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Ski runs as an alternative habitat for threatened grassland plant species in Japan

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Abstract: Land use changes have been major drivers of global biodiversity declines during the last century. Although ski resort developments generally cause biodiversity loss in mountainous grassland and forest ecosystems of East Asia, Europe and North America, they can sustainably harbor grassland species which have largely been lost via various land use changes during the last decades. In this study, we surveyed distributions of native endangered and threatened grassland plant species in ski run grasslands of Sugadaira area in the central Japan. We found that ski run grasslands converted from old pastures were habitats of eight native endangered and threatened grassland species, which have been drastically declining in recent decades. Richness of these plant species increased with direct sunlight duration and soil pH: more open ski runs and those with soil pH of approx. 5.0–5.8 exhibited higher richness. According to our results, we discussed the potential of ski runs as an alternative habitat type of native endangered and threatened grassland plants.

Keywords: endangered plant species; Japan; semi-natural grassland; ski run; soil pH; sunlight duration.

Nomenclature: Yonekura & Kajita (2003) for vascular plants .

Abbreviations: EN = endangered; NT = near threatened; VU = vulnerable.

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Introduction

Land use changes have been major drivers of global biodiversity loss during the last century (Sala et al. 2000; Gerstner et al. 2014). Negative effects of land use changes on biodiversity and the underlying mechanisms have been intensively examined in both natural and semi-natural ecosystems worldwide (Butchart et al. 2010; Newbold et al. 2015). Grassland biodiversity in the Palaearctic realm has also been threatened by several types of land use changes (Dengler et al. 2014; Wesche et al. 2016), among which grassland abandonment and conversion to arable lands have exerted a prevailing threat to grassland biodiversity in this region (Török & Dengler 2018).

Ski resort development is a typical land use change, which has negative impacts on biodiversity of mountainous grassland ecosystems in East Asia, Europe and North America (Tsuyuzaki 1994; Wipf et al. 2005; Rolando et al. 2007; Burt & Rice 2009; Roux-Fouillet et al. 2011). In ski runs, machine grading and artificial snow application are known to increase bare ground coverage and/or to change soil moisture and nutrient conditions and therefore influence plant diversity and composition (Tsuyuzaki 1995; Tsuyuzaki 2002; Rolando et al. 2007; Burt & Rice 2009; Roux-Fouillet et al. 2011). Soil erosion caused by machine grading leads to low water content and reduction in soil depth (Tsuyuzaki 1990; Watson 1985). After grading, introduced vegetation cover to preventing soil erosion would promote high dominance of alien plant species at the pioneer vegetation stage (Tsuyuzaki 1995; Tsuyuzaki 2002).

Although ski resort developments generally degrade biodiversity in the alpine zones, they have the potential to maintain semi-natural grassland biodiversity which has largely been lost via various land use changes during the last decades below the timberline in the Palaearctic region (Rolando et al. 2007; Ushimaru et al. 2018). This is because typical mowing management once a year maintains semi-natural grassland conditions on ski runs. However, the potential of ski run grasslands as an alternative habitat for native grassland plants has not been examined in Japan.

In this study, we surveyed the distribution of native endangered and threatened grassland plant species in ski run grasslands in Sugadaira area, Nagano prefecture in the central Japan (Fig. 1). In the study area, old pastures conversion to ski runs in the early 20th has maintained grassland conditions continuously for more than 100 years on the slopes. Ski runs are typically surrounded by secondary forests and *Larix kaempferi* plantations which have established on abandoned pastures (Fig. 1). We examined richness of native endangered and threatened grassland plant species on ski run grasslands and how distributions of these species were related to vegetation and environmental factors. According to our results, we discuss the potential of ski run grasslands as alternative habitat for semi-natural grassland biodiversity.

Study area

The study was conducted in 13 ski runs in Sugadaira- and Minenohara-plateau ski resorts in the Sugadaira area, Nagano Prefecture, Japan (Fig. 1; 36.512°–36.561° N, 138.304°–138.360° E, 1325–1510 m a.s.l.). In the study area, the mean annual temperature was 6.5℃, with a minimum monthly average of -6.2℃ in January, and a maximum monthly average of 19.4℃ in July. The mean annual precipitation was 1197.4 mm during 1986–2015. These meteorological data were recorded by nearby automated meteorological data acquisition system (36.532° N, 138.325° E, 1253 m a.s.l.) by the Japanese Meteorological Agency.

