

Effect of mowing on population maintenance of the endangered silver-studded blue butterfly, *Plebejus subsolanus iburiensis* (Lepidoptera: Lycaenidae), throughout its life cycle

Masato Hayamizu

hayamizu-masato@hro.or.jp

Hokkaido Research Organization

Naoyuki Nakahama

University of Hyogo

Atsushi Ohwaki

J. F. Oberlin University

Gohta Kinoshita

National Institute of Genetics

Yoko Uchida

Hokkaido Research Organization

Nobuyoshi Koyama

Maruseppu Insectarium

Kazutaka Kida

Maruseppu Insectarium

Research Article

Keywords: semi-natural grassland, nationally rare species of wild fauna and flora, species diversity, management

Posted Date: August 21st, 2023

DOI: <https://doi.org/10.21203/rs.3.rs-3259067/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Journal of Insect Conservation on March 27th, 2024. See the published version at <https://doi.org/10.1007/s10841-024-00552-9>.

Effect of mowing on population maintenance of the endangered silver-studded blue butterfly, *Plebejus subsolanus iburiensis* (Lepidoptera: Lycaenidae), throughout its life cycle

Masato Hayamizu^{1*}, Naoyuki Nakahama^{2,3*}, Atsushi Ohwaki⁴, Gohta Kinoshita⁵, Yoko Uchida¹, Nobuyoshi Koyama⁶, Kazutaka Kida⁶

¹ Forestry Research Institute, Hokkaido Research Organization, Higashiyama, Koshunai, Bibai, Hokkaido 079-0198, Japan

² Institute of Natural and Environmental Sciences, University of Hyogo, Sanda City, Hyogo, 669–1546, Japan

³ The Museum of Nature and Human Activities, Hyogo, 6 Yayoigaoka, Sanda Hyogo 669–1546, Japan

⁴ College of Arts and Sciences, J. F. Oberlin University, Machida, Tokyo 194-0294, Japan

⁵ Ecological Genetics Laboratory, National Institute of Genetics, Mishima, Shizuoka 411-8540, Japan

⁶ Maruseppu Insectarium, Kamimuri, Maruseppu, Engaru Town, Hokkaido, Japan

*These authors contributed equally to the study.

Correspondence: Masato Hayamizu

Email; hayamizu-masato@hro.or.jp

ORCID: 0000-0002-4186-0328

26 **Abstract**

27 *Introduction:* The decline in semi-natural grasslands is posing a threat to several grassland
28 insect species, including the silver-studded blue butterfly, *Plebejus subsolanus* ssp.
29 *iburiensis*, which is nationally rare species of wild fauna in Japan.

30 *Aims:* This study aimed to investigate the impact of mowing on larval and adult populations
31 of *P. subsolanus* in a conservation area and to identify suitable habitat management methods
32 for this species and other butterflies. We surveyed the number of larvae and adults of *P.*
33 *subsolanus*, other butterfly species, and the height, cover, and number of inflorescences of
34 the host plant (*Vicia unijuga*), in both mowed and unmowed areas.

35 *Results:* Larvae only appeared in the mowed area, and the cover and height of host plant were
36 markedly higher in the mowed area. Furthermore, the number of adult *P. subsolanus* was
37 substantially higher in the mowed areas. However, no statistical differences were observed
38 in the number of other butterfly species, species richness, inflorescences or number of
39 flowering plants between the mowed and unmowed areas.

40 *Discussion:* The mowed area is an important habitat for both larvae and adults of *P.*
41 *subsolanus*. Although there were no differences in the number of other butterfly species and
42 flowering plants between the mowed and unmowed areas, the vegetation height was
43 negatively correlated with these variables.

44 *Implications for insect conservation:* Our results show that the creation of areas with reduced
45 vegetation height could be effective in the conservation management of butterfly and floral
46 communities, including *P. subsolanus* and its host plants.

47 **Keywords;** semi-natural grassland, nationally rare species of wild fauna and flora, species
48 diversity, management

1. Introduction

The global decline in semi-natural grasslands, which are maintained by human activities, has been a long-standing issue since the 20th century (Henwood 2010; Nunez et al. 2020; Endress et al. 2022). This decline has become more pronounced due to recent various human activities, including urbanization (Noda et al. 2019), agricultural expansion (Wright and Wimberly 2013), and climate change (Wu et al. 2021). Semi-natural grasslands in East Asia are characterized by distinct and rich biodiversity, with unique flora and fauna and have high conservation value (Ushimaru et al. 2018; Ohwaki 2018). Therefore, conservation efforts are crucial in preserving the remaining ecosystems of semi-natural grasslands in East Asia.

Mowing is a crucial management method to maintain the ecosystems of semi-natural grasslands (Endels et al. 2007; Nakahama et al. 2016; Tälle et al. 2016; Wintergerst et al. 2021). However, the positive and negative effects of mowing on the grassland biodiversity depend on how and where it is applied. On the positive side, mowing can promote grassland conservation by removing the biomass of competitive dominant herbs and preventing the growth of woody vegetation, which can facilitate coexistence of less competitive herbaceous plants (Huhta et al. 2001). On the negative side, improper mowing may pose a threat to the persistence of grassland ecosystems (Uchida and Ushimaru 2014). For example, mowing at inappropriate periods, such as during the reproductive stage, can substantially reduce genetic diversity and reproductive success (Brys et al. 2004; Nakahama et al. 2016). Hence, to conserve endangered species in semi-natural grasslands, it is necessary to clarify management methods that consider the appropriate timing and frequency of mowing based on the life cycles of the organisms that use them as habitat.

The silver-studded blue, *Plebejus subsolanus*, is a grassland butterfly distributed in the central Honshu and Hokkaido islands. The Japanese populations have been classified into three subspecies, all of which were listed in the national Red List (Ministry of the Environment 2020). *Plebejus subsolanus* ssp. *iburiensis*, is a critically endangered butterfly species that inhabits semi-natural grasslands in Hokkaido, Japan (Nagamori et al. 2016; Ministry of the Environment 2023). This butterfly species has a unique relationship with its sole host plant, *Vicia unijuga* (Fabaceae) in Hokkaido (Nagamori et al. 2016; Fig. 1). Eggs are oviposited at the base of the host plant, leaf, and stems (Fig. 1). After overwintering in the egg stage, the larvae emerge and feed on the host plants from April to May (Fig. 1). During early and middle June, the larvae sequentially become pupae, but the location of pupation remains unknown. Adult butterflies feed on nectar and flowers, including host plant inflorescences, emerge in large numbers in July, and mate around host plants (Fig. 1).

