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Original Research Article

How should we view temperate semi-natural grasslands? Insights from butterflies in Japan

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ABSTRACT

In humid temperate regions, it has been commonly thought that closed forests represent original states and grasslands are unstable human artifacts that persist only as “semi-natural” states. This perspective underrates grasslands, because it makes the recent decline in grassland excusable. A contrasting perspective was recently proposed for temperate Europe and North America, stating that grasslands are intrinsically natural and stable, and hence could have survived without human presence during the postglacial age. However, few quantitative analyses have been performed to test the validity of these two perspectives. Considering that the evolutionary history of species is reflected in species traits, analyzing traits of grassland species in relation to habitat stability is expected to identify the intrinsic nature of grasslands (stable or unstable) and test the validity of these two perspectives. Here, using temperate Japanese butterflies, I compared ecological traits, geographic range, endemism and habitat types in the Eurasian continent between grassland species and forest (stable habitat) and ruderal (unstable habitat) species. I found that grassland butterflies shared similar ecological traits with forest butterflies, but not with ruderal butterflies. Moreover, grassland butterflies were primarily associated with natural and stable steppes and meadows in the Eurasian continent. Furthermore, Japanese grassland species are evolutionarily unique, nurturing many endemic subspecies with narrow geographic ranges. These results indicate that grasslands should not be regarded as unstable, transient, and artificial, but as intrinsically natural and stable in humid temperate regions. These grasslands may have persisted in a stable state without human intervention during the Holocene due to natural disturbances and severe environmental conditions, which are currently immensely suppressed or altered by human. Such perspective also holds true for humid temperate regions in Europe and North America. Thus, temperate semi-natural grasslands should be conserved with high priority in these regions considering that few natural grasslands are left resulting from the present intensive land use pressures and disturbance suppression.

1. Introduction

In forested temperate regions in Europe and temperate mountain areas in the USA and East Asia, natural grasslands are rare and grasslands usually persist in “semi-natural” conditions. In this case, their persistence depends on moderate human

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intervention activities, such as mowing, grazing, and burning (Dengler et al., 2014; Habel et al., 2013; Pärtel et al., 2005; Ushimaru et al., 2018; Weigl and Knowles, 2014). These semi-natural grasslands have shown a continuous and rapid decline since the 20th century due to agricultural intensification and abandonment (Eriksson et al., 2002; Koyanagi and Furukawa, 2013; Ogura, 2012; van Swaay, 2002) As a result, many grassland species are presently endangered since they mainly inhabit semi-natural grasslands owing to the scarcity of natural grasslands in these regions (Habel et al., 2013; Nakamura, 2011). The scarcity of natural grasslands and dependence on human management for the persistence of semi-natural grasslands has led to the prevailing perspective that grasslands are unstable and transient human artifacts in humid temperate Europe (Vera, 2000; WallisDeVries et al., 2002), USA (Weigl and Knowles, 2014) and East Asia (Fukushima, 2017; Numata, 1969; Takahashi and Naito, 1997). In addition, the widespread belief that closed forests are the original state of humid temperate regions seems to be a reason for the naturalness of grasslands being deprecated (Fukushima, 2017; Vera, 2000; Weigl and Knowles, 2014). This perspectives lower the conservation value of grassland species in these regions because it has been generally considered that these species would not persist until today without the continuous human intervention since prehistoric times (Takahashi and Naito, 1997; Vera, 2000), which makes even some biologists think that the loss of grassland species is excusable (Weigl and Knowles, 2014). Although conservation biologists have searched for proper management measures for conserving semi-natural grasslands biodiversity (Balmer and Erhardt, 2000; Helm et al., 2006; Kruess and Tscharntke, 2002; Öckinger et al., 2006, 2012; Pöyry et al., 2006; Tscharntke et al., 2002; Uchida et al., 2016), the validity of the conventional perspective on humid temperate grasslands needs to be tested as it may cause the underestimation of the value of these grasslands.

Since the end of the 20th century, several authors proposed a contrasting perspective, stating that, during the Holocene, grasslands may have persisted on floodplains and mountainous cliffs in forested Europe without human intervention and under the pressures of large mammalian herbivores and fire (Pärtel et al., 2005; Pykälä, 2000; Svenning, 2002; Vera, 2000). In Japan, plants and butterflies observed in semi-natural grasslands are known to originate from the temperate Eurasian steppes and meadows (Hiura, 1971; Murata, 1988; Tabata, 1997). However, since Eurasian steppes are natural and stable grassland habitats that have persisted for millions of years (Dengler et al., 2014), it is contradictory that, in Japan, species derived from these stable habitats are currently mainly associated with unstable and transient semi-natural grasslands that need human intervention. Nevertheless, there have been few quantitative studies that test the validity of the conventional and contrasting perspectives and resolve the contradictory situation. Resolving this contradiction by clarifying the intrinsic nature (i.e., stability of habitats) and evolutionary history of grassland species could be important to test which of the two perspectives is likely to be valid in humid temperate regions. The intrinsic nature and evolutionary history of species are reflected in the ecological traits of species (Southwood, 1977). Butterflies are excellent subjects for this purpose owing to the considerable information available on their ecological traits, preferred biotopes and biogeography (Thomas, 2005).

