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Threatened herbivorous insects maintained by long-term traditional management practices in semi-natural grasslands

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ABSTRACT

Biodiversity declines have been driven by land-use changes in semi-natural grasslands worldwide. This is thought to be because threatened species are unable to compete with generalist species, which are better adapted to the new environments created by modern land-use management. Many studies have separately examined biodiversity declines resulting from land abandonment and intensified use, however few have examined their unified effects on biodiversity. In addition, we still do not fully understand the relative importance of decreasing habitat area in comparison to changes in land-use practice with regard to biodiversity. To clarify the roles of these interconnected variables, we compared the diversity of threatened and common herbivorous insects and plants among four land-use types (traditional, annual burning, annual mowing, and abandoned) during 2012 and 2013. Next, we examined whether a relationship exists between herbivorous insects and environmental variables (species richness of plants, as well as current and historical grassland areas). We showed that land-use changes (annual burning, annual mowing and/or land abandonment) diminished the diversity of threatened butterflies, orthopterans, and plants. Herbivorous insects were affected by land-use practices rather than grassland area. Our results suggest that to conserve threatened species in semi-natural grasslands, we should reintroduce traditional land-use practices in areas that currently experience modern practices, such as annual mowing and burning. The reintroduction of traditional management practices would allow for the recovery of plant biodiversity, thereby increasing herbivorous insect diversity.

1. Introduction

In recent decades, biodiversity declines have been driven by multiple anthropogenic factors (McNeely et al., 2001; Sala et al., 2000), especially land-use changes in semi-natural grasslands (Benton et al., 2003; Kleijn et al., 2011; Uchida and Ushimaru, 2014). Traditional agricultural activities enhance biodiversity by maintaining unique semi-natural ecosystems (Benton et al., 2003; Billeter et al., 2008; Kleijn et al., 2011; Tilman et al., 2001), however the switch to modern land-use practices has considerably decreased the availability of suitable habitats for many species in semi-natural ecosystems (e.g., Buse et al., 2015; Kruess and Tscharntke, 2002; Uchida and Ushimaru, 2014). Many threatened species are diminishing as a result of decreases in traditional semi-natural habitats, and may not be able to survive in habitats exposed to modern land-use practices (Luoto et al., 2003; Tscharntke et al., 2005; Uchida and Ushimaru, 2014; Uematsu et al., 2010).

Land abandonment may reduce the diversity of grassland specialists by facilitating an expansion of competitive dominant species and by promoting succession from grasslands to forests (Marini et al., 2009; Storkey et al., 2011; Uematsu et al., 2010). In addition, more frequent or irregularly-timed management practices, such as the intensified use of agricultural lands, also leads to biodiversity declines (e.g., Abadie et al., 2011; Andreasen et al., 1996; Warren et al., 2001). Although many studies have examined biodiversity declines resulting from land abandonment and intensified use separately, few have examined their unified effects on biodiversity (but see Uchida and Ushimaru, 2014, 2015). Furthermore, maintaining grassland size is important to the preservation of biodiversity (Cousins et al., 2007; Krauss et al., 2004), although the effects of decreasing habitat areas in semi-natural grasslands has generally been studied in isolation from changes in land-use practices. Therefore understanding the unified effects of changes in habitat quality and quantity on biodiversity is important. Among the various consequences of habitat loss and change, decreases in plant diversity are particularly alarming, as

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several studies have demonstrated that declines in producers reduces diversity at higher trophic levels (Joern, 2005; Haddad et al., 2009; Pöyry et al., 2009; Uchida and Ushimaru, 2014). Additionally, despite the many threatened insect species inhabiting semi-natural grasslands, still fewer studies focus on the connection between declines in herbivorous insect diversity and plant communities due to land-use changes (but see Pöyry et al., 2009; Uchida and Ushimaru, 2014).

Moreover, while human activities clearly affect changes in biodiversity, the relative importance of past versus present activities has been comparatively overlooked (Krauss et al., 2010; Kuussaari et al., 2009; Lindborg and Eriksson, 2004). The phenomenon of a delayed biodiversity loss in response to environmental change (i.e., extinction debt) implies that current diversity patterns partially reflect historical land-use practices and landscape areas (Buse et al., 2015; Helm et al., 2006; Krauss et al., 2010). Thus, to fully understand biodiversity declines in semi-natural grasslands, it is necessary to examine relationships between current biodiversity and historical grassland use (Gustavsson et al., 2007; Kuussaari et al., 2009).