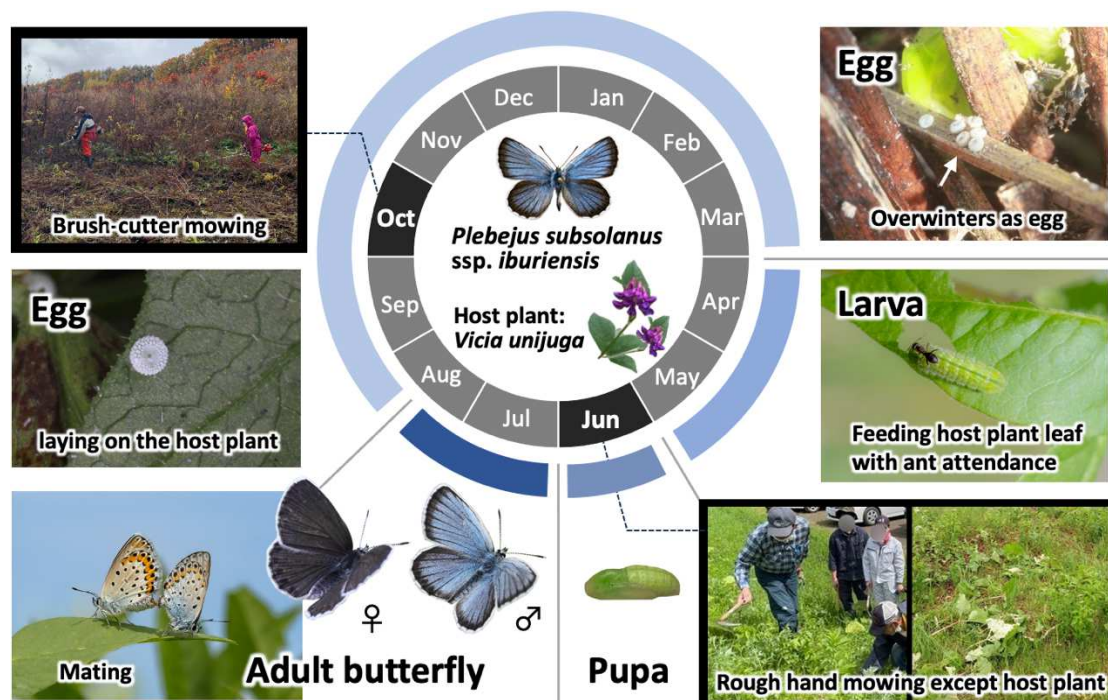


Fig. 1 Life cycle of the *Plebejus subsolanus* ssp. *iburiensis* and mowing management in the current study

Human land-use changes since the late 20th century in Hokkaido have caused rapid habitat loss and decline, resulting in a high risk of extinction for *P. subsolanus* ssp. *Iburiensis* (Nagamori et al. 2016). This subspecies is classified as critically endangered by the Ministry of the Environment of Japan (2020), listed as endangered in the Ministry of the Environment's Red Data Book as class IA (CR) (Ministry of the Environment 2020). Furthermore, it was designated as a "nationally rare species of wild fauna and flora in Japan" under the law for conservation of species in Japan in March 2016 (Ministry of the Environment 2023). Despite monitoring for this butterfly species in Engaru Town in Hokkaido since 2016, which is the only conservation area for *P. subsolanus* ssp. *iburiensis* in Japan, a specific habitat management plan has not yet been determined.

The aim of this study was to investigate the impact of mowing on conservation in a *P. subsolanus* conservation area located in Hokkaido, Japan. Specifically, we tested the effects of mowing on the abundance of both larvae and adults by avoiding mowing at the time of larval and adult emergence, which was done in mid-June (pupal stage) and in October (egg stage). We also assessed how habitat conditions, such as vegetation height, other butterflies, and flowering plants, differed with and without mowing, and whether these conditions changed over multiple years.

2. Materials and methods

2.1 Study site

The study site was an approximately 3.4 ha of gently sloping grassland surrounded by the forest of the Japan Self-Defense Force (JSDF) soldiers on Camp Engaru, Hokkaido Prefecture, Japan, which is designated as a conservation area for *P. subsolanus* by the

Maruseppu Insect Club, the Maruseppu Education Center, and the JSDF (Fig. 2). An area of approximately 1 ha within this area was the mowed area. JSDF members and the Maruseppu Insect Club have mowed vegetation twice a year since 2019 (in June and in October). During the pupal period of 2020 and 2021 (middle to late June), rough hand mowing of only the surrounding, tall-stemmed plants (except *V. unijuga*) was conducted using mowing sickles to maintain *V. unijuga*, a host plant of *P. subsolanus* (Fig. 1). In October 2020 and 2021, after the butterfly adult emergence was completely ended (egg season), all plants in the mowed area (1 ha) were cut with a brush-cutter to remove woody plants (Fig. 1). Although the site has long been managed by the JSDF as a ski practice area, prior to 2018, detailed timing and frequency on mowing locations and frequency are not available.

2.2 Field survey and data collection

Plebejus subsolanus and other adult butterflies were surveyed in July in both 2021 and 2022, corresponding with the emerging period of *P. subsolanus* (Nagamori et al. 2016; Nakahama et al. 2022). Larvae of *P. subsolanus* was surveyed once in late May 2022. For the larval stage survey, a total of 15 quadrats (1×1 m) were placed, nine within the mowed area and six in the unmowed area (Fig. 2B). We measured the number of *P. subsolanus* larva, percentage cover and height of *V. unijuga*, and average vegetation height in each quadrat.