The habitat templet theory (Southwood, 1977) helps to understand the intrinsic nature of the habitats where a species has evolved. This theory relates the stability of habitats with the ecological traits of species. It predicts that species that utilize spatially and temporally stable habitats tend to be univoltine, oligophagous and sedentary, whereas species that utilize unstable and unpredictable habitats tend to be multivoltine, polyphagous and mobile (Southwood, 1977, 1988). Since forests (stable) and human modified open (HMO) areas (unstable) are at opposite extremes along the successional gradient of habitat stability, comparing the ecological traits of grassland species to those associated with forests and HMO areas could help fathom the intrinsic nature of grasslands. Thus, if species closely associated with (semi-natural) grasslands are originally inhabitants of unstable habitats reflecting the conventional perspective of humid temperate grasslands, their ecological traits are expected to be similar to those of HMO species, whereas if grassland species are derived from stable habitats, such as the Eurasian steppes, their ecological traits are expected to be similar to those of forest species (Fig. 1). Moreover, to understand the evolutionary origin of these species, it should be helpful to examine which types of habitats (stable steppes and meadows or other unstable, man-made biotopes) the Japanese grassland butterfly species are associated with in the Eurasian continent. Furthermore, as mobility affects species' geographic ranges, mobile species (inhabitants of unstable habitats) tend to have larger geographic ranges, whereas sedentary species (inhabitants of stable habitats) tend to have narrower geographic ranges (Fig. 1; Dennis et al., 2004; Gaston, 2003). Endemism (existence of endemic species/subspecies) should also be taken into account, as high proportions of endemic species raise conservation priorities (Myers et al., 2000; Thomas, 1991); this would also provide information on the biogeographical position of the Japanese grasslands within East Asia.

In this study, I compiled information on ecological traits, endangered status, geographic range, endemism, and Eurasian habitats of all Japanese temperate butterflies from the published literature. The aim of the present study is to test the validity of the two perspectives regarding humid temperate grasslands by comparing the various species traits between species closely associated with grasslands and those associated with forests or HMO areas. Given the Japanese grassland species originate from natural and stable steppes and meadows, I predicted that, contrary to the conventional view, ecological traits, geographic range, and endemism of grassland species are closer to those of stable forest species than those of unstable HMO species. I discuss the intrinsic nature, evolutionary history, and conservation priorities of Japanese grassland species. I also discuss the persistence of grasslands in Japan during the Holocene on the assumption of human absence and showed an integrated view of grasslands throughout the forested temperate regions in the Northern hemisphere by reviewing research in humid temperate Europe and USA.

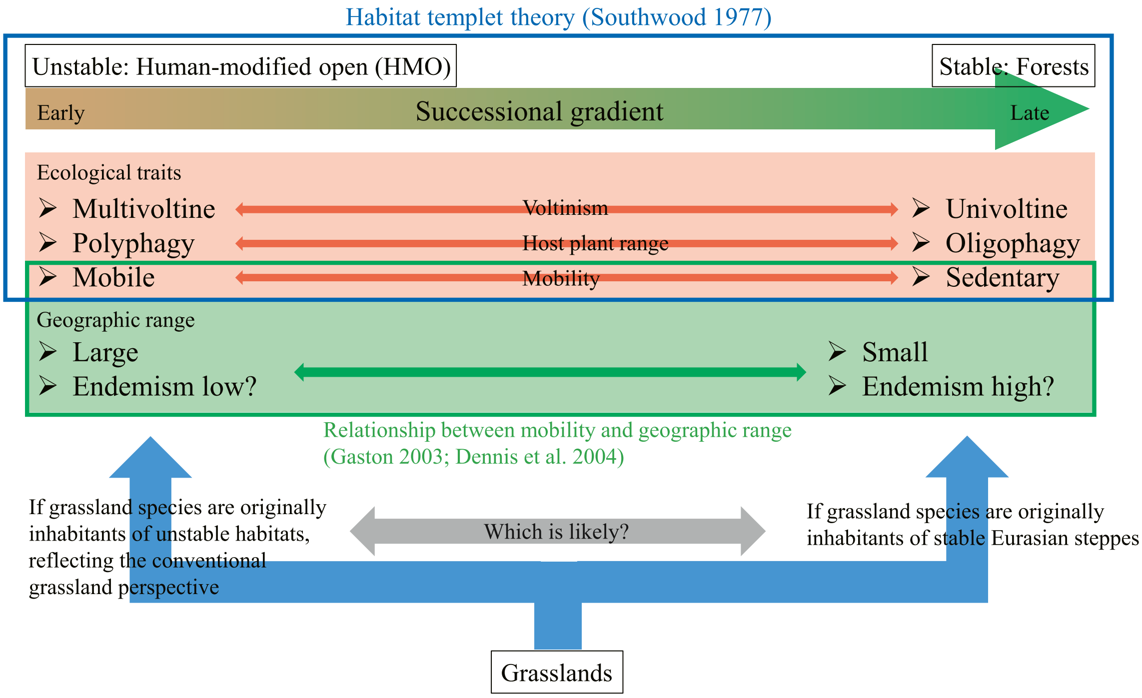

Fig. 1. Schematic view explaining the theoretical framework of the relationships between stability of habitats, evolution of species' ecological traits, and geographic range. To understand the intrinsic nature of grassland species, the ecological traits and geographic range of grassland species are compared with those of forest and human-modified open-habitat species.