Japanese grasslands are suitable for studying how biodiversity decline is affected by the complex interaction between decreases in habitat areas, changes in land use practices, and historical anthropogenic activities. Although relatively small in size, Japan has very high biodiversity and was designated as one of the 35 biodiversity hotspots in the world (Conservation International, 2015). Over the past century, semi-natural grasslands in Japan have rapidly declined from approximately 5,000,000–430,000 ha (<10% remaining; Ogura, 2006), severely limiting the habitats of many threatened species. Additionally, land-use changes of agricultural lands (land abandonment and intensified use) have occurred in many regions of Japan (Katayama et al., 2015; Uematsu et al., 2010). Furthermore, while research on biodiversity conservation in semi-natural grasslands is common throughout Europe and North America, investigations focusing on East Asia are very scarce.

In this study, we describe declines in species richness and diversity of herbivorous insects (butterflies and orthopterans) and plants due to land-use changes (annual burning, annual mowing and land abandonment) in the semi-natural grasslands of Japan. The following questions were addressed: (1) Do land-use changes (annual burning, annual mowing, and land abandonment) cause biodiversity declines? (2) Which is more important for maintaining biodiversity, management practices or grassland areas? (3) Are declines in herbivorous insects more rapid than declines in plant species?

2. Materials and methods

2.1. Study area, sites, and belt-plots

The study was conducted on semi-natural grasslands in southern Nagano Prefecture (ca. $8 \times 10\,km^2$ [ca. 7150 ha]; 35°50′N, 137°41′E), Japan. This relatively small area has many endangered grassland species (Nagano Prefecture, 2004; Uchida et al., in press). The study sites were located in a mountainous region, with elevations between 1100 and 1243 m. The study site landscape was 19.6% grasslands and 67.7% forests in 1948, but only 2.0% grasslands and 87.4% forests in 2010. The mean annual temperature was 7.4 °C, with a minimum monthly average temperature of −4.9 °C in January and a maximum of 20.0 °C in August during the period of 1981–2010. The mean annual precipitation was 2065.4 mm. Climate records were collected from a nearby automated meteorological data acquisition point (35°94′N, 137°60′E) of the Japan Meteorological Agency.

We compared the diversity of butterflies, orthopterans, and plants among different management practices (traditional, annual burning, annual mowing, and land abandonment). We examined 36 belt-plots (each belt-plot: $5\,m \times 30\,m$) in 12 sites, and all sites were surveyed for two years (2012 and 2013). Land management practices are as follows:

(a) Traditionally managed sites (Tra: three sites with three belt-plots per site, nine belt-pots in total) were maintained by both burning and mowing, once every two years. Farmers divided each meadow into two areas: half of the meadow was burned in the spring (mid-April) and mowed in the autumn (early September) during the first year, while the other half was left intact (Fig. S1). In the following year, the intact half was burned and mowed, while the previously managed half was kept intact. All cut material was removed from the sites as winter fodder. This management pattern has been practiced for at least 300 years in this study region.
(b) Annual burning sites (Bur: three sites with three belt-plots per site, nine belt-plots in total) were originally under traditional management, but switched to the current management practices 7–13 years ago (Fig. S1).
(c) Annual mowing sites (Mow: three sites with three belt-plots per site, nine belt-plots in total) were originally under traditional management, but switched to the current management practices before the start of our study (Fig. S1). Two of the Mow sites were mowed in August, and had been converted to conifer plantations 8 years ago (Fig. S1), where farmers remove herbs that shade the saplings. These sites are similar to semi-natural grasslands because the conifer saplings were very short (Fig. S1). The other Mow site had been changed from traditional management practices to annual mowing in late April 9 years ago.
(d) Abandoned sites (Aba: three sites with three belt-plots per site, nine belt plots in total) were changed from traditional management practices to land abandonment 6–13 years ago (Fig. S1).

We summarized site information variables (study site area [ha], grassland areas within 1-km radius of each site [ha], distance of sites within land-use type [m], distance between each belt-plot in each site [m], and slope angle [°]) in Table S1. The distribution of the study sites was not random, distance between Tra sites was shorter than the distance between Bur sites (Table S1).

2.2. Herbivorous insect surveys

The butterfly community in each study site was surveyed monthly from May to September in 2012 and 2013 (five times per year). Butterfly species identity and abundance were recorded using the visual observation count method for 20 min within each belt-plot, at a height of 5 m under warm, sunny conditions (Uchida and Ushimaru, 2014; Pollard and Yates, 1994). The identity and abundance of orthopteran species were surveyed twice (August and September) in 2012 and five times (monthly from May to September) in 2013. Two methods were used: 1) sweep-net (42-cm diameter) with 100 sweeps per belt plot and 2) visual observation for 30 min per belt-plot. For statistical analyses, we pooled the data from all surveys in each year.

2.3. Plant surveys

The plant community in each of the 36 belt-plots was surveyed monthly from May to September in 2012 (five times per year). During each survey, all flowering species in each belt plot were recorded. In the same time period, we also established and surveyed two plots ($0.5\,m \times 0.5\,m$), located at regular intervals along each belt-plot (6 plots per site). In total, there were 72 plots