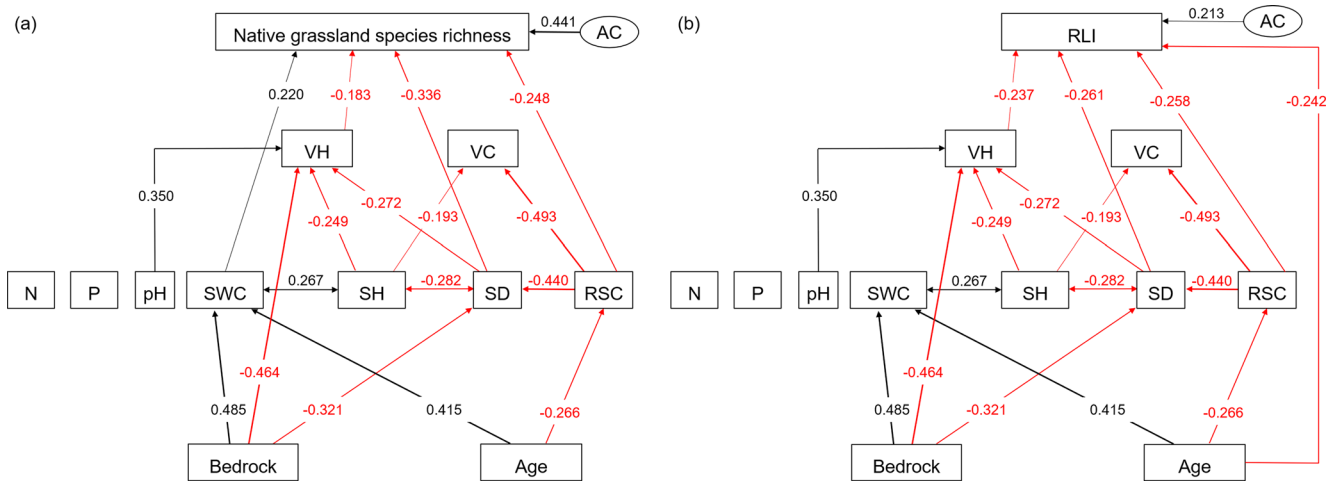


FIGURE 4 The SEM (structural equation modeling) results for (a) native grassland species richness and (b) red list index, RLI. Only relationships that were statistically significant ($P < 0.05$) are depicted. Black and red arrows indicate positive and negative effects, respectively. Positive arrows originating from bedrock represent that lava has a higher value than scoria. Abbreviations are as follows: AC, spatial autocovariate; age, the age of the bedrock; bedrock, type of the bedrock; N, total extractable nitrogen content; P, soil phosphorus content; pH, soil pH; RSC, rock and stone cover; SD, soil depth; SH, soil hardness; SWC, soil water content; VC, vegetation cover; VH, vegetation height.