For the adult butterfly survey, we applied the line transect method and established 3 × 30 m lines (Pollard and Yates 1993), three in the mowed area and four in the unmowed area (Fig. 2B). The survey was implemented for 15 min per line during periods with warm and sunny conditions (air temperature: 23–28 °C). Within the lines, we measured the number of *P. subsolanus* adults and other adult butterfly species, the number of *V. unijuga*

inflorescences, the inflorescence number of insect-pollinated plants, and vegetation height. An inflorescence of flowering plants was counted as one unit because individual butterflies land on inflorescences. The survey lines for adults were set at the same location in both years.

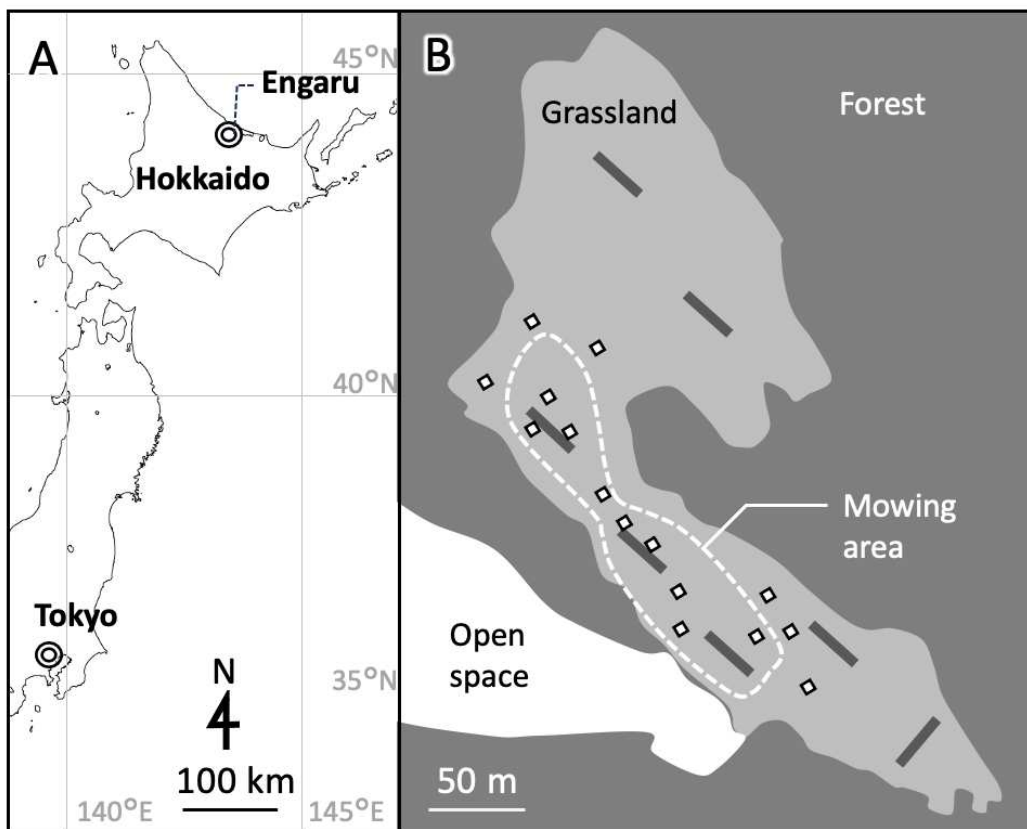


Fig. 2 Location of Engaru Town, Hokkaido, where the study site was located (A). (□) in the figure B indicates the location of the quadrat established during the larval stage survey conducted in May, and the thick line indicates the location of the line census (3×30 m) conducted during the adult stage in July (B)

2.3 Statistical analysis

We compared the vegetation height in the mowed and unmowed areas during the larval stage using *t*-tests to determine whether the difference was significant. To analyze the effects of mowing on the larvae and adults of *P. subsolanus*, *V. unijuga* (the host plant), other

insect-pollinated plants, and other butterflies, we applied generalized linear mixed models (GLMMs), assuming a Poisson distribution. In the larval period, the explanatory variable was the presence or absence of mowing, and the response variables were the number of *P. subsolanus* larvae, cover degree, and height of *V. unijuga*. In the adult period, the presence or absence of mowing was used as an explanatory variable, while the number of *P. subsolanus* adults, the number of *V. unijuga* inflorescences, the inflorescence number of insect-pollinated plants, the number of other butterfly species, and vegetation height were used as response variables. For the period of adult butterfly data, the survey year was used as a random effect.

To assess how butterflies were affected by vegetation height and inflorescences in July, GLMMs, assuming a negative binominal distribution, were applied. The explanatory variable was vegetation height. The responsible variables were numbers of other butterfly species and individuals, inflorescence number of insect-pollinated plants, or number of inflorescences of *V. unijuga*. For the period of adult butterfly data, the survey year was used as a random effect.

To examine whether *P. subsolanus* could serve as indicators of other butterfly communities, the correlations between the number of *P. subsolanus* adults and the number of species and individuals of other butterfly adults were evaluated using Spearman's correlations. All statistical analyses were performed using R software (R Development Core Team 2023)

3. Results

3.1 Effect of mowing on the larval period

168 A total of 13 *P. subsolanus* larvae were observed. Larvae appeared in nine of the
169 mowed quadrats and none were observed in the unmowed quadrats. The number of larvae
170 per quadrat was higher in the mowed area (mean: 1.44 larvae/m²) than in the unmowed area
171 (mean: 0.00 larvae/m²) (Deviance test, $P < 0.001$, Fig. 3A). The cover degree and height of
172 *V. unijuga* within the mowed plots were higher than those in the unmowed plots (Wald test,
173 $P < 0.001$, Table 1, Fig. 3B, C). Vegetation height was lower in the mowed quadrats than in
174 the unmowed quadrats (t -test, $P < 0.001$, Fig. 3D).