2. Materials and methods

2.1. Selection of temperate butterfly species in Japan

There are approximately 240 native butterfly species in Japan. Since the target region in the present study is temperate (semi-natural) grasslands, I selected temperate butterfly species (hereafter "temperate species") and excluded species mainly confined to other climatic regions (Fig. 2). Considering that species from sub-tropical to tropical (southern) regions have higher average numbers of generations than temperate species, the species with distributions that reach the sub-tropical lowlands of Southeast Asia and those that are only distributed in the Ryukyu Islands of Japan (from the Amami and Okinawa Islands to the Yaeyama Islands) were omitted. Similarly, species completely confined to boreal and alpine areas of Japan were omitted because their geographic distributions are biased toward northern areas compared to those of temperate species. However, even if a species is distributed in the Ryukyu Islands, the species was treated as temperate species if its main geographic range is within temperate areas, but not sub-tropical lowland East Asia (e.g., *Polygonia c-aureum*, *Eurema mandarina* and *Colias erate*). As a result, 139 species of temperate butterflies were selected (Fig. 2, Supplementary material Table A1).

2.2. Classification of temperate species into forest, grassland and HMO species

The 139 temperate species were classified into forest, grassland, and HMO species based on a recent guidebook of Japanese butterflies (Japan Butterfly Conservation Society, 2012) (Fig. 2). In this guidebook, butterfly habitats are classified into 11 biotopes (forest, forest edge, open forest, grassland, wetland, agricultural land, riparian area, urban park, residential area, alpine area, and rocky area) to describe the habitats of the respective butterfly species. For example, it illustrates that *Luehdorfia japonica* occurs only in "forest," while *Pieris rapae* occurs in "agricultural land," "urban park," "residential area," and "riparian area." In this study, forest species were defined as those whose habitats must include "forest" and may also include "forest edge," "open forest," "agricultural land" (i.e., secondary forests in traditional agricultural areas), and "riparian area" (i.e., riparian forests), but never include any open areas (Supplementary material Table A1). The forest species as defined in this study inhabit natural and semi-natural (secondary) forests, but not modified urban forests or isolated woodlands. Grassland species were defined as those whose habitats must include "grassland" and may also include "wetland," "forest edge," "open forest," "agricultural land" (i.e., semi-natural grassy strips in traditional agricultural areas), "riparian area" (i.e., riparian grasslands), and "alpine area" (i.e., alpine meadows) (Kitahara and Watanabe, 2003; Uchida and Ushimaru, 2014), but never include "forest" or modified open areas, such as

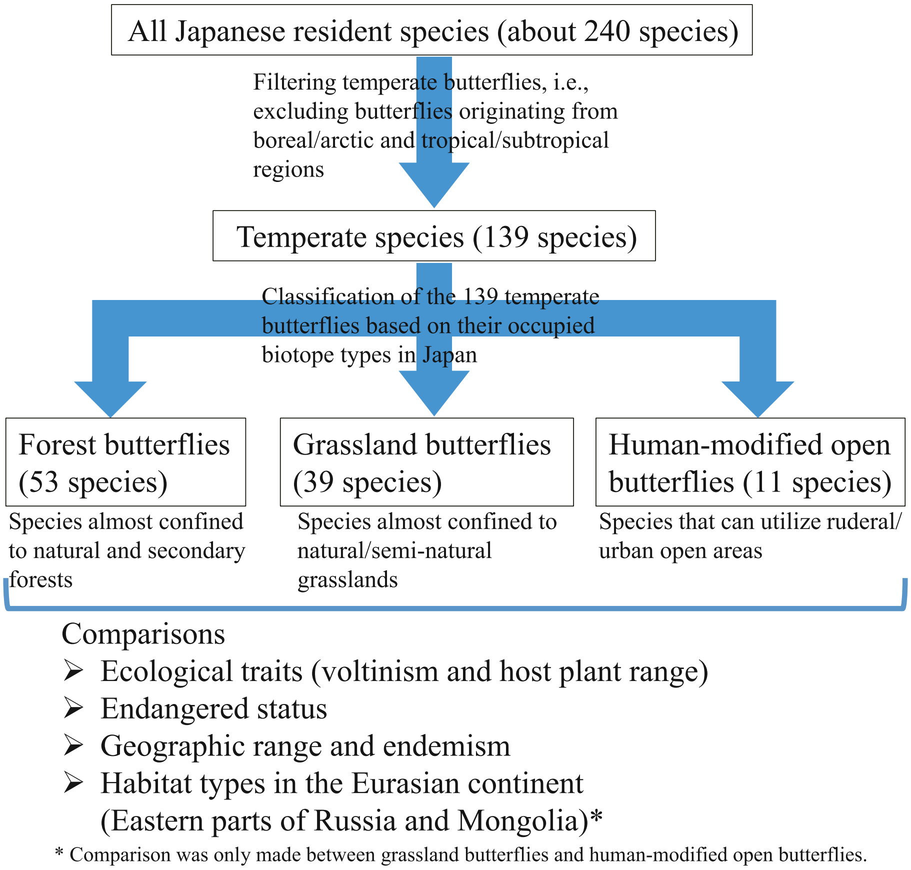

Fig. 2. Schematic view explaining the selection procedure of temperate forest, grassland, and human-modified open-habitat butterflies from 240 species of the entire Japanese butterfly pool.

“urban park” and “residential area” (Table A1). The grassland species as defined here are strongly associated with natural and semi-natural grasslands, but not with unstable and modified open biotopes. Although some grassland species utilize both natural and semi-natural grasslands in Japan, the majority of them depend to a great extent on semi-natural grasslands because of the scarcity of natural grasslands. The HMO species were defined as those that utilize unstable and modified open biotopes i.e., “agricultural land” (farmlands themselves), “urban park,” and/or “residential area” as well as grasslands, but not utilize “forest” (Table A1). In addition to the above habitat criteria, grassland and HMO butterflies was also required to have herbs/grasses or shrubs as host plants, but not trees (Supplementary material Table A1). Both grassland and HMO species are associated with open vegetation, but differ in the utilization of human-modified biotopes. Consequently, 53 forest, 38 grassland, and 11 HMO species were identified and used for the analyses (Fig. 2). Temperate species that possess other habitat associations were exclude.