All study ski runs are distributed in cool temperate zone, where the climax vegetation are broad-leaved deciduous forests. For all the study ski runs, semi-natural grassland conditions have been maintained by annual mowing (mowing once in September) as a typical ski run maintenance. Cut plant materials were left in situ for all the runs every year. Wild vertebrate herbivore grazing seldom oc-

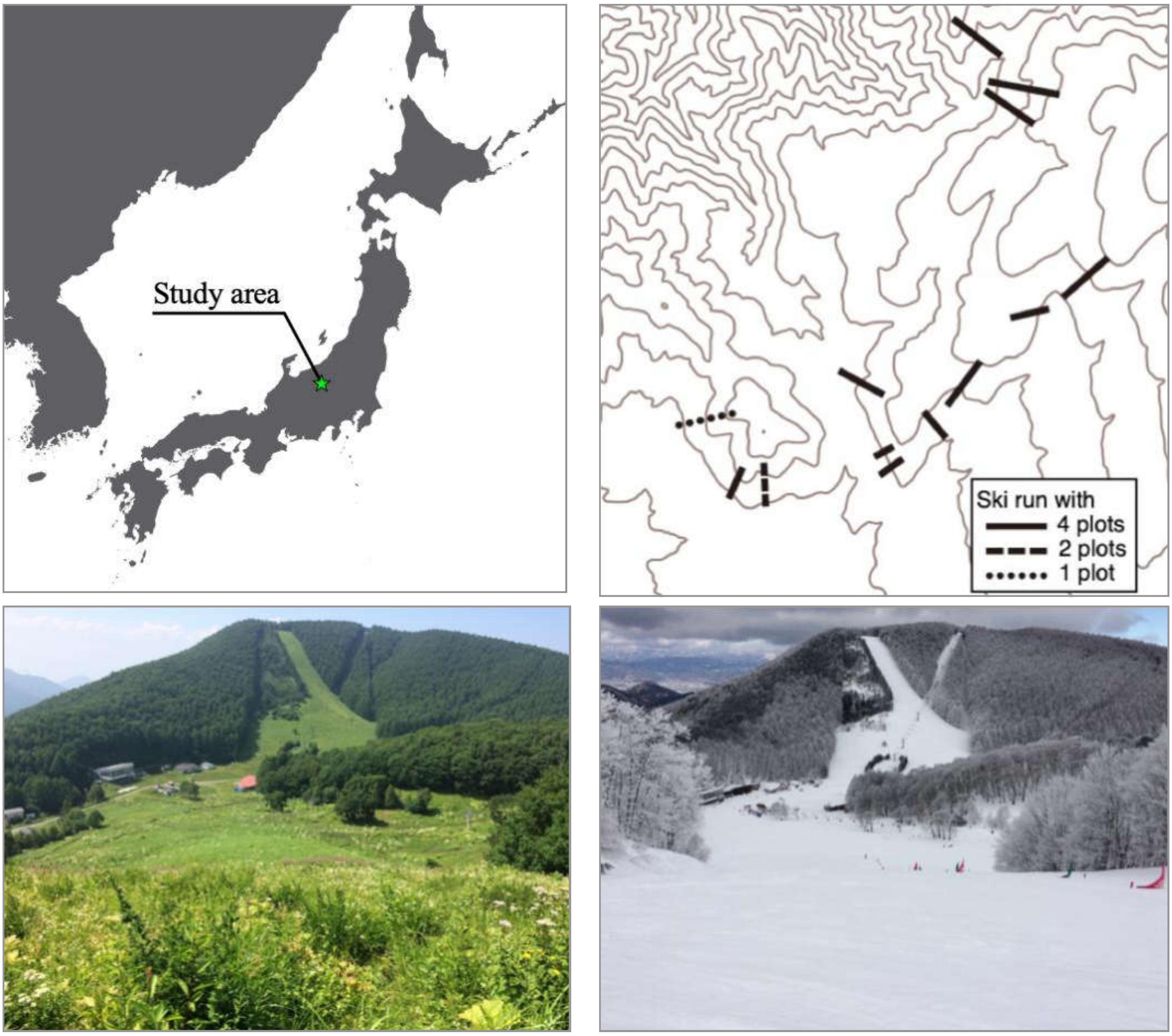

Fig. 1. Location of study area (Sugadaira area), Nagano prefecture, Japan (a), distribution of study runs and plots with 50-m contour line (b) and the study ski runs are indicated by bold, broken and dotted lines (the numbers of plots were 4, 2 and 1, respectively). Photos of a ski run in summer (c) and winter (d) are shown.