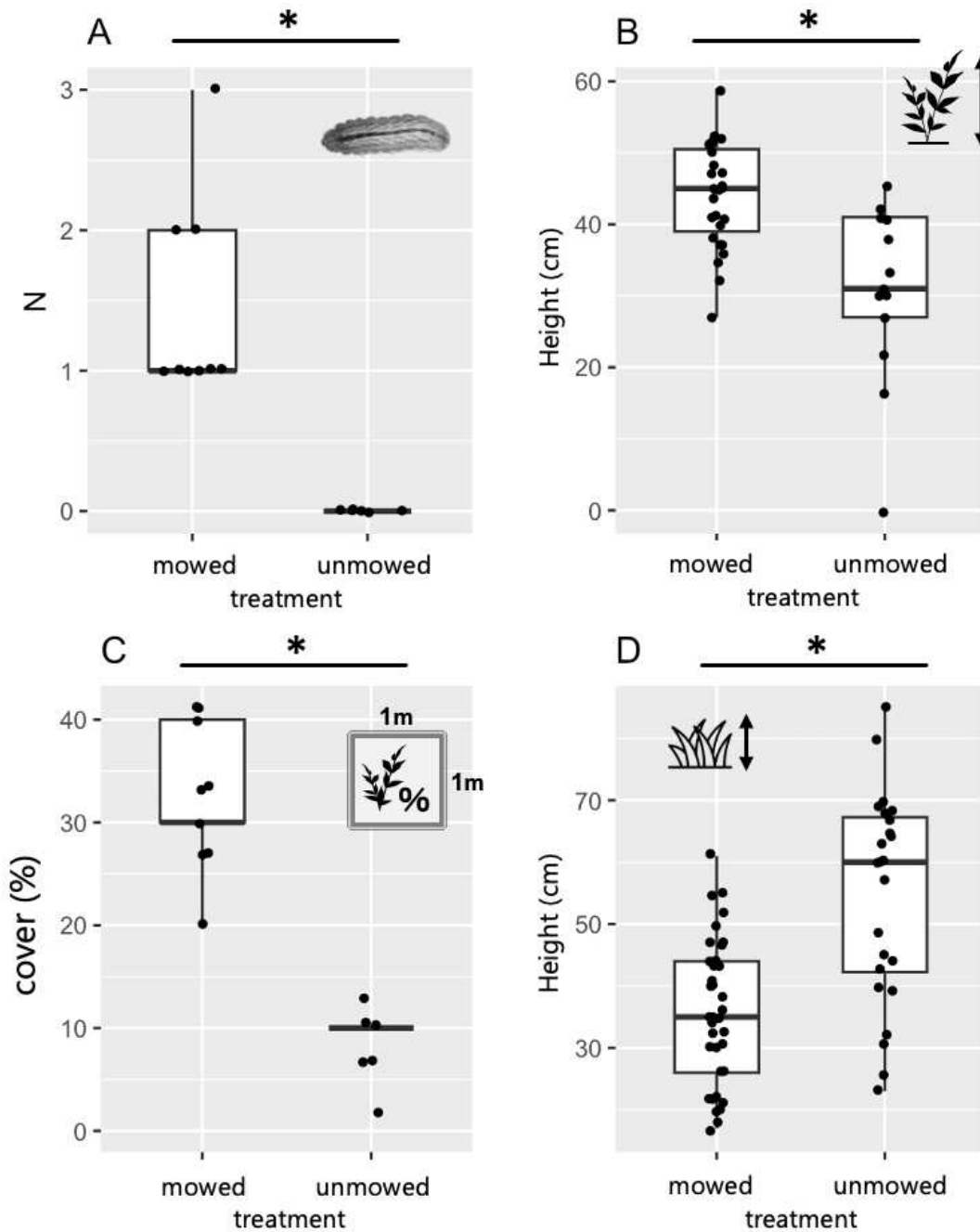


Fig. 3 The results of mowing on the larval period (horizontal axis categories). The vertical axes are the number of larvae of *Plebejus subsolanus* (A), *Vicia unijuga* height (cm) (B), coverage (%) (C), and other vegetation height (cm) (D) in mowed and unmowed plots. * denotes statistically significant differences ($P < 0.05$).

3.2 Effect of mowing on adult period

The number of *P. subsolanus* adults was higher (Wald test, $P < 0.001$) in the mowed lines (mean: 5.67/90 m² in both years) than in the unmowed lines (mean: 0.50–0.75/90 m², Table 1, Fig. 4A). The number of inflorescences of *V. unijuga* was also higher in the mowed lines (Wald test, $P < 0.001$, Table 1, Fig. 4B). Both the number of flowering plants and vegetation height were not different between the mowed and unmowed lines (Wald test, $P > 0.05$, Table 1, Fig. 4C, D).

Table 1 Generalized linear mixed models (GLMM) analyzing the effect of mowing on *P. subsolanus*, host plant (*Vicia unijuga*), other butterflies and flowering plants.

Season	Response variable	Coefficient [#]	SE	<i>P</i> value	
May (Larval period)	No. of <i>P. subsolanus</i>	21.67	-	$P < 0.001$	*
	Coverage of <i>Vicia unijuga</i>	1.352	0.153	$P < 0.001$	*
	Height of <i>V. unijuga</i>	11.537	3.087	$P = 0.003$	*
July (Adult period)	No. of <i>P. subsolanus</i>	2.627	1.098	$P = 0.017$	*
	No. of <i>V. unijuga</i> inflorescence	2.141	0.984	$P = 0.030$	*
	No. of butterflies	0.666	0.342	$P = 0.051$	
	Butterfly species	0.270	0.288	$P = 0.349$	
	Inflorescence of flowering plants	0.133	0.287	$P = 0.644$	
	Species of flowering plant	0.126	0.183	$P = 0.492$	

Vegetation height	0.205	0.145	$P = 0.158$
-------------------	-------	-------	-------------

191 Footnote: The coefficients are shown as the differences from unmowed plots (unmowed plots
192 were the baseline). P -values for the number of *P. subsolanus* larvae represent the results of
193 likelihood ratio tests. Random effects of survey year were used for all variables in the analysis
194 of the adult period. Asterisks (*) represent a statistical significance ($P < 0.05$); SE, standard
195 error.