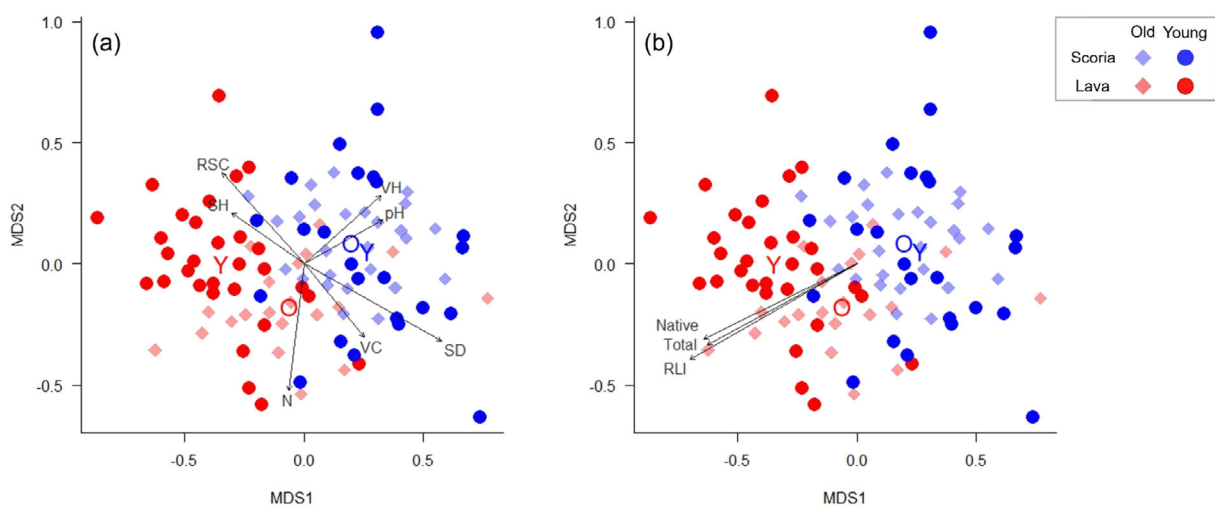


FIGURE 5 Comparison of species composition between bedrock types using multidimensional scaling (MDS). Ordination was conducted according to the Jaccard index between plots. Each point represents each 1-m² plot, and shorter distances between points indicate greater similarity in species composition between plots. The letters represent the centroids of each bedrock type: Y, young bedrock type; O, old bedrock type; red, lava; blue, scoria. The results of vector fitting analysis for (a) environmental factors (N, total extractable nitrogen content; pH, soil pH; RSC, rock and stone cover; SD, soil depth; SH, soil hardness; VC, vegetation cover; VH, vegetation height) and for (b) plant diversity indices (native, native grassland species richness; RLI, red list index; total, total plant species richness).

4 | DISCUSSION

Plant diversity was the highest in young lava grasslands characterized by less developed soil formation than older lava and scoria grasslands even with burning-only management. This result aligns with the previous findings of slow and shallow soil formation on lava flows (Candra et al., 2023; Zehetner et al., 2022) and supports the shallow soil hypothesis, SsH (Magnes et al., 2021). In contrast, soil nutrients did not vary between bedrock types and had no effects on plant diversity, a finding inconsistent with Zehetner et al. (2022) and providing no

support for the oligotrophic soil hypothesis, OsH (Wassen et al., 2005). Furthermore, species composition differed largely between lava and scoria grasslands. Species with higher RLI; values were identified as indicator species of young lava grasslands, whereas those of young scoria grasslands were species with lower RLI; values. Thus, the higher richness and unique composition observed in young lava grasslands than in other grassland types were attributed to high richness of threatened species, suggesting that burning-only management would effectively maintain grassland plant diversity on young lava flows.

4.1 | Influences of bedrock types on soil physicochemical and vegetation properties

In lava grasslands, especially in young lava grasslands, soil formation appears to be less advanced than in scoria grasslands, aligning with SsH (Figures 3e–g and 4). Lava typically weathers more slowly than scoria (Candra et al., 2023; Zehetner et al., 2022). Thus, the shallow soil formation on lava is considered to reflect the slow weathering of lava than that of scoria. Additionally, the invasion of woody species often enhances weathering of bedrock as their roots extend deep into the ground (Anderson, 1988). Woodland vegetation often spreads on lava flows (Ellsworth & Kauffman, 2010; Kato et al., 2005; Kitayama et al., 1995; Zehetner et al., 2022). In fact, in the study area, *Quercus* species sometimes dominates on the lava flows (Figure 1g). However, anthropogenic fire management suppresses the invasion and establishment of trees and enhances grassland vegetation on various bedrock types, including lava flows (Figure 1h; Ellsworth & Kauffman, 2010; Fynn et al., 2004; Nagata & Ushimaru, 2016; Valkó et al., 2014). Therefore, in the study area, in addition to the characteristic of slow weathering of lava, burning likely damages trees, further limiting the progression of bedrock weathering by their roots. This combined effect may contribute to the less advanced soil formation in lava grasslands.

Soil nutrient contents did not vary among bedrock types, contrary to the previous study in the Galápagos islands (Zehetner et al., 2022). Additionally, we found that soil nutrients are not important determinants of vegetation properties in this study area, although the above-ground biomass of communities, correlated with the vegetation height, decreases under nutrient limitation in other grassland ecosystems (Uematsu & Ushimaru, 2013; Wassen et al., 2005). Meanwhile, young lava grasslands exhibited the lowest pH, which in turn caused low vegetation height. Low pH often limits nutrient uptake for plants, likely leading to low vegetation height (Lambers et al., 2008). These together suggest that very low pH indirectly increases plant diversity by suppressing the growth of dominant plants in young lava grasslands.