Table 1. The mean and standard deviation (SD) of environmental variables in the study plots.

	Vegetation height (cm)	Aboveground biomass (g)	Soil water content (%)	Soil pH	Slope angle (°)	Sunlight duration (min)
Mean ± SD	75.54 ± 32.98	16.97 ± 9.79	39.75 ± 8.43	5.177 ± 0.271	18.66 ± 6.88	760.1 ± 109.9

curred in the ski runs, although Japanese deer have invaded the study area very recently.

Vegetation survey

We set four 2 × 10 m (20 m^2) belt plots on each of the 13 ski runs. Plots were positioned at the center and the edge of upper and lower positions of each run (Fig. 1). The width of study ski runs ranged from 26 to 167 m (mean ± SD: 78 ± 3 m). We focused on ski run areas directly converted from old pasture and as such areas were of limited distribution in two runs, we used data from only 1 or 2 plots on these runs (Fig. 1). Locations of old pasture were checked using past aerial photographs taken in 1947, 1965, 1973, 1975, 1991 (Geographical Information Authority of Japan, GIAJ, http://mapps.gsi.go.jp/maplibSearch.do#1). We thus set a total of 47 plots on the 13 runs.

We conducted vegetation surveys twice in the late June and the early August for each plot in 2015. During the survey of each plot, we recorded the presence of all native endangered and threatened grassland plant species listed in the National Red list (Ministry of the Environment of Japan). To define “grassland” species, we referred to Wild Flowers of Japan Herbaceous Plants I - III (Satake et al. 1981). For the following analyses, we pooled two survey data sets and counted the richness of the red list species in each plot.

Vegetation and environmental factors

We recorded vegetation height, aboveground biomass, soil water content, soil pH, sunlight duration, and slope angle for each plot in August 2015 (Table 1). At five points within each plot (1, 3, 5, 7 and 9 m from the edge of the plot on the center line), we measured the height (in cm) of the highest aboveground plant part within a 10-cm radius at each point and averaged them as vegetation height per plot for the following analyses. To measure aboveground biomass, we clipped all of the above-ground living vascular plant material from two additional 0.25 × 0.25 m subplots just beside each plot, dried the material at 70°C for 72 h, and weighted the dry biomass for each subplot. We used the mean aboveground biomass per plot for the analyses.

At the same time of biomass sampling, we collected soil samples at a depth of 0-5 cm using a cylindrical soil corer with a diameter of 5-cm and a height of 5-cm (ca. 100 cm^3) from the two subplots. For each plot, the two fresh soil samples were mixed then weighted, dried at 70 °C for 72 h, and weighted again. Soil water content (SWC in %) was calculated as follows (Nagata & Ushimaru 2016):

$$SWC = \frac{fresh\ soil\ weight\ (g) - dry\ soil\ weight\ (g)}{fresh\ soil\ weight\ (g)} \times 100$$

In addition, soil pH was measured by mixed and dried soil samples, in a 2:5 (w:w) dry soil:distilled water mixture using a HI 991221 Direct Soil pH measurement instrument (HANNA Instruments, Smithfeild, RI, US). We took a hemispherical photograph at 1-m above ground height of the center of each plot in late August, when the weather was cloudy. For each site, we calculated direct sunlight duration at the summer solstice (in minutes; hereafter direct sunlight duration) as an index of light conditions during the growing season using a hemispherical photograph analysis program, CanopOn 2 (http://takenaka-akio.org/etc/canopon2/).

Statistical analyses

To examine the effects of vegetation and environmental factors on endangered grassland species richness, we constructed a generalized linear model (GLM) with Poisson distribution and log-link function in which vegetation height, aboveground biomass, soil water content, soil pH, sunlight duration, and slope angle were incorporated as the explanatory variables, the number of endangered and threatened species per plot was incorporated as the response variable. Because vegetation height was highly correlated with the aboveground biomass in our data set (Pearson correlation coefficient: r = 0.578, P < 0.001, n = 47) and the variance inflation factor value (VIF; the value = 2.6) of vegetation height in the full model was higher than those of other variables and over 2.0 (Brauner & Shacham 1998), we reconstructed a GLM without vegetation height as the explanatory variable.