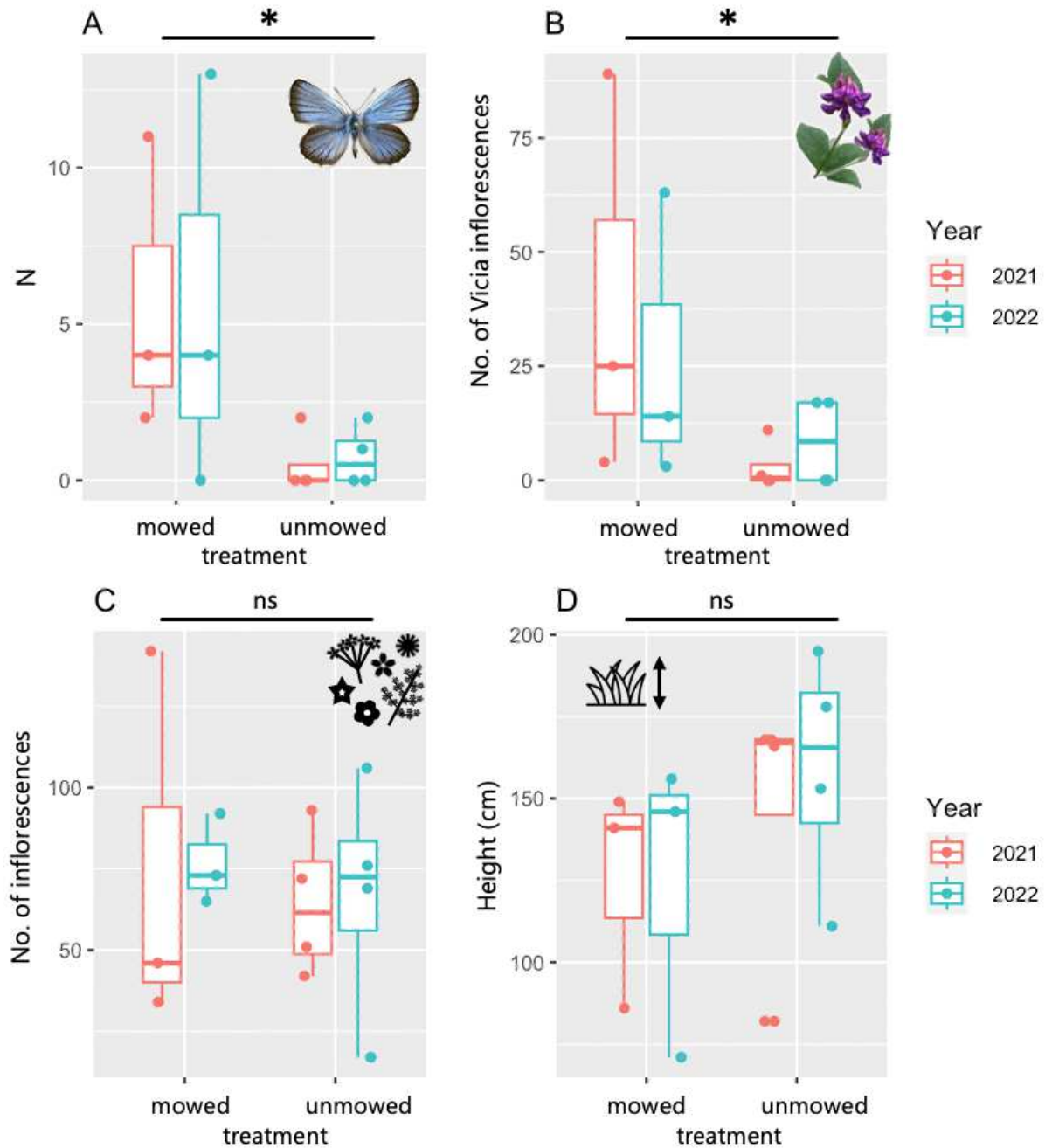


Fig. 4 The effects of mowing in the adult period (horizontal axis categories). Vertical axes are the number of adult *Plebejus subsolanus* (A), the number of *Vicia unijuga* inflorescences (B), inflorescences of other flowering plants (C), and vegetation height (D) in mowed and unmowed plots. * denotes statistically significant differences ($P < 0.05$)

3.3. Relationship between vegetation variables, *P. subsolanus*, and other butterflies

A total of 248 butterfly individuals of 18 species were recorded over the two years, including the *P. subsolanus*, with 156 individuals from 13 species recorded in 2021 and 92 individuals from 10 species recorded in 2022.

The vegetation height had no effect on the number of *P. subsolanus* (GLMM, $P = 0.135$, Fig 5A). The numbers of butterfly species and individuals and vegetation height were negatively correlated (GLMM, butterfly species: $P < 0.001$, No. of butterflies: $P < 0.001$, Fig 5B, C). Both the number of inflorescences of flowering plants and the number of inflorescences of *V. unijuga* were negatively correlated with vegetation height (GLMM, overall number of inflorescences: $P < 0.001$, number of inflorescences of *Vicia unijuga*: $P < 0.001$, Fig. 5D, E).

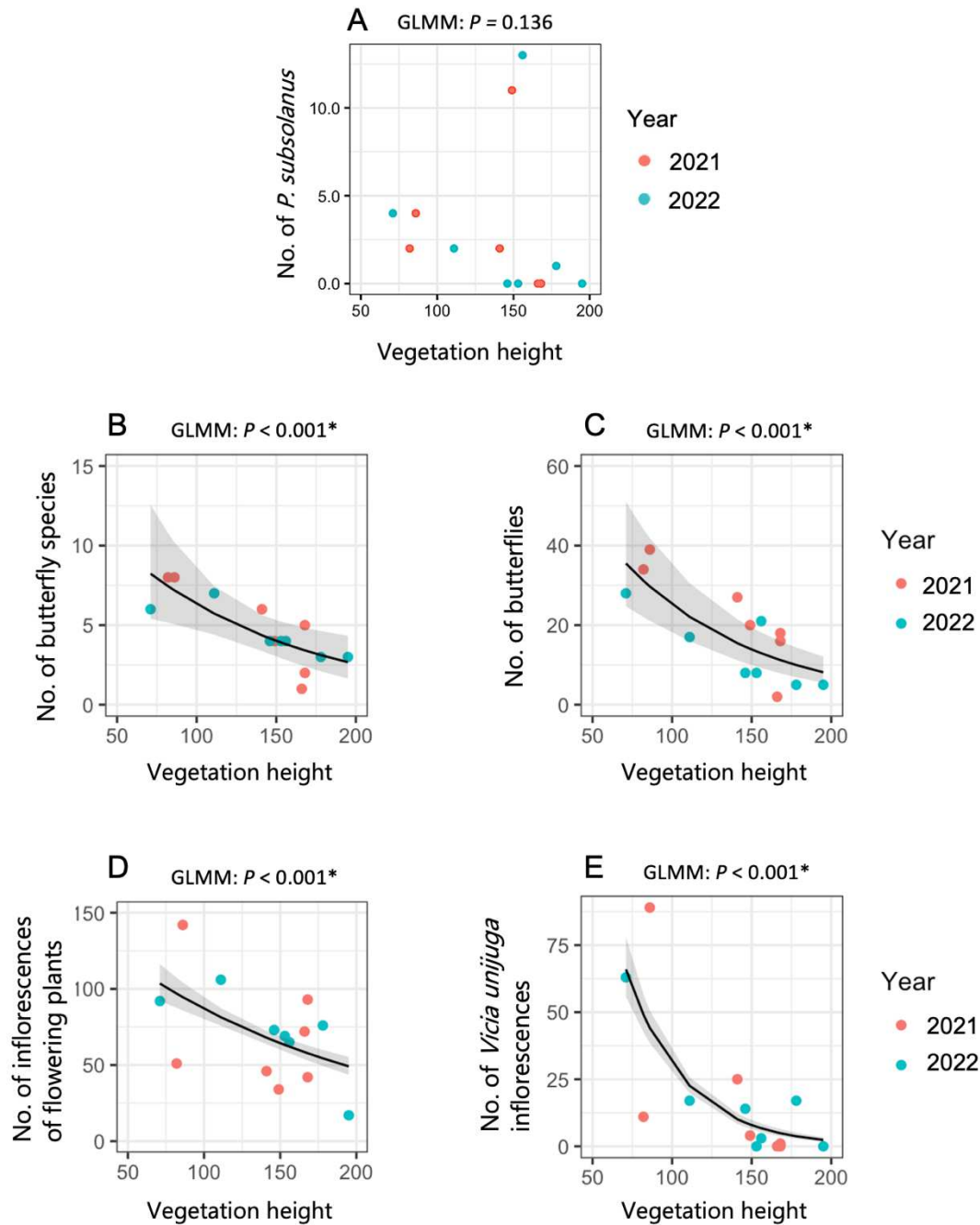


Fig. 5 Relationship between vegetation height and each response variable during the *Plebejus subsolanus* adult stage. Number of *P. subsolanus* adults (A), number of butterfly species (B), number of butterfly individuals (C), overall number of inflorescences (D), and number of inflorescences of *Vicia unijuga* (E). Regression curves indicated by solid lines show generalized linear mixed model results (gray area, 95 % confidence interval)

4. Discussion

The present study demonstrated that suitable mowing practices which take into account the entire life cycle of *Plebejus subsolanus* have positive effects on both larval and adult populations. Larvae of *P. subsolanus* were only present in mowed areas with higher abundance of host plant (height and cover) and low vegetation height, indicating that the combination of bush-cutter mowing in autumn and rough hand mowing in June could provide a suitable habitat. The higher number of adult *P. subsolanus* in the mowed area than in unmowed areas during the two-year monitoring period emphasizes the success in mowing for adult populations over two years. Our results also suggest that mowing does not have a negative effect on other butterfly species and flowering plants in the conservation area.

4.1 The mowing effect on *P. subsolanus* and host plants

In this study, both larvae and adults showed a preference for mowed areas, with adults exhibiting this preference over two consecutive years. The mowed areas were rich in host plant inflorescences, which could have attracted adult butterflies. Although the egg-laying preferences of female butterfly adults were not quantitatively determined, previous studies indicate that this species tends to lay eggs in relatively open areas, such as habitat margins and the borders of bare areas (Ohwaki 2019). Additionally, larvae of *P. argyrognomon*, a semi-natural grassland species of the same genus, have been found to be more frequently parasitized by generalist flies on the higher host plants, resulting in lower survival rates as vegetation height increases (Yeh et al. 2021). Thus, mowing may have had a positive effect on the survival rate of larvae as well as on food and egg-laying sites for adult butterflies.

The response of host plants to mowing provides critical information for population maintenance of *P. subsolanus*. It is widely known that reducing vegetation height can mitigate the competition between plant species in grasslands (Nagata and Ushimaru 2016). In the current study, the higher number of flowers and higher cover and height of *V. unijuga* after either June or October mowing may be due to the mowing effect. Previous research has shown that the abundance of above-ground parts of *V. unijuga* is greater in brightly lit forest margins, replanting areas, and semi-natural grasslands where mowing is conducted regularly than inside shelterbelt forest (Nakahama et al. 2022). Therefore, the higher cover, height, and number of inflorescences of *V. unijuga* observed in the mowed areas in this study may be due to mowing, which has weakened competition between the host plant and other surrounding plants.

4.2 The effect of mowing on butterfly communities and flowering plants

We found that the mowing conducted in this study did not impact the diversity of butterfly species or flowering plants (Table 1). Because mowing can regulate vegetation height (Tälle et al. 2016), it may not always be beneficial for organisms that depend on specific fine-scale sites within semi-natural grasslands (Konvicka et al. 2023). During our survey of the *P. subsolanus* larval stage, we observed markedly lower vegetation height in mowed sites than in unmowed sites. However, during our adult stage surveys, vegetation height had recovered to similar levels as the unmowed sites after a few weeks (Fig. 4). Furthermore, there were low vegetation height lines in both mowed and unmowed areas over the two years (Fig. 4). Hence, our results indicate that mowing management applied in this study had minimal effect on the regulation of vegetation height in summer, which might have reduced the adverse effects of mowing on butterflies and flowers.

