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Research article

Patterns of plant diversity loss and species turnover resulting from land abandonment and intensification in semi-natural grasslands

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ABSTRACT

Land-use changes cause biodiversity loss in semi-natural ecosystems worldwide. Biotic homogenization has led to biodiversity loss, mainly through declines in species composition turnover. Elucidating patterns of turnover in species composition could enhance our understanding of how anthropogenic activities affect community assembly. Here, we focused on whether the decreasing patterns in plant diversity and turnover of species composition resulting from land-use change vary in two regions. We estimated the species diversity and composition of semi-natural grasslands surrounding paddy fields in *satoyama* landscapes. We examined the differences in species diversity and composition across three land-use types (abandoned, traditional, and intensified) in two regions (Hyogo and Niigata Prefectures, Japan), which were characterized by different climatic conditions. We then assessed alpha-, beta-, and gamma-diversity to compare the patterns of diversity losses in the two regions as a result of land-use changes. In each region, gamma-diversity was consistently higher in the traditional sites compared to abandoned or intensified sites. The analyses revealed that most of the beta-diversity in traditional sites differed significantly from those of abandoned and intensified sites in both regions. However, the beta-diversity of total and perennial species did not differ between traditional and abandoned sites in the Hyogo region. We noted that the beta-diversity of total and perennial species in intensified sites was much lower than that in the traditional sites of the Niigata region. Overall, the patterns of alpha- and gamma-diversity loss were similar in both study regions. Although the biotic homogenization was caused by intensified land-use in the Niigata region, this hypothesis did not completely explain the loss of biodiversity in the abandoned sites in the Hyogo region. The present study contributes to the growing body of work investigating changes in biodiversity as a result of both biotic homogenization and differentiation in semi-natural ecosystems. Conservationists and policy makers should focus on patterns of species composition responded to land-use changes that continue to increase worldwide.

1. Introduction

The value of traditional agricultural habitats for biodiversity conservation has gained increased recognition (Pykälä, 2000; Foley et al., 2005; Tscharntke et al., 2005; Kleijn et al., 2011). Extensive management practices generate high levels of alpha and beta diversity at the regional scale in the semi-natural grasslands of agro-ecosystems (e.g., Ekroos et al., 2010; Uchida and Ushimaru, 2015). In Asian countries, including Japan, human management practices (e.g., mowing and tree thinning) have maintained *satoyama* landscapes to obtain dairy food, fodder, and wood fuel (Berglund et al., 2014; Fukamachi, 2017). The *satoyama* landscapes is defined as a mosaic landscape, including semi-natural grasslands, paddy fields, and secondary forests (Ministry of the Environment 2010; Uchida and Ushimaru, 2014; Fukamachi, 2017). The semi-natural grasslands that surround paddy fields in *satoyama* are maintained by

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periodic mowing, and harbor a high degree of alpha diversity of plants and insects, including endangered species (Matsumura and Takeda, 2010; Uematsu et al., 2010; Koyanagi et al., 2014; Uchida and Ushimaru, 2014, 2015). However, only small fractions of these landscapes remain today as a result of land-use changes. In Japan, ~10% of the total area of paddy fields has been abandoned and ~75% of the total area of paddy fields has been consolidated (Uematsu et al., 2010).

In semi-natural ecosystems, land abandonment has promoted the succession of vegetation, which has, in turn, decreased grassland biodiversity (Marini et al., 2009; Uematsu et al., 2010; Uchida and Ushimaru, 2014; Queiroz et al., 2014; Normile, 2016). Intensified use (i.e., nitrogen input, high disturbance management, and land consolidation) has also been identified as a major driver of decreased biodiversity in semi-natural ecosystems (Andreasen et al., 1996; Pöyry et al., 2009; Uematsu et al., 2010; Abadie et al., 2011; Uchida and Ushimaru, 2014). Although abandoned and intensified semi-natural grasslands may lead to loss of biodiversity, most studies have examined both of the land-use forms separately (Clough et al., 2007; Jakobsson et al., 2016). Furthermore, patterns of community assembly differed among regions (Dyer et al., 2007; Freestone and Osman, 2011; Myers et al., 2013); however, studies for comparison of changes in biodiversity in semi-natural grasslands among regions were limited (but see Clough et al., 2007; Flohre et al., 2011).