2.3. Ecological traits, endangered status, geographic range, endemism, and Eurasian habitats

The ecological traits (voltinism and larval host plant range), endangered status, geographic range, and endemism were compared between grassland and forest/HMO species. The voltinism of each species was classified as univoltine or multivoltine (Shirozu, 2006), while host plant range was classified into four ranks (1: monophagous; 2: narrowly oligophagous, feeding on only one plant genus; 3: widely oligophagous, feeding on one plant family; or 4: polyphagous, feeding on more than one plant family) (Saito et al., 2016). *Shirozua jonasi* (forest butterfly) was omitted because it is a commensal species with *Lasius* ants and feeds on aphids and scale insects. The endangered status of each species was also classified into four ranks (1: endangered or critically endangered, 2: vulnerable, 3: near threatened, or 4: non-red-list species) based on the 2017 Red List of Threatened Species of Japan (Ministry of the Environment, Japan, 2017). When several subspecies were assigned to different categories of the Red List, the status of the most threatened subspecies was used. The geographic range of each species was classified into four ranks (1: endemic to Japan; 2: Pan-Japan Sea; 3: temperate East Asia; or 4: expanding to other temperate regions, such as Europe and North America, Fig. 3) (Gorbunov and Kosterin, 2003, 2007; Kim and Seo, 2012; Shirozu, 2006). For convenience, species that are distributed only within the Japanese archipelago, the Kurile Islands, and Sakhalin were classified as "endemic to Japan" because their geographic ranges are largely within the chain of the Japanese Islands (Fig. 3). The endemism of each species was classified into three ranks (1: endemic species, 2: endemic subspecies, or 3: non-endemic). All the above information is summarized in Table 1 and shown in detail in Table A1.

In addition, based on English-language literature from the Asian part of Russia (Gorbunov and Kosterin, 2003, 2007) and Mongolia (Tshikolovets et al., 2009), the habitat use in the Eurasian continent was consulted for grassland and HMO species and assigned to four categories: "species mainly associated with natural steppes and meadows (including open forests and clear-cuts)," "species that are able to utilize human modified areas (settlements, roads, fields, and waste lands)," "species mainly associated with forests," and "species absent in these regions". Clear-cuts were regarded as analogues of grasslands considering several studies have shown that many grassland species also utilize clear-cuts as habitats in Europe (Ibbe et al., 2011; Viljur and Teder, 2016) and Japan (Ohwaki et al., 2018b). The details of habitat use of each species in the Asian part of Russia and Mongolia are shown in Supplementary material Table A2.

2.4. Statistical analysis

An overview of the analytical procedures and the results of the statistical analyses are shown in Table 1. Differences in the ecological traits (voltinism and host plant range), endangered status, geographic range, endemism, and habitat use in the Eurasian continent were tested between grassland and forests/HMO species using generalized linear mixed models (GLMMs) and cumulative link mixed models (CLMMs). The differences between forest and HMO butterflies were not tested because the focus of this study was comparison between grassland and other habitats species, rather than the differences between forest and HMO species. When response variables were binary {voltinism (univoltine or multivoltine) and habitat use in the Eurasian continent (steppes/meadows or modified open biotopes)}, GLMMs (binomial and logit link) were performed with individual species regarded as independent data, butterfly group (grassland vs. forest/HMO) as explanatory variable, and tribe and family of each species as nested random factors (tribe nested within family). The remaining four items (host plant range, endangered status, geographic range, and endemism) have ordered ranks. For each of these ordered items, CLMMs were applied with individual species regarded as independent data, rank for each species as response variable, butterfly group (grassland vs. forest/HMO) as explanatory variable, and tribe and family of each species as nested random factors. A cumulative linear model (CLM: a method dropping random factors from CLMM) is the cumulative probability of the ith species falling in the jth rank or below. The CLM can be written as $\mathrm{logit}\,(P(Y_i \leq j)) = \theta_j - \beta(\mathrm{grassland}_i)$ (Christensen, 2015), where θ_j is