Because a single threatened species, *Platycodon grandiflorus* was frequently observed in the study plots, we also examined the effects of vegetation height, aboveground biomass, soil pH, soil water content, slope angle, and sunlight duration on the presence/absence of the species in each plot using a GLM with binomial distribution and logistic-link function. In the model, all the variables were explanatory variables and the presence/absence (1/0) of the species was the response variable. Because the study runs and plots were not randomly distributed within the study area, the effects of spatial autocorrelation on the analytical results should be also considered. We calculated the spatial auto-covariates from the latitude and longitude measurements of the study plots, incorporating values into each GLM, which was achieved through a simple extension of the GLM by adding a distance-weighted function of neighboring response values as the explanatory variable (Dormann et al. 2007). The significance of each explanatory variable was examined with a Wald test. For all analyses, we used the statistical software R v3.3.2 and the vegan package v2.4.1 (R core Team 2016).

Table 2. Observed endangered and threatened species and their Red list category (The Ministry of the Environment of Japan, EN: endangered, VU: vulnerable, NT: near threatened), life form and the number of center and edge plots where the species occurred.

Family	Scientific Name	RL	Life form	No. of plots	
				Center	Edge
Boraginaceae	*Lithospermum erythrorhizon*	EN	Perennial	0	1
Apocynaceae	*Vincetoxicum atratum*	VU	Perennial	0	2
	Vincetoxicum pycnostelma	NT	Perennial	2	1
Plantaginaceae	*Veronica onoei*	VU	Perennial	4	4
Campanulaceae	*Platycodon grandiflorus*	VU	Perennial	10	9
Caprifoliaceae	*Triosteum sinuatum*	VU	Perennial	1	1
Asteraceae	*Tephroseris flammea* subsp. *glabrifolia*	VU	Perennial	3	0
Ranunculaceae	*Pulsatilla cernua*	VU	Perennial	1	1

Results

In total, we found eight endangered and threatened native grassland species in the study plots (Fig. 2 and Table 2). The GLM for their richness revealed significantly positive effects of soil pH and direct sunlight duration on the species richness and non-significant effects of any of the other variables (Fig. 3 and Table 3). The presence of *P. grandiflorus* increased with direct sunlight duration, whereas the other variables did not have any significant effects on the *P. grandiflorus* presence (Fig. 4 and Table 3).

Discussion

Eight endangered and threatened grassland species including a single EN species, *Lithospermum erythrorhizon*, were found in study ski run grasslands, suggesting that ski resort developments have a potential to harbor these grassland plant species of conservation importance in Japan. Since semi-natural grasslands have been declining rapidly via several types of land use change during the last century in Japan as well as in other areas in the Palaearctic realm (Dengler et al. 2014; Nagata & Ushimaru 2016; Uchida et al. 2016; Török & Dengler 2018; Ushimaru et al. 2018), it is valuable information that the new land use, ski run use can retain habitats for native endangered and threatened grassland plants.

Higher soil pH (c. 5.0–5.8, see Table 1) within the acid range of the study ski runs was suggested to be preferred by the study species. Rare species, including some endangered grassland species are known to have narrower ecological niches compared to common species with respect to soil biogeochemical parameters in Europe and Japan (Kleijn et al. 2008; Uematsu & Ushimaru 2013). The unimo-

Fig. 2. Photos of native endangered and threatened grassland plants on ski run grasslands in the Sugadaira area, Nagano prefecture, Japan. Upper row from left to right: *Lithospermum erythrorhizon*, *Vincetoxicum atratum*, *V. pycnostelma, Veronica onoei*. Lower row from left to right: *Platycodon grandiflorus*, *Triosteum sinuatum, Tephroseris flammea* subsp. *glabrifolia* and *Pulsatilla cernua*. Photos: Y.A. Yaida & A. Ushimaru.

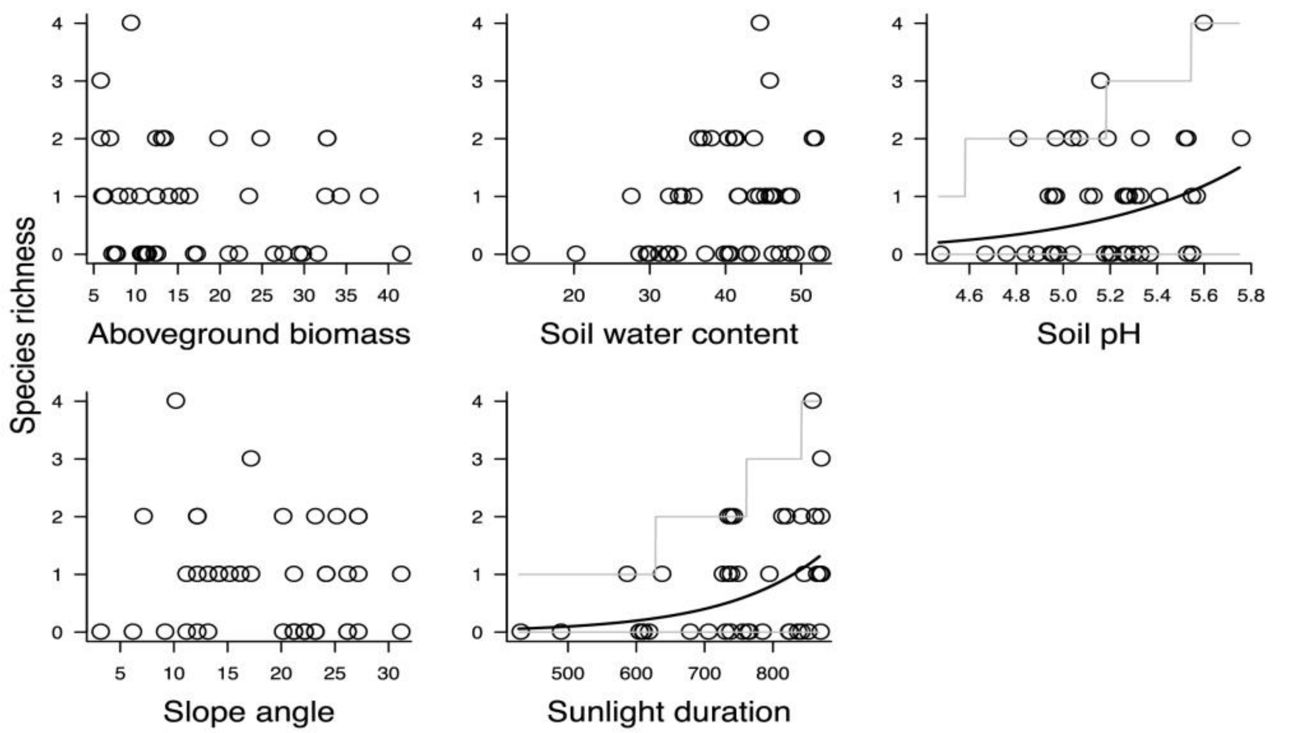

Fig. 3. Relationships of native endangered and threatened grassland species richness with vegetation and environment variables. The regression lines (black) and the 95% prediction intervals (grey) are drawn for the significant explanatory variables (GLM, Table 3). The regression line was calculated using fixed values (i.e. means) for the other explanatory variables.

Table 3. The GLM results for native endangered and threatened grassland plant richness and the presence/absence of *Platycodon grandiflorus*. Estimated coefficients, SEs, *z* values and *p* values by Wald test are shown. Variables with statistically significant effects ($p < 0.05$) are indicated in bold.

Explanatory variables	Estimate	SE	*z*	*p* (> |z|)
Response variable: native endangered and threatened grassland plant richness				
Intercept	-1.418×10	4.359	−3.253	<0.01
Aboveground biomass	-5.251×10^{-3}	1.860×10^{-2}	−0.282	0.778
Soil water content	2.810×10^{-2}	2.387×10^{-2}	1.177	0.239
Soil pH	**1.562**	**6.645×10^{-1}**	**2.352**	**<0.05**
Slope angle	-2.786×10^{-2}	2.811×10^{-2}	−0.991	0.322
Sunlight duration	**7.043×10^{-3}**	**2.505×10^{-3}**	**2.811**	**<0.01**
Spatial auto-covariance	-2.537×10^{-5}	3.590×10^{-5}	−0.707	0.480
Response variable: the presence/absence of *P. grandiflorus*				
Intercept	-2.699×10	1.115×10	−2.420	<0.05
Aboveground biomass	1.502×10^{-2}	4.418×10^{-2}	0.340	0.734
Soil water content	4.374×10^{-2}	5.166×10^{-2}	0.847	0.397
Soil pH	2.716	1.665	1.631	0.103
Slope angle	6.008×10^{-3}	6.046×10^{-2}	0.099	0.921
Sunlight duration	**1.282×10^{-2}**	**5.419×10^{-3}**	**2.366**	**<0.05**
Spatial auto-covariance	8.017×10^{-5}	1.022×10^{-4}	0.784	0.433

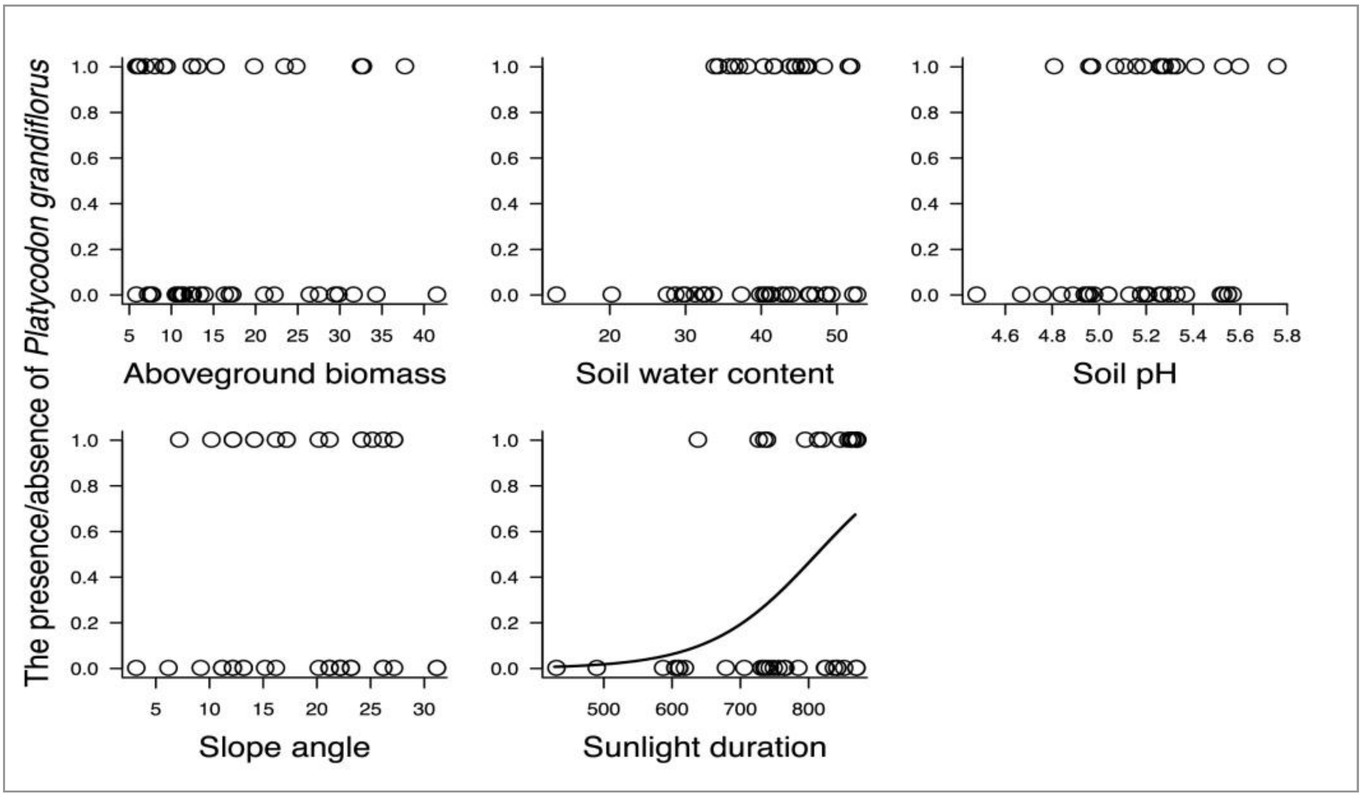

Fig. 4. Relationship between the *Platycodon grandiflorus* presence/absence (1/0) and vegetation and environmental variables. The regression line for the significant explanatory variable (GLM, Table 3) is drawn while the other explanatory variables are fixed as mean values.

dal relationship between soil pH and rare species richness was reported in Japanese hay meadows, such that plots with soil pH of c. 4.7–5.7 had higher rare species richness than those with lower and higher soil pH (Nagata & Ushimaru 2016). The pH range with higher endangered and threatened species richness in this study is consistent with the pH range of the previous study (Nagata & Ushimaru 2016).

The endangered and threatened grassland species richness and the *Platycodon grandiflorus* presence significantly increased with the sunlight duration on ski runs, indicating that more open grasslands without neighboring forests were preferred by the species. The findings suggest that endangered and threatened grassland plants may require sufficient light conditions. Meanwhile, the species richness was influenced neither by the vegetation height nor the aboveground biomass, although endangered and threatened species are often distributed in habitats with low aboveground biomass and vegetation height in Europe and Japan (Venterink et al. 2003; Wassen et al. 2005; Nagata & Ushimaru 2016). The annual mowing management might maintain enough low vegetation height and aboveground biomass for such species everywhere in the study ski runs whereas the establishments of secondary forests and conifer plantations might cause habitat degradation for the endangered and threatened grassland species via reducing direct sunlight.

Our findings give important insights to conservation planning for semi-natural grassland biodiversity in Japan. First, to maintain ski runs like semi-natural grasslands is effective to provide habitats for endangered and threatened grassland species. Ski runs are known to function as a habitat of an endangered butterfly species, *Melitaea ambigua* as well (Nakahama et al. 2018). Second, open and wide ski runs with soil pH of c. 5.0–5.8 would be more ideal for conserving endangered and threatened grassland species. Therefore, abandonment and narrowing of ski runs and artificial snow (ammonium sulfate) application and surface soil removal by machine grading, both of which will change soil properties (c.f. Watson 1985; Tsuyuzaki 1990; Tatemoto & Nakamura 1998; Roux-Fouillet et al. 2011), should be avoided. Unfortunately, some ski runs and their managements have been abandoned during the last decades due to economic reasons (Nakamura 1999) whereas other runs have been more intensively managed with machine grading and snow application (A. Ushimaru personal observation). We should inform resort companies, national and local governments, local residents, conservationists and researchers that ski runs have functioned as habitats for endangered grassland plants by providing more open grassland conditions for more than 70 years. Although this study concentrated on endangered and threatened plant species which were distributed in low densities, diversity and composition of whole grassland plant and animal species on ski runs should be examined to clarify the potential of ski runs as a new habitat type for the whole semi-natural grassland community in future.

Author contributions

Y.A.Y., T.K. and A.U. planned the research. All authors conducted field works. Y.A.Y. and A.U. conducted statistical analyses and wrote the first manuscript and all authors critically revised the manuscript.

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References

Brauner, N. & Shacham, M. 1998. Role of range and precision of the independent variable in regression of data. *AIChE Journal* 44: 603–611.

Burt, J.W. & Rice, K.J. 2009. Not all ski slopes are created equal: disturbance intensity affects ecosystem properties. *Ecological Applications* 19: 2242–2253.

Butchart, S.H.M., Walpole, M., Collen, B., Strien, A. van, Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C. & Watson, R. 2010. Global biodiversity: indicators of recent declines. *Science* 328: 1164–1168.

Dengler, J., Janišová, M., Török, P. & Wellstein, C. 2014. Biodiversity of Palaearctic grasslands: a synthesis. *Agriculture, Ecosystems & Environment* 182: 1–14.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., (…) & Wilson, R. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30: 609–628.

Gerstner, K., Dormann, C.F., Stein, A., Manceur, A.M. & Seppelt, R. 2014. Effects of land use on plant diversity – a global meta-analysis. *Journal of Applied Ecology* 51: 1690–1700.

Kleijn, D., Bekker, R.M., Bobbink, R., Graaf, M.C.C.D. & Roelofs, J.G.M. 2008. In search for key biogeochemical factors affecting plant species persistence in heathland and acidic grasslands: a comparison of common and rare species. *Journal of Applied Ecology* 45: 680–687.

Nagata, Y.K. & Ushimaru, A. 2016. Traditional burning and mowing practices support high grassland plant diversity by providing intermediate levels of vegetation height and soil pH. *Applied Vegetation Science* 19: 567–577.

Nakahama, N., Uchida, K., Ushimaru, A. & Isagi, Y. 2018. Historical changes in grassland area determined the demography of semi-natural grassland butterflies in Japan. *Heredity* 121: 155–168.

Nakamura, T. 1999. A review of scientific studies on ski areas in Japan. *Japanese Journal of Ecology* 49: 261–264. [In Japanese]

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A. & Purvis, A. 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520: 45–50.

R Core Team. 2016. R: *A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

Rolando, A., Caprio, E., Rinaldi, E. & Ellena, I. 2007. The impact of high-altitude ski-runs on alpine grassland bird communities. *Journal of Applied Ecology* 44: 210–219.

Roux-Fouillet, P., Wipf & S., Rixen, C. 2011. Long-term impacts of ski piste management on alpine vegetation and soils. *Journal of Applied Ecology* 48: 906–915.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., (…) & Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.

Satake, Y., Ohwi, J., Kitamura, S., Watari, S. & Tominari, T. 1981. Wild Flower of Japan: Herbaceous Plants. Vols. I–III. Heibonsha, Tokyo, JP. [In Japanese]

Tatemoto, Y. & Nakamura, T. 1998. The actual situation of using ammonium sulfate in skiing areas. *Japan Outdoor Education Journal* 2-1: 13–19. [In Japanese]

Török, P. & Dengler, J. 2018. Palaearctic grasslands in transition: overarching patterns and future prospects. In: Squires, V.R., Dengler, J., Feng, H. & Hua, L. (eds.) *Glasslands of the world: diversity, management and conservation*, pp. 15–26. CRC Press, Boca Raton, US.

Tsuyuzaki, S. 1990. Species composition and soil erosion on a ski area in Hokkaido, northern Japan. *Environmental Management* 14: 203–207.

Tsuyuzaki, S. 1994. Environmental deterioration resulting from ski-resort construction in Japan. *Environmental Conservation* 21: 121–125.

Tsuyuzaki, S. 1995. Ski slope vegetation in central Honshu, Japan. *Environmental Management* 19: 773–773.

Tsuyuzaki, S. 2002. Vegetation development patterns on skislopes in lowland Hokkaido, northern Japan. *Biological Conservation* 108: 239–246.

Uchida, K., Takahashi, S., Shinohara, T. & Ushimaru, A. 2016. Threatened herbivorous insects maintained by long-term traditional management practices in semi-natural grasslands. *Agriculture, Ecosystems & Environment* 221: 156–162.

Uematsu, Y. & Ushimaru, A. 2013. Topography- and management-mediated resource gradients maintain rare and common plant diversity around paddy terraces. *Ecological Applications* 23: 1357–1366.

Ushimaru, A., Uchida, K. & Suka, T. 2018. Grassland biodiversity in Japan: threats, management and conservation. In: Squires, V.R., Dengler, J., Feng, H. & Hua, L. (eds.) *Grasslands of the world: diversity, management, and conservation*, pp. 197–218. CRC Press, Boca Raton, US.

Venterink, H.O., Wassen, M.J., Verkroost, A.W.M. & Ruiter, P.C.D. 2003. Species richness–productivity patterns differ between N-, P-, and K-limited wetlands. *Ecology* 84: 2191–2199.

Wassen, M.J., Venterink, H.O., Lapshina, E.D. & Tanneberger, F. 2005. Endangered plants persist under phosphorus limitation. *Nature* 437: 547–550.

Watson, A. 1985. Soil erosion and vegetation damage near ski lifts at Cairn Gorm, Scotland. *Biological Conservation* 33: 363–381.

Wesche, K., Ambarlı, D., Kamp, J., Török, P., Treiber, J. & Dengler, J. 2016. The Palaearctic steppe biome: a new synthesis. *Biodiversity and Conservation* 25: 2197–2231.

Wipf, S., Rixen, C., Fischer, M., Schmid, B. & Stoeckli, V. 2005. Effects of ski piste preparation on alpine vegetation. *Journal of Applied Ecology* 42: 306–316.

Yonekura, K. & Kajita, T. 2003. *BG Plants: index of Japanese names and scientific names (YList)*. URL: http://ylist.info/index.html. [in Japanese]