Patterns of beta-diversity provide fundamental insights into the maintenance of biodiversity (Chase, 2010; Anderson et al., 2011; Kraft et al., 2011). Such patterns could be used to elucidate the effects of anthropogenic activities (e.g. Benton et al., 2003; Clough et al., 2007; Vellend et al., 2007; Ekroos et al., 2010) and/or environmental gradients (e.g. Kraft et al., 2011; Myers et al., 2013) on community assembly. In recent decades, biodiversity loss was caused by biotic homogenization (i.e. decreases in beta-diversity; Table S1) due to anthropogenic impacts, and is considered a rapidly growing ecological issue (McKinney and Lockwood, 1999; Olden and Rooney, 2006; Smart et al., 2006; Pool and Olden, 2011; Tabarelli et al., 2012; Mori et al., 2015). Although land-use changes usually lead to declines in local species diversity, knowledge about biotic homogenization as a result of bidirectional land-use changes (including land abandonment and intensification) in semi-natural ecosystems is poorly understood (Ekroos et al., 2010; Flohre et al., 2011; Uchida and Ushimaru, 2015). Anthropogenic activities could potentially decrease the niche selection of many species, resulting in the homogenization of community composition (e.g. Vellend et al., 2007; Mori et al., 2015). In contrast, recent studies have shown that the loss of species diversity due to land-use changes is not necessarily explained by decreases in the beta-diversity. For instance, land-use changes might increase the observed beta-diversity (i.e., biotic differentiation between sites) due to decreases in alpha-diversity (e.g., Naaf and Wulf, 2010; Uchida and Ushimaru, 2015). Further studies need to be conducted to examine whether the biotic homogenization and/or biotic differentiation lead to biodiversity loss.

We hypothesized that regional biodiversity loss due to land abandonment and intensification would be associated with low alpha-, beta-, and gamma-diversity of plant species (Table S1) in both regions. To address this hypothesis, we compared the patterns of biodiversity (alpha-, beta-, and gamma-diversity) among three land-use types (traditional, abandoned, and intensified) in the two study regions (Hyogo and Niigata Prefectures) Japan. We assessed changes in diversity indices comparing two different regions (Hyogo region and Niigata region, see section 2.1.) that had different climatic conditions (Table S2). It is important to consider differences in the responses of life-history groups to understand the patterns of species loss owing to land-use changes (Pykälä, 2005; Uematsu et al., 2010; Uchida and Ushimaru, 2014). We therefore also considered species life-history traits because annual species are more disturbance-resistant than perennial species, and often dominate the vegetation of highly disturbed environments (Aarssen, 2000; Begon et al., 2006), which may lead to the loss of beta-diversity in semi-natural grasslands.

2. Materials and methods

2.1. Study areas

The study was conducted on semi-natural grasslands surrounding paddy terraces in southeast Hyogo and southeast Niigata Prefectures in Japan. The Hyogo region is approx. $45 \times 50\,km^2$ (34°42′ N, 135° 13′ E), while the Niigata region is approx. $10 \times 20\,km^2$ (37°06′ N, 138° 49′ E) (Fig. S1). In both study areas, semi-natural grasslands were maintained by periodic mowing on the levees of the paddy field margins, irrigation ponds, and the edges between paddy fields and secondary forests (Fig. S2; Matsumura and Takeda, 2010; Koyanagi et al., 2014; Uchida and Ushimaru, 2014). Mowing was considered a form of disturbance for plants, and mowing frequency varied between study terraces depending on land-use type (Koyanagi et al., 2014; Uchida and Ushimaru, 2014).

We separated the two regions for the subsequent analyses, because climatic factors of each region were very different. In the Hyogo region, the mean annual temperature was 16.7 °C, and the mean annual precipitation was approximately 1220 mm during 1981–2010 (Table S2). This region is characterized by a temperate climate and is rarely covered by snow. The Niigata region is characterized by heavy snow in winter (>2 m in depth) and has a mean annual temperature of 11.7 °C and a mean annual precipitation of approximately 2500 mm (Table S2). In the Niigata region, paddy terraces are spread on slopes that were formed after landslides that occurred thousands of years ago on the unconsolidated sediment of the tertiary deposits (Rural Areas Development Division, Niigata Pref. 1978). Local villagers suggested that primitive terraced paddies were established approximately 500 years ago. These meteorological data were recorded by an automated meteorological data acquisition system by the Japan Meteorological Agency in Kobe, Hyogo Prefecture (34°41.8′ N, 135°12.7′ E, 5.3 m alt.) and Toka-machi, Niigata Prefecture (37°8.6′ N, 138°43.6’ E, 170 m alt.), respectively.

2.2. Land-use types

We interviewed farmers on how they manage semi-natural grasslands. Paddy terraces were categorized into three land-use types in both regions. These three land-use types were formally managed using traditional management practices. Explanations of land-use type as follows:

A) Abandoned sites (ABA) are sites where farmers ceased rice cultivation and the mowing of semi-natural grasslands 3–20 years ago. Paddy terrace abandonment leads to succession from a semi-natural grassland to a secondary forest, with grassland-specific plant diversity decreasing over several years (Uematsu et al., 2010; Uchida and Ushimaru, 2014). Mowing frequency in ABA sites was basically 0 times per year, although two ABA sites were mowed by farmers once every four years.
B) Traditional sites (TRA) are sites where paddy terraces have been managed for more than 100 years in both regions. This management practice maintains high biodiversity and high numbers of threatened species (Matsumura and Takeda,