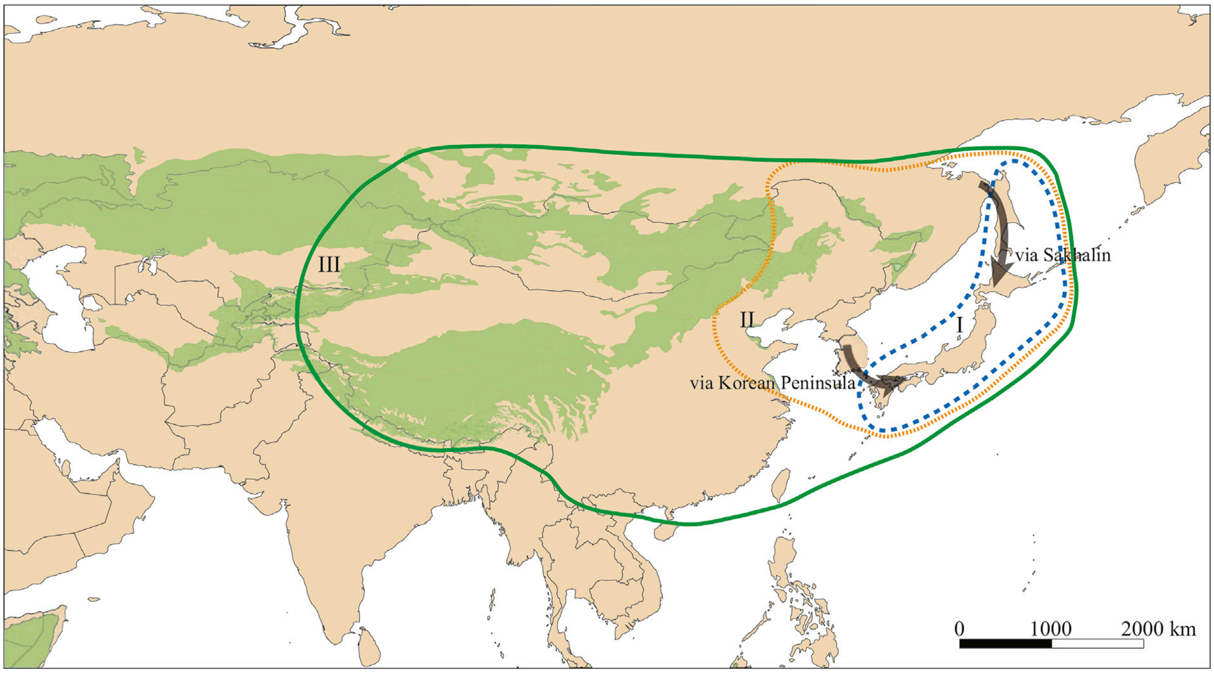

Fig. 3. Map of the approximate geographic ranges of temperate Japanese butterflies. I (blue dashed line): geographic range of the species that are largely endemic to Japan (including Sakhalin and the Kurile Islands). II (orange dotted line): geographic range of the species that are only within the Pan-Japan Sea region. III (green line): geographic range of the species that are endemic to temperate areas of East Asia. Two possible immigration routes into the Japanese archipelagoes are shown with arrows. The world map was made with Natural Earth (2018) and grassland distributions (light green areas) were based on Dixon et al. (2014). Ecoregions where grasslands occupied less than 10% of the given ecoregion were not classified as grasslands (Dixon et al., 2014). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Overview of the analytical procedures and results of the generalized linear mixed models (GLMMs) for voltinism and habitats in the Eurasian continent, and cumulative link mixed models (CLMMs) for host plant range, endangered status, geographic range, and endemism between grassland species vs. forest/HMO species. Family and Tribe were treated as nested random factors. Values of the coefficient (SE in parentheses) are shown as the differences from those of the grassland species.

Tested variables	Variable characteristics	Model	Compared group (grassland vs.)	Results
Voltinism	Binomial	GLMM	Forest	Coeff.: 0.244 (0.850) $P = 0.774$
		GLMM	HMO	Coeff.: 3.561 (1.437) $P = 0.013$
Host plant range	Ordered (4 ranks)	CLMM	Forest	Coeff.: 0.100 (0.517) $P = 0.847$ Threshold coeff. 1|2: 2.769 (0.539) 2|3: 0.345 (0.431) 3|4: 1.174 (0.458)
		CLMM	HMO	Coeff.: 1.014 (0.758) $P = 0.181$ Threshold coeff. 1|2: 2.285 (0.597) 2|3: 0.750 (0.467) 3|4: 1.289 (0.534)
Endangered status	Ordered (4 ranks)	CLMM	Forest	Coeff.: 2.577 (0.679) $P < 0.001$ Threshold coeff. 1|2: 2.937 (0.615) 2|3: 2.495 (0.580) 3|4: 1.788 (0.530)
		–[1]	HMO	Did not work[1]
Geographic range	Ordered (4 ranks)	CLMM	Forest	Coeff.: 1.379 (0.661) $P = 0.037$ Threshold coeff. 1|2: 2.056 (0.564) 2|3: 1.431 (0.530) 3|4: 2.048 (0.608)
		CLMM	HMO	Coeff.: 0.769 (0.726) $P = 0.289$ Threshold coeff. 1|2: 3.797 (1.042) 2|3: 2.638 (0.641) 3|4: 0.524 (0.410)
Endemism	Ordered (3 ranks)	CLM[2]	Forest	Coeff.: 0.228 (0.406) $P = 0.575$ Threshold coeff. 1|2: 1.994 (0.376) 2|3: 0.081 (0.278)
		CLM[2]	HMO	Coeff.: 0.998 (0.748) $P = 0.182$ Threshold coeff. 1|2: 3.715 (1.016) 2|3: 0.005 (0.325)
Habitats in the Eurasian continent[3]	Binomial	GLMM	HMO	Coeff.: 4.322 (0.253) $P = 0.088$

1: Either CLMM or CLM did not work.

2: As CLMM did not work, CLM was performed instead.

3: For the analysis of the habitats in the Eurasian continent, a comparison was made only between grassland and HMO species, both of which depend on open biotopes.

the intercept for the jth cumulative logit ($P(Y_i \le j)$) and β is the regression parameter of grassland relative to the other habitat (forest or HMO). A CLMM is an extension of a CLM with the addition of random factors. I adopted GLMMs and CLMMs instead of GLMs and CLMs since various species traits are often intercorrelated with phylogeny. Ecological similarity is particularly marked at the tribe level (e.g., hairstreaks and fritillaries; Supplementary material Table A1). Therefore, to remove the effects of phylogeny-related similarities, GLMMs and CLMMs were performed with tribe treated as a random factor nested within family. However, as CLMMs did not work well for the analyses of endemism, only CLMs were performed. Furthermore, for the comparison of endangered status between grassland and HMO species, unfortunately, both CLM and CLMM did not work well (Table 1).

All statistical analyses were performed using the software R version 3.1.3 (R Core Team, 2015), with package “lme4” (Bates et al., 2015, p. 4) for GLMMs and package “ordinal” (Christensen, 2015) for CLMMs.

3. Results

In general, although many comparisons lacked statistical significances, various traits of grassland species showed more similarities to those of forest species than to those of HMO species (Fig. 4; Table 1). Regarding voltinism and host plant range, grassland and forest species are mostly composed of univoltine and oligophagous species that feed on one plant species or genus, while HMO species are mainly composed of multivoltine and polyphagous species that feed on one or more plant families (Fig. 4a and b; Table 1). The proportions of univoltine species significantly differed between grassland and HMO species. For endangered status, grassland species accounted for the largest proportion of species included in the 2017 Red List of Threatened Species of Japan, whereas HMO species did not include red-list species (Fig. 4c). In relation to geographic range and endemism, no significant differences were detected between grassland and HMO species. However, grassland species had higher proportions of species with narrower geographic ranges (Pan-Japan Sea and temperate East Asia) and endemic subspecies than HMO species, but forest species had, on average, the narrowest geographic range and the highest proportion of endemic species (Fig. 4d and e; Table 1). Regarding the habitats in the Eurasian continent, five grassland species and one HMO species are mainly associated with forests and three grassland species are absent from the Asian part of Russia and Mongolia. Excluding these nine species, the majority of grassland species are confined to natural steppes and meadows in the Eurasian continent, whereas the majority of the HMO species are able to utilize human-modified biotopes in the continent (Fig. 4f; Tables 1, 2, and A2).

4. Discussion

The results of the present study clearly showed that ecological traits of Japanese grassland species are similar to those of forest species (inhabitants of stable biotopes), but different from those of HMO species that can utilize unstable, early successional, and human-modified biotopes (Fig. 4a and b). Furthermore, grassland species are mainly associated with natural and stable steppes and meadows in the Eurasian continent (Fig. 4f). These facts indicate that although Japanese grassland butterflies appear to be mainly associated with transient semi-natural grasslands at present, they are intrinsically inhabitants of stable grasslands and meadows. Therefore, the existing belief that semi-natural grasslands are unstable, early successional, or artificial is misleading and fails to appreciate the intrinsic ecological nature of these ecosystems. In addition, more than fifty percent of Japanese grassland butterflies are endangered and endemic subspecies that possess restricted geographic ranges (within Pan-Japan Sea region or temperate East Asia; Fig. 4c—e), indicating that Japanese grassland species are evolutionarily unique to a specific area of East Asia, but are currently facing an extinction crisis.

Several European ecologists searched for associations between habitat types and various butterfly traits. Studies on British butterflies showed that grassland species have fewer voltinism, narrower host plant range, and lower mobility, whereas ruderal species have opposite traits and forest species are somewhat intermediate (Dennis et al., 2004; Shreeve et al., 2001). The study on French butterflies showed that although there are no differences in voltinism and host plant range, grassland species have lower mobility than forest and ruderal species (Stefanescu et al., 2005). The results of these European studies generally match those of the present study in Japan but differ in the traits of forest species. This could be related to differences in forest butterfly faunas between Europe and East Asia (including Japan). Europe has a poor forest butterfly fauna mainly composed of mobile species (Dennis et al., 2004; van Swaay et al., 2006), whereas East Asia has rich forest butterfly fauna with many life-history specialists (Ohwaki et al., 2007; Table A1). However, if we focus on grassland butterflies, Europe and Japan share many butterflies with the same taxonomic position at the genus or species level {e.g. *Maculinea*, *Plebejus* (Lycaenidae), *Melitaea* and *Coenonympha* (Nymphalidae); van Swaay et al., 2006}. The majority of grassland species currently depend on semi-natural grasslands in Europe (Dover et al., 2011; Kuussaari et al., 2007) and some of them are endemic to Europe (Pärtel et al., 2005; van Swaay, 2002). In the mountain ranges of USA, temperate semi-natural grasslands also contain many endemic relict species, thus being the remnants of ancient stable grasslands that persisted due to the presence of mega herbivores (Weigl and Knowles, 2014). Therefore, taking into account the present study and previous knowledge from Europe (Pärtel et al., 2005; Pykälä, 2000; Svenning, 2002) and North America (Weigl and Knowles, 2014), a review of conventional perspective regarding temperate semi-natural grasslands is needed, promoting a unified view where temperate semi-natural grasslands throughout the Northern Hemisphere are basically remnants of ancient, intrinsically stable, natural steppes and meadows that contained endemic species and lineages in each region.

The conventional perspective assumed that temperate grasslands in forested regions were lost throughout the Holocene with the emergence of warm and humid climatic conditions. Thus, another question arises: did grasslands really persisted in humid temperate regions since the onset of the Holocene in Japan in the absence of human intervention? The present study does not provide answers. However, although past human activities seem to have expanded grasslands since prehistoric times (Dengler et al., 2014; Pärtel et al., 2007; Suka et al., 2012), several natural drivers are thought to have prevented forest succession and maintained natural grasslands and meadows during the Holocene (Pärtel et al., 2005; Svenning, 2002; Ushimaru et al., 2018). First, flooding have sustained grasslands and meadows in floodplains during the previous and present (Holocene) interglacial periods (Gao et al., 2000; Härdtle et al., 2006; Svenning, 2002). *Plebejus argyrognomon* and the extinct populations of *Melitaea scotosia* in the Kanto district are dependent to alluvial formation on floodplains or wetlands in stream valleys. Second, wildfire naturally creates and maintains areas of open vegetation. Although wildfire is considered uncommon in Japan and its regime is not well-understood, the pacific side of Japan is very dry during winter and early spring (Nakashizuka and Iida, 1995; Suka et al., 2012). Nakashizuka and Iida (1995) suggested that deciduous oak forests, which are

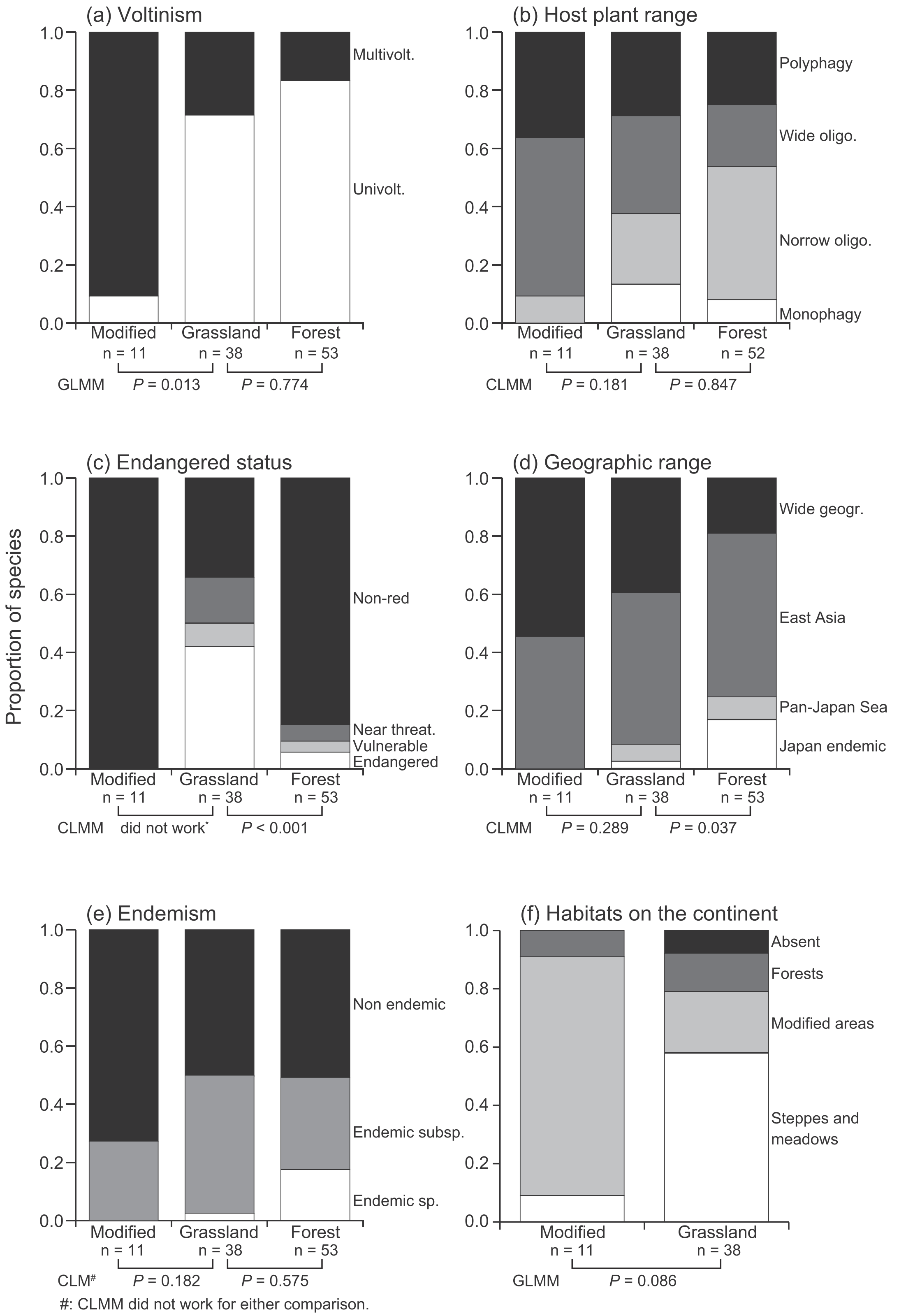

Fig. 4. Proportion of species native to grasslands, forests and human modified open (HMO) areas. a: Voltinism; b: Host plant range (*Shirozua jonasi* was omitted); c: Endangered status; d: Geographic range; e: Endemism; f: Habitats on the Eurasian continent. P-values of the generalized linear mixed models (GLMMs) and cumulative link (mixed) models (CL(M)Ms) between grassland and forest/HMO butterflies are also shown (see also Table 1).

* Either CLM or CLMM did not work.

\# As a CLMM did not work, a CLM was applied.

Table 2
Associations of grassland and HMO butterflies with natural steppes/meadows and human modified open areas in the Eurasian continent of the Asian part of Russia and Mongolia.