Our results indicated that soil water content increases with the age of the bedrock and on lava flows than scoria in the SEM. However, this study does not provide an explanation for the mechanism that produces such results. Moreover, the GLM did not show significant differences in soil water content among bedrock types, suggesting that the influence of bedrock properties on soil water content was weak in this study area.

The SEM showed direct negative effects of lava flows on vegetation height. In the Galápagos islands, woodland vegetation results in higher vegetation height on lava flows than those on pumice deposits (Zehetner et al., 2022). In this study area, the annual burning has maintained grasslands with lower vegetation height on lava flows than scoria deposits. The mechanism behind the lower vegetation height in lava grasslands than scoria grasslands could not be elucidated from this study. There is a tendency for vegetation height and cover to decrease as soil hardness increases in plots, consistent with patterns known from previous studies (Dong et al., 2012; Onodera

et al., 2000). Soil hardness is positively correlated with soil water content and negatively correlated with soil depth. Although the effect is modest, it indicates an indirect influence of bedrock properties on vegetation properties through soil hardness.

A relationship is observed where shallower soil depth corresponds to higher vegetation height, contradicting findings from Bernard-Verdier et al. (2012). However, due to the stronger direct negative impact of lava on vegetation height, field observations show lower vegetation height in lava grasslands than scoria grasslands. Moreover, the negative correlation between vegetation height and soil depth is particularly pronounced in old scoria grasslands (Figure S6c), suggesting that it is not a mechanism explaining the differences in vegetation height between bedrock types.

Additionally, in plots with a high rock and stone cover, vegetation cover was lower, aligning with findings from previous research (Magnes et al., 2021). This indicates that in grasslands with a newer bedrock formation, there is a direct negative impact of rock and stone cover on vegetation cover.

4.2 | Factors influencing plant diversity

In this study area, shallow soil conditions and low vegetation height caused high plant diversity like in other global grasslands (Dembicz et al., 2021; Nagata & Ushimaru, 2016). Under shallow soil conditions, slow-growing and nutrient-conservative species tend to dominate over taller species with rapid growth and high nutrient acquisition strategies (Bernard-Verdier et al., 2012; Dembicz et al., 2021; Garnier & Navas, 2012; Grime, 1977). Shorter (or dwarf) herbs are often competitively excluded in tall grassland vegetation due to shading and covering by taller plants (Eskelinen et al., 2022; Hautier et al., 2009). Thus, shallow soil and low vegetation height likely facilitated higher plant diversity of slower-growing or shorter grassland plants via mitigating competition for light and nutrients by suppressing the dominance of competitive species in young lava grasslands.

In the SEMs, total and native grassland species richness increased with higher soil water content, supporting the previous finding (Uematsu & Ushimaru, 2013). Moreover, on lava flows or when the bedrock formation was older, soil water content became higher. This suggests that plant richness is indirectly influenced by bedrock types through influencing soil water content. However, there is no significant difference in soil water content between bedrock types, suggesting that soil water content does not exert a significant impact on the differences in plant species richness between bedrock types in the study area.

RLI decreased with increasing rock and stone cover, supporting a previous study (Magnes et al., 2021). In locations with high rock and stone cover, the available surface area for plant growth might be physically reduced. Meanwhile, Dembicz et al. (2021) reported an increase in species richness with increasing exposed rocks when meta-analyzing diverse types of Palearctic grasslands. The discrepancy in results might be due to the following reason: when comparing different grassland types, rocky grasslands likely exhibit higher diversity

than other types, but physically limited surface soil area may reduce plant diversity within rocky grasslands.

Only RLI was directly and negatively influenced by the bedrock age, although we could not explain the mechanism underlying this result. Endangered species thrive in phosphorus-limited grasslands (Wassen et al., 2005), but no indirect impact from the bedrock age through soil nutrients was observed in this study. The plant-available inorganic nitrogen and phosphorus often increase with the passage of years after lava formation (Kitayama et al., 1995; Vitousek et al., 1992), but no such trends were observed in the study area. We found that the study area exhibited relatively oligotrophic soils than those on volcanic materials in other regions of Japan (Tsutsumi et al., 2022). As the entire study area is nutrient-poor, there might be no evident indirect impact through soil nutrients on threatened species diversity.

4.3 | Comparison with other burning-managed grasslands

Our and previous studies suggest that the effects of burning on grassland plant species richness and vegetation height vary considerably depending on the bedrock type. Young lava grasslands exhibited higher diversity and lower vegetation height than both burning-managed grasslands on volcanic ash soils in Japan (Koyama et al., 2017; Nagata & Ushimaru, 2016) and scoria grasslands in this study. Plant richness in volcanic ash grasslands managed only by prescribed burning in other regions (3–29 species in Koyama et al., 2017; 18–34 species in Nagata & Ushimaru, 2016) is lower than that in young lava grasslands (17–42 species) and comparable to that in scoria grasslands (6–29 species). Additionally, the impact of wildfires on species richness differed between serpentine and non-serpentine areas in California grasslands (Harrison et al., 2003). Moreover, even with the same burning-only management, vegetation height varied within the same bedrock type (this study; Nagata & Ushimaru, 2016). Whether these differences in species richness and vegetation height among grasslands are caused by soil environmental factors remains an open question. The comparison of soil properties between grasslands on different bedrocks will further reveal the impacts of soil physico-chemical properties on vegetation height and diversity of common and threatened plants in burning-managed grasslands.

4.4 | Effectiveness of burning management

Previous studies have shown to decrease diversity in grasslands on volcanic ashes (Koyama et al., 2017; Koyanagi et al., 2013; Nagata & Ushimaru, 2016). However, this study revealed that lava grasslands, especially young lava grasslands, can harbor high plant diversity even with burning-only management. Plant richness in lava grasslands was also comparable to that of volcanic ash grasslands managed through both prescribed burning and mowing (9–35 species in Koyama et al., 2017; 23–53 species in Nagata & Ushimaru, 2016). The high

plant diversity on young lava bedrock is likely attributed to the limited soil development and suppressed vegetation height. Natural grasslands, thriving in warm and humid climatic zones, can establish not only on lava plateaus but also on nutrient-poor specific rocks such as limestone and serpentine (Hayakawa, 2002; Proctor & Woodell, 1971; Ushimaru et al., 2020). Based on our results, semi-natural grasslands on shallow and nutrient-poor soils or on specific bedrocks might sustain high plant diversity even managed only by prescribed burning, but may transition to forests when ceasing the management (Ellsworth & Kauffman, 2010; Nagata & Ushimaru, 2016; Ohwaki et al., 2018).

As this study did not compare burned grasslands with unburned ones, it remains unclear whether burning-only management contributes to maintaining diversity than no management. Nevertheless, in Japanese volcanic ash grasslands, plant species richness is higher under burning-only management than under abandonment (Koyama et al., 2017; Uchida, Takahashi, et al., 2016), suggesting the positive effects of burning-only management on grassland plant diversity. This result aligns with previous studies conducted in Mediterranean and South African grasslands (Bonanomi et al., 2022; Fynn et al., 2004; but see Van Dyke et al., 2004). Furthermore, our results do not clarify whether burning-only management can maintain species richness comparable to that of traditional management combining burning and mowing in the lava grasslands. To address these issues, we need to conduct experiments reintroducing mowing alongside burning and preparing intact grasslands to evaluate the effectiveness of burning-only management in the study area in the future.

There will be an increase in abandoned semi-natural grasslands with the ongoing population decline in rural areas. Therefore, prescribed burning, which can maintain a wide range of grassland environments with low labor, could be an effective means of grassland conservation (Tsuda et al., 2002; Valkó et al., 2014; Yoder, 2004). Indeed, there has been an increase in grasslands managed exclusively through prescribed burning throughout Japan (Ushimaru et al., 2018). Identifying environments where high plant diversity can be maintained through prescribed burning not only elucidates the survival conditions of grassland plants in Japan but also proves essential for the conservation and restoration of grassland environments and grassland plant species in the future.

AUTHOR CONTRIBUTIONS

Airi A. Asada, Atushi Ushimaru, and Atsushi Ohwaki conceptualized the research and designed the methodology; Airi A. Asada managed fieldwork; Airi A. Asada, Atushi Ushimaru, Yuki A. Yaida, Fuma Kawakami, Atsushi Ohwaki, and Masaki Masuda collected data; Airi A. Asada and Atushi Ushimaru analyzed the data and led the writing of the manuscript; all authors contributed critically to all drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available upon request from the GrassPlot database (v.2.15), following its Bylaws (<https://edgg.org/databases/GrassPlot>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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