The vegetation height across the study sites was negatively correlated with the number of butterfly species, number of individual butterflies, the number of inflorescences of flowering plants, and host plants over the two years, regardless of whether the vegetation was mowed or not. This pattern is consistent with many previous studies conducted on temperate grasslands (Ohwaki 2019). The study site also served as a critical habitat for butterfly and flower communities in areas with low vegetation height. In addition, heterogeneous habitats with a mix of areas of low and high vegetation height have been shown to be important for grassland butterfly species, as males and females utilize areas of spatially distinct vegetation structure (Konvicka et al. 2023). Therefore, although this study stressed the importance of low vegetation height areas in maintaining butterfly and flowering plant diversity, further research may clarify the contribution of high vegetation height to overall diversity and the number of *P. subsolanus* at this study site.

4.3 Implications for habitat conservation and management

The study demonstrated that the mid-June and October mowing practices adopted in this study for two years had a positive effect on the conservation of the endangered *P. subsolanus* population. The timing of mowing was based on the life cycle of the species, with non-feeding (pupal and egg) stages selected to avoid damage to the larval and adult stages. This approach facilitated an optimal habitat for crucial life cycle processes such as larval feeding, adult nectaring, and reproduction. Even if the overall vegetation height was not sufficiently lowered by the egg-stage mowing (late autumn), rough hand mowing during the pupal stage (mid-June) may have facilitate the growth of host plants, which result in increased oviposition by adults. The few remaining habitat environments for this species in Hokkaido include regularly mowed grasslands along railroad and pasture edges (Nagamori

et al. 2016), lowland windbreak regeneration areas and forest edges, and small grasslands in the vicinity (Hayamizu et al. 2020; Nakahama et al. 2022). Continuing appropriate mowing practices in these known habitats is essential for conservation. However, this study did not investigate whether mowing in areas where *P. subsolanus* has been absent or extirpated would make them suitable habitat for the species. Moreover, while larvae are typically accompanied by ants, this study could not verify the effect of mowing season on ant populations and behavior. Future research which addresses these issues will provide valuable insights into management strategies for creating new grassland habitats suitable for *P. subsolanus*.

The conservation area in this study had been preserved as a semi-natural grassland for an extended period due to partial management of the forest as a JSDF ski-training area. The management of ski slopes and their former sites has been shown to provide vital habitats for various prairie species, including endangered species, and is considered to have high conservation value for other organisms (Yeh et al. 2021; Oki et al. 2022). Our study also revealed that mowing had no significant negative impact on other butterflies or flowering plants, indicating their preference for areas with low vegetation height in this habitat. Thereby, secondary benefit of the reduction in vegetation height due to mowing is that it provides suitable habitat for other butterflies and flowering plants. However, the conservation site where this study was conducted is relatively small (1 ha), the application of mowing management practices to other geographically distant *P. subsolanus* habitats is limited. Given the substantial population declines confronting semi-natural grassland organisms, particularly endangered species, as a result of habitat loss and fragmentation (Inoue & Nakagoshi, 2001; Uchida & Ushimaru, 2014; Nakahama et al., 2018; Ohwaki, 2018), it is essential to integrate the life cycle of endangered species and other community responses to

grass cutting habitat management, even on a small scale. For a comprehensive understanding of ecosystem management of semi-natural grasslands, future research should also take into account additional factors such as location and human land use differences among isolated habitats.

Acknowledgements We would like to thank the Japan Self-Defense Force, the Engaru Town Maruseppu Education Center, and the Maruseppu Insect Club for their cooperation. Dr. Kenta Iwasaki has been of great help to me in setting up the study and in preliminary research.

Author contributions All authors conceptualised and designed the study and all of them participated equally in collecting the data in the field. The first draft of the manuscript was written by MH, NN, and AO. All statistical analysis was performed by MH, NN, and AO. GK, YU, NK, and KK commented on previous versions of the manuscript. All authors approved the final manuscript.

Funding This work was supported by the Hokkaido Research Organization, JSPS KAKENHI Grants-in-Aid for Scientific Research (Grant Number 21H02221), the Environment Research Technology Development Fund (JPMEERF20224M02) of the Environmental Restoration and Conservation Agency provided by the Ministry of Environment of Japan, and by Pro Natura Foundation Japan's 31st and 33rd Pro Natura Fund.

Availability of data The data used in this study are available from the authors on request.

Statements and Declarations

336 **Competing interests** The authors declare no competing interests.

337 **Consent to participate** Not applicable.

338 **Consent for publication** Not applicable.

339 **Ethical approval** Not applicable.

340

341 **References**

342 Brys R, Jacquemyn H, Endels P, Blust GD, Hermy M (2004) The effects of grassland
343 management on plant performance and demography in the perennial herb *Primula veris*:
344 Plant performance and demography of a grassland herb. *J Appl Ecol* 41:1080–1091.
345 <https://doi.org/10.1111/j.0021-8901.2004.00981.x>

346 Endels P, Jacquemyn H, Brys R, Hermy M (2007) Reinstatement of traditional mowing
347 regimes counteracts population senescence in the rare perennial *Primula vulgaris*. *Appl*
348 *Veg Sci* 10:351–360. <https://doi.org/10.1111/j.1654-109X.2007.tb00434.x>

349 Endress BA, Averett JP, Steinmetz S, Quaempts EJ (2022) Forgotten forbs: Standard
350 vegetation surveys underrepresent ecologically and culturally important forbs in a
351 threatened grassland ecosystem. *Conserv Sci Pract* 4:e12813.
352 <https://doi.org/10.1111/csp2.12813>

353 Hayamizu M, Iwasaki K, Nitta N, Nakahama N (2020) Endangered wild fauna and flora in
354 shelterbelts of Hokkaido: The relationship between habitat and shelterbelt management.
355 *Koshunai-Kihou* 194:11–16

356 Henwood WD (2010) Toward a strategy for the conservation and protection of the world's
357 temperate grasslands. *Gr Plains Res* 20:121–134

358 Huhta A, Rautio P, Tuomi J, Laine K (2001) Restorative mowing on an abandoned semi-
 359 natural meadow: Short-term and predicted long-term effects. *J Veg Sci* 12:677–686.
 360 <https://doi.org/10.2307/3236908>

361 Inoue M, Nakagoshi N (2001) The effects of human impact on spatial structure of the
 362 riparian vegetation along the Ashida river, Japan. *Landsc Urban Plan* 53:111–121.
 363 [https://doi.org/10.1016/S0169-2046\(00\)00145-6](https://doi.org/10.1016/S0169-2046(00)00145-6)

364 Konvicka M, Hula V, Vlasanek P, Zimmermann K, Faltýnek Fric Z (2023) Within-habitat
 365 vegetation structure and adult activity patterns of the declining butterfly *Euphydryas*
 366 *Aurinia*. *J Insect Conserv* 27:335–346. <https://doi.org/10.1007/s10841-023-00459-x>

367 Ministry of the Environment, Government of Japan (2020) The Red List of insects of
 368 Japan. <https://www.env.go.jp/press/107905.html>. Accessed 31 Jan 2022 (in Japanese)

369 Ministry of the Environment, Government of Japan (2023) The list of the nationally
 370 endangered species of wild fauna and flora.
 371 <http://www.env.go.jp/nature/kisho/domestic/list.html>. Accessed 1 Apr 2023 (in
 372 Japanese)

373 Nagamori T, Nagamori H, Shibata T, et al (2016) The complete guide to butterflies of
 374 Hokkaido. Hokkaido University Press, Sapporo (in Japanese)

375 Nagata YK, Ushimaru A (2016) Traditional burning and mowing practices support high
 376 grassland plant diversity by providing intermediate levels of vegetation height and soil
 377 pH. *Appl Veg Sci* 19:567–577. <https://doi.org/10.1111/avsc.12252>

378 Nakahama N, Hayamizu M, Iwasaki K, Nitta N (2022) Management and landscape of
 379 shelterbelts contribute to butterfly and flowering plant diversity in northern Japan. *Ecol*
 380 *Res* 37:780–790. <https://doi.org/10.1111/1440-1703.12342>

381 Nakahama N, Uchida K, Ushimaru A, Isagi Y (2016) Timing of mowing influences genetic
 382 diversity and reproductive success in endangered semi-natural grassland plants. *Agric*
 383 *Ecosyst Environ* 221:20–27. <https://doi.org/10.1016/j.agee.2016.01.029>
 384 Nakahama N, Uchida K, Ushimaru A, Isagi Y (2018) Historical changes in grassland area
 385 determined the demography of semi-natural grassland butterflies in Japan. *Heredity*
 386 121:155–168. <https://doi.org/10.1038/s41437-018-0057-2>
 387 Noda A, Kondoh A, Nishihiro J (2019) Changes in land cover and grassland area over the
 388 past 120 years in a rapidly urbanised area in Japan. *OE* 4:e37669.
 389 <https://doi.org/10.3897/oneeco.4.e37669>
 390 Nunez S, Alkemade R, Kok K, Leemans R (2020) Potential biodiversity change in Central
 391 Asian grasslands: Scenarios for the impact of climate and land-use change. *Reg Environ*
 392 *Change* 20:39. <https://doi.org/10.1007/s10113-020-01619-4>
 393 Ohwaki A (2018) How should we view temperate semi-natural grasslands? Insights from
 394 butterflies in Japan. *Glob Ecol Conserv* 16:e00482.
 395 <https://doi.org/10.1016/j.gecco.2018.e00482>
 396 Ohwaki A (2019) Entire-area spring burning versus abandonment in grasslands: Butterfly
 397 responses associated with hibernating traits. *J Insect Conserv* 23:857–871.
 398 <https://doi.org/10.1007/s10841-019-00181-7>
 399 Oki K, Soga M, Amano T, Koike S (2022) Abandonment of ski pistes impoverishes
 400 butterfly communities. *Biodivers Conserv* 31:2083–2096.
 401 <https://doi.org/10.1007/s10531-022-02422-9>
 402 Pollard E, Yates TJ (1993) Monitoring butterflies for ecology and conservation. Springer
 403 Science & Business Media, London.

404 R Core Team (2023) R. R: A Language and Environment for Statistical Computing, version
 405 4.2.2. <http://www.R-project.org>. Vienna, Austria
 406 Tälle M, Deák B, Poschlod P, et al (2016) Grazing vs. mowing: A meta-analysis of
 407 biodiversity benefits for grassland management. *Agric Ecosyst Environ* 222:200–212.
 408 <https://doi.org/10.1016/j.agee.2016.02.008>
 409 Uchida K, Ushimaru A (2014) Biodiversity declines due to abandonment and
 410 intensification of agricultural lands: Patterns and mechanisms. *Ecol Monogr* 84:637–
 411 658. <https://doi.org/10.1890/13-2170.1>
 412 Ushimaru A, Uchida K, Suka T (2018) Grassland biodiversity in Japan: Threats,
 413 management and conservation. In: *Grasslands of the world*. CRC Press
 414 Wintergerst J, Kästner T, Bartel M, Schmidt C, Nuss M (2021) Partial mowing of urban
 415 lawns supports higher abundances and diversities of insects. *J Insect Conserv* 25:797–
 416 808. <https://doi.org/10.1007/s10841-021-00331-w>
 417 Wright CK, Wimberly MC (2013) Recent land use change in the Western Corn Belt
 418 threatens grasslands and wetlands. *Proc Natl Acad Sci U S A* 110:4134–4139.
 419 <https://doi.org/10.1073/pnas.1215404110>
 420 Wu G, Cheng Z, Alatalo JM, Zhao J, Liu Y (2021) Climate warming consistently reduces
 421 grassland ecosystem productivity. *Earths Future* 9:EF001837:e2020.
 422 <https://doi.org/10.1029/2020EF001837>
 423 Yeh Y, Deto H, Miyashita T (2021) Parasitism rate of *Plebejus argyrognomon*
 424 (Lepidoptera: Lycaenidae) under different levels of mowing management. *Entomol Sci*
 425 24:32–34. <https://doi.org/10.1111/ens.12448>
 426