	Habitats in the continent		
	Only in natural steppes/meadows and open forests	Also in human modified open areas	Other biotopes (forests and/or edges)
Grassland butterflies	*Pyrgus maculatus* *Leptalina unicolor* *Ochlodes venatus* *Hesperia Florinda* *Parnassius hoenei* *Leptidea amurensis* *Niphanda fusca* *Glaucopsyche lycormas* *Shijimiaeoides divinus* *Maculinea teleius* *Plebejus subsolanus* *Melitaea scotosia* *Melitaea ambigua* *Melitaea protomedia* *Brenthis ino* *Fabriciana nerippe* *Argyronome ruslana* *Clossiana Iphigenia* *Coenonympha hero* *Coenonympha oedippus* *Minois dryas* *Ypthima motschulskyi*	*Gonepteryx rhamni* *Plebejus argus* *Plebejus argyrognomon* *Fabriciana adippe* *Speyeria aglaja* *Argyronome laodice* *Inachis io* *Aglais urticae*	*Aeromachus inachus* *Ochlodes ochraceus* *Carterocephalus silvicola* *Polytremis pellucida* *Brenthis daphne*
HMO butterflies	*Leptidea morsei*	*Parnara guttata* *Papilio machaon* *Pieris rapae* *Pieris melete* *Anthocharis scolymus* *Colias erate* *Lycaena phlaeas* *Everes argiades* *Polygonia c-aureum*	*Ypthima argus*

Note that three species that are absent from the Asian part of Russia and Mongolia (*Pelopidas jansonis, Parnassius citrinarius and Zizina emelina*) are not listed here.

among the dominant forest types in temperate East Asia, are associated with fire disturbance. Semi-natural grasslands are often adjacent to deciduous oak forests within the same climatic zone. As wildfires are largely suppressed under the present land-use regime (Nakashizuka and Iida, 1995), they may have been more frequent than we believe and may have contributed to the persistence of grassland ecosystems in the absence of humans. Third, infertile soils and winter frost are also known to impede the growth of tall trees (Svenning, 2002; Wesche et al., 2016). Japan is located on a volcanic arc and many semi-natural grasslands are located in the volcanic and cool mountainous areas, with adverse edaphic and climatic conditions (Shoji, 2003). In an abandoned semi-natural grassland on volcanic lava at the foot of Mt. Fuji, where grassland is affected by harsh edaphic conditions and probably by frost (minimum winter temperature $< -15\,^{\circ}\mathrm{C}$), grassland still remains and harbors several endangered plants and butterflies even after its abandonment for over 60 years (Ohwaki et al., 2018a). In such situation, grasslands could be preserved by wildfire occurring at intervals of approximately 100 years. Furthermore, several volcanic mountains have repeatedly erupted during the Holocene (Geological Survey of Japan, AIST, 2017), which may be responsible for maintaining grasslands around them. Fourth, landslides and avalanches may have contributed to the persistence of meadows in mountainous areas along rivers and valleys. In Inner Asia and Far East Asia, natural meadows develop along river valleys in mountain ranges (Erdős et al., 2018) and support rich grassland butterfly faunas in forested zones (Gorbunov and Kosterin, 2003). Populations of *Maculinea teleius* and *Glaucopsyche lycormas* inhabit the exposed steep slopes of mountain valleys and coastal cliffs in Japan, where grassy or meadow vegetation is naturally maintained. Finally, large herbivores help to sustain natural open vegetation (Barnosky et al., 2016; Veldman et al., 2015). Although the reasons (anthropogenic activities or climate change) for the extinction of the megafauna in Japan during the last glacial period (*Mannuthus primigenius*, *Palaeoloxodon naumani* and *Sinomegaceros yabei* in Hokkaido and *P. naumani*, *Cervus praenipponicus*, *S. yabei*, *Bison priscus*, *Alces alces* and *Bos promigenius* in Honshu-Shikoku-Kyushu islands) remain controversial (Bartlett et al., 2016; Iwase et al., 2012), if humans contributed to these extinctions to a certain extent, some megaherbivores may have survived and preserved the Japanese grasslands during the Holocene in the absence of human intervention. Therefore, infrequent natural disturbances, as well as harsh environmental conditions may serve to stably maintain natural grasslands and meadows in humid temperate regions (Pärtel et al., 2005; Svenning, 2002; Vera, 2000). However, natural disturbances are immensely suppressed because of their disastrous effects on humans, thus preventing the creation and maintenance of natural grasslands and meadows (Ushimaru et al., 2018). Furthermore, many floodplains are converted into cultivated lands and residential areas for human use. In such circumstances, as grasslands seldom persist in natural conditions, semi-natural grasslands must be maintained by mowing, burning, and grazing as alternatives to natural disturbances (Pärtel et al., 2005; Svenning, 2002).

Although I emphasized the stability and evolutionary importance of the Japanese (semi-natural) grasslands based on various traits of grassland butterflies, little is known regarding the persistence and evolutionary history of the grasslands. Nakahama et al. (2018) examined the demography of the grassland butterfly *Melitaea ambigua* over the past 10 000 years in Japan and found that although the population size increased from 6000 to 3000 years ago, probably due to increase in human activities, this butterfly had persisted during thousands of years since the onset of the Holocene (10 000–6000 years ago), when human impacts would be negligible. Therefore, grassland species could persist without the existence of human activities during the Holocene, even though population sizes would be small. However, there are no other studies that investigated the persistence and estimated divergence times of grassland species between Japan and the Eurasian continent. Furthermore, processes of grassland formation are expected to be complicated, probably with different immigration routes and timings and speciation into several subspecies (Fig. 3). Therefore, to understand grasslands history and antiquity and promote the conservation of semi-natural grasslands in Japan, phylogenetic analyses are needed in a wide range of grassland species over an East Asian geographic scale.

Declarations

Author contributions

A.O. conceived the ideas, assembled the data from the literature, made the analyses and wrote the manuscript.

Conflicts of interest

I have no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2018.e00482.

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