A study of mechanisms of biodiversity declines due to land-use changes in agricultural ecosystems

Uchida, Kei

(Degree)
博士（理学）
(Date of Degree)
2014-09-25
(Date of Publication)
2016-09-25
(Resource Type)
doctoral thesis
(Report Number)
甲第6255号
(URL)
https://hdl.handle.net/20.500.14094/D1006255

Doctoral dissertation

A study of mechanisms of biodiversity declines due to land-use changes in agricultural ecosystems

(農業生態系における，土地利用形態の変化が引き起こす

生物多様性低下のメカニズムに関する研究)

Kei UCHIDA

内田圭

Graduate school of Human Development and Environment

Kobe University

神戸大学大学院人間発達環境学研究科 人間環境学専攻

September, 2014

Table of contents

Summary

In this thesis, I describe patterns of decline in α- and β-diversity of plants and herbivorous insects (butterflies and orthopterans) due to land abandonment and intensification and discuss their underlying mechanisms in semi-natural agricultural (paddy field) landscapes. Land abandonment and intensification can change semi-natural grassland conditions in various ways. First, land-use changes are often accompanied by changes in the surrounding landscape. Second, land-use changes inevitably coincide with changes in the anthropogenic disturbance (mowing, burning, and grazing) regime. Third, declines in consumer diversity may be driven by changes in the diversity of food resources (i.e., plant diversity) due to changes in land use. Together, these changes can lead to rapid biodiversity declines.

In Chapter 2, I report on my examination of how plant and herbivorous insect diversity declines due to land-use changes. The α- diversity of plant had a unimodal patterns with disturbance regime (mowing frequency) and decreased with the loss of surrounding secondary forests, whereas herbivorous insects decreased with declining plant diversity and also displayed a unimodal relationship with mowing frequency. Furthermore, my results suggest that the number of individuals of most herbivorous species decreased randomly after the loss of plant richness.

In Chapter 3, I discuss a comparison of spatial and temporal additive (β_{add}) and multiplicative (β_{W}) partitionings of plant, butterfly, and orthpteran species richness among land use types and their dependence on mowing frequency and surrounding landscape attributes. Land-use changes decreased between-plot diversity (β-diversity) at the within-terrace scale, as well as plot-scale (α-) diversity in agricultural landscapes. The spatial and temporal β_{add} for plant, butterfly, and orthopteran species were

highest in traditionally managed terraces. By contrast, the spatial and temporal β_w of plants and orthopterans in abandoned and intensive terraces were, respectively, significantly higher than and equal to those in traditional terraces, whereas spatial and temporal butterfly β_w did not vary with land-use type.

Chapter 4 reports results from my test of the biotic homogenization and random loss hypotheses as explanations of local β-diversity decline due to land abandonment and intensification. I compared β-diversity indices (additive partitioning of species richness (β_{add}) and Jaccard's and the Bray-Curtis dissimilarity indices) for terrace pairs among three land-use (abandoned, traditional, and intensified) types. I demonstrated that β_{add} for traditional terrace pairs was significantly higher than that for land-use-changed terrace pairs, whereas Jaccard's and the Bray-Curtis dissimilarity indices for traditional terrace pairs were significantly lower than or did not differ from those for abandoned and/or intensified terrace pairs. My results did not support the biotic homogenization hypothesis but generally support the random loss hypothesis.

Overall, my findings suggest that land abandonment and intensification drive plant, butterfly, and orthopteran species diversity declines at the plot, within-terrace, and local scales around paddy terraces. Declines in plant richness and changes in mowing frequency more strongly contributed to the loss of butterflies and orthoptera than did changes to the surrounding landscape. Additionally, my results suggest that conservation priority should be given to rare species that are at greater risk from land-use abandonment and intensification. By conserving these rare species, α-diversity and within-terrace and local β-diversity (γ-diversity) will be maintained.

Chapter 1.

General introduction

General introduction

Biodiversity loss is a major global issue. During the past century, biodiversity declines have been accelerated due to multiple anthropogenic factors, including land-use changes, nitrogen deposition, introduction of alien species, and climate change (Sala *et al.* 2000). Recent extinction rates are estimated to be 100–1000 times higher than historical rates (Pimm *et al.* 1995; Pimm & Raven 2000; Pereira & Daily 2006). To date, 193 parties have signed *The Convention on Biological Diversity* (CBD), which took effect on 29 December 1993, setting goals for significantly reducing the rate of biodiversity loss by 2020 (Secretariat of the Conservation on Biological diversity 2010).

Worldwide, people have developed ways to utilize and manage their natural environments through activities such as agriculture, forestry, and fisheries to meet the need for food, goods, and energy production. Based on traditional knowledge and practices accumulated locally over generations, the coexistence of biodiversity and production activities has been maintained in semi-natural ecosystems. Because the balance between production activities and biodiversity has been dramatically altered in recent decades, the International Partnership for the Satoyama Initiative has begun to promote collaboration in the conservation and restoration of sustainable semi-natural environments via broader global recognition of their value. By managing and using biological resources sustainably to maintain biodiversity, humans will be able to enjoy a stable supply of various ecosystem services well into the future (IPSI 2014, http://satoyama-initiative.org/en/about/).

Biodiversity crisis in semi-natural ecosystems

Conservation of semi-natural ecosystems is crucial for maintaining future biodiversity (Tilman *et al.* 2001; Foley *et al.* 2005), as agricultural lands occupy approximately 40% of all terrestrial areas worldwide (Ramankutty & Foley 1999). Although agricultural ecosystems harbor unique biodiversity compared with natural ecosystems, semi-natural landscapes have experienced major changes in recent decades. Consequently, biodiversity loss mainly due to land-use changes in agro-ecosystems has become a central issue for biological conservation (e.g., Krebs *et al*. 1999; Tilman *et al*. 2001; Benton, Vickery & Wilson 2003; Billeter *et al*. 2008). Thus, the value of traditional agricultural habitats has been increasingly recognized in recent decades (Pykälä 2000; Tscharntke *et al.* 2005; Knop *et al.* 2006; Kleijn *et al.* 2011).

Globally, the commercialization of agriculture and declines in rural populations have caused changes in land use and agricultural practices (Kruess & Tscharntke 2002; Knop *et al.* 2006; Pöyry *et al.* 2006, 2009; Öckinger & Smith 2007; Kleijn *et al.* 2009; Uematsu & Ushimaru 2013), which in turn have driven rapid semi-natural biodiversity declines. Intensified use (i.e., nitrogen input and land consolidation) of agricultural lands increased after World War II and has been identified as a major driver of biodiversity declines in semi-natural ecosystems (Robinson & Sutherland 2002; Benton, Vickery & Wilson 2003; Tscharntke *et al.* 2005). Species declines of multiple taxa in agro-ecosystems due to intensified land use have been increasingly reported during the last two decades, particularly in birds (Krebs *et al.* 1999; Benton *et al.* 2002; Thomas *et al.* 2004; Donald *et al.* 2006), arthropods (Sotherton & Self 2000; Warren *et al.* 2001; Benton *et al.* 2002; Thomas *et al.* 2004; Conrad *et al.* 2006; Öckinger & Smith 2007), and plants (Andreasen *et al.* 1996; Sotherton & Self 2000; Thomas *et al.* 2004; Uematsu *et al.* 2010). On the other hand, land abandonment, which promotes subsequent vegetation succession, is also known to cause species declines (Matsumura & Takeda 2010; Uematsu *et al.* 2010). Because many endangered species occur in traditionally managed agricultural landscapes, integrating conservation efforts to combine high biodiversity and productive agricultural systems will be especially important (Pimentel *et al.* 1992; Bengtsson *et al.* 2003; Bennet *et al.* 2006; Tscharntke *et al.* 2005).

In general, most species associated with farmland habitats are found in non-crop habitats such as semi-natural grassland conditions at field boundaries and in pastures and meadows (Svensson *et al.* 2000; Clausen *et al.* 2001; Kells & Goulson 2003; Clough *et al.*2007). Traditional management practices, such as low-intensity mowing and grazing, have maintained high plant and animal diversity in these semi-natural grasslands (Fig. 1-1, Tscharntke *et al.* 2005; Kleijn *et al.* 2011; Uematsu & Ushimaru 2013; Uchida & Ushimaru 2014). Recently, however, land-use changes have resulted in intensification and abandonment of traditional management practices (Krebs *et al.* 1999; Tilman *et al.* 2001; Benton, Vickery & Wilson 2003; Young *et al.* 2005). Thus, traditional semi-natural conditions have declined, threatening species in semi-natural grasslands worldwide (Ekroos, Heliölä & Kuussaari 2010; Kleijn *et al.* 2011; Koyanagi & Furukawa 2013).

In Japan, biodiversity in agricultural landscapes has declined drastically following the widespread loss and fragmentation of semi-natural grasslands. Over the past century, Japanese semi-natural grassland (pasture and meadow) area has declined from approximately 5,000,000 ha to 430,000 ha (i.e., <10% remains) (Ogura 2006), of which some 185,000 ha occurs on the margins (levees) of paddy fields (The Ministry of Internal Affairs and Communications Japan 2013). Paddy fields cover 6.5% of the total land area in Japan, but by 2005, approximately 10% had been abandoned (Ministry of Agriculture, Forestry and Fisheries 2005), while approximately 75% had been consolidated to allow intensified agriculture (Himiyama & Kikuchi 2007). Thus, abandoned and intensified (consolidated) paddy areas are prevalent throughout Japan and have caused rapid species declines in semi-natural grasslands on paddy levees (Fukamachi *et al*. 2005; Matsumura & Takeda 2010, Uematsu *et al.* 2010; Uematsu & Ushimaru 2013; Uchida & Ushimaru 2014).

Many studies have described within-plot diversity (α-diversity) declines in plants and herbivorous insects in semi-natural grasslands due to land-use changes (Kruess & Tscharntke 1994; Wettstein & Schmid 1999; Di Giulio *et al.* 2001; Kruess & Tscharntke 2002) and have provided hypotheses about the mechanisms underlying declines in plant (e.g., Pykälä 2005; Hautier *et al.* 2009; Kleijn *et al.* 2009; Uematsu *et al.* 2010) and herbivorous insect richness (e.g., Kruess & Tscharntke 2002; Pöyry *et al.* 2006). However, the proposed mechanisms have not been examined sufficiently (but see Öckinger & Smith 2007; Pöyry *et al.* 2009). Moreover, few studies have examined the ways in which land-use changes reduce between-plot diversity (β-diversity) (Clough *et al.* 2007; Ekroos, Heliölä & Kuussaari 2010; Abadie *et al.* 2011; Karp *et al.* 2012) despite its importance in maintaining local and regional species pools. Some studies have shown that intensified land use leads to reduced β-diversity in plants, herbivorous insects, and birds in agricultural landscapes, indicating that biological diversity in human-dominated agricultural landscapes has been reduced in recent decades, resulting in ecological homogenization (Clough *et al.* 2007; Ekroos, Heliölä & Kuussaari 2010; Abadie *et al.* 2011; Karp *et al.* 2012). Furthermore, most studies have examined biodiversity declines due to land abandonment and due to intensification separately; therefore a mechanism that can explain both sources of decline simultaneously would be useful.

Aims of the thesis

In this thesis, I describe patterns of decline in the *α*- and *β*-diversity of plants and herbivorous insects (butterflies and orthopterans) due to land-use changes and discuss their underlying mechanisms in semi-natural agricultural (paddy field) landscapes. Land abandonment and intensification can change semi-natural grassland conditions in various ways. First, land-use changes are often accompanied by changes in the surrounding landscape (Tscharntke *et al.* 2005; Pöyry *et al.* 2009; Ekroos, Heliölä & Kuussaari 2010). Second, land-use changes inevitably coincide with changes in the anthropogenic disturbance (mowing, burning, and grazing) regime (Pöyry *et al.* 2006; Kleijn *et al.* 2011). Third, declines in consumer diversity may be driven by changes in the diversity of food resources (i.e., plant diversity) due to changes in land use. Together, these changes can lead to rapid biodiversity declines.

I examined the cumulative effects of these changes on plant and herbivorous insect diversity in semi-natural grasslands along paddy field margins at three spatial scales: plot-scale (*α*-) diversity, site-scale (within-site *β*-) diversity, and local-scale (inter-site *β*-) diversity. In Chapter 2, I address plant and herbivorous insect *α*-diversity declines and their relationship with land abandonment and intensification at 31 study sites in southeastern Hyogo Prefecture, Japan (Kobe, Sanda, Miki, and Takarazuka Cities and Inagawa Town). In Chapter 3, I examine within-site (within-terrace) *β*-diversity declines in plants and herbivores due to land-use changes in the same study area. In Chapter 4, I examine declines in local (inter-terrace) *β*- and *γ*-diversity due to land-use changes. In the final chapter, I summarize my findings and discuss the overall patterns of biodiversity decline due to land abandonment and intensification. In the current chapter, I propose a unified explanation for declines in biodiversity due to land abandonment and intensification and make recommendations for conserving biodiversity in semi-natural grasslands around agricultural land.

Fig. 1-1. The Photographs shows my study environment: semi-natural grassland around agricultural lands (paddy terraces).

Chapter 2.

Alpha diversity declines due to land abandonment and intensification of agricultural lands: patterns and mechanisms

Introduction

In recent decades, biodiversity declines due to land-use changes in agricultural landscapes, and their causes, have become central issues in ecology (e.g., McNeely *et al.* 1995; Krebs *et al.* 1999; Tilman *et al.* 2001; Billeter *et al.* 2008). Traditional management practices, such as low-intensity grazing and mowing, maintain high plant and animal diversity in agricultural landscapes (Tscharntke *et al.* 2005; Kleijn *et al.* 2011), whereas recent land-use changes, including both abandonment and intensification, may cause declines in biodiversity through both habitat loss and changes in habitat quality (Kruess & Tscharntke 1994; Wettstein & Schmid 1999; Di Giulio *et al.* 2001; Kruess & Tscharntke 2002). Although many studies have described biodiversity decline due to land-use changes, and have provided hypotheses addressing the underlying mechanisms in plants (e.g., Pykälä 2005; Hautier *et al.* 2009; Kleijn *et al.* 2009; Uematsu *et al.* 2010) and herbivorous insects (e.g., Kruess & Tscharntke 2002; Pöyry *et al.* 2006), the proposed mechanisms have not been sufficiently examined, especially for herbivorous insects (but see, Öckinger & Smith 2007; Pöyry *et al.* 2009). Furthermore, most studies have examined declines in biodiversity due to land-use abandonment and intensification separately, and therefore a unified mechanism that can explain both sources of decline together would be valuable.

Several hypotheses addressing the mechanisms of decline in herbivorous insects around agricultural land have been suggested (Table 2-1). First, declines in the diversity of herbivorous insects may be driven by changes in the diversity of food resources (i.e., plant diversity) due to changes in land use (the resource diversity hypothesis, RDH). Indeed, a decline in arthropod diversity often results from a decline in plant diversity (Siemann *et al.* 1998; Haddad *et al.* 2001; 2009; Petermann *et al.* 2010), with some exceptions (Kricheva *et al.* 2000; Hawkins & Potter 2003).

Butterfly diversity decreases with decreasing plant species richness and/or floral abundance due to habitat loss and fragmentation (Kuussaari *et al.* 2007; Öckinger & Smith 2007; Pöyry *et al.* 2009). In tallgrass prairie, orthopteran diversity increases with increased plant species richness caused by changes in the burning interval (Joern 2005).

Second, patterns of biodiversity decline can be explained by changes in the disturbance regime according to the intermediate disturbance hypothesis (IDH, Grime 1973; Horn 1975; Connell 1978; Huston 1979, 1994). The IDH predicts that species diversity would be maximized under traditional low-impact management that provides an intermediate level of disturbance to agricultural land (Pöyry *et al.* 2006; Kleijn *et al.* 2011). On abandoned agricultural land, diversity may decrease due to a low level or absence of anthropogenic disturbance (Pöyry *et al.* 2006; Uematsu *et al.* 2010). Intensified land-use with stronger and/or more frequent disturbances can also lead to diversity loss (Ekroos, Heliölä & Kuussaari 2010).

Third, land-use changes in surrounding landscapes can cause declines in herbivorous insects (the landscape change hypothesis, LCH; Bergman *et al.* 2004; Tscharntke *et al.* 2005), although some studies have shown that landscape variables have weak or no effects on herbivore diversity (Collinge 2003; Kuussaari *et al.* 2007; Pöyry *et al.* 2009). For example, habitat isolation and fragmentation should limit species immigration, especially for species that have patchy populations with frequent dispersal among habitats, leading to a loss of diversity (Tscharntke *et al.* 2005; Rodoriguez-Estrella 2007). In addition, reductions in the area of semi-natural grasslands often lead to decreases in butterfly richness and density (Öckinger & Smith 2007).

Table 2-1. Summary of the four hypotheses which were tested in this study

Hypothesis	General predictions	Organism	Specific predictions from the hypothesis for diversity in each land-use type		
			abandoned terrace	traditional terrace	intensive terrace
Resource diversity hypothesis (RDH)	Declines of herbivorous insect diversity due to changes in diversity of food resources (i.e., plant diversity)	Butterfly	Low diversity due to low availability of larval host and nectar flower plant diversity	High diversity due to high availability of larval host and nectar flower plant diversity	Low diversity due to low availability of larval host and nectar flower plant diversity
		Orthoptera	Low diversity due to low availability of plant diversity	High diversity due to high availability of plant diversity	Low diversity due to low availability of plant diversity
Intermediate disturbance hypothesis (IDH)	Species diversity would be maximized under traditional low-impact management that provides an intermediate level of disturbance	Plant	Low diversity due to over-dominance of competitive species caused by no or less frequent disturbances	High diversity is maintained by coexistence of many species under the intermediate levels of disturbance	Low diversity due to over-dominance of disturbance tolerant species under frequent disturbances
		Butterfly & Orthoptera	Smaller and/or specialist species would have a low diversity due to infrequent disturbances	High diversity is maintained by coexistence of many species under the intermediate levels of disturbance	Larger species with a high biomass and low growth rate and/or generalists may decrease under frequent disturbances
Land-use change hypothesis (LCH)	Changes in surrounding landscapes enhances habitat isolation and fragmentation, which would limit species immigration, especially for larger and generalist species	Plant	Low diversity due to decreasing surrounding traditional terraces	High diversity is maintained by surrounding traditional terraces and secondary forests	Low diversity due to decreases in surrounding traditional terraces and secondary forests
		Butterfly & Orthoptera	Low diversity due to decreasing surrounding traditional terraces	High diversity is maintained by surrounding traditional terraces and secondary forests	Low diversity due to decreases in surrounding traditional terraces and secondary forests
More individuals hypothesis (MIH)	Positive correlations between herbivore richness and the number of herbivore individuals, and between plant biomass production and the number of herbivore individuals	Butterfly & Orthoptera	Low individual number and richness dut to low plant biomass production	High individual number and richness supported by high plant biomass production	Low individual number and richness dut to low plant biomass production

Fourth, the more individuals hypothesis (MIH), which assumes positive correlations between species richness and the number of individuals, and between biomass production and the number of individuals (Srivastava & Lowton 1998; Yee & Juliano 2007), can predict diversity declines due to land-use changes because of decrease in the number of herbivores via a reduction in biomass production, i.e., the quantity of resources. The MIH has rarely been applied to biodiversity loss in agricultural lands. Because these four hypotheses are complementary rather than mutually exclusive, I should examine them together to fully understand how land abandonment and intensification influence herbivore communities (Joern 2005; Öckinger & Smith 2007; Pöyry *et al.* 2009; Kleijn *et al.* 2011).

Because not all species respond equally to land-use changes in agricultural landscapes, it is essential to address differences in responses among species and/or ecological trait groups to understand the mechanisms driving species loss (Table 2-1, Kleijn *et al.* 2009; Uematsu *et al.* 2010; Uematsu & Ushimaru 2013). The ecological requirements for the maintenance of diversity may vary among trait groups within a taxon (Wootton 1998; Duffy *et al.* 2003; Pöyry *et al.* 2006). For example, body size may influence susceptibility of each species to land-use changes (Holland *et al.* 2005; Hambäck *et al.* 2007; 2010; cf. Davies *et al.* 2000). Larger species often have higher dispersal ability and are more affected by changes in surrounding landscapes, whereas smaller species with low flight ability are more susceptible to changes in local habitat conditions (Tscharntke *et al.* 2005; Hambäck *et al.* 2007, 2010). Furthermore, species with different body sizes may respond differently to changes in the disturbance regime (Huston 1979, 1994). Larger species with a high biomass and low growth rate tend to decrease with frequent disturbances, while smaller species tend to have a low diversity when disturbances are infrequent (Huston & Wolverton 2011). The diversity–disturbance relationship also varies among herbivorous insects with respect to the degree of larval-host specialization, such that specialists prefer more frequently disturbed conditions than generalists (Pöyry *et al.* 2006). Compared to specialists, generalist species may also require larger landscape scales for the maintenance of their populations (Tscharntke *et al.* 2005). Moreover, rare species (species with a low abundance) are generally more susceptible to land-use changes than common species, according to the random loss hypothesis (Suding *et al.* 2005), which is assumed in the MIH (Srivastava & Lowton 1998). Thus, the relationships between susceptibility to land-use changes and species traits such as body size, the degree of specialization to food resources, and abundance, are all worth examining to understand effects of land abandonment and intensification on herbivorous insect diversity.

To clarify how the diversity of herbivorous insects declines due to land abandonment and intensification, I examined the above four hypotheses (RDH, IDH, LCH and MIH) together. I compared the species richness and diversity of two herbivorous insect groups (butterflies and orthopterans) in semi-natural grasslands among three land-use management types: abandoned, traditional, and intensified agricultural lands (see *Materials and Methods*: *Study area, paddy terraces, and plots*). I also investigated plant community variables (richness of total, larval-host and flowering species and vegetation height), variables in the mowing (disturbance) frequency and the surrounding landscapes in the grasslands, to examine their effects on herbivore diversity. Then I address the following four questions: (1) Do land-use abandonment and intensification cause diversity declines in plants and herbivorous insects? (2) Do changes in plant community variables, disturbance regime, and the surrounding landscape drive herbivore declines? (3) Are there differences in the susceptibility to land abandonment and intensification between plants and herbivores or among functional groups of plants and herbivores? (4) What types of species are more susceptible to land abandonment and intensification? I discuss the answers to these questions in the context of the four hypotheses for declines in diversity introduced earlier. Then I propose a unified explanation for declines in biodiversity due to land abandonment and intensification, which have often been studied separately.

Materials and Methods

Study area, paddy terraces, and plots

This study was conducted in 124 plots across 31 agricultural areas (paddy terraces) in the southeast area of Hyogo Prefecture, western Japan (ca. 19 × 30 km^2, 34°48’–57’ N, 135°03’–24’ E). The mean annual temperature was 13.8℃ with a minimum monthly average of –2.4℃ in January and a maximum monthly average of 31.6℃ in August. The mean annual precipitation was 1,239.9 mm during 1981–2010. During the growing seasons (from April to October) in 2011 and 2012, mean air temperatures were 20.3℃ and 20.4℃, total precipitation was 1498 and 1266 mm, and the average hours of sunshine per month were 168 and 178 h, respectively. Thus, the climate was similar between the two study years. These meteorological data were recorded by a nearby automated meteorological data acquisition system (34°53.7’ N, 135°12.7’ E, 150 m alt.) by the Japan Meteorological Agency.

In the study area, semi-natural grasslands were maintained on the levees of paddy fields and irrigation ponds, and at the edges between paddy fields and secondary forests (dominated by *Pinus densiflora* and *Quercus serrata*), by periodic mowing (Fig. S2-1). Here, mowing is considered to act as a disturbance agent for plants and herbivores. Mowing frequency varied among terraces depending on land-use type (see next section). Semi-natural grasslands around paddy fields are estimated to cover approximately 30% of the total area of paddy terraces in Japan (Tabata 1997).

The paddy terraces were categorized into three land-use types (Fig. S2-1): abandoned terraces, where farmers had ceased rice cultivation and the mowing of semi-natural grasslands 3–15 (mean 9.8) years ago; traditional terraces, which are paddy terraces that have been managed in traditional ways for at least 100 years; and intensive terraces, characterized as land-consolidated paddy terraces, which underwent land consolidation 12–31 (mean 20) years ago. Paddy terrace abandonment initiates succession from *semi-natural grassland* to secondary forest, and decreases grassland-specific plant diversity within several years (Uematsu *et al.* 2010). In contrast, paddy consolidation converts small, irregular, and poorly drained paddy fields into large, quadrangular, well-drained fields to improve productivity and to allow mechanized farming (Uematsu *et al.* 2010). Although the number of grassland plant species increased with years after consolidation in intensive terraces, Matsumura & Takeda (2010) found that richness had not recovered to the level of that in traditional terraces even after > 20 years. Distances between each abandoned or intensive terraces and traditional terraces varied from 0.10 to 25.55 km (mean 12.33 km) and from 0.11 to 33.57 km (mean 14.18 km), respectively. I interviewed all farmers and were informed that little to no insecticide is used for paddy crops and no insecticides are applied to semi-natural grasslands. In most cases, one farmer managed a single terrace.

I set four 5 × 50 m belt plots in semi-natural grasslands on each study terrace. I studied 32 abandoned plots in 8 abandoned terraces, 52 traditional plots in 13 traditional terraces, and 40 intensive plots in 10 intensive terraces in 2011. In 2012, I removed two study terraces because the areas had been developed for other land uses; therefore, 116 plots in 29 terraces were used in this study, including 28 plots in 7 abandoned terraces, 48 plots in 12 traditional terraces, and 40 intensive plots in 10 intensive terraces.

Anthropogenic disturbance

I recorded the number of mowing events in each plot during my survey period to determine the disturbance frequency in 2011 and 2012. During late April and late September, I measured vegetation height (cm) at 15 points within each plot and calculated the mean vegetation height for each month (Fig. S2-2). I compared the mowing frequency among the different land-use types using a generalized linear mixed model (GLMM, Poisson error and log link) in which mowing frequency per year was the response variable and land-use type was the explanatory variable. Terrace identity was incorporated into the models as a random term because four plots within each terrace could be a source of pseudoreplication. I evaluated the significance of the partial regression coefficients of the explanatory variables using a Wald test. The mowing frequency in traditional plots was significantly higher and lower than in abandoned and intensive plots, respectively (Fig. S2-3). The mean vegetation height decreased with increasing mowing frequency (GLMM and Wald test, $t = –7.388$, $P < 0.01$ in 2011, $t = –6.397$, $P < 0.01$ in 2012; Fig. S2-4).

Landscape variables

For each study terrace, I calculated the areas of abandoned, traditional, and intensive terraces, secondary forest, and residential land within a 1- km radius from the center of the terrace (Fig. S2-5), using ArcGIS Spatial Analyst 9.3 (ESRI) with a land-use map (Geospatial Information Authority of Japan) and aerial photographs from Google maps (Google 2013).

I conducted a principal components analysis (PCA) on the above five area-variable data sets to reduce landscape variables for the diversity analyses. I found that two primary axes explained 77.3% of the total variance. The PCA axis 1 value increased with the area of secondary forest and decreased with the area of both abandoned and intensive terraces and residential land; thus the negative values indicate large land-use changes around the terraces (Fig. S2-6). The PCA axis 2 value increased with the area of both intensive terraces and residential land and decreased with the area of both traditional and abandoned terraces, thus the high positive values indicate more human impact around the terraces (Fig. S2-6). For each plot, I also measured the length for which the study grassland plot neighbored secondary forest (i.e., forest edge length within the study plot) as another landscape variable, which would influence plant and insect communities.

Plant survey

I surveyed the plant community in each study plot monthly from late April to late September in 2011 and 2012 (six times per year). During each survey, I walked along the plots and recorded all vascular plant species and flower abundance (the number of flowers) for all flowering species, except for wind-pollinated species. Using the flower abundance data, I calculated the inverse Simpson's index of diversity (1/D, Simpson 1949; Hill 1973) of flowers. This index accounts for variation in relative abundance, unlike simple species richness. In October 2011, I conducted an intensive vegetation survey during which I recorded all of the vascular plants within each plot. Aboveground biomass (g m^{-2}) was estimated after the aboveground parts of plants from the four subplots (0.25 m^2) within each plot were clipped, dried at 70°C for 24 h, and weighed (Fig. S2-2). The mean biomass per plot was strongly and positively correlated with the mean vegetation height per plot (Pearson's correlation coefficient, $r = 0.87$, $P < 0.01$).

Herbivorous insect survey

On the same days that I conducted monthly vegetation surveys, butterfly species and abundance (the number of individuals) in each plot were recorded using the standardized transect count method (Pollard & Yates 1994). The butterfly survey was implemented for 15 min per plot (60 min per terrace) under sunny and warm conditions. Hesperioidea (skippers) and Papilionoidea (butterflies) species were defined as butterflies in this study (Fig. S2-7).

Orthoptera species and abundance were surveyed using a sweep-net (42-cm-diameter) with 200 sweeps per plot. To minimize the effects of differences in vegetation height among the plots, I swept from the bottom to the top of the leaf layer during a single sweep. Orthoptera surveys were conducted twice (between mid-August and early October) per year for each plot in 2011 and 2012. Sweeping is considered a good method for estimating the species richness and abundance of orthopterans in grassland vegetation (Joern 2005). After collecting orthopterans in the field, I identified the species and counted the number of individuals of each species (Fig. S2-8). The insect surveys were conducted in the same way during the two study years, such that the sampling intensity did not differ between years.

Functional grouping

Plants—To examine differences in the responses to land-use changes among plant groups with different life-history traits, I divided plant species into three groups: annual, perennial, and woody. These groups differ in disturbance resistance, flowering position, and mating system. Generally, annuals are more disturbance-resistant than perennial and woody species, and they often dominate and reproduce by selfing in frequently disturbed vegetation (Baker 1974; Aarssen 2000; Begon *et al.* 2006). Meanwhile, the reproduction of perennial herb species would be limited under frequently disturbed or undisturbed conditions. This is because they often produce larger, animal-pollinated flowers only after plants grow taller than annuals and compete against woody species for light at much taller vegetation heights (Pykälä 2005).

Butterflies—First, I categorized butterflies into three body-size groups: small (10.4–17.6 mm body length), medium (17.6–24.8 mm), and large (24.8–32.1 mm). I estimated the body size of each species by measuring life-sized photos of specimens in the butterfly guide *The Standard Butterflies in Japan* (Shirouzu 2006). I did not collect specimens, because many endangered species are present at the study sites. All photographed individuals of each species in the book were measured (n = 6–24, all measured individuals n = 846; Table S2-1). This categorization was based on the range of body sizes in the studied species (10.4–32.1 mm). Second, I divided the butterflies into three larval-host groups (Table S2-1): monophagous species (specialists on a specific plant species or genus), oligophagous species (species that feed on various species within a specific plant family), and polyphagous species (generalist feeders that use more than one plant family). Host plant identification was also based on descriptions in *The Standard Butterflies in Japan* (Shirouzu 2006). Third, I divided butterflies into rare (<1 individual per terrace per year in either year, Table S2-1) and common species (all others) according to their abundance in traditional terraces. Finally, I divided butterfly species into their families: Papilionidae, Pieridae, Lycaenidae, Nymphalidae and Hesperiidae (Table S2-1).

Orthoptera—First, I categorized orthopterans into three body-size groups, small (8.1–16.3 mm body length), medium (16.3–24.4 mm), and large (24.4–40.7 mm), except for an outlier, *Acrida cinerea* (56.4 mm). I measured the body sizes of specimens in the laboratory (n = 1–40, all measured individuals n = 791; Table S2-2). Second, I divided them into three mandibular groups (Table S2-2): sharp (herb feeder), flat (grass feeder), and mixed type (generalist) (Isley 1944; Petterson 1984; ElEla *et al.* 2010), determined using a microscope in the laboratory. The host plants of orthopterans have not been thoroughly studied in Japan (Ichikawa *et al.* 2006). Third, I divided the orthopterans into rare and common following the same criteria used for butterfly species. Finally, I divided species into their families: Tettigoniidae, Meconematidae, Phaneroperidae, Eneopteridae, Tetrigidae, Pyrgomorphidae, and Acrididae (Table S2-2). Because of the small sample size, I did not use data for Eneopteridae, Meconematidae and Pyrgomorphidae for family analyses.

Statistical analyses

Land-use type–diversity relationships—I compared the richness of plant species and the richness and 1/D of butterflies and orthopterans among land-use types. First, I pooled the data from six (plant and butterfly) or two (Orthoptera) surveys, and created an annual data set for each plot. I also pooled data from the intensive plant survey conducted in October 2011. I used GLMMs (with Poisson error and log link for richness analyses and Gaussian error and identity link for 1/D analyses), in which the richness of plants, and richness and 1/D of butterflies or orthopterans per plot were the response variables and land-use type (abandoned, traditional, and intensive) was the explanatory variable. Terrace identity was incorporated into the models as a random term. I evaluated the significance of the partial regression coefficients of the explanatory variables using a Wald test. I also compared herbivore richness among land-use types for each survey (butterflies: six times, Orthoptera: twice).

Relationships of plant richness with disturbance and landscape variables—I examined the relationships between plant richness, and the disturbance regime (mowing frequency) and the landscape variables (forest edge length and PCA axis 1 and 2 values), using a GLMM (Poisson error and log link). The IDH predicts that species richness will show a unimodal relationship with the mowing frequency, whereas the LCH predicts significant effects of the landscape variables. In the full GLMM models, mowing frequency and its square, forest edge length, and PCA axis 1 and 2 values were used as the explanatory variables, and the richness of each group of plants was used the response variable. I used raw values of these explanatory variables in the analyses. Terrace identity was incorporated into the models as a random term. To evaluate the significance of the effects of the explanatory variables on species richness, I used a model selection procedure based on Akaike's information criterion (AIC): the model with the smallest AIC was considered the best model (Johnson & Omland 2004). The significance levels of the estimated partial regression coefficients of the explanatory variables in the best model were examined by determining if the 95% confidence intervals (CIs) of the estimated coefficients included zero. For further evaluation of the relative importance of selected variables in the best models, I compared AICs between the best models and those without one of the variables included in the best model: a larger difference in AIC value indicated a higher contribution of the variable to the plant richness.

Relationships of herbivore diversity with plants, disturbance, and landscape variables—I examined the relationships of butterfly diversity (richness and 1/D) with plant parameters (flower 1/D, larval-host plant richness), the disturbance regime (mowing frequency), and landscape variables (forest edge length and PCA axis 1 and 2 values), using GLMMs (Poisson error and log link for richness, Gaussian error and identity link for 1/D). In the full models, the explanatory variables were the flower 1/D of annuals, perennials and woody species, richness of the annual, perennial and woody larval-host species, mowing frequency and its square, and all landscape variables. The response variables were the richness or 1/D of total butterfly species or each trait group. I used raw values of these explanatory variables in the analyses. Terrace identity was incorporated into the models as a random term. Flower 1/D and larval-host plant richness are indicators of adult and larval resource diversity, respectively. The full models included some explanatory variables that could potentially have been excluded; model selection based on AIC was conducted for the above models. The significance levels of the partial regression coefficients of the explanatory variables and the relative importance of selected variables were assessed as described above.

In the same way, I examined the relationships of the richness and 1/D of orthopteran and plant parameters (richness of annual and perennial grass and forb species), with mowing frequency and landscape variables using GLMMs (Poisson error and log link for richness, Gaussian error and identity link for 1/D). In the full models, the explanatory variables were the richness of annual and perennial grass and forb species, mowing frequency and all landscape variables, and the response variable was the richness and 1/D of all orthopterans or each trait group. Terrace identity was incorporated into the models as a random term. Annual and perennial plant species richness could be used as an indicator of the orthopteran resource availability (the species studied do not feed on woody species).

Relationships between abundance and richness and between productivity and abundance of herbivores—To test the MIH, I examined the relationships between abundance (total number of individuals) and richness of herbivorous insects and between productivity and abundance of herbivores, using GLMM (Poisson error and log link). The MIH predicts an increase in species richness with total abundance that further increases with productivity. In the first GLMM analysis, I used log-transformed abundance as the explanatory variable and total species richness as the response variable. Terrace identity was incorporated into the models as a random term.

In the second GLMM analysis, productivity, abundance, and terrace identity were the explanatory variable, response variable, and random term, respectively. I used vegetation height growth (cm) between the first and second surveys, i.e., the growth rate per month in spring, for each plot as an indicator of productivity. Because the unpredictable occurrence of mowing by farmers prevented us from collecting productivity data in some terraces, I only performed the analysis on data from a limited number of plots (13 plots on 4 intensive terraces, 42 plots on 10 traditional terraces, 32 plots at 8 abandoned terraces in 2011; and 8 plots on 2 intensive terraces; and 27 plots at 8 traditional terraces, 28 plots at 7 abandoned terraces in 2012).

Relationships between species traits and species loss and decline—To assess which species traits (body size, degree of host specialization, and abundance) were related to species loss and decline due to land-use changes, I pooled all terrace data in 2011 and 2012 and examined the relative abundance of each species (the rank-abundance relationship) in traditional terraces and the total and individual abundance of each butterfly and orthopteran species in abandoned and intensive terraces. First, I categorized the insect species based on whether they were present in abandoned and intensive terraces, separately. Then I calculated the expected range (95%, from the lower 2.5% to the upper 97.5%) of each species in abandoned and intensive terraces. For the calculations, I developed a null model assuming neutrality, with the same properties as the data sets of butterflies or orthopterans in abandoned and intensive terraces (i.e., the total number of individuals: 842 and 1192 butterfly individuals, and 371 and 1515 orthopteran individuals for abandoned and intensive terraces, respectively). For example, in a single butterfly-in-intensive terrace model trial, 1192 individuals were assigned to randomly selected butterfly species in proportion to the relative abundance of each species in traditional terraces, in accordance with recent neutral models of community structure (Bell 2000; Hubbell 2001). I repeated this randomization trial 50,000 times. Using this data set, I generated a frequency distribution of abundance for each butterfly species, and then calculated the expected range of abundance of each butterfly species in abandoned terraces. I examined whether the observed abundance of each species was out of the expected range. Based on this result, I divided species into three categories (significantly decreased, expected, and significantly increased) for abandoned and intensive terraces, separately.

I first examined the effects of species traits on species loss and the decline of butterfly and orthopteran species in abandoned and intensive terraces, separately. In the species loss analyses, the presence/absence (0/1) of each species was the response variable and body size (mm), the degree of host specialization (butterfly: monophagaous, oligophagaous, or polyphagous; Orthoptera: sharp, flat, or mixed) and abundance (total number of individuals in traditional terraces) were the explanatory variables in a generalized linear model (GLM, binomial distribution and logit link). Two species (*Zizina otis* and *Libythea lepita*), which were not found in traditional terraces, were excluded. Furthermore, I tested the effects of species traits on the decline of butterfly and orthopteran species in abandoned and intensive terraces, separately, using a GLM (binomial distribution and logit link). I used data for species whose expected range of abundance did not include zero. The response variable was whether the species was significantly decreased or not (i.e., significantly decreased species, 1; expected and significantly increased species, 0) and the explanatory variables were body size, larval-host group (or mandibular type), and abundance in traditional terraces. I also examined the relationship of species abundance in traditional terraces with body size and larval-host group or mandibular type in butterflies and orthopterans, using a GLM with Poisson errors, in which abundance was the response variable and body size, and larval-host group or mandibular type were the explanatory variables.

All statistical analyses were performed using the software R (version 2.13.1; R Development Core Team 2008).

Results

In total, 477 plant species, 61 species and 3,713 individual butterflies, and 33 species and 4,232 individual orthopterans were recorded in 2011; and 468 plant species, 58 species and 2,902 individual butterflies, and 28 species and 1,957 individual orthopterans were recorded in 2012 (Tables S2-1, S2-2, and S2-3). Although the climate and sampling methods did not differ between years, the numbers of butterfly and orthopteran individuals were much lower in 2012 that in 2011.

Differences in richness and diversity among land-use types

Traditional plots had significantly higher species richness of total and perennial plants than both abandoned and intensive plots (Fig. 2-1a and c). Annual species richness was similar between traditional and intensive plots and was significantly higher in these than in abandoned plots (Fig. 2-1b), whereas woody species richness was similar between traditional and abandoned plots and significantly higher in these than in intensive plots (Fig. 2-1d). The richness and 1/D of butterfly and orthopteran species were also significantly higher in traditional plots among the three land-use types (Fig. 2-1e–h). This trend was consistent throughout the seasons in both 2011 and 2012 (GLMM and Wald-test, $P < 0.01$, Fig. S2-9), except for the fourth butterfly survey in 2011, in which both species richness and 1/D did not differ between traditional and abandoned plots (GLMM and Wald-test, $P > 0.1$, Fig. S2-9).

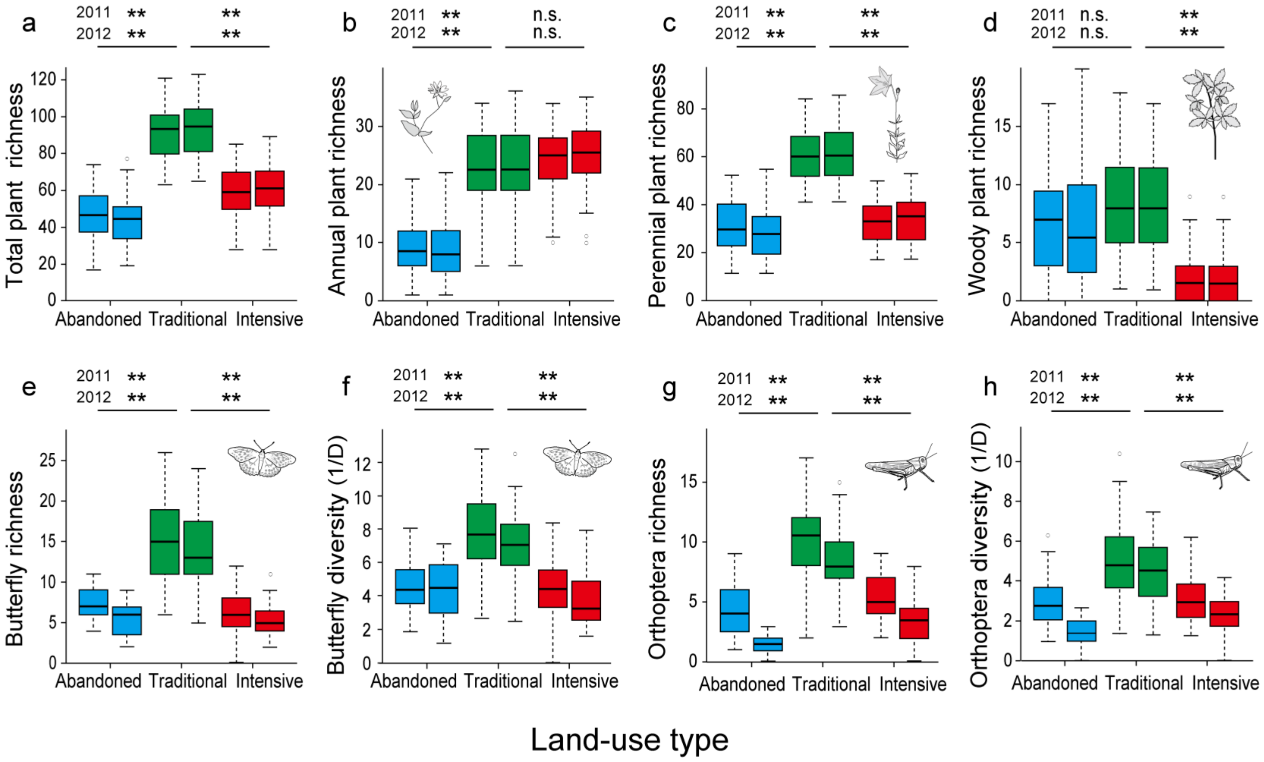


Fig. 2-1. Comparisons of plant species richness and the species richness and diversity (the inverse Simpson's index of diversity, 1/D) of butterfly and orthopteran species among abandoned, traditional and intensive plots (left box, 2011; right box, 2012). Box plots represent medians (bold black horizontal line), and first and third quartiles (box perimeters). $^{**}P < 0.01$, n.s. not significant.

Relationships of plant richness with disturbance and landscape variables

Richness of total plant species and all life-history groups had a significant unimodal relationship with the mowing frequency in 2011 and 2012 (Fig. 2-2 a, c, and e, Table S2-4), except for woody species richness, which linearly decreased with the mowing frequency in 2011 (Fig. 2-2 g, Table S2-4). The estimated richness of total, perennial, and woody species was maximized with a mowing frequency of less than twice a year (Fig. 2-2 a, e, and g), whereas annual plant richness was at a maximum with a mowing frequency of more than three times a year (Fig. 2-2 c). The richness of total, perennial, and woody species increased with forest edge length and PCA axis 1 value (Fig. 2-2 b, f, and h, Table S2-4), whereas the richness of annual species increased with the PCA axis 2 value (Fig. 2-2 d, Table S2-4).

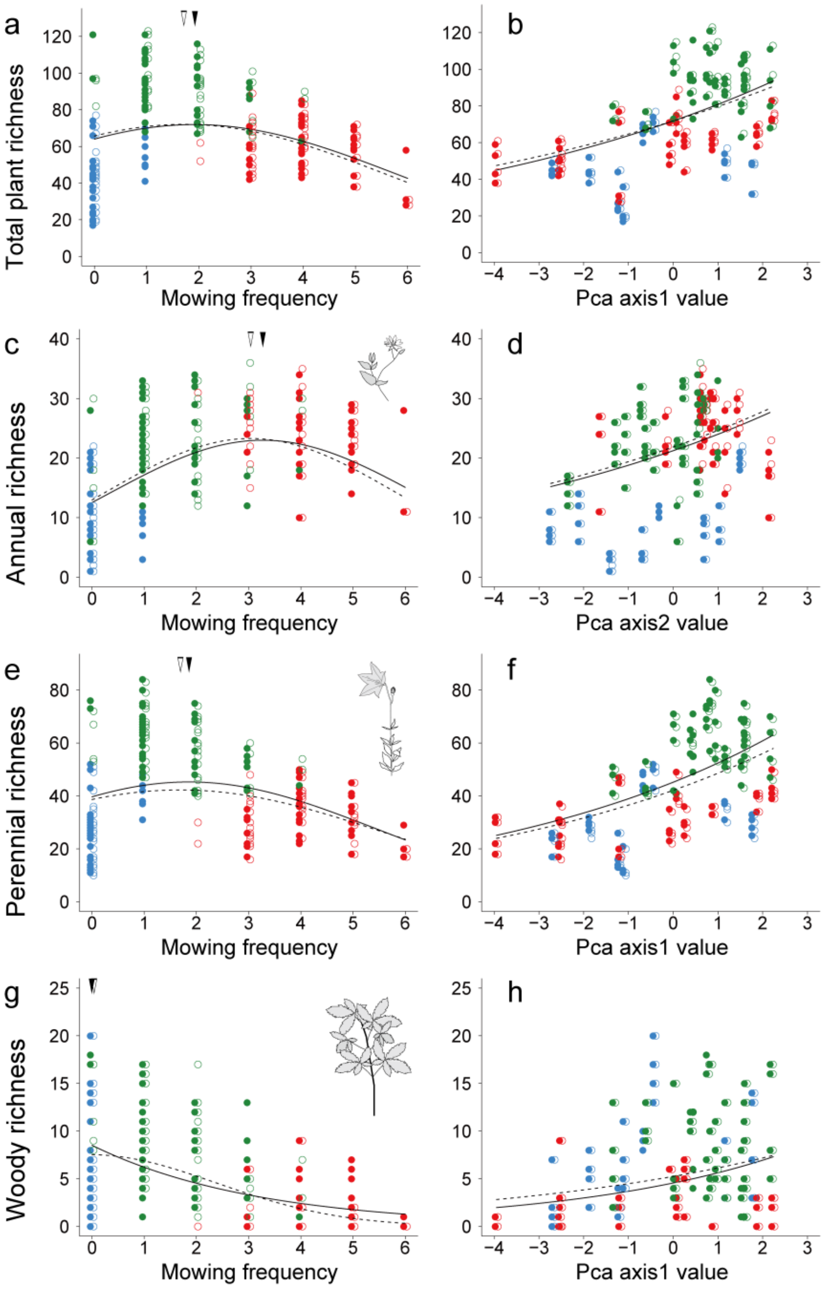


Fig. 2-2. Relationships of species richness of each plant life-history group with the mowing frequency and the PCA axis 1 or 2 value in 2011 and 2012. Closed and open circles represent the species richness in 2011 and 2012, respectively (blue dot, abandoned; green, traditional; red, intensive). Bold (2011) and dashed lines (2012) represent the estimated species richness from the best generalized linear mixed model. The upside-down closed and open triangles indicate the mowing frequency at which the estimated species richness was highest in 2011 and 2012, respectively (see Table S2-4 for details). To avoid data point overlaps, small increments (2011: -0.03, 2012: +0.03 to x coordinates) have been added. The regression line for each predictor was drawn using fixed values (i.e., the means) for the other predictors.

Relationships of herbivore diversity with plant, disturbance, and landscape variables

Total butterfly richness and 1/D increased with larval-host plant richness in both 2011 and 2012 (Fig 2-3a and c, Tables S2-5 and S2-6). Flower 1/D rarely influenced the richness and 1/D of butterflies, and butterfly richness increased only with perennial flower 1/D in 2012 (Tables S2-5 and S2-6). Total orthopteran richness and 1/D increased with richness of perennial grass and/or forb species in both years (Fig 2-3e, f, h, and i, Tables S2-7 and S2-8). Both butterfly and orthopteran richness had a unimodal relationship with mowing frequency, although peaks differed between the two herbivore groups: butterfly and orthopteran richness at their maxima with mowing frequencies of 1–2 times per year and 2–3 times per year, respectively (Fig 2-3b and g). Conversely, butterfly and orthpteran 1/D had no relationships with the mowing frequency; an exception was that in 2012 butterfly 1/D which significantly decreased with mowing frequency (Fig. 2-3d and j). No landscape variables had significant effects on total butterfly and orthopteran richness or 1/D (Tables S2-5–S2-8).

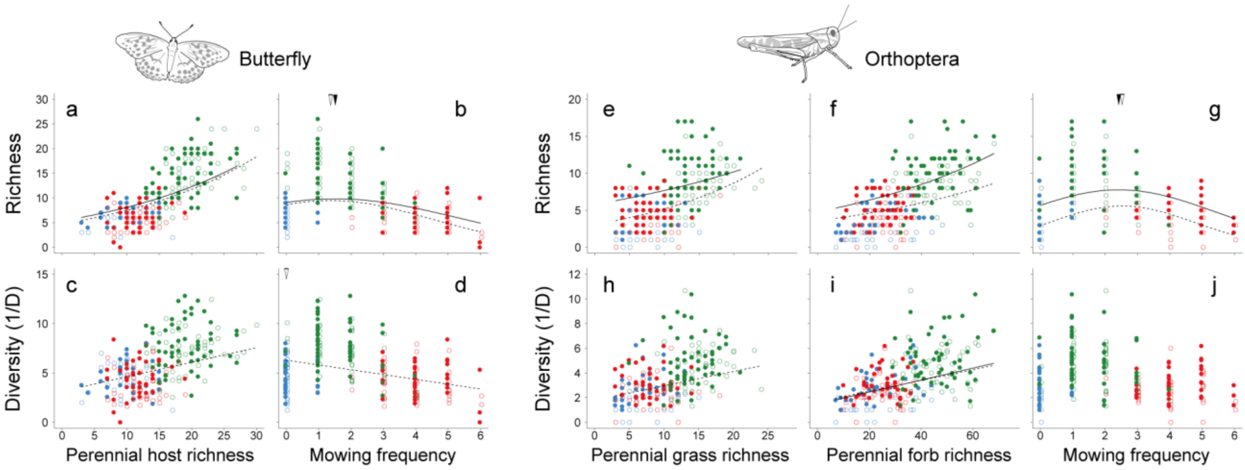


Fig. 2-3. Relationships of species richness and diversity (the inverse Simpson's index of diversity, 1/D) of herbivorous insects with the resource of perennial plant variables and the mowing frequency in 2011 and 2012. Closed and open circles represent the species richness and diversity (1/D) in 2011 and 2012, respectively (blue dot, abandoned; green, traditional; red, intensive). Bold (2011) and dashed lines (2012) represent the estimated species richness of butterfly and orthoptera, from the generalized linear mixed model. The upside-down closed and open triangles indicate the mowing frequency at which the estimated species richness and diversity (1/D) was the highest. To avoid data point overlap, small increments (2011: -0.03, 2012: +0.03 to x coordinates) have been added. The regression line for each predictor was drawn using fixed values (i.e., the means) for the other predictor.

Differences among butterfly functional groups

The richness of both annual and perennial larval-hosts and/or the flower 1/D of perennials had significant positive effects on the richness and 1/D of all body-size groups in one or both years (Fig. 2-4a, c, and e, Tables S2-5 and S2-6, Fig. S2-10). There were unimodal relationships of richness and 1/D of medium- and large-sized groups with mowing frequency in one or both years (Fig. 2-4d and f, Tables S2-5 and S2-6, Fig. S2-10), whereas no relationships were found between richness and 1/D of the small-sized group and mowing frequency (Fig. 2-4b, Tables S2-5 and S2-6, Fig. S2-10), except for 1/D in 2012. There were no large differences in the peaks of richness or 1/D against mowing frequency among the body-size groups (Fig. 2-4d and f, Tables S2-5 and S2-6, Fig. S2-10). Both the richness and 1/D of medium-sized butterflies increased with PCA axis 1 value in 2011, and decreased with PCA axis 2 value in 2012 (Tables S2-5 and S2-6). The 1/D of the small-sized butterfly group increased with forest edge length in 2011, and landscape variables had no effects on the richness and 1/D of large butterflies (Tables S2-5 and S2-6).

The richness and/or 1/D of all larval-host groups significantly increased with perennial larval-host plant richness and/or perennial flower 1/D in one or both years (Fig. 2-5a and c, Tables S2-5 and S2-6, Fig. S2-11) and were affected by the mowing frequency in one or both years (Fig. 2-5b, d, and f, Tables S2-5 and S2-6, Fig. S2-11), such that their estimated peaks tended to occur in more frequently mowed plots for specialists (monophagaous or oligophagous species) than for generalists (polyphagous species), although the trend was not consistent between years (Fig. 2-5b, d, and f, Tables S2-5 and S2-6, Fig. S2-11).

The richness and 1/D of rare and common butterfly species increased significantly with larval-host perennial plant richness in both years (Fig. 2-6a and c, Tables S2-5 and S2-6, Fig. S2-12). Perennial flower 1/D and annual and woody larval-host plant richness had significantly positive effects on rare or common species richness and 1/D, but consistent effects were not found (Tables S2-5 and S2-6). The richness of rare species had a unimodal relationship with the mowing frequency in both years, whereas 1/D significantly linearly decreased with the mowing frequency (Fig. 2-6b, Tables S2-5 and S2-6, Fig. S2-12). The richness and 1/D of common species had a significant unimodal relationship with mowing frequency only in 2012 (Fig. 2-6d, Tables S2-5 and S2-6, Fig. S2-12). Landscape variables had no effect on the richness and 1/D of rare or common species (Tables S2-5 and S2-6).

Differences among orthopteran functional groups

Plant species richness, especially for perennial grasses and/or forbs, had significant positive effects on the richness and 1/D of all body-size groups in one or both years (Fig. 2-4g, h, k, m, and n, Tables S2-7 and S2-8, Fig. S2-10). Mowing frequency significantly influenced the richness and/or 1/D of medium and large orthopteran species in both years (Fig. 2-4 l and o, Tables S2-7 and S2-8, Fig. S2-10), but mowing frequency had no effect on the richness or 1/D of small species (Fig. 2-4 i, Tables S2-7 and S2-8, Fig. S2-10). The peak values of large species occurred in more frequently-mowed plots than those of medium-sized species in 2011 (Fig. 2-4l and o, Tables S2-7 and S2-8, Fig. S2-10). The PCA axis 2 value had a significantly negative effect on both the richness and 1/D of small species in 2011 and medium-sized species in 2012 (Tables S2-7 and S2-8).

The richness and 1/D of sharp and flat mandibular species significantly increased with perennial grass or forb species in both years (Fig. 2-5g, h, j, and k, Tables S2-7 and S2-8, Fig. S2-11). The predicted relationships between the sharp mandibular type and forbs species, and between the flat type and grass species were not consistently found (Tables S2-7 and S2-8). The richness and 1/D of the mixed type increased with perennial grass and/or forb species in one or both years (Fig. 2-5m and n, Tables S2-7 and S2-8, Fig. S2-11). Mowing frequency significantly affected the richness and 1/D of sharp and flat types in both years, but had no effect on the richness and 1/D of the mixed type in both years (Fig. 2-5i, l, and o, Tables S2-7 and S2-8, Fig. S2-11). The peaks of estimated richness were found more frequently in mowed plots for the flat than for the sharp type (Fig. 2-5i and l).

The richness and 1/D of rare and common orthopterans increased with the richness of perennial grasses and/or forb species in both years (Fig. 2-6e, f, h, and i, Tables S2-7 and S2-8, Fig. S2-12). Only the richness of common orthpteran species had a unimodal relationship with the mowing frequency (Fig. 2-6j, Tables S2-7 and S2-8, Fig. S2-12). The PCA 2 value had a negative effect on both the richness and 1/D of rare orthopteran species, but only in 2012 (Tables S2-7 and S2-8). Other landscape variables had no significant effects on the richness or 1/D for both type of species (Tables S2-7 and S2-8).

Differences among taxonomic groups of herbivores

The richness and 1/D of all butterfly families significantly increased with the richness of the perennial larval-host and/or the 1/D of perennial flowers in one or both years (Tables S2-9, Figs. S2-13 and S2-14). Note that the richness and 1/D of Papilionidae had no relationship with larval-host plant richness in both years. Mowing frequency had significant effects on the richness and/or 1/D of all butterfly families in one or both years, except the 1/D of Lycaenidae species (Tables S2-9, Figs. S2-13 and S2-14). The peaks of estimated richness against the mowing frequency differed largely among butterfly families (Tables S2-9).

In 2011, forest edge length had a positive effect on Hesperiidae richness and 1/D, whereas both factors increased with the PCA axis 1 value for Lycaenidae and Nymphalidae species (Tables S2-9).

The richness and 1/D of all orthopteran families had significant relationships with the richness of perennial grass and/or forb species in one or both years (Tables S2-10, Figs. S2-13 and S2-14). Mowing frequency significantly influenced richness and 1/D of all families in one or both years, except for the 1/D of Tetrigidae species (Tables S2-10, Figs. S2-13 and S2-14). The peaks of estimated richness against the mowing frequency differed largely among orthopteran families (Tables S2-10). Forest edge length and the PCA axis 2 value had significant negative effects on the richness and 1/D of Acrididae, respectively, whereas the PCA axis 1 value had a positive effect on Tettigoniidae richness (Tables S2-10).

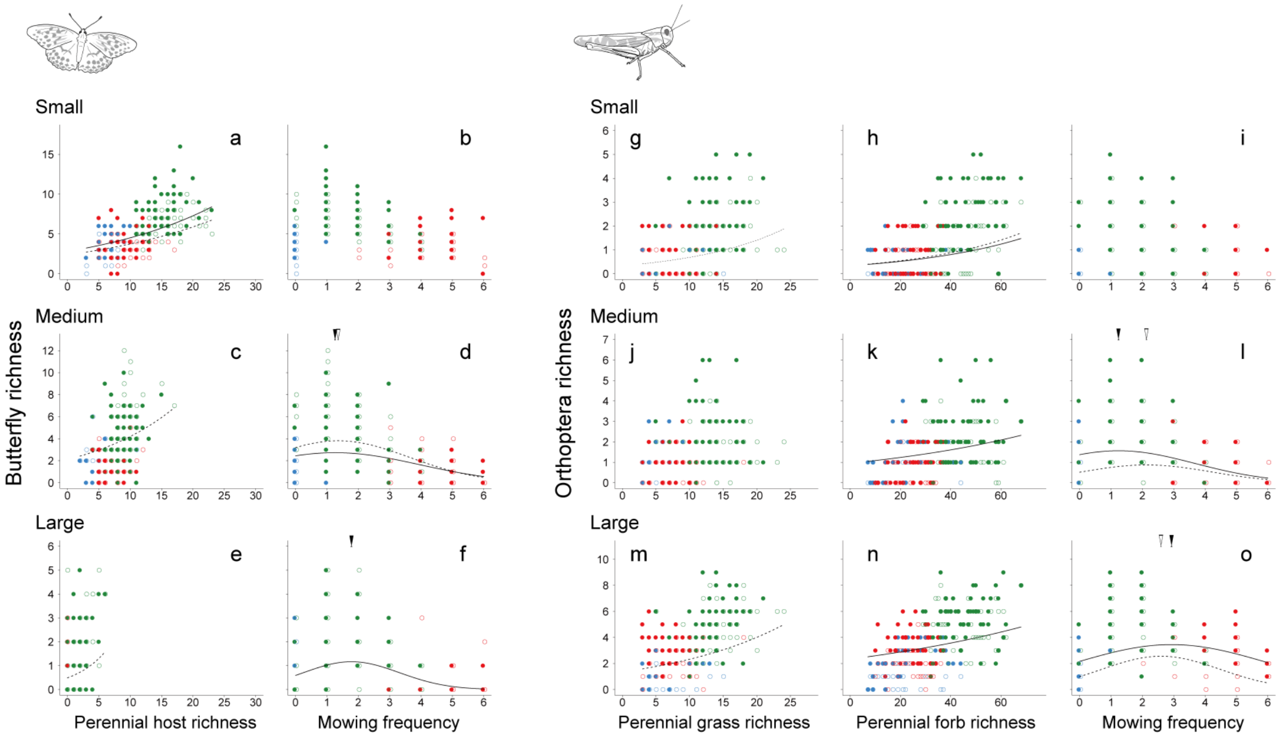


Fig. 2-4. Relationships of the species richness of herbivorous insects of body-size groups with the resource of perennial plant variables and the mowing frequency in 2011 and 2012. Closed and open circles represent the species richness in 2011 and 2012, respectively (blue dot, abandoned; green, traditional; red, intensive). Bold (2011) and dashed lines (2012) represent the estimated species richness of butterfly and orthoptera, from the generalized linear mixed model. The upside-down closed and open triangles indicate the mowing frequency at which the estimated the species richness was the highest. To avoid data point overlap, small increments (2011: -0.03, 2012: +0.03 to x coordinates) have been added. The regression line for each predictor was drawn using fixed values (i.e., the means) for the other predictor.

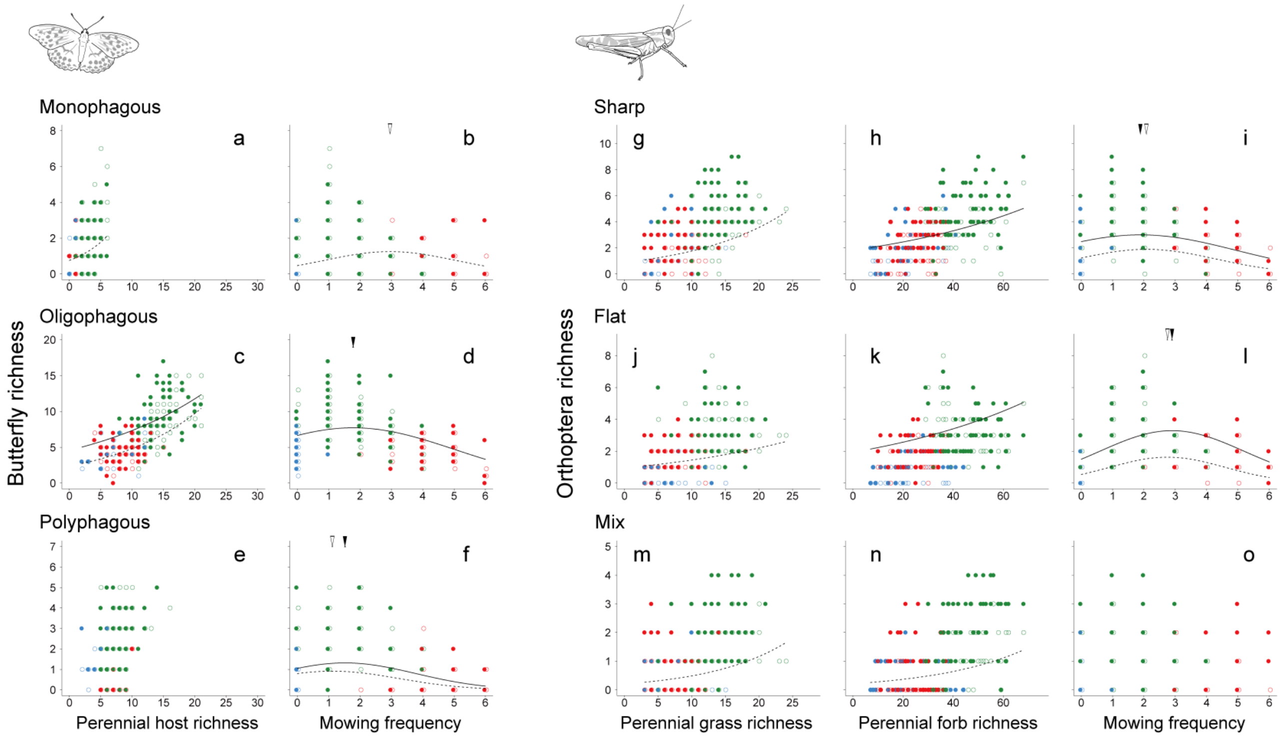


Fig. 2-5. Relationships between the species richness of herbivorous insects of larval-host/mandibular groups and the resource of perennial plant variables and the mowing frequency in 2011 and 2012. Closed and open circles represent the species richness in 2011 and 2012, respectively (blue dot, abandoned; green, traditional; red, intensive). Bold (2011) and dashed lines (2012) represent the estimated species richness of butterfly and orthoptera, from the generalized linear mixed model. The upside-down closed and open triangles indicate the mowing frequency at which the estimated the species richness was the highest. To avoid data point overlap, small increments (2011: -0.03, 2012: +0.03 to x coordinates) have been added. The regression line for each predictor was drawn using fixed values (i.e., the means) for the other predictor.

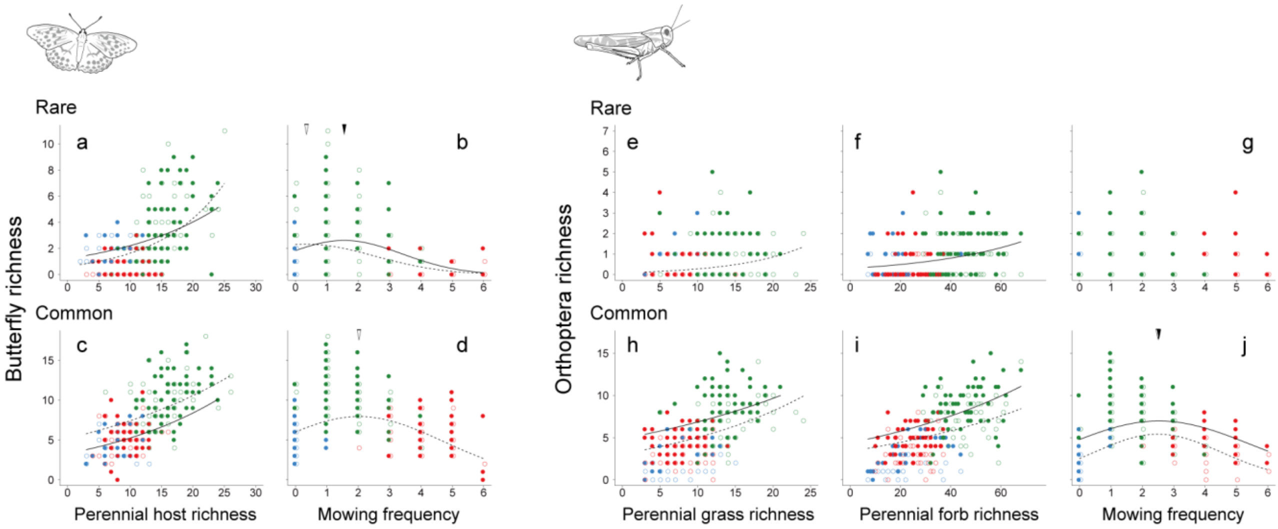


Fig. 2-6. Relationships of the species richness of herbivorous insects of abundance (No. of individuals) groups with the resource of perennial plant variables and the mowing frequency in 2011 and 2012. Closed and open circles represent the species richness in 2011 and 2012, respectively (blue dot, abandoned; green, traditional; red, intensive). Bold (2011) and dashed lines (2012) represent the estimated species richness of butterfly and orthoptera, from the generalized linear mixed model. The upside-down closed and open triangles indicate the mowing frequency at which the estimated the species richness was the highest. To avoid data point overlap, small increments (2011: -0.03, 2012: +0.03 to x coordinates) have been added. The regression line for each predictor was drawn using fixed values (i.e., the means) for the other predictor.

Relationships of richness with abundance and productivity in herbivores

The richness of butterfly and orthopteran species significantly increased with their respective abundances in both years (Fig. 2-7). Note that I obtained better fits using log-transformed abundance than non-transformed abundance (butterfly: non-transformed AIC = 116.2 and 111.4 in 2011 and 2012, log-transformed AIC = 74.0 and 66.5 in 2011 and 2012, respectively; Orthoptera: non-transformed, AIC = 104.6 and 97.8 in 2011 and 2012, log-transformed, AIC = 84.7 and 45.4 in 2011 and 2012, respectively). In contrast, the abundance of butterfly and orthopteran species did not increase with productivity, except for butterfly abundance in 2011 (Fig. S2-15).

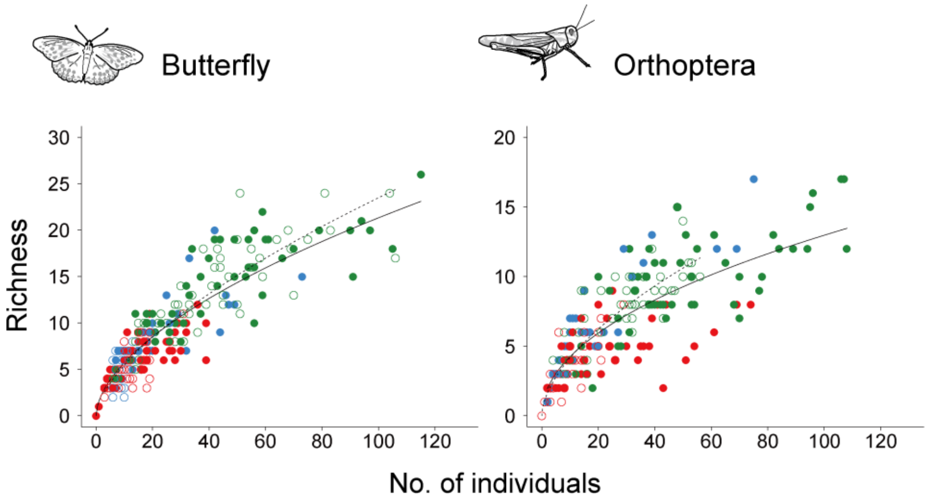


Fig. 2-7. The relationships between number of individuals and species richness of two herbivorous insect groups in 2011 and 2012. Closed and open circles represent data for 2011 and 2012, respectively (blue, abandoned; green, traditional; red, intensive). Bold (2011) and dashed lines (2012) represent the estimated species richness from the best generalized linear mixed models (GLMMs; see text for details). To avoid data point overlaps, small increments (2011: -0.03, 2012: +0.03 to x coordinates) have been added.

Relationships of species loss in terraces with land-use and species traits

My null model analyses revealed that expected range of abundance of butterfly species of rank > 27 (abandoned) and > 31 (intensive), and orthopteran species of rank > 17 (abandoned) and > 22 (intensive) included zero (Fig. 2-8 and 2-9). Note that species ranks for butterflies and orthopterans were based on the relative abundances of each species in traditional terraces.

Species loss of butterflies in abandoned and intensive terraces was significantly negatively correlated with abundance, such that species with a lower abundance in traditional terraces were more rarely observed in abandoned and intensive terraces (Fig. 2-8, Tables S2-11). Body size and larval-host plant type had no relationships with butterfly species loss in abandoned or intensive terraces (Tables S2-11). Abundance had marginally negative effects on the species loss of orthopterans in both abandoned and intensive terraces, whereas body size and mandibular type had no significant effects (Fig. 2-9, Tables S2-11). The species decline analyses revealed that no species traits had significant effects on the decline of butterfly or orthopteran species in either abandoned or intensive terraces (Fig. 2-9, Tables S2-11). Only abundance had a marginally significant negative effect on butterfly species decline in intensive terraces (Fig. 2-8, Tables S2-11). The abundance of butterfly species in traditional terraces significantly decreased with body size (GLM, coefficient = – 0.122, $P < 0.01$) and was significantly higher in oligophagous and polyphagous species than in monophagous species (GLM, oligophagous species, coefficient = 1.773, $P < 0.01$; polyphagaous species, coefficient = 1.552, $P < 0.01$). In contrast, the abundance of orthopteran species significantly increased with body size (GLM, coefficient = 0.023, $P < 0.01$) and was lower in mixed mandibular-type species than in those with sharp or flat mandibular parts (GLM, sharp type: coefficient = 0.328, $P < 0.01$; flat type, coefficient = 1.228, $P < 0.01$).

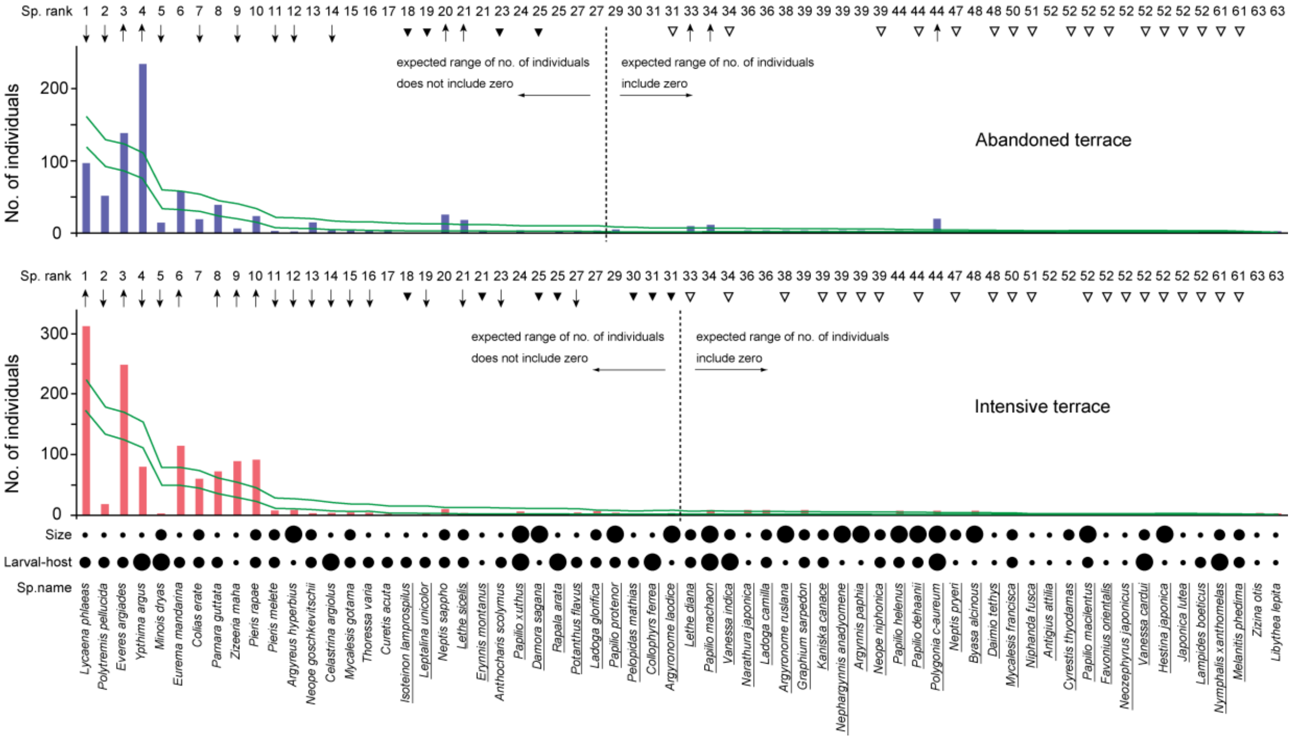


Fig. 2-8. Total number of individuals of each butterfly species for abandoned (up) and intensive (bottom) terraces in 2011 and 2012. Species (Sp.) rank is according to the order of abundance in traditional terraces. Bold green lines represent the expected abundance (upper 97.5% and lower 2.5%) calculated from the rank-abundance relationship of traditional terraces and the total butterfly abundance for each land-use type (see *statistical analyses* for details). Up and down arrows indicate that the abundance were more than and less than the expected range. Upside-down triangles indicate an abundance of zero (i.e., no of individuals of the species were observed in the land-use type). For species whose rank was lower than the dashed lines, the expected range of abundance did not include zero, whereas the range included zero for species with a higher rank than the dash lines. Note that the sizes of the closed circles for body size indicate the herbivorous insect body-size groups: small, medium and large. The size of the closed circles of the larval-host indicate small-monophagous, medium-origophagous and large-polyphagous. Underlined species (Sp.) names indicate rare species (see *statistical analyses* for details).

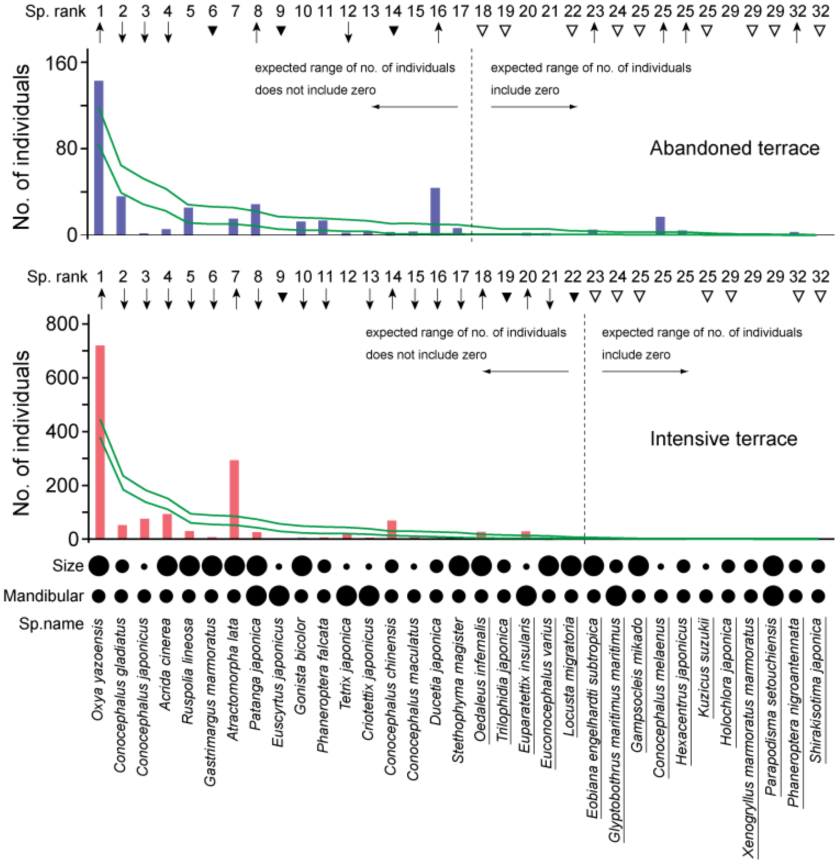


Fig. 2-9. Total number of individuals of each orthopteran species for abandoned (up) and intensive (bottom) terraces in 2011 and 2012. Species (Sp.) rank is according to the order of abundance in traditional terraces. Bold green lines represent the expected abundance (upper 97.5% and lower 2.5%) calculated from the rank-abundance relationships of traditional terraces and the total orthopteran abundance for each land-use type (see *statistical analyses* for details). Up and down arrows indicate that the abundance were more than and less than the expected range of abundance. Upside-down triangles indicate an abundance of zero (i.e., no individuals of the species were observed in the land-use type). For species whose rank was lower than the dashed lines, the expected abundance range did not include zero, whereas the range included zero for species with higher ranks than the dashed lines. Note that the sizes of the closed circles for body size indicate the herbivorous insect body-size: small, medium and large. The sizes of the closed circles of mandibular groups indicate medium-sharp or flat and large-mix. Underlined species (Sp.) names indicate rare species (see *statistical analyses* for details).

Discussion

I demonstrated that land abandonment and intensification caused a decline in plant and insect diversity (Fig. 2-1). This trend was consistent throughout the seasons in both 2011 and 2012 (Fig. S2-9). The IDH and LCH explained the decline in plant richness well (Fig. 2-2, Table S2-4). Total plant species richness was maximized at an intermediate mowing frequency (approximately two times per year), which produced the highest richness of perennial herbs. The maximum diversities of faster-growing annual plants and more slowly growing woody plants were shifted to higher and lower frequencies of mowing, respectively, as predicted by dynamic equilibrium model (Huston 1979, 1994). Perennial and woody species decreased with land-use changes in the surrounding landscapes, whereas annual species increased as the human impacts on surrounding landscapes increased. Declines in herbivorous insects were explained by the RDH and IDH and partly by the MIH, but not by the LCH (Figs. 2-3– 2-7). Herbivore declines occurred in accordance with declines in plant richness and changes in the mowing frequency in abandoned and intensive paddy terraces.

The richness and diversity responses of herbivore functional groups to changes in plant richness, disturbance frequency, and the surrounding landscapes were generally inconsistent with predictions, although some differences in responses among groups were found for both butterflies and orthopterans. This may suggest that the population size of most species decreased randomly with respect to traits due to land abandonment and intensification. I found significant and marginally significant trends where butterfly and orthopteran species with low abundance in traditional terraces were more frequently lost in abandoned and/or intensive terraces (Figs. 2-8 and 2-9, Table S2-11), further supporting the random loss hypothesis (Suding *et al.* 2005).

The four hypotheses of herbivorous insect decline

Resource diversity hypothesis (RDH)—The richness and diversity of butterfly and orthopteran species significantly increased with larval- and adult-resource plant richness (Figs. 2-3– 2-6), supporting the RDH and previous findings (Siemann *et al.* 1998; Haddad *et al.* 2001, 2009; Petermann *et al.* 2010). My results indicate that the richness of host plants, especially perennials, plays an important role in maintaining the richness and diversity of herbivorous insects in semi-natural grasslands around paddy terraces. Note that plant richness was not correlated with aboveground biomass in my study system, such that abandoned terraces with the highest plant biomass had the lowest plant species richness. Thus, plant diversity, rather than plant biomass, is key for maintaining herbivore diversity. Generally, different butterfly and orthopteran species depend on different plant species for their lifecycles; therefore, a decline in plant diversity due to land-use changes has a large impact on herbivore diversity (Joern 2005; Kuussaari *et al.* 2007; Öckinger & Smith 2007; Pöyry *et al.* 2009).

Intermediate disturbance hypothesis (IDH)—The IDH successfully explained the decline in biodiversity due to land abandonment and intensification. I found significant unimodal relationships between the richness of herbivorous insects and mowing frequency wherein the greatest richness was found at a mowing frequency of 1–3 times per year (butterflies: 1–2 times per year, orthopterans: 2–3 times per year), which usually occurred on traditional terraces (Fig. 2-3, Fig. S2-3). As stated above, the GLMM analyses with multi-explanatory variables revealed that herbivorous insect species significantly increased not only with plant richness but also with an intermediate mowing frequency (Fig. 2-3), which peaked at a mowing frequency of approximately twice per year (Fig. 2-2). These results suggest that a mowing frequency of 1–3 times per year enhances herbivore richness directly, as well as indirectly by enhancing plant diversity. Little or no disturbance in abandoned terraces would influence grassland thermal conditions, because the dominance of tall grasses and herbs largely limits direct sunlight in the middle and lower layers of vegetation. Changes in thermal conditions might negatively affect thermoregulation for some herbivores (e.g., Joern 2005). Farmers frequently mowed at a vegetation height less than 10cm and immediately removed cut plant material from the levees in intensive terraces (Uchida & Ushimaru unpublished data). Butterfly larvae and immature orthopterans might be removed from grasslands with cut plant material whereas adults were frequently found to escape from mowed levees.

The responses of plant and herbivore richness to the disturbance gradient across all terrace types were generally consistent with the pattern predicted by the IDH (Grime 1973; Horn 1975; Connell 1978; Huston 1979, 1994) and previous suggestions that species richness might be maintained by traditional extensive agricultural practices (Pöyry *et al.* 2006; Kleijn *et al.* 2011). Recent no/fewer anthropogenic disturbances (Pöyry *et al.* 2006; Uematsu *et al.* 2010) and stronger and/or more frequent disturbances (Ekroos, Heliölä & Kuussaari 2010) due to land abandonment and intensification, respectively, have decreased agricultural biodiversity. My multi-factor analyses revealed the utility of the IDH for explaining plant and herbivore richness patterns in semi-natural grasslands around paddy terraces. Conversely, the inverse Simpson’s diversity of herbivores decreased or had no relationship with mowing frequency, but significantly increased with plant richness. This suggests that an intermediate mowing frequency did not directly increase the evenness of abundance among herbivore species, but indirectly enhanced it by increasing plant richness. I could not explain the inconsistency between the richness and diversity patterns and this issue will be examined in future research.

Landscape change hypothesis (LCH)—Land consolidation is prevalent throughout Japan and is often conducted over several terraces concurrently, so that intensive terraces tend to be surrounded by other intensive terraces rather than traditional terraces, while abandonment areas also often occur in the same region (Fig. S2-5, Uematsu *et al.* 2010; Uematsu & Ushimaru 2013). The total richness and diversity of butterflies and orthopterans were not influenced by landscape variables, although the richness and diversity of some functional groups were negatively influenced by surrounding land-use changes (PCA axis1 value) and increased human impacts (PCA axis 2 value). In contrast, plant richness increased with the PCA axis1 value, suggesting that surrounding land-use changes had indirect negative effects on herbivores. Landscape variables often had weak or no effects on herbivore diversity, similar to the results of previous studies (Collinge 2003; Kuussaari *et al.* 2007; Pöyry *et al.* 2009; but see Bergman *et al.* 2004; Tscharntke *et al.* 2005).

More individuals hypothesis (MIH)— I found significantly positive correlations between species richness and the total number of individuals for both butterflies and orhopterans (Fig. 2-7). Furthermore, many rare species were lost following land abandonment and intensification. This seems to support the MIH (Suding *et al.* 2005; Yee & Juliano 2007; c.f. Srivastava and Lawton 1998). The large number of individuals more likely maintains the persistence of rare species, leading to high species richness (Suding *et al.* 2005; Yee & Juliano 2007; Chiari *et al.* 2010). However, my results showed no conspicuous relationships between productivity and abundance of herbivores (Fig. S2-15), which is inconsistent with the underlying assumption of the MIH (Srivastava & Lawton 1998). Abandoned terraces with high productivity, and intensive terraces with a similar range of productivity to those of traditional terraces, harbored fewer number of individuals than traditional terraces (Fig. S2-15). The MIH has been previously investigated in ecosystems with either a low rate of or no disturbances (Srivastava & Lawton 1998; Yee & Juliano 2007; Pautasso *et al.* 2008). With frequent anthropogenic disturbances, the total abundance of herbivores might be influenced by disturbance and plant diversity rather than productivity (Fig. 2-3, Figs. S2-5, S2-6, S2-7, S2-8, and S2-15). Thus, I found that the MIH partly explained the decline of herbivorous insects in abandoned and intensive terraces.

Differences in richness and diversity patterns among different trait groups

The richness and diversity patterns of herbivore functional groups were generally inconsistent with predictions, although there were some significant differences among trait groups. Richness and diversity of all size groups decreased with a decline in plant richness for both butterflies and orthopterans. The richness and diversity peaked at more-frequently disturbed plots for larger butterflies and orthopterans than for medium-sized ones, whereas small-sized species did not correlate with mowing frequency (Fig. 2-4). Furthermore, small- and medium-sized butterflies and orthopterans were more influenced by landscape variables than were larger species (Figs. S2-5, S2-6, S2-7, and S2-8). These patterns are inconsistent with the general prediction that smaller species would be strongly affected by local resource availability and decreased mowing frequency, whereas larger species would be more susceptible to an increased mowing frequency and changes in surrounding landscapes (Tscharntke *et al.* 2005; Huston & Wolverton 2011). Pöyry *et al.* (2006) reported that generalist species preferred less disturbed conditions than did specialists. My butterfly results seem to support this finding, but the trend was inconsistent between the two study years (Fig. 2-5). No such trend was found for orthopterans (Fig. 2-5). Moreover, for both butterflies and orthopterans, specialists were more influenced by landscape variables than were generalists. This finding is the opposite of the prediction made by Tscharntke *et al.* (2005). Additionally, I found no large differences in responses to plant richness among larval-host types of butterflies and mandibular types of orthopteran species. The richness of rare butterflies responded in a similar manner to host plant diversity and mowing practice to that of common butterflies (Fig. 2-6), whereas the diversity responses to mowing frequency differed between rare and common species. Rare orthopterans were influenced by plant diversity and increased human impacts on the surrounding landscape, whereas common species were influenced by plant diversity and the mowing frequency.

Therefore, the differences among insect trait groups were not well explained by theoretical predictions. Unfortunately, I are unable to propose alternative ideas to explain my results based on my current data, and therefore future research should be conducted to examine the generality of my findings. Conversely, differences in richness patterns among plant life-history groups can be explained by the IDH and LCH. The richness of annual and woody plants increased at more, and less, disturbed plots, respectively, compared with perennials, which is consistent with predictions of IDH. Furthermore, my findings that annuals increased with human impacts on the surrounding landscapes increased (PCA axis 2 value) and that perennial and woody plant species increased with the amount of surrounding secondary forest increased (forest edge length and PCA axis 1 value) are not surprising based on common knowledge.

Differences in richness and diversity patterns among insect families

Peaks in the richness and diversity of Nymphalidae and Hesperiidae were found at less-frequently mowed (< 1 per year) plots (Figs. S2-13 and S2-14). Many species belonging to these families forage on grass species, and tall perennial grasses such as *Miscanthus sinensis* and *Pleioblastus* spp. were dominant in abandoned and traditional grasslands that experienced infrequent mowing (Matsumura & Takeda 2010). Thus, the dominance of a certain plant group might be responsible for the observed richness (diversity)-disturbance relationships in these butterfly families.

Most large orthopteran species belonged to the family Acrididae, which prefer shorter vegetation and were often found on the ground, perhaps because a heavy body is unsuitable for moving on leaves of taller vegetation. Phaneroperidae species prefer relatively taller vegetation (Ichikawa *et al.* 2006). These behavioral differences may be responsible for the difference in peaks with mowing frequency between the two families.

Species loss and decline due to land abandonment and intensification

I found that many rare butterfly and orthopteran species were lost in the abandoned and/or intensive terraces (Figs. 2-8 and 2-9). Thus land abandonment and intensification together resulted in the loss of rare species in the study area. Note that species abundances in traditional terraces for both insect groups were correlated with body-size and the degree of food specialization, suggesting that larger and monophagous butterflies and small and mixed-mandibular orthopterans tended to be more susceptible to land abandonment and intensification (Figs. 2-8 and 2-9). However, I did not detect any trends in the species decline analyses. These results may suggest that plant richness declines due to land abandonment and intensification lead to a decline in carrying capacity, which has an equal impact on most herbivore species so that species with a low abundance are lost randomly (Sunding *et al.* 2005). This would also explain the differences between the predictions and my findings on the patterns of richness and diversity of herbivore trait groups.

General significance

This study provides a unified explanation for declines in biodiversity due to land abandonment and intensification, which have often been studied separately. I demonstrated that declines in herbivorous insects due to land-use changes can be explained by multiple factors, such as a decline in plant richness, changes in disturbance frequency, and increases in land-use changes and human impacts around the study site. Changes in the disturbance regime resulted in a direct decline in the richness of both butterfly and orthopteran species, and an indirect decline through diminished plant richness. To the best of my knowledge, this is the first report to demonstrate that the intermediate disturbance hypothesis explains a decline in biodiversity due to a combination of land-use abandonment and intensification. I also demonstrated that perennial plants played a key role in maintaining the total butterfly and orthopteran richness. To date, there are no reports demonstrating that a decline in a particular plant life-history group causes a decline in herbivorous insects. Surrounding land-use changes had only minor negative effects on herbivore diversity, suggesting that many of the herbivores studied had a limited foraging range. My results also show that herbivore declines due to changes in land use might have occurred randomly, irrespective of species traits. This may indicate that more species will become extinct due to land abandonment and intensification because the area of abandoned and consolidated agricultural land is still increasing (Uematsu *et al.* 2010; Uematsu & Ushimaru 2013). These results suggest that enhancing plant richness by maintaining traditional mowing practices is essential to conserving herbivore diversity around paddy terraces. To generalize my findings, future studies should investigate different types of agricultural land and different regions, while considering the IDH, changes in landscape and host plant diversity for higher trophic levels.

Supporting information

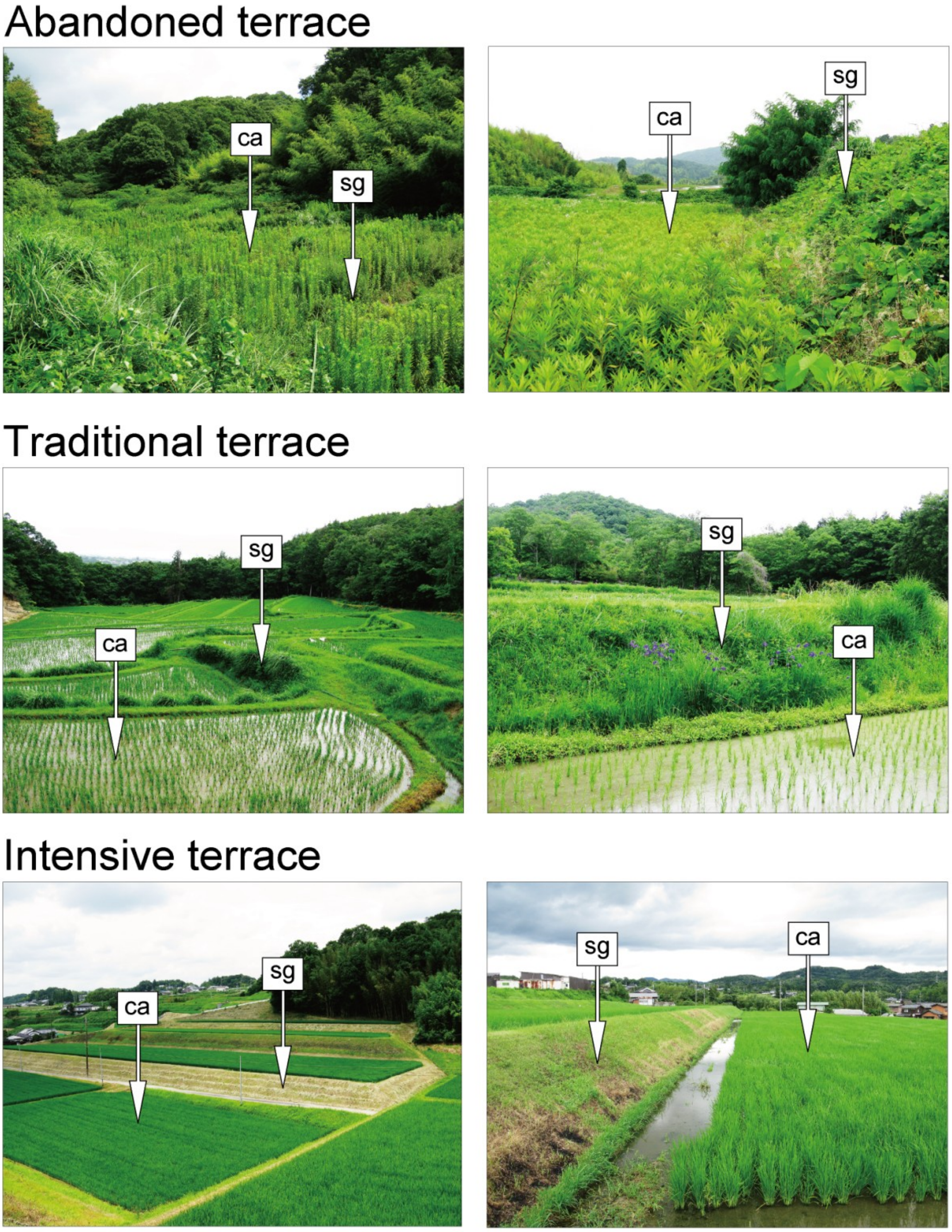


Fig. S2-1. Photographs of three land-use types of paddy terraces: ca, cropped or previously cropped area; sg, semi-natural grassland on paddy levees.

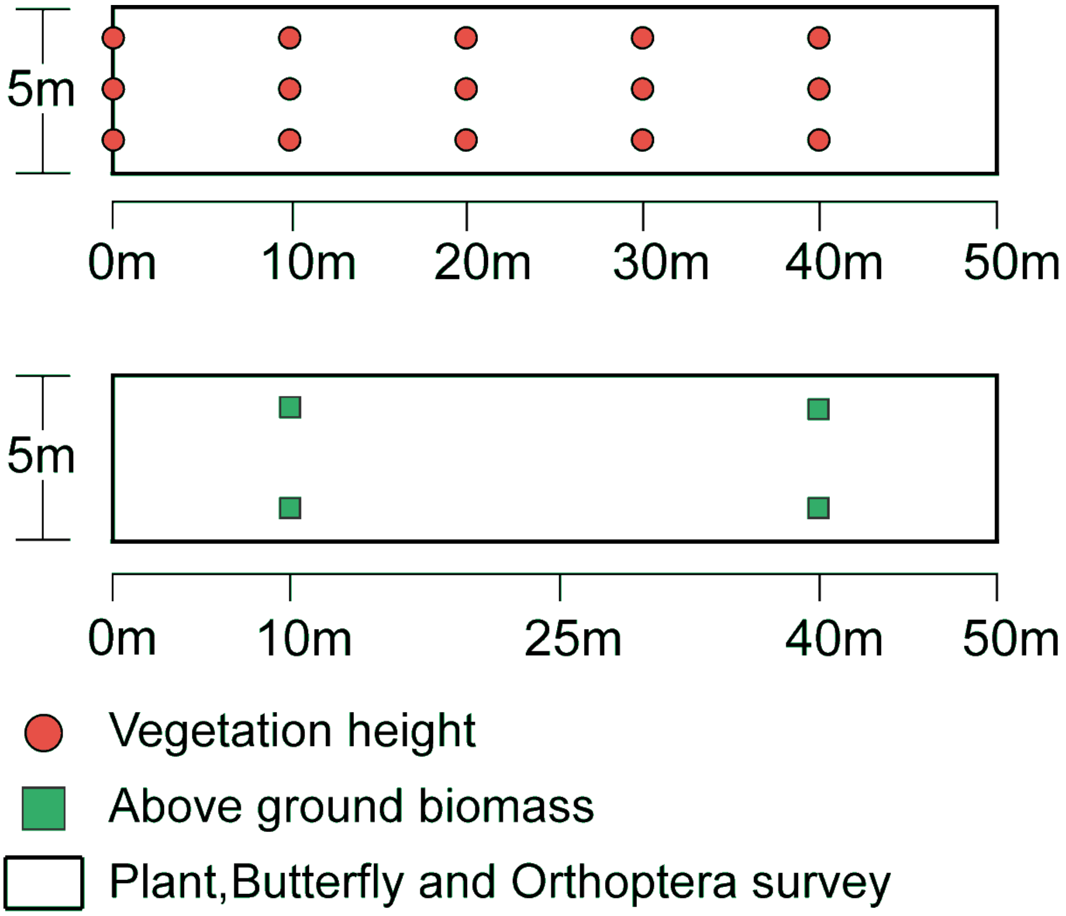


Fig. S2-2. Survey design used in this study. See *Materials and Methods* for details.

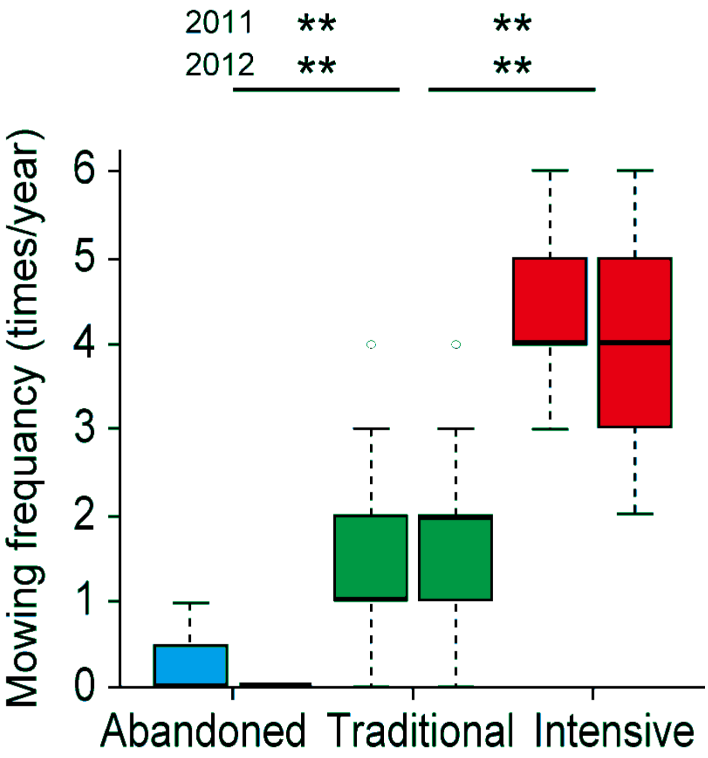


Fig. S2-3. Comparisons of mowing frequency among land-use types in 2011 and 2012 (left box, 2011; right box, 2012; blue, abandoned; green, traditional; red, intensive). ***P* < 0.01.

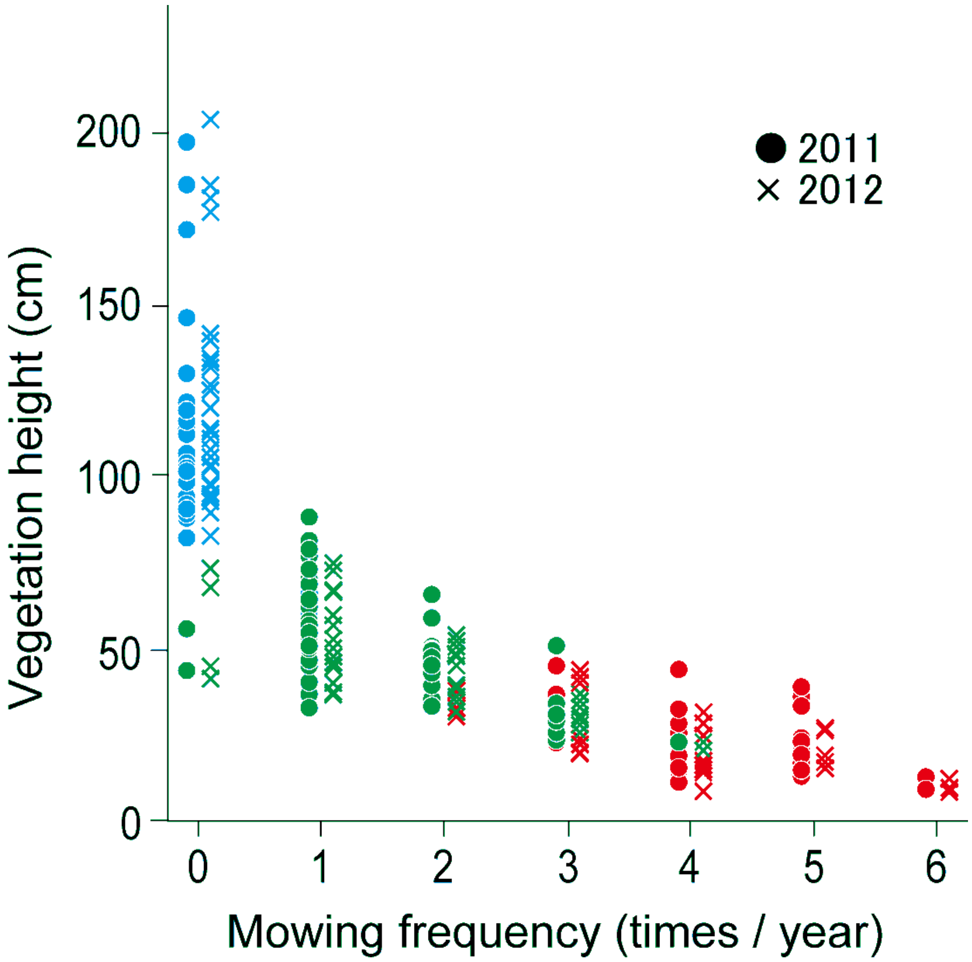


Fig. S2-4. Relationships between mowing frequency and vegetation height in 2011 and 2012 (blue, abandoned; green, traditional; red, intensive). *P* < 0.01 in 2011 and 2012.

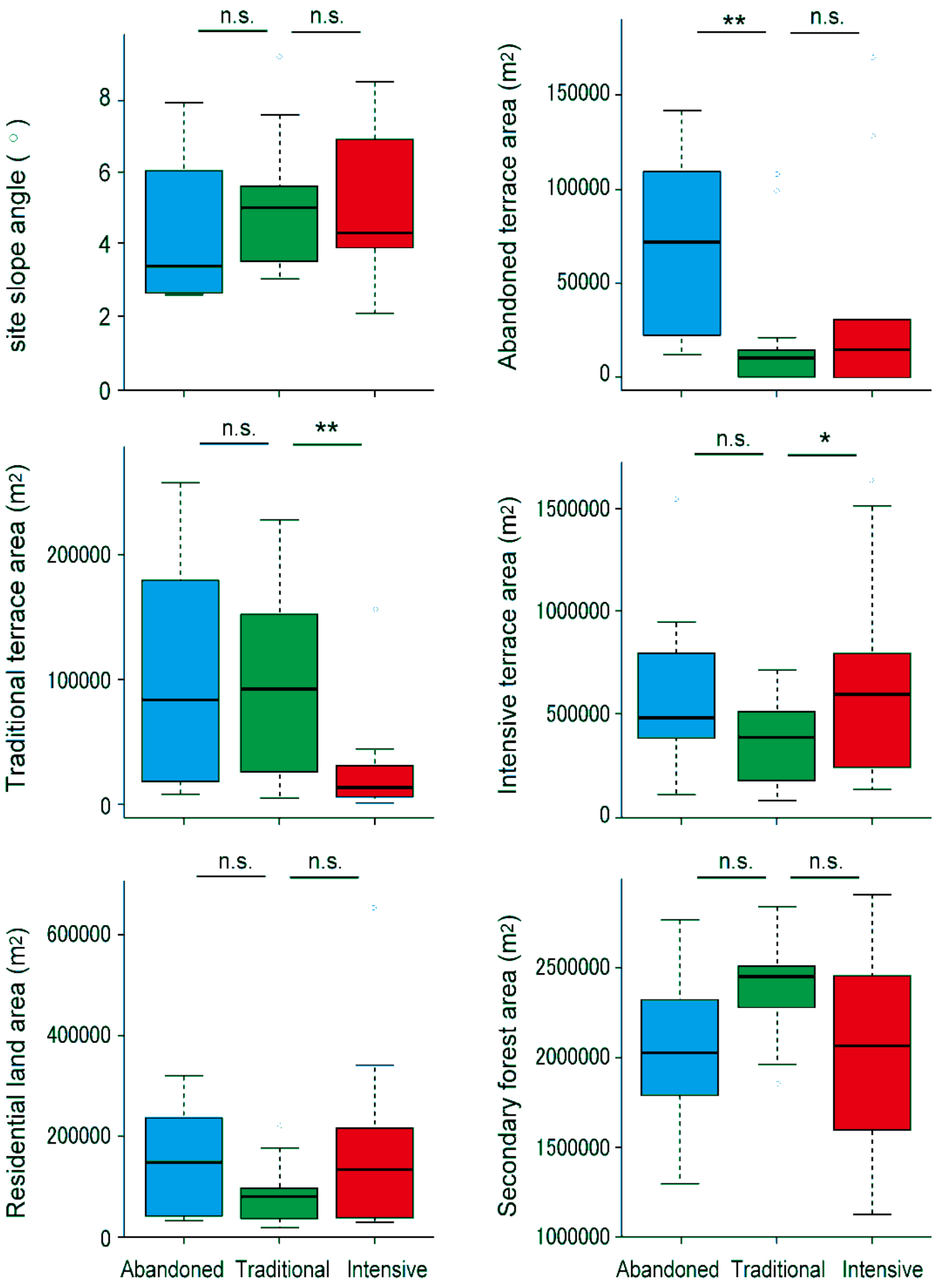
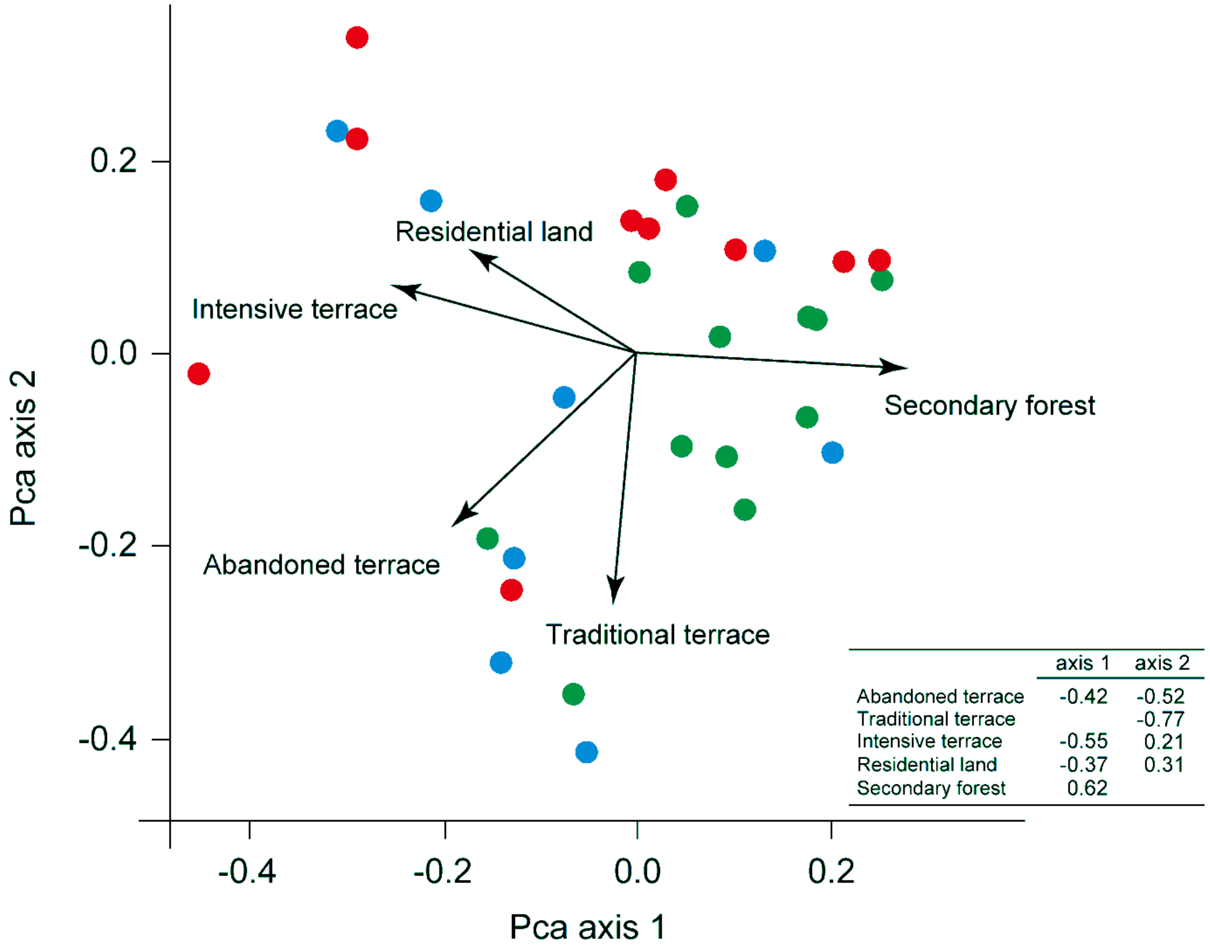


Fig. S2-5. Comparisons of surrounding landscape variables (site slope angle, areas of abandoned, traditional and intensive terrace, residential land and secondary forest within a 1-km radius from each terrace) among land-use types (blue, abandoned; green, traditional; red, intensive). *$P < 0.05$, **$P < 0.01$, n.s. not significant.



	axis 1	axis 2
Abandoned terrace	-0.42	-0.52
Traditional terrace		-0.77
Intensive terrace	-0.55	0.21
Residential land	-0.37	0.31
Secondary forest	0.62	

Fig. S2-6. Bi-plot showing the first two PCA axis of surrounding landscape variables (five environment types, intensive terrace area, traditional terrace area, abandoned terrace area, residential land area and secondary forest area) that explain 77.3% of the total variance (axis 1: 49.2%, axis 2: 28.1%). The PCA axis 1 increased with secondary forest area and decreased with areas of intensive and abandoned terrace and residential lands. Meanwhile the PCA axis 2 increased with areas of intensive terrace and residential lands and decreased with areas of traditional and abandoned terrace.

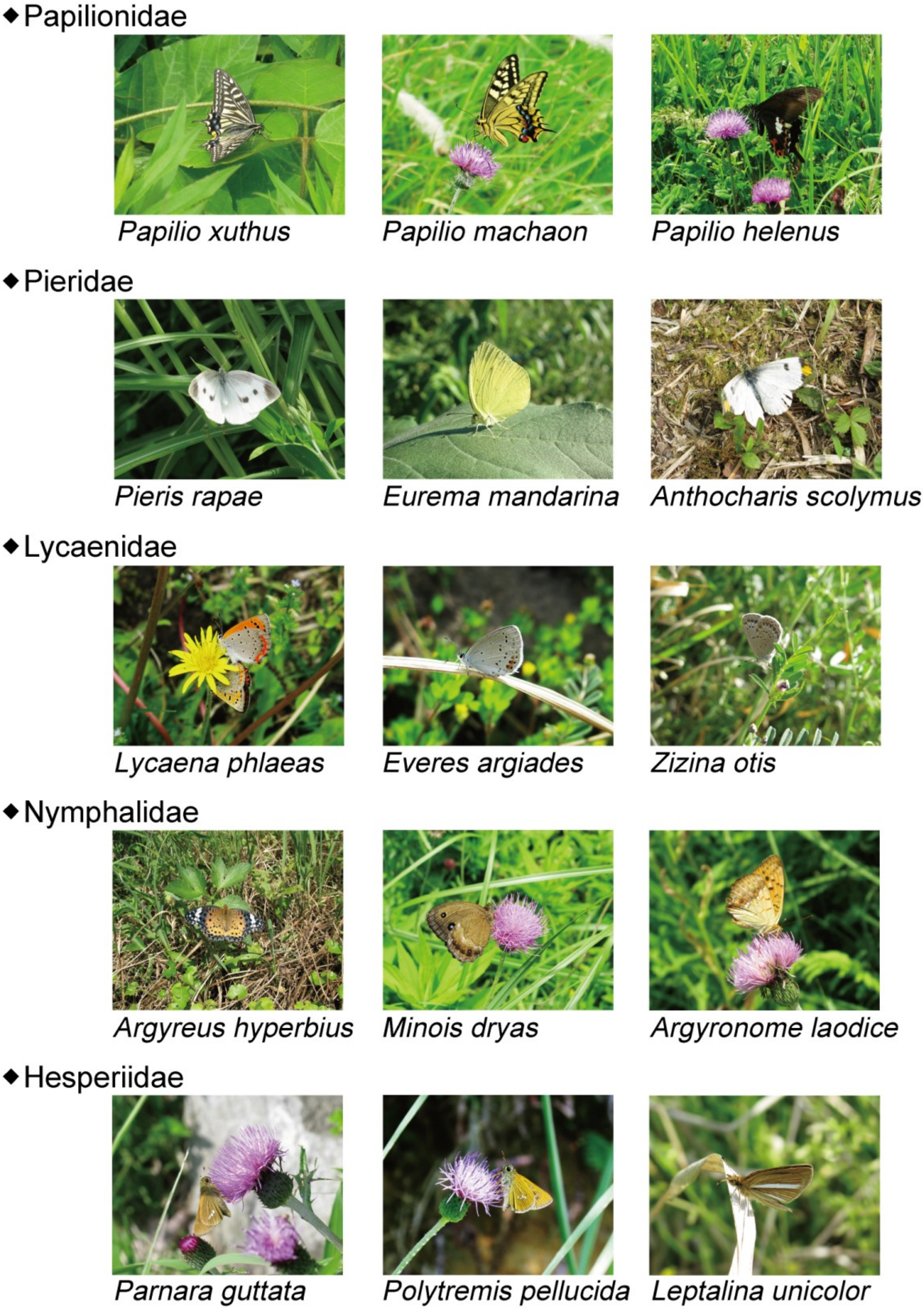


Fig. S2-7. Photographs of butterflies. The left species for each family was dominant in the study area.

◆Tettigoniidae

Conocephalus gladiatus *Eobiana engelhardti subtropica*

◆Meconematidae

Kuzicus suzukii

◆Phaneropteridae

Phaneroptera falcata *Phaneroptera nigroantennata*

◆Eneopteridae

Euscytus japonicus

◆Tetrigidae

Tetrix japonica *Criotettix japonicus*

◆Pyrgomorphidae

Atractomorpha lata

◆Acrididae

Gastrimargus marmoratus *Gonista bicolor*

Fig. S2-8. Photographs of Orthoptera. The left species for each family was dominant in the study area.

Table S2-1. List of 65 butterfly species that were found in 124 and 116 study plots in 2011 and 2012, respectively. Larval-host type: M, monophagous; O, oligophagous; P, polyphagous.

Family	Species name	Average body size (mm & category)		Larval-host type	number of measured individuals	Total abundance		Abundance per site					
						2011	2012	Abandoned		Traditional		Intensive	
								2011	2012	2011	2012	2011	2012
Papilionidae	*Byasa alcinous* (Klug, 1836)	27.1	L	M	n = 18	5	2	0.1	0.0	0.3	0.1	0.0	0.1
	Graphium sarpedon (Linnaeus, 1758)	24.5	M	O	n = 13	11	2	0.1	0.1	0.6	0.1	0.2	0.0
	Papilio xuthus Linnaeus, 1767	27.2	L	P	n = 6	31	7	0.4	0.0	1.7	0.0	0.6	0.0
	Papilio machaon Linnaeus, 1758	27.7	L	P	n = 7	17	7	0.9	0.4	0.6	0.3	0.2	0.0
	Papilio helenus Linnaeus, 1758	32.2	L	O	n = 11	10	2	0.3	0.0	0.5	0.1	0.1	0.1
	Papilio protenor Cramer, 1775	31.8	L	O	n = 12	18	8	0.5	0.1	1.0	0.4	0.1	0.2
	Papilio macilentus Janson, 1877	28.7	L	O	n = 9	2	0	0.0	0.0	0.2	0.0	0.0	0.0
	Papilio dehaanii C. & R. Felder, 1864	31.4	L	O	n = 15	3	5	0.0	0.0	0.2	0.4	0.0	0.0
									0.0				
Pieridae	*Anthocharis scolymus* Butler, 1866	17.1	S	O	n = 12	14	15	0.0	0.0	1.0	1.3	0.1	0.0
	Pieris rapae (Linnaeus, 1758)	19.6	M	O	n = 8	152	94	1.9	1.1	6.5	3.9	5.3	3.9
	Pieris melete (Ménétriès, 1857)	21.0	M	O	n = 20	53	28	0.1	0.0	3.6	2.1	0.5	0.3
	Eurema mandarina (de l'orza, 1869)	15.6	S	O	n = 20	259	157	5.1	2.3	11.8	7.4	6.4	5.2
	Colias erate (Esper, 1805)	20.4	M	O	n = 12	197	109	2.0	0.4	10.8	7.2	4.1	2.0
Lycaenidae	*Curetis acuta* Moore, 1877	16.6	S	O	n = 12	37	17	0.4	0.3	1.9	1.1	0.9	0.2
	Narathura japonica (Murray, 1875)	13.5	S	M	n = 15	9	7	0.3	0.0	0.4	0.5	0.2	0.1
	Japonica lutea (Hewitson, 1865)	12.0	S	M	n = 10	0	2	0.0	0.0	0.0	0.2	0.0	0.0
	Antigius attilia (Bremer, 1861)	10.8	S	M	n = 20	3	2	0.1	0.1	0.1	0.1	0.1	0.0
	Favonius orientalis (Murray, 1875)	14.6	S	M	n = 16	1	1	0.0	0.0	0.1	0.1	0.0	0.0
	Neozephyrus japonicus (Murray, 1874)	13.7	S	M	n = 20	2	2	0.3	0.0	0.0	0.2	0.0	0.0
	Collophrys ferrea (Butler, 1866)	10.9	S	P	n = 14	13	3	0.0	0.1	1.0	0.2	0.0	0.0
	Rapala arata (Bremer, 1861)	13.8	S	P	n = 10	2	25	0.1	0.0	0.1	2.1	0.0	0.0
	Lycaena phlaeas (Linnaeus, 1761)	13.1	S	O	n = 10	599	572	8.9	3.6	29.2	32.0	14.9	16.3
	Niphanda fusca (Bremer & Grey, 1852)	16.3	S	M	n = 16	3	0	0.0	0.0	0.2	0.0	0.0	0.0
	Zizina otis (Fabricius, 1787)	10.4	S	M	n = 24	3	2	0.0	0.0	0.0	0.0	0.3	0.2
	Zizeeria maha (Kollar, 1844)	11.0	S	M	n = 24	148	104	0.6	0.0	6.4	6.3	6.0	2.8
	Everes argiades (Pallas, 1771)	10.6	S	O	n = 12	611	345	13.0	4.9	28.0	17.1	14.3	10.6
	Celastrina argiolus (Linnaeus, 1758)	11.8	S	P	n = 10	23	35	0.1	0.3	1.5	2.7	0.3	0.1
	Lampides boeticus (Fabricius, 1798)	12.9	S	O	n = 6	0	2	0.0	0.0	0.0	0.2	0.0	0.0
Nymphalidae	*Libythea lepita* Moore,1858	14.4	S	M	n = 8	0	2	0.0	0.1	0.0	0.0	0.0	0.1
	Vanessa cardui (Linnaeus, 1758)	21.2	M	P	n = 5	1	1	0.0	0.0	0.1	0.1	0.0	0.0
	Vanessa indica (Herbst, 1794)	24.4	M	P	n = 5	5	7	0.0	0.0	0.4	0.6	0.0	0.0
	Polygonia c-aureum (Linnaeus, 1758)	26.5	L	P	n = 10	14	15	1.3	1.4	0.3	0.3	0.0	0.1
	Nymphalis xanthomelas (Esper, 1781)	24.8	M	P	n = 8	1	0	0.0	0.0	0.1	0.0	0.0	0.0
	Kaniska canace (Linnaeus, 1763)	24.5	M	O	n = 12	9	2	0.3	0.0	0.5	0.2	0.0	0.0
	Cyrestis thyodamas Doyère, 1840	21.2	M	M	n = 15	2	1	0.0	0.0	0.1	0.1	0.1	0.0
	Argyronome laodice (Pallas, 1771)	30.7	L	M	n = 18	8	7	0.0	0.0	0.6	0.6	0.0	0.0
	Argyronome ruslana (Motschulsky, 1866)	31.1	L	M	n = 15	5	8	0.3	0.1	0.2	0.6	0.0	0.0
	Nephargynnis anadyomene (C. & R. Felder, 1862)	30.8	L	M	n = 15	7	3	0.1	0.0	0.5	0.3	0.0	0.0
	Damora sagana (Doubleday, 1847)	29.6	L	M	n = 15	19	7	0.0	0.0	1.5	0.6	0.0	0.0
	Argynnis paphia (Linnaeus, 1758)	29.8	L	M	n = 19	5	6	0.1	0.1	0.3	0.4	0.0	0.0
	Nymphalinae spp.	—	—	M	—	2	0	0.0	0.0	0.2	0.0	0.0	0.0
	Argyreus hyperbius (Linnaeus, 1763)	26.1	L	M	n = 8	46	33	0.0	0.1	3.3	2.2	0.3	0.6
	Neptis pryeri Butler, 1871	19.7	M	M	n = 20	3	3	0.0	0.0	0.2	0.3	0.0	0.0
	Neptis sappho (Pallas, 1771)	18.9	M	O	n = 12	46	25	2.0	1.3	1.7	1.0	0.8	0.4
	Ladoga camilla (Linnaeus, 1764)	20.2	M	O	n = 16	16	3	0.1	0.3	0.8	0.1	0.5	0.0
	Ladoga glorifica (Fruhstorfer, 1909)	21.3	M	O	n = 8	13	15	0.1	0.1	0.9	1.0	0.0	0.2
	Hestina japonica (C. & R. Felder, 1862)	27.4	L	M	n = 15	1	1	0.0	0.0	0.1	0.1	0.0	0.0
	Ypthima argus Butler, 1866	13.6	S	P	n = 15	459	367	20.8	9.9	19.2	21.7	4.4	3.8
	Mycalesis francisca (Stoll,1780)	18.7	M	O	n = 10	4	0	0.0	0.0	0.3	0.0	0.0	0.0
	Mycalesis gotama Moore, 1858	17.8	M	O	n = 15	23	33	0.0	0.7	1.8	1.9	0.0	0.5
	Minois dryas (Scopoli, 1763)	20.3	M	P	n = 16	147	116	1.8	0.0	10.2	9.6	0.1	0.1
	Melanitis phedima (Cramer, 1780)	25.2	M	O	n = 9	1	0	0.0	0.0	0.1	0.0	0.0	0.0
	Lethe diana (Butler, 1866)	18.8	M	O	n = 16	13	9	0.6	0.4	0.6	0.5	0.0	0.0
	Lethe sicelis (Hewitson, 1862)	21.6	M	O	n = 12	18	31	1.0	1.4	0.7	1.7	0.1	0.1
	Neope goschkevitschii (Ménétriès, 1857)	21.4	M	O	n = 16	32	48	1.0	1.0	1.8	3.3	0.0	0.2
	Neope niphonica Butler, 1881	20.8	M	O	n = 20	5	4	0.0	0.0	0.4	0.3	0.0	0.0
Hesperiidae	*Daimio tethys* (Ménétriès, 1857)	14.6	S	M	n = 20	4	1	0.0	0.0	0.3	0.1	0.0	0.0
	Erynnis montanus (Bremer, 1861)	16.1	S	M	n = 16	12	18	0.0	0.1	0.9	1.4	0.0	0.0
	Leptalina unicolor (Bremer & Grey, 1852)	15.2	S	O	n = 15	32	4	0.0	0.0	2.4	0.3	0.1	0.0
	Isoteinon lamprospilus C. & R. Felder, 1862	17.3	S	O	n = 10	36	0	0.0	0.0	2.8	0.0	0.0	0.0
	Thoressa varia (Murray, 1875)	14.8	S	O	n = 20	40	21	1.3	0.0	2.2	1.5	0.2	0.3
	Potanthus flavus (Murray, 1875)	14.8	S	O	n = 16	9	25	0.4	0.9	0.4	1.6	0.1	0.0
	Polytremis pellucida (Murray, 1875)	17.5	S	O	n = 15	277	394	2.9	4.0	18.9	29.5	0.8	1.2
	Pelopidas mathias (Fabricius, 1798)	15.7	S	O	n = 8	6	11	0.0	0.1	0.5	0.8	0.0	0.0
	Parnara guttata (Bremer & Grey, 1852)	17.5	S	O	n = 11	166	126	3.1	1.7	7.0	7.7	5.0	2.2

Table S2-2. List of 33 Orthoptera species that were found in 124 and 116 study plots in 2011 and 2012, respectively. Mandible type: S, sharp; F, flat; M, mix.

Family	Species name	Average body size (mm & category)		Mandibular type	number of measured individuals	Total abundance		Abundance per site					
						2011	2012	Abandoned		Traditional		Intensive	
								2011	2012	2011	2012	2011	2012
Tettigoniidae	*Gampsocleis mikado* Burr, 1899	40.7	L	S	n = 2	2	1	0.0	0.0	0.2	0.1	0.0	0.0
	Eobiana engelhardti subtropica (Bey-Bienko, 1949)	24.9	M	S	n = 15	15	2	0.9	0.0	0.6	0.2	0.0	0.0
	Ruspolia lineosa (Walker, 1869)	30.5	L	S	n = 40	202	79	3.0	0.3	11.5	6.2	2.9	0.3
	Euconocephalus varius (Walker, 1869)	37.6	L	S	n = 6	15	7	0.1	0.0	1.0	0.6	0.1	0.0
	Conocephalus maculatus (le Guillou, 1841)	14.1	S	S	n = 33	38	33	0.4	0.0	2.6	2.3	0.1	0.6
	Conocephalus chinensis (Redtenbacher, 1891)	17.6	M	S	n = 40	68	66	0.0	0.0	2.8	2.2	3.1	4.0
	Conocephalus gladiatus (Redtenbacher, 1891)	20.5	M	S	n = 40	468	226	3.4	1.3	31.0	16.5	3.8	1.9
	Conocephalus japonicus (Redtenbacher, 1891)	15.5	S	S	n = 40	387	154	0.1	0.1	25.1	11.3	6.0	1.8
	Conocephalus melaenus (de Haan, 1843)	16.2	S	S	n = 16	16	7	1.4	0.9	0.2	0.1	0.3	0.0
	Hexacentrus japonicus Karny, 1907	23.7	M	S	n = 6	6	3	0.3	0.3	0.2	0.1	0.2	0.0
Meconematidae	*Kuzicus suzukii* (Matsumura et Shiraki, 1908)	13.8	S	S	n = 1	1	2	0.0	0.0	0.1	0.2	0.0	0.0
Phaneropteridae	*Phaneroptera falcata* (Poda, 1761)	18.1	M	S	n = 40	99	23	1.6	0.0	6.2	1.8	0.5	0.1
	Phaneroptera nigroantennata Brunner von Wattenwyl, 1878	19.1	M	S	n = 3	3	0	0.3	0.0	0.1	0.0	0.0	0.0
	Ducetia japonica (Thunberg, 1815)	20.0	M	S	n = 40	73	27	4.3	1.4	3.0	1.3	0.0	0.1
	Shirakisotima japonica (Matsumura et Shiraki, 1908)	22.7	M	S	n = 1	1	0	0.0	0.0	0.1	0.0	0.0	0.0
	Holochlora japonica Brunner von Wattenwyl, 1878	24.2	M	S	n = 3	3	0	0.1	0.0	0.2	0.0	0.0	0.0
Eneopteridae	*Xenogryllus marmoratus marmoratus* (de Haan, 1844)	19.4	M	S	n = 3	3	0	0.0	0.0	0.2	0.0	0.1	0.0
	Euscyrtus japonicus Shirak, 1930	10.1	S	M	n = 35	78	46	0.0	0.0	6.0	3.8	0.0	0.0
Tetrigidae	*Criotettix japonicus* (de Haan, 1843)	11.9	S	M	n = 40	80	15	0.5	0.0	5.5	1.2	0.5	0.1
	Euparatettix insularis Bey-Bienko, 1951	8.1	S	M	n = 16	29	32	0.1	0.0	1.3	0.5	1.1	2.6
	Tetrix japonica (Bolivar, 1887)	10.2	S	M	n = 24	87	40	0.1	0.0	4.5	3.3	2.8	0.1
Pyrgomorphidae	*Atractomorpha lata* (Motschousky, 1866)	27.6	L	S	n = 12	374	133	1.5	0.4	9.3	6.5	24.2	5.2
Acrididae	*Parapodisma setouchiensis* Inoue, 1979	16.2	L	M	n = 4	4	0	0.0	0.0	0.2	0.0	0.2	0.0
	Patanga japonica (Bolivar, 1898)	36.4	L	M	n = 5	142	83	2.8	0.9	7.8	5.8	1.9	0.8
	Oxya yazoensis Shiraki, 1910	29.7	L	F	n = 5	1400	630	15.1	3.1	58.1	34.3	52.4	19.7
	Acrida cinerea (Thunberg, 1815)	56.4	L	F	n = 10	322	151	0.6	0.0	18.5	11.2	7.7	1.7
	Gonista bicolor (de Haan, 1842)	34.0	L	F	n = 8	76	49	1.0	0.6	5.0	3.8	0.3	0.0
	Glyptobothrus maritimus maritimus (Mistshenko, 1951)	19.2	M	M	n = 2	2	5	0.0	0.0	0.2	0.4	0.0	0.0
	Stethophyma magister (Rehn, 1902)	38.6	L	F	n = 15	41	20	0.8	0.0	2.5	1.7	0.3	0.0
	Locusta migratoria (Linnaeus, 1758)	35.7	L	F	n = 4	4	8	0.0	0.0	0.3	0.7	0.0	0.0
	Gastrimargus marmoratus (Thunberg, 1815)	36.8	L	F	n = 15	134	84	0.0	0.0	9.8	6.8	0.7	0.3
	Oedaleus infernalis Saussure, 1884	32.1	L	F	n = 15	48	18	0.0	0.0	1.9	0.9	2.3	0.7
	Trilophidia japonica Saussure, 1888	21.8	M	F	n = 11	11	13	0.0	0.0	0.8	1.1	0.0	0.0

Table S2-3. List of plant families and their species richness in 124 and 116 study plots in 2011 and 2012, respectively.

Family name	Total richness		Richness of land-use					
			Abandoned		Traditional		Intensive	
	2011	2012	2011	2012	2011	2012	2011	2012
Annual								
Acanthaceae	1	1	1	1	1	1	1	1
Apiaceae	1	1	1	1	1	1	1	1
Asteraceae	18	18	12	12	15	15	15	15
Boraginaceae	2	2	1	1	2	2	2	2
Brassicaceae	5	5	2	2	4	4	4	4
Cannabaceae	1	1	1	1	0	0	0	0
Caryophyllaceae	3	3	2	2	2	2	3	3
Chenopodiaceae	2	1	0	0	2	1	0	0
Clusiaceae	1	1	1	1	1	1	1	1
Commelinaceae	2	2	2	2	2	2	2	2
Crassulaceae	1	1	1	1	1	1	1	1
Cyperaceae	7	7	0	0	5	5	4	4
Euphorbiaceae	6	6	2	2	5	5	5	5
Fabaceae	13	13	8	8	12	12	11	11
Gentianaceae	2	2	0	0	2	2	0	0
Geraniaceae	1	1	0	0	1	1	1	1
Lamiaceae	3	3	2	2	3	3	2	2
Molluginaceae	1	1	0	0	1	1	0	0
Moraceae	1	1	1	0	1	1	1	1
Onagraceae	2	2	1	1	2	2	2	2
Orobanchaceae	1	0	0	0	1	0	0	0
Plantaginaceae	1	1	1	1	1	1	1	1
Poaceae	16	16	8	8	15	15	14	14
Polygonaceae	8	8	5	5	8	8	4	4
Pontederiaceae	1	1	0	0	1	1	1	1
Rubiaceae	2	2	1	1	2	2	2	2
Scrophulariaceae	8	8	3	3	8	8	3	3
Solanaceae	1	1	1	1	1	1	1	1
Perennial								
Alismataceae	3	3	1	1	2	2	2	2
Amaranthaceae	1	1	1	1	1	1	1	1
Apiaceae	3	3	1	1	3	3	1	1
Aristolochiaceae	2	2	1	1	2	2	1	1
Asclepiadaceae	3	3	3	3	2	2	0	0
Aspleniaceae	1	1	1	1	1	1	0	0
Asteraceae	32	31	17	15	26	25	15	15
Blechnaceae	1	1	1	1	1	1	0	0
Boraginaceae	1	1	1	1	0	0	0	0
Campanulaceae	6	6	3	1	6	6	2	2
Caryophyllaceae	3	3	1	1	3	3	2	2
Chloranthaceae	1	1	1	1	0	0	0	0
Clusiaceae	1	1	1	1	1	1	1	1
Convolvulaceae	1	1	0	0	1	1	0	0
Cucurbitaceae	1	1	1	1	1	1	1	1
Cyperaceae	25	26	13	12	22	25	13	14
Dennstaedtiaceae	2	2	2	2	1	1	1	1
Dioscoreaceae	4	4	2	2	3	3	2	2
Droseraceae	2	2	0	0	2	2	0	0
Dryopteridaceae	3	3	3	3	1	1	1	1
Equisetaceae	1	1	1	1	1	1	1	1
Fabaceae	16	16	10	10	13	13	10	10
Gentianaceae	1	1	1	1	1	1	0	0
Geraniaceae	1	1	1	1	1	1	1	1
Gleicheniaceae	1	1	0	0	1	1	0	0
Haloragaceae	1	1	0	0	1	1	1	1
Iridaceae	4	4	1	1	4	4	1	1
Juncaceae	5	5	2	2	5	5	3	3
Lamiaceae	11	11	8	7	10	10	5	5
Liliaceae	20	19	7	6	15	15	4	4
Lindsaeaceae	1	1	0	0	1	1	0	0
Lycopodiaceae	1	1	0	0	1	1	0	0
Lythraceae	1	1	1	1	1	1	1	1
Menispermaceae	1	1	1	1	1	1	1	1
Onagraceae	2	2	1	1	1	1	2	2
Ophioglossaceae	1	1	1	1	1	1	1	1

Table S2-3. Continued.

Family name	Total richness		Richness of land-use					
			Abandoned		Traditional		Intensive	
	2011	2012	2011	2012	2011	2012	2011	2012
Perennial								
Orchidaceae	4	4	1	1	4	4	1	1
Osmundaceae	1	1	1	1	1	1	0	0
Oxalidaceae	2	2	2	2	2	2	2	2
Phytolaccaceae	1	1	1	1	1	0	0	0
Plantaginaceae	2	2	2	2	1	1	2	2
Poaceae	42	41	24	22	33	33	25	26
Polygalaceae	1	1	0	0	1	1	1	1
Polygonaceae	6	6	4	4	5	5	4	4
Polypodiaceae	1	0	1	0	0	0	0	0
Primulaceae	3	3	2	1	3	3	3	3
Pteridaceae	1	1	1	1	1	1	0	0
Ranunculaceae	4	4	3	3	4	4	3	3
Rosaceae	8	8	7	7	7	7	6	6
Rubiaceae	6	6	4	4	3	3	4	4
Santalaceae	1	1	0	0	1	1	1	1
Saururaceae	1	1	1	1	1	1	1	1
Saxifragaceae	4	4	2	2	3	3	0	0
Schizaeaceae	1	1	1	1	1	1	1	1
Scrophulariaceae	2	2	1	1	2	2	2	2
Smilacaceae	1	1	1	1	1	1	1	1
Solanaceae	2	2	1	1	0	0	1	1
Thelypteridaceae	6	6	3	3	5	5	2	2
Typhaceae	1	1	1	1	0	0	0	0
Urticaceae	3	3	0	0	3	3	1	1
Valerianaceae	1	1	0	0	1	1	0	0
Verbenaceae	2	2	0	0	0	0	2	2
Violaceae	5	5	3	3	5	5	4	4
Vitaceae	2	2	1	1	2	2	1	1
Woodsiaceae	2	2	2	2	2	2	0	0
Woody								
Aceraceae	2	2	1	1	1	1	0	0
Anacardiaceae	3	3	3	3	3	3	3	3
Apocynaceae	1	0	1	0	0	0	0	0
Aquifoliaceae	3	3	2	2	3	3	0	0
Araliaceae	3	2	3	2	1	0	0	0
Betulaceae	4	4	2	2	3	3	3	3
Caprifoliaceae	7	7	4	4	4	4	1	1
Celastraceae	2	2	2	2	0	0	0	0
Clethraceae	1	1	1	1	1	1	0	0
Cornaceae	2	2	1	1	0	0	1	1
Cupressaceae	1	1	0	0	1	1	0	0
Ebenaceae	1	1	1	1	1	1	1	1
Elaeagnaceae	2	2	2	2	1	1	0	0
Ericaceae	7	7	4	4	7	7	2	2
Euphorbiaceae	2	2	1	1	2	2	1	1
Fabaceae	3	3	3	3	2	2	2	2
Fagaceae	6	6	4	4	5	5	3	3
Hydrangeaceae	3	3	3	3	3	3	1	1
Lardizabalaceae	2	2	1	1	2	2	1	1
Lauraceae	2	1	2	1	0	0	0	0
Moraceae	1	1	1	1	1	1	1	1
Myrsinaceae	1	1	1	1	1	1	0	0
Oleaceae	2	2	1	1	1	1	0	0
Pinaceae	1	1	0	0	1	1	1	1
Rhamnaceae	1	1	1	1	1	1	0	0
Rosaceae	10	10	7	7	10	10	3	3
Rutaceae	1	1	1	1	1	1	0	0
Salicaceae	3	2	0	0	3	2	0	0
Theaceae	3	3	2	2	3	3	1	1
Thymelaeaceae	1	1	0	0	1	1	0	0
Ulmaceae	2	2	1	1	0	0	2	2
Verbenaceae	1	1	1	1	0	0	0	0
Vitaceae	2	2	1	1	2	2	1	1
total species richness	477	468	274	259	395	392	252	254

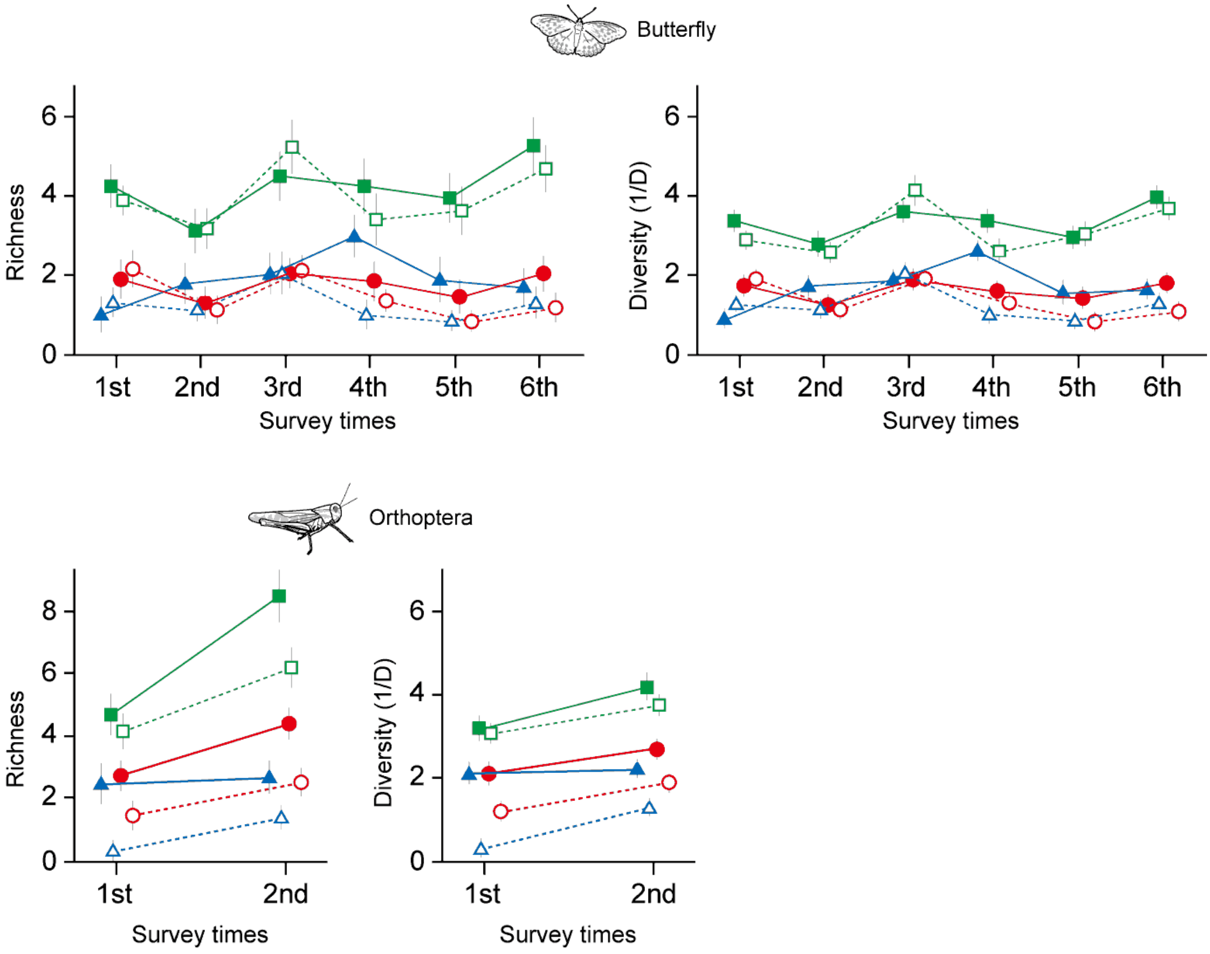


Fig. S2-9. Seasonal variation in richness and 1/D of two herbivorous insect groups. The triangle, square, and circle indicate abandoned, traditional, and intensive terrace, respectively. Closed and open symbols indicate data in 2011 and 2012, respectively. To avoid data point overlaps, small increments (2011: -0.1, 2012: +0.1 to x coordinates) have been added.

Table S2-4. Estimated coefficients of explanatory parameters (mowing frequency and land-scape variables) in the best generalized linear mixed model for plant species-richness in 2011 and 2012. Boldface indicates that the 95% confidence interval for the partial regression coefficient did not include zero. AIC, Akaike's information criterion. Shown to the upper right of each number is the relative importance among the explanatory variables.

		mowing frequency		land-scape variables			AIC value	
Plant species	year	primary	quadric	forest edge length	pca axis 1 value	pca axis 2 value	best	full
Total species	2011	**0.121**	**-0.032**^{1}	**0.003**^{2}	**0.118**^{3}		264.7	266.0
	2012	**0.108**	**-0.032**^{1}	**0.003**^{2}	**0.104**^{3}		250.9	252.5
Annual	2011	**0.371**	**-0.057**^{1}			**0.122**^{2}	198.6	201.4
	2012	**0.386**	**-0.063**^{1}			**0.120**^{2}	181.3	184.8
Perennial	2011	**0.143**	**-0.038**^{1}	**0.002**^{3}	**0.149**^{2}		213.4	215.4
	2012	**0.106**	**-0.031**^{2}	**0.002**^{3}	**0.143**^{1}		209.0	210.9
Woody	2011	**- 0.315**^{2}		**0.014**^{1}	**0.215**^{3}		257.4	261.1
	2012	**-0.005**	**-0.086**^{1}	**0.011**^{2}	**0.157**^{3}		233.0	234.2

Table S2-5. Estimated coefficients of explanatory parameters (butterfly adult and larva resources: flower diversity (1/D) and host plant species, mowing frequency and land-scape variables) in the best generalized linear mixed model for butterfly species richness in 2011 and 2012. Boldface indicates that the 95% confidence interval for the partial regression coefficient did not include zero. AIC, Akaike's information criterion. Shown to the upper right of each number is the relative importance among the explanatory variables.

		Flower diversity (1/D)			Larva host plant species richness			mowing frequency		land-scape variables			AIC value	
Butterfly richness	year	annual	perennial	woody	annual	perennial	woody	primary	quadric	forest edge length	pca axis 1 value	pca axis 2 value	best	full
Total species	2011			0.079	**0.030**^{3}	**0.042**^{1}	**0.035**^{4}	**0.015**	**-0.035**^{2}				124.3	131.7
	2012		**0.039**^{3}			**0.045**^{1}		**0.141**	**-0.051**^{2}				113.2	120.3
Body size														
Small	2011		**0.030**^{2}	**0.099**^{3}		**0.048**^{1}	0.031			0.004			88.8	97.4
	2012		**0.041**^{2}			**0.045**^{1}		0.141	-0.038				65.6	76.6
Medium	2011				0.061			**0.176**	**-0.070**^{1}		**0.134**^{2}		135.0	145.0
	2012		**0.068**^{2}		**0.077**^{4}	**0.069**^{3}		**0.263**	**-0.097**^{1}	0.004		**-0.117**^{5}	113.1	119.2
Large	2011		0.051		**0.420**^{2}			**0.762**	**-0.214**^{1}		0.121		132.6	142.6
	2012		**0.115**^{1}		**0.450**^{3}	**0.195**^{2}							136.7	147.0
larval-host														
Monophagous	2011		**0.098**^{1}	0.156		0.121					**0.164**^{2}		124.9	131.9
	2012		**0.176**^{1}			**0.170**^{4}		**0.669**	**-0.113**^{3}			**-0.310**^{2}	107.0	116.3
Oligophagous	2011					**0.047**^{1}		**0.169**	**-0.047**^{2}	**0.004**^{3}	0.049		116.1	125.1
	2012				0.026	**0.070**^{1}		0.039	-0.029	0.003			80.9	90.5
Polyphagous	2011					0.060	**0.132**^{2}	**0.299**	**-0.098**^{1}				98.8	108.1
	2012		0.056			0.069		**0.245**	**-0.110**^{1}				99.5	110.8
No. of individuals														
Rare	2011					**0.060**^{3}	**0.111**^{2}	**0.456**	**-0.147**^{1}				150.7	161.3
	2012		0.073			**0.072**^{2}		**0.074**	**-0.010**^{1}				151.1	160.9
Common	2011			0.073	0.027	**0.047**^{1}		0.086	-0.027	0.003			109.2	118.4
	2012		**0.046**^{3}			**0.035**^{2}		**0.278**	**-0.069**^{1}		-0.052		91.6	98.7

Table S2-6. Estimated coefficients of explanatory parameters (butterfly adult and larva resources: flower diversity (1/D) and host plant species, mowing frequency and land-scape variables) in the best generalized linear mixed model for butterfly diversity (1/D) in 2011 and 2012. Boldface indicates that the 95% confidence interval for the partial regression coefficient did not include zero. AIC, Akaike's information criterion. Shown to the upper right of each number is the relative importance among the explanatory variables.

		Flower diversity (1/D)			Larva host plant species richness			mowing frequency		land-scape variables			AIC value	
Butterfly diversity (1/D)	year	annual	perennial	woody	annual	perennial	woody	primary	quadric	forest edge length	pca axis 1 value	pca axis 2 value	best	full
Total species	2011				**0.223**^{1}	0.080	**0.238**^{2}	0.438	-0.157				506.1	514.0
	2012				**0.145**^{4}	**0.147**^{1}	**0.190**^{3}	**-0.490**^{2}					459.8	468.3
Body size														
Small	2011		**0.090**^{4}		**0.136**^{2}		**0.138**^{3}	0.300	-0.096	**0.017**^{1}			400.0	406.3
	2012		**0.081**^{2}				0.084	**0.500**	**-0.134**^{1}				336.1	347.3
Medium	2011							0.208	-0.087		**0.208**^{2}		420.8	432.9
	2012	-0.095			**0.234**^{2}	**0.174**^{1}		0.084	-0.087			**-0.281**^{3}	353.0	360.0
Large	2011		**0.076**^{2}		**0.390**^{3}	**0.164**^{4}		**0.290**	**-0.082**^{1}				351.9	361.0
	2012		**0.142**^{1}		0.293	**0.267**^{2}					-0.120		313.1	325.7
larval-host														
Monophagous	2011		**0.115**^{1}			0.104	**0.167**^{2}				0.107		293.3	299.5
	2012		**0.189**^{1}			**0.228**^{2}							291.7	300.5
Oligophagous	2011					**0.108**^{2}		**0.669**	**-0.184**^{1}	**0.016**^{3}			463.3	472.4
	2012				0.080	**0.151**^{2}		**-0.382**^{1}		**0.012**^{3}	-0.162		391.3	401.6
Polyphagous	2011		**0.048**^{4}			**0.115**^{1}	**0.115**^{2}	**-0.134**^{3}					260.3	270.0
	2012	-0.057	**0.059**^{1}			0.064		0.005	-0.045	-0.006			253.4	259.5
No. of individuals														
Rare	2011					**0.188**^{1}	**0.242**^{2}	**-0.195**^{3}					454.0	466.4
	2012		**0.210**^{3}			**0.198**^{1}		**-0.349**^{2}			-0.191		422.7	433.6
Common	2011				**0.159**^{2}	**0.111**^{1}		0.338	-0.119	0.014			452.9	462.3
	2012					**0.128**^{2}		**0.723**	**-0.226**^{1}		-0.242		409.8	419.3

Table S2-7. Estimated coefficients of explanatory parameters (orthoptera resources: richness of annual and perennial of grass and forb, mowing frequency and land-scape variables) in the best generalized linear mixed model for orthoptera species richness in 2011 and 2012. Boldface indicates that the 95% confidence interval for the partial regression coefficient did not include zero. AIC, Akaike's information criterion. Shown to the upper right of each number is the relative importance among the explanatory variables.

Orthoptera richness	year	Plant species richness				mowing frequency		land-scape variables			AIC value	
		annual		perennial		primary	quadric	forest edge length	pca axis 1 value	pca axis 2 value	best	full
		grass	forb	grass	forb							
Total species	2011			**0.028**^{3}	**0.014**^{1}	**0.263**	**-0.054**^{2}				116.5	123.3
	2012			**0.052**^{2}	**0.013**^{3}	**0.514**	**-0.102**^{1}				121.0	127.3
Body size												
Small	2011	**0.090**^{3}		0.047	**0.022**^{2}					**-0.251**^{1}	120.8	129.7
	2012			**0.072**^{1}	**0.024**^{2}						109.9	120.8
Medium	2011		0.016		**0.013**^{2}	**0.210**	**-0.085**^{1}				105.9	113.3
	2012		**0.038**^{3}	0.039		**0.493**	**-0.116**^{2}			**-0.214**^{1}	89.6	94.2
Large	2011			0.030	**0.011**^{2}	**0.319**	**-0.054**^{1}				80.8	88.7
	2012			**0.060**^{2}	0.012	**0.728**	**-0.140**^{1}		-0.079	-0.087	93.9	99.5
Mandibular												
Sharp	2011			0.025	**0.015**^{1}	**0.203**	**-0.053**^{2}				100.4	104.2
	2012		0.020	**0.071**^{1}		**0.420**	**-0.101**^{2}				98.6	106.2
Flat	2011				**0.014**^{2}	**0.544**	**-0.094**^{1}	-0.005		-0.082	80.6	85.3
	2012			**0.042**^{3}	0.015	**0.801**	**-0.146**^{1}		-0.111	**-0.155**^{2}	87.1	92.9
Mix	2011			0.051	0.021						126.7	139.4
	2012			**0.087**^{1}	**0.028**^{2}						93.6	102.7
No. of individuals												
Rare	2011				**0.026**^{1}						143.3	154.0
	2012			**0.114**^{1}						**-0.443**^{2}	99.3	110.7
Common	2011			**0.034**^{3}	**0.014**^{1}	**0.300**	**-0.060**^{2}				98.3	104.4
	2012			**0.049**^{2}	**0.013**^{3}	**0.609**	**-0.122**^{1}				117.5	125.4

Table S2-8. Estimated coefficients of explanatory parameters (orthoptera resources: richness of annual and perennial of grass and forb, mowing frequency and land-scape variables) in the best generalized linear mixed model for orthoptera diversity (1/D) in 2011 and 2012. Boldface indicates that the 95% confidence interval for the partial regression coefficient did not include zero. AIC, Akaike's information criterion. Shown to the upper right of each number is the relative importance among the explanatory variables.

		Plant species richness				mowing frequency		land-scape variables			AIC value	
Orthoptera diversity (1/D)	year	annual		perennial		primary	quadric	forest edge length	pca axis 1 value	pca axis 2 value	best	full
		grass	forb	grass	forb							
Total species	2011			0.078	**0.049**^{1}					-0.293	432.6	442.4
	2012			**-0.116**^{2}	**0.044**^{1}						409.1	414.4
Body size												
Small	2011	**0.106**^{1}		**0.047**^{3}						**-0.254**^{2}	276.9	283.6
	2012	0.039		**0.083**^{1}							242.7	251.6
Medium	2011				**0.025**^{1}	**-0.162**^{2}					298.8	308.3
	2012	-0.054	**0.040**^{1}	**0.048**^{3}		**0.401**	**-0.088**^{4}			**-0.183**^{2}	242.7	244.9
Large	2011			0.062	0.020						338.0	343.5
	2012		**-0.038**^{4}	**0.091**^{2}	**0.026**^{3}	**0.844**	**-0.151**^{1}	-0.008	-0.158		296.8	299.8
Mandibular												
Sharp	2011	**0.144**^{3}		**0.084**^{2}		**-0.232**^{1}		**0.011**^{4}		-0.177	382.0	387.7
	2012		0.028	**0.089**^{1}		**0.259**	**-0.071**^{2}				304.4	311.0
Flat	2011		**-0.028**^{4}		**0.024**^{1}	**0.523**	**-0.080**^{2}	**-0.008**^{3}			251.4	256.7
	2012			**0.067**^{1}		**0.571**	**-0.095**^{2}			-0.160	264.4	271.6
Mix	2011				**0.025**^{1}						288.7	300.9
	2012			**0.051**^{1}	0.013						221.8	229.4
No. of individuals												
Rare	2011				**0.020**^{1}					-0.143	304.1	314.4
	2012			**0.063**^{1}					-0.089	**-0.185**^{2}	221.0	231.3
Common	2011			**0.095**^{2}	**0.044**^{1}						397.1	407.3
	2012			**0.095**^{2}	**0.044**^{1}			-0.010			376.9	382.6

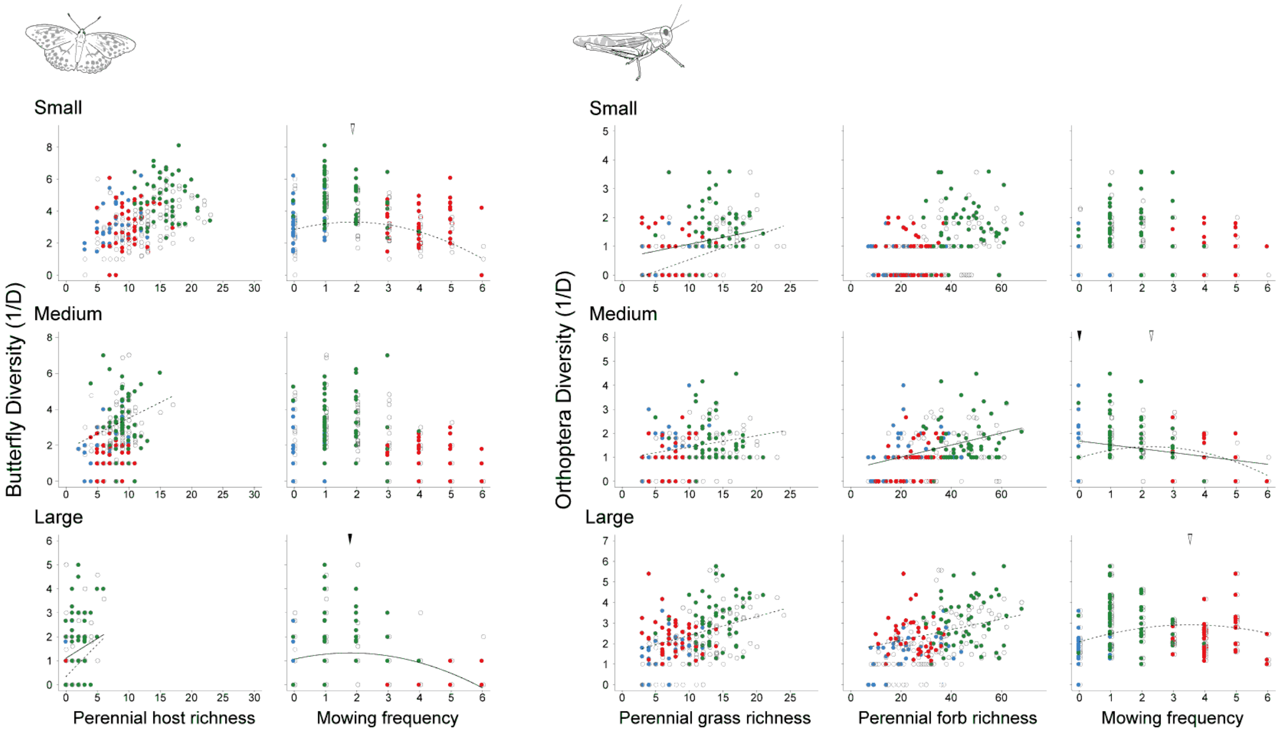


Fig. S2-10. Relationships between the diversity (1/D) of herbivorous insects of body-size groups and resource of perennial plant variables and mowing frequency in 2011 and 2012. Closed and open circles represent the 1/D in 2011 and 2012, respectively (blue dot, abandoned; green, traditional; red, intensive). Bold (2011) and dashed lines (2012) represent the estimated 1/D of butterfly and orthoptera, from the GLMM. The upside-down closed and open triangles indicate the mowing frequency at which the estimated 1/D was the highest. To avoid data point overlap, small increments (2011: -0.03, 2012: +0.03 to x coordinates) has been added. The regression line for each predictor was drawn using fixed values (i.e., the means) for the other predictors.

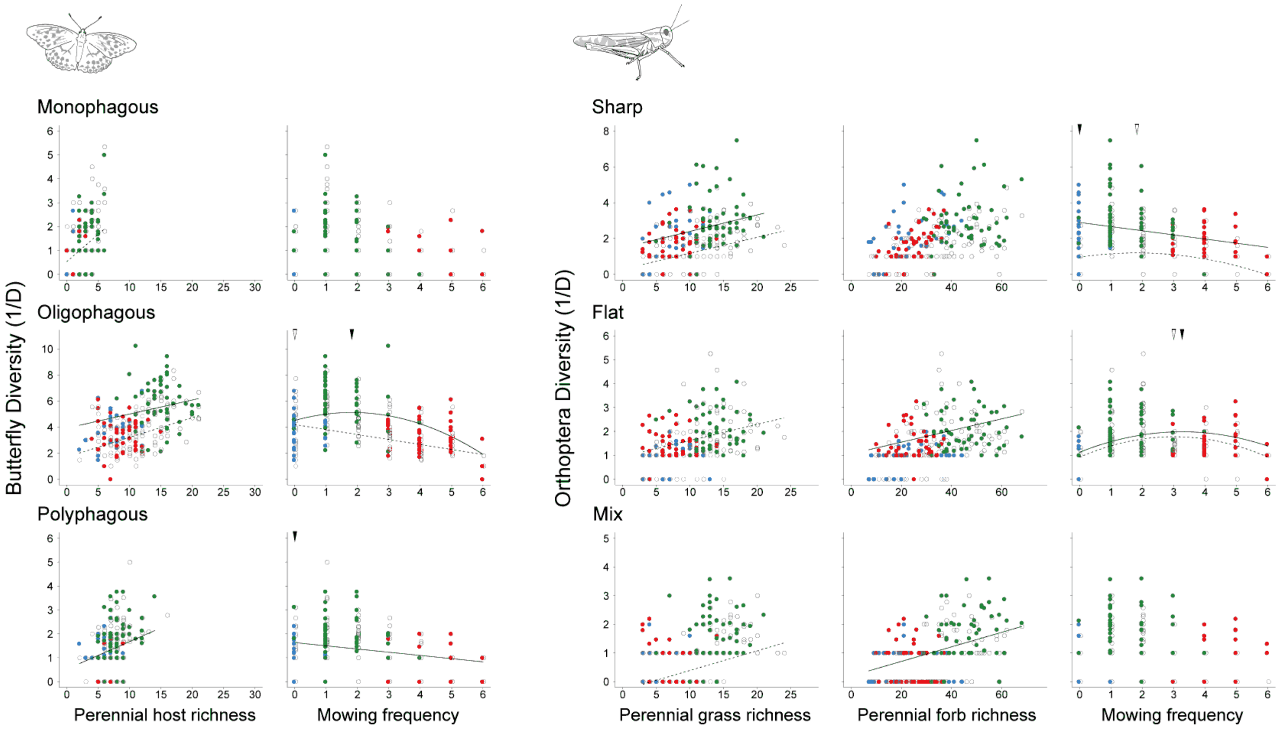


Fig. S2-11. Relationships between the diversity (1/D) of herbivorous insects of larval-host/mandibular groups and resource of perennial plant variables and mowing frequency in 2011 and 2012. Closed and open circles represent the 1/D in 2011 and 2012, respectively (blue dot, abandoned; green, traditional; red, intensive). Bold (2011) and dashed lines (2012) represent the estimated 1/D of butterfly and orthoptera, from the GLMM. The upside-down closed and open triangles indicate the mowing frequency at which the estimated 1/D was the highest. To avoid data point overlap, small increments (2011: -0.03, 2012: +0.03 to x coordinates) has been added. The regression line for each predictor was drawn using fixed values (i.e., the means) for the other predictors.

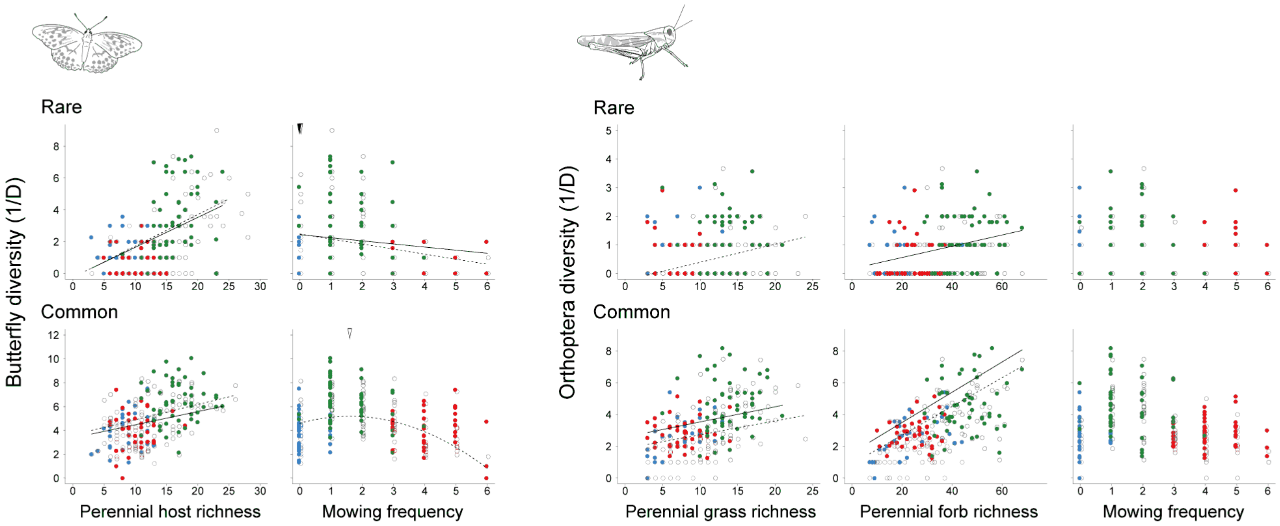


Fig. S2-12. Relationships between the diversity (1/D) of herbivorous insects of abundance (No. of individuals) groups and resource of perennial plant variables and mowing frequency in 2011 and 2012. Closed and open circles represent the 1/D in 2011 and 2012, respectively (blue dot, abandoned; green, traditional; red, intensive). Bold (2011) and dashed lines (2012) represent the estimated 1/D of butterfly and orthoptera, from the GLMM. The upside-down closed and open triangles indicate the mowing frequency at which the estimated 1/D was the highest. To avoid data point overlap, small increments (2011: -0.03, 2012: +0.03 to x coordinates) has been added. The regression line for each predictor was drawn using fixed values (i.e., the means) for the other predictors.

Table S2-9. Estimated coefficients of explanatory parameters (butterfly adult and larva resources: flower diversity (1/D) and host plant species, mowing frequency and land-scape variables) in the best generalized linear mixed model for butterfly richness and diversity (1/D) in 2011 and 2012. Boldface indicates that the 95% confidence interval for the partial regression coefficient did not include zero. AIC, Akaike's information criterion. Shown to the upper right of number is the relative importance among the explanatory variables.

		Flower diversity (1/D)			Larva host plant species richness			mowing frequancy		land-scape variables			AIC value	
Butterfly taxonomic groups	year	annual	perennial	woody	annual	perennial	woody	primary	qadric	forest edge length	pca axis 1 value	pca axis 2 value	best	full
Richness														
Papilionidae	2011							**1.170**	**- 0.299**^{1}	0.009			115.4	129.3
	2012		0.094										90.9	107.1
Pieridae	2011		**0.049**^{1}					**0.310**	**- 0.063**^{2}				109.2	122.9
	2012				0.110	**0.194**^{1}		**0.456**	**- 0.094**^{2}				99.3	108.1
Lycaenidae	2011					**0.136**^{1}					**0.079**^{2}		63.1	73.8
	2012		**0.059**^{1}			**0.102**^{3}		**0.344**	**- 0.067**^{2}				82.7	91.9
Nymphalidae	2011					0.057	0.176	**0.139**	**- 0.081**^{1}		**0.134**^{2}		126.7	134.9
	2012		**0.073**^{2}			**0.062**^{3}		**0.136**	**- 0.095**^{1}				120.4	130.2
Hesperiidae	2011		0.043			**0.084**^{2}		0.171	- 0.073	**0.011**^{1}			110.3	119.2
	2012		0.046			**0.094**^{2}		**0.210**	**- 0.114**^{1}				95.3	105.1
Diversity (1/D)														
Papilionidae	2011							**0.669**	**- 0.184**^{1}	0.107			295.4	308.4
	2012		**0.037**^{1}										171.0	186.3
Pieridae	2011		0.051					**0.439**	**- 0.090**^{1}				325.0	339.2
	2012			-0.187		**0.267**^{1}		**0.557**	**- 0.119**^{2}				284.0	293.1
Lycaenidae	2011		**0.068**^{1}	0.164		**0.122**^{2}						0.110	268.8	277.3
	2012				**0.251**^{1}						0.152		264.1	274.9
Nymphalidae	2011					0.100		**- 0.388**^{1}			**0.257**^{2}		386.1	397.0
	2012		**0.138**^{2}			**0.120**^{2}		**- 0.333**^{1}					342.1	355.0
Hesperiidae	2011					**0.129**^{1}		**- 0.149**^{3}		**0.013**^{2}			285.5	297.4
	2012					**0.090**^{2}		**0.078**	**- 0.055**^{1}				236.7	246.7

Table S2-10. Estimated coefficients of explanatory parameters (orthoptera resources: richness of annual and perennial of grass and forb, mowing frequency and land-scape variables) in the best generalized linear mixed model for orthoptera richness and diversity (1/D) in 2011 and 2012. Boldface indicates that the 95% confidence interval for the partial regression coefficient did not include zero. AIC, Akaike’s information criterion. Shown to the upper right of number is the relative importance among the explanatory variables.

		Plant species richness				mowing frequancy		land-scape variables			AIC value	
Orthoptera taxonomic groups	year	annual		perennial		primary	qadric	forest edge length	pca axis 1 value	pca axis 2 value	best	full
		grass	forb	grass	forb							
Richness												
Tettigoniidae	2011		**0.033**^{2}	**0.038**^{4}		**0.289**	**- 0.081**^{1}		**0.113**^{3}	-0.116	96.8	100.3
	2012		0.029	**0.082**^{1}		**0.395**	**- 0.090**^{2}				94.6	101.9
Phaneropteridae	2011				**0.018**^{2}	**- 0.462**^{1}					86.8	96.1
	2012					**0.870**	**- 0.344**^{1}				83.1	92.7
Tetrigoidae	2011			0.061	**0.032**^{1}	**0.194**^{2}				-0.193	118.7	127.3
	2012			0.095	**0.030**^{1}						86.7	98.9
Acrididae	2011				**0.015**^{1}	**0.404**	**- 0.075**^{2}				85.4	91.4
	2012			**0.062**^{2}		**0.843**	**- 0.160**^{1}			**-0.177**^{3}	84.3	90.4
Diversity (1/D)												
Tettigoniidae	2011	**0.107**^{1}	0.026	**0.050**^{2}		0.151	-0.065	0.006		- 0.142	307.7	309.8
	2012		0.024	**0.083**^{1}		**0.318**	**- 0.068**^{2}				270.6	277.2
Phaneropteridae	2011		-0.017		**0.012**^{2}	**- 0.162**^{1}					185.8	194.4
	2012				**0.009**^{1}	**- 0.068**^{2}					161.7	172.8
Tetrigoidae	2011				**0.021**^{1}						244.3	254.4
	2012			**0.040**^{1}				0.004			166.9	178.5
Acrididae	2011				**0.027**^{1}			**- 0.008**^{2}			286.6	294.3
	2012			**0.073**^{1}		**0.675**	**- 0.120**^{2}			- 0.187	271.1	275.3

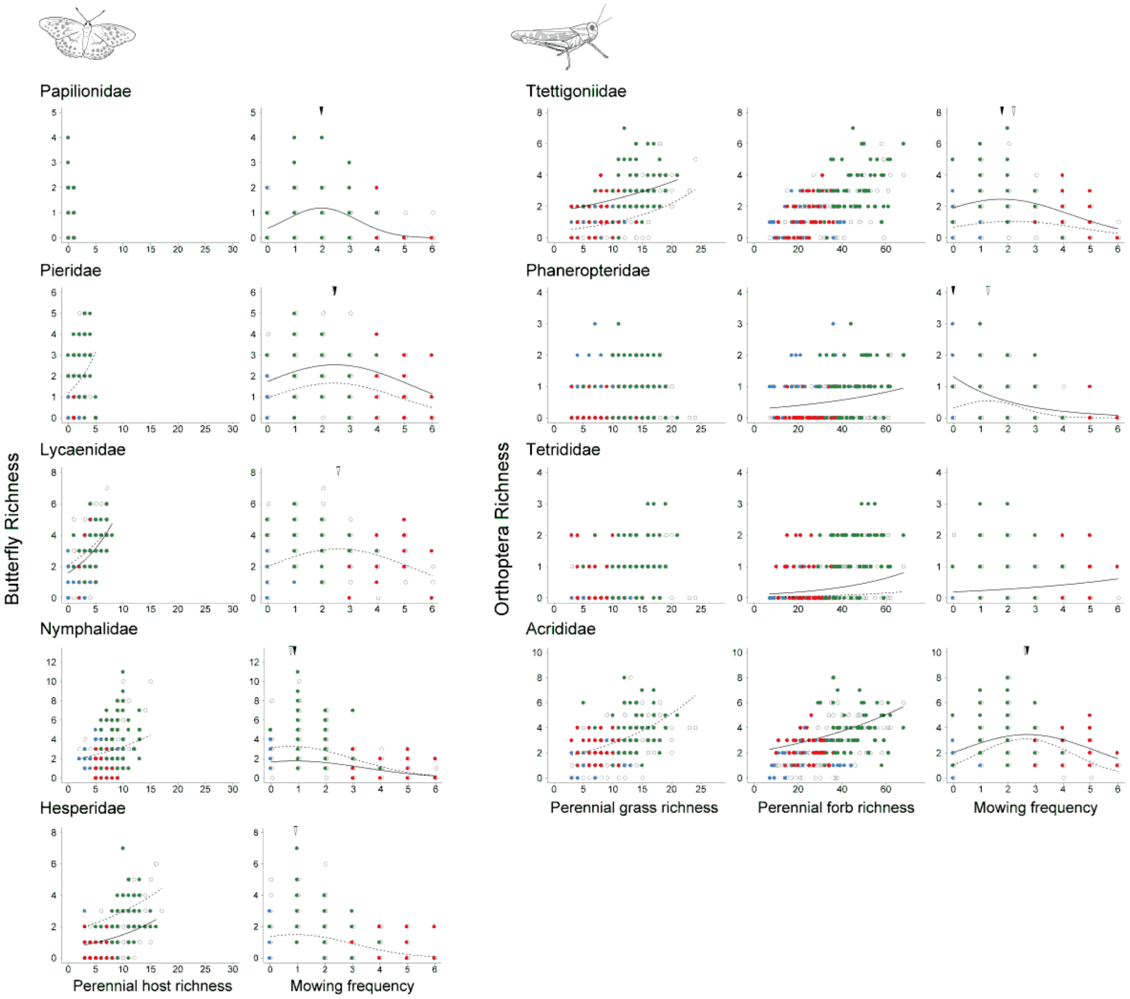


Fig. S2-13. Relationships between the species richness of herbivorous insects of taxonomic groups and resource of perennial plant variables and mowing frequency in 2011 and 2012. Closed and open circles represent the richness in 2011 and 2012, respectively (blue dot, abandoned; green, traditional; red, intensive). Bold (2011) and dashed lines (2012) represent the estimated richness of butterfly and orthoptera, from the GLMM. The upside-down closed and open triangles indicate the mowing frequency at which the estimatedrichness was the highest. To avoid data point overlap, small increments (2011: -0.03, 2012: +0.03 to x coordinates) has been added. The regression line for each predictor was drawn using fixed values (i.e., the means) for the other predictor.

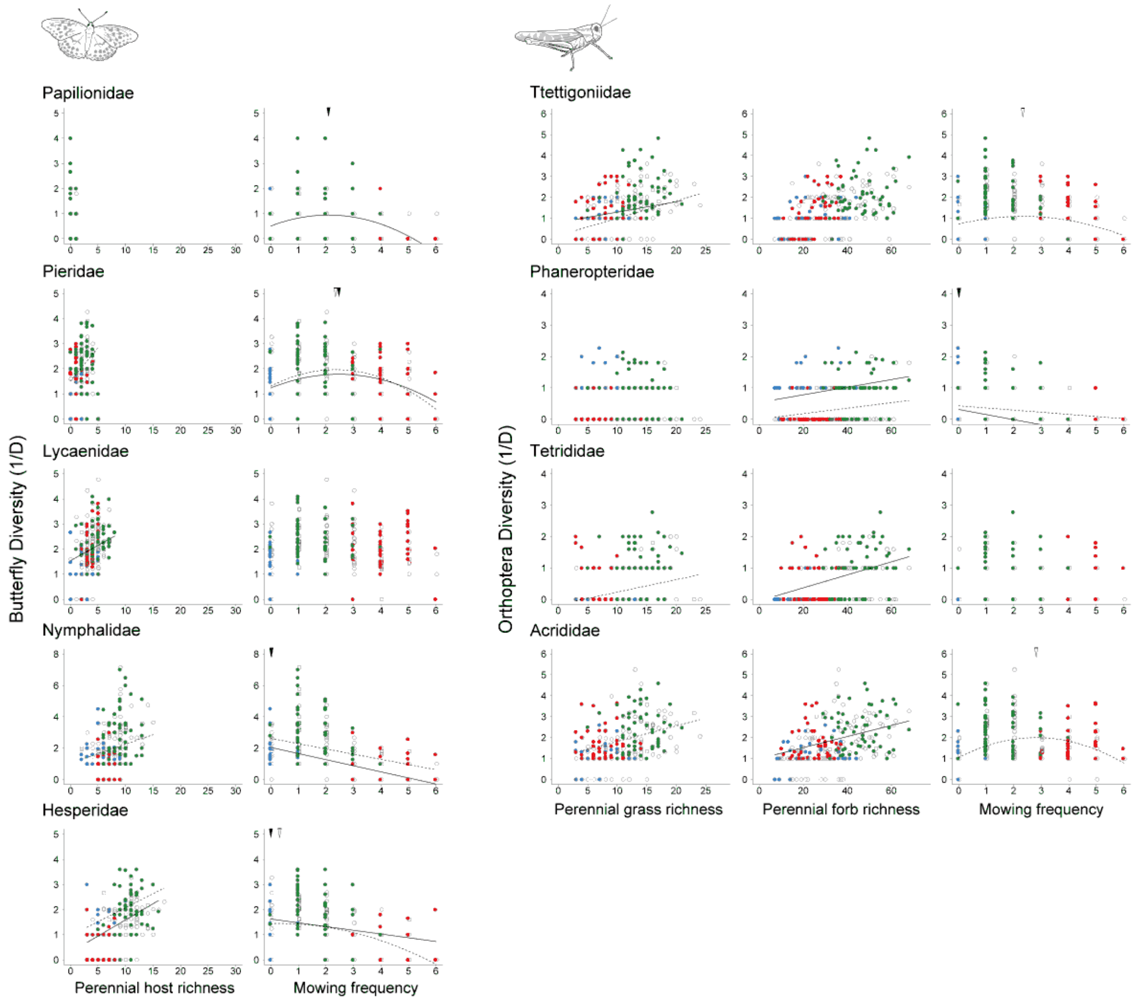


Fig. S2-14. Relationships between the diversity index (1/D) of herbivorous insects of taxonomic groups and resource of perennial plant variables and mowing frequency in 2011 and 2012. Closed and open circles represent the richness in 2011 and 2012, respectively (blue dot, abandoned; green, traditional; red, intensive). Bold (2011) and dashed lines (2012) represent the estimated richness of butterfly and orthoptera, from the GLMM. The upside-down closed and open triangles indicate the mowing frequency at which the estimatedrichness was the highest. To avoid data point overlap, small increments (2011: -0.03, 2012: +0.03 to x coordinates) has been added. The regression line for each predictor was drawn using fixed values (i.e., the means) for the other predictor.

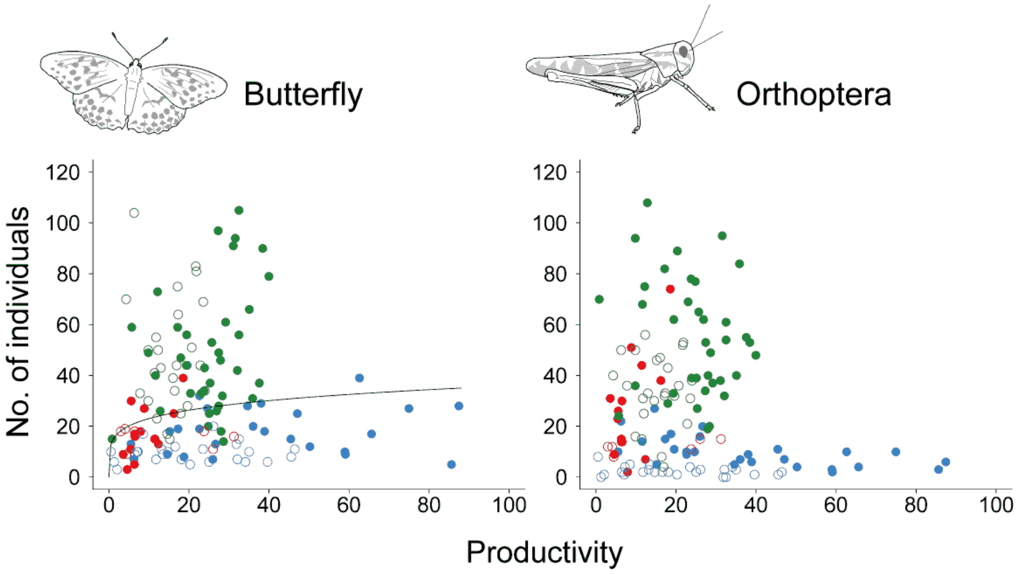


Fig. S2-15. The productivity–no. of individuals relationships for two herbivorous insect groups in 2011 and 2012. Closed and open circles represent data for 2011 and 2012, respectively (blue, abandoned; green, traditional; red, intensive). Bold (2011) and dashed lines (2012) represent the estimated species richness from the best GLMMs (see text for details). To avoid data point overlaps, small increments (2011: -0.03, 2012: +0.03 to x coordinates) have been added.

Table S2-11. This table shows that relationships between species traits and species loss and decline. In order to assess which species traits (abundance, body size and larval-host type or mandibular type) is more related with species loss and decline due to land-use changes. Boldface indicates that the significant or marginal coefficient from z-value, using GLM. *$P<0.05$, '$P<0.1$. 1: Monophagous group was used as a baseline. 2: Mix-mandibular type group was used as a baseline.

		Species loss								Species decline							
		Abandoned terrace				Intensive terrace				Abandoned terrace				Intensive terrace			
Herbivorous insect	Trait	Estimate	df	z-value	p	Estimate	df	z-value	p	Estimate	df	z-value	p	Estimate	df	z-value	p
Butterfly																	
	Abundance	**0.069**	**63**	**2.440**	**0.015***	**0.063**	**63**	**2.519**	**0.012***	0.001	27	0.629	0.529	**0.088**	**31**	**-1.708**	**0.088'**
	body size	0.018	63	0.383	0.702	-0.015	63	-0.315	0.753	-0.064	27	-0.676	0.499	-0.114	31	-1.323	0.186
	Larval host type[1]																
	Oligophagous	-0.203	63	-0.281	0.779	0.383	63	0.534	0.594	-0.893	27	-0.751	0.453	-0.309	31	-0.264	0.792
	Polyphagous	0.268	63	0.296	0.768	-0.016	63	-0.017	0.986	0.072	27	0.051	0.960	1.079	31	0.678	0.498
Orthopteran																	
	Abundance	**0.012**	**32**	**1.763**	**0.078'**	**0.028**	**32**	**1.891**	**0.059'**	0.001	16	0.457	0.648	-0.002	21	-0.874	0.382
	body size	-0.005	32	-0.098	0.922	0.030	32	0.513	0.610	-0.022	16		0.722	0.079	21	1.070	0.285
	Mandibular type[2]																
	Sharp	1.936	32	1.517	0.129	0.767	32	0.578	0.563	-0.343	16	-0.082	0.830	1.081	21	0.701	0.483
	Flat	-0.986	32	-0.666	0.506	-0.637	32	-0.392	0.695	-0.168	16	-0.414	0.679	-0.591	21	-0.293	0.770

Chapter 3.

Within-site beta diversity of spatial and temporal scales declines due to land abandonment and intensification of agricultural lands

Introduction

Spatial and temporal heterogeneity in ecological environments is an important factor that can enhance the species pool (total number of species) within a given area (Whittaker 1975; Huston 1994), which is target for biodiversity conservation. Land-use changes during recent decades, including both land abandonment and agricultural intensification, are considered to have reduced the species pool in agricultural landscapes worldwide (Sala *et al.* 2000; Tilman *et al*. 2001). These land-use changes are bidirectional in terms of anthropogenic impacts, which have been suspended in abandoned agricultural areas and increased in intensified areas. Many studies have reported decreases in plot-scale diversity (α-diversity) of plants and herbivorous insects as a result of agricultural land-use changes and have presented hypotheses for the underlying mechanisms (Kruess & Tscharntke 2002; Pöyry *et al.* 2006, 2009; Öckinger & Smith 2007; Kleijn *et al.* 2009; Uematsu & Ushimaru 2013; Uchida & Ushimaru 2014). In contrast, only a few studies have examined the ways in which land-use changes reduce among-plot diversity (β-diversity) (Clough *et al.* 2007; Ekroos, Heliölä & Kuussaari 2010; Abadie *et al.* 2011; Karp *et al.* 2012), despite its importance in maintaining species pools. A limited number of studies have shown that intensified land use leads to reduced β-diversity in plants, herbivorous insects, and birds in agricultural landscapes, indicating that biological diversity in human-dominated landscapes tends to be simplified over time, resulting in a type of ecological homogenisation (Clough *et al.* 2007; Ekroos, Heliölä & Kuussaari 2010; Abadie *et al.* 2011; Karp *et al.* 2012). Although the causal mechanisms have not been fully explored, ecological generalists and species that can tolerate human impacts may be prevalent in intensified lands. Moreover, little is known about the ways in which land abandonment influences β-diversity in agricultural ecosystems.

In agricultural landscapes, ecological heterogeneity at multiple spatio-temporal scales is a key factor in maintaining high biodiversity (Benton, Vickery & Wilson 2003). Loss of heterogeneity resulting from bidirectional land-use changes can cause declines in β-diversity at both spatial and temporal scales (Benton, Vickery & Wilson 2003). Several studies have examined reductions in β-diversity resulting from land-use changes at very large spatial scales (i.e. > 100 km^2) (Clough *et al.* 2007; Flohre *et al.* 2011; Karp *et al.* 2012). In contrast, changes in β-diversity at small spatial scales (field scale, < 1 ha) have not been adequately explored (e.g. Benton, Vickery & Wilson 2003, Abadie *et al.* 2011), although small-scale processes can affect biodiversity patterns at regional and larger scales (Huston 1999; Collins, Glenn & Briggs 2002). Contemporary agricultural practices tend to simplify landscapes and diminish spatial heterogeneity, which can lead to reduced temporal heterogeneity (Benton, Vickery & Wilson 2003). In turn, reduced temporal heterogeneity is expected to accelerate declines in diversity in agricultural areas (Benton, Vickery & Wilson 2003; Tylianakis, Klein & Tscharntke 2005), although these dynamics have not been sufficiently explored in field studies. Thus, my understanding of the ways in which bidirectional land-use changes reduce both spatial and temporal β-diversity at the small (within-field) scale in agricultural landscapes remains incomplete.

Diversity losses in animal species resulting from land-use changes have been explained by several hypotheses. First, a decline in producers will lead to reduced diversity of primary consumers and organisms at higher trophic levels (I refer to this as the plant-decline hypothesis). For example, land abandonment and intensification often decrease α-diversity of herbivorous insects by diminishing plant α-diversity (e.g. Kruess & Tscharntke 2002; Pöyry *et al.* 2009; Uchida & Ushimaru 2014). Causal relationships between plant and consumer β-diversity have not been examined extensively, although a positive correlation has been implied by previous studies (e.g. Clough *et al.* 2007). To better understand the observed reductions in β-diversity in herbivorous insects in agricultural areas, the influence of land use on β-diversity of plant communities should be examined (e.g. Joern 2005; Öckinger & Smith 2007; Pöyry *et al.* 2009). Patterns of biodiversity loss can also be explained by changes in disturbance regime (Kruess & Tscharntke 2002; Joern 2005; Pöyry *et al.* 2006; Kleijn *et al.* 2011). Although traditional low-impact management approaches are thought to cause intermediate levels of disturbance that maximise biodiversity, recent bidirectional land-use changes (land abandonment and intensification) impose extreme disturbance regimes (none vs. overly frequent disturbance, respectively), which in turn cause diversity declines (this idea is based on the intermediate disturbance hypothesis; Grime 1973; Connel 1978; Pöyry *et al.* 2006; Kleijn 2011; Uchida & Ushimaru 2014). The lack of disturbance or a too-frequent disturbance regime may favour dominance by competitive or disturbance-tolerant species, respectively, over wider areas, leading to declines in spatial and temporal β-diversity as well as α-diversity. Third, land-use changes often occur at the landscape scale, diminishing α-, β- and γ-diversity at spatio-temporal scales (I refer to this as the landscape-change hypothesis; Ekroos, Heliölä & Kuussaari 2010; Abadie *et al.* 2011). These three hypotheses must be examined to understand the lasting negative effects of landscape abandonment and use intensification on β-diversity.

Two calculations of β-diversity from α- and γ-diversity are used most often: the additive and multiplicative diversity partitioning indices (Veech & Crist 2010; Anderson *et al.* 2011). The additive diversity partitioning is calculated as $\gamma - \alpha$ (Lande 1996; Veech *et al.* 2002; Crist *et al.* 2003; Clough *et al.* 2007; Flohre *et al.* 2011) and largely depends on the absolute values of α- and γ-diversity. In contrast, Whittaker's multiplicative diversity partitioning is calculated as $\frac{\gamma}{\alpha}$ and is largely influenced by the relative values of α- and γ-diversity (Veech & Crist 2010; Anderson *et al.* 2011). Although low values of both measurements indicate homogenisation of species composition within a given spatio-temporal scale, the two measurements are not necessarily correlated. To better understand the processes involved in β-diversity losses, both additive and multiplicative diversity partitioning should be examined.

In the present study, I examined β-diversity declines of two herbivorous insect groups (butterflies and orthopterans) at the small (within-field) scale resulting from bidirectional land-use changes in semi-natural grasslands on paddy field margins, and tested the above three hypotheses concerning biodiversity declines in agricultural landscapes. In Japanese paddy terraces, topography and traditional management practices generate resource gradients that facilitate high plant β-biodiversity in semi-natural grasslands that surround paddy fields (Uematsu *et al.* 2010; Uematsu & Ushimaru 2013). Recent land abandonment and intensification are expected to reduce the heterogeneity of plant species distributions within paddy terraces (Uematsu *et al.* 2010; Uematsu & Ushimaru 2013) and thus to reduce herbivore β-diversity. I compared the spatial and temporal β-diversity of plants, butterflies, and orthopterans in semi-natural grasslands within paddy terraces, the management practices, and surrounding landscapes among three land-use management types: abandoned, traditional, and intensified agricultural lands. Based on my results, I addressed the following questions: (1) Do land-use abandonment and intensification cause spatial and temporal β-diversity declines in plants and herbivorous insects within paddy terraces? (2) Do differences exist in the relationships between land-use type and β-diversity between additive and multiplicative diversity partitioning, and if so, what causes these differences? (3) Do changes in plant β-diversity, disturbance regime, and the surrounding landscape drive declines in herbivore β-diversity? I then discuss β-diversity losses within paddy terraces in relation to the hypotheses mentioned above.

Materials and methods

Study area, paddy terraces, and plots

The study was conducted in 124 plots across 31 agricultural areas (paddy terraces) in south-eastern Hyogo Prefecture, western Japan (~15 × 30 km^2, 34°48′–57′ N, 135°03′–24′ E). The mean annual temperature was 13.8°C, with a minimum monthly average of –2.4°C in January and a maximum monthly average of 31.6°C in August. The mean annual precipitation was 1240 mm during 1981–2010. These meteorological data were recorded by a nearby automated meteorological data acquisition system (34°53.7′ N, 135°12.7′ E, 150 m a.s.l.) by the Japan Meteorological Agency.

In the study area, semi-natural grasslands were maintained by periodic mowing on the levees of paddy fields and irrigation ponds and at the edges between paddy fields and secondary forests dominated by *Pinus densiflora* and *Quercus serrata* (Uematsu *et al.* 2010). Here, mowing is considered to act as a disturbance agent for plants and herbivores. Mowing frequency varied among terraces depending on land-use type (see next section). Semi-natural grasslands around paddy fields are estimated to cover ~30% of the total area of paddy terraces in Japan (Tabata 1997).

The paddies were categorised into three land-use types: abandoned terraces, where farmers had ceased rice cropping and mowing of semi-natural grasslands 3–15 years ago; traditional terraces, managed by traditional methods for at least 100 years; and intensive terraces, which underwent land-consolidation 12–31 years ago. In most cases, the same farmer managed a single terrace. The areas of the studied paddy terraces varied as follows: abandoned terraces, 0.33–0.86 ha (mean = 0.48 ha); traditional terraces, 0.30–0.91 ha (mean = 0.50 ha); and intensive terraces, 0.38–0.86 ha (mean = 0.68 ha). The distance between abandoned and traditional terraces varied from 0.10 to 25.55 km (mean = 12.33 km), and intensive and traditional terraces were separated by 0.11–33.57 km (mean = 14.18 km). The distance between plots within abandoned, traditional, and intensive terraces varied from 23.8 to 67.2 m (mean = 41.0 m), from 20.5 to 95.0 m (mean = 47.4 m), and from 28.1 to 82.7 m (mean = 47.5 m), respectively. Interviews with all farmers indicated that they used little to no insecticide for paddy crops and did not apply insecticides to semi-natural grasslands.

I established four 5 × 50-m belt plots in semi-natural grasslands on paddy field margins at each study terrace. I studied 32 plots in eight abandoned terraces, 52 plots in 13 traditional terraces, and 40 plots in 10 intensive terraces in 2011. In 2012, I removed two terraces from the study because the areas had been developed for other land uses; therefore, 116 plots in 29 terraces were used in total, including 28 plots in seven abandoned terraces, 48 plots in 12 traditional terraces, and 40 plots in 10 intensive terraces.

Anthropogenic disturbance

I recorded the number of mowing events in each plot during my survey period to determine the disturbance frequency in 2011 and 2012. I compared the mowing frequency among the different land-use types using a generalised linear mixed model (GLMM, Poisson errors and log link) in which the mowing frequency per year for each plot was the response variable and land-use type was the explanatory variable. Terrace identity was incorporated into the models as a random term because the four plots within each terrace could be a source of pseudoreplication. I evaluated the significance of the partial regression coefficients of the explanatory variables using a Wald test. Mowing frequency in traditional plots was significantly higher than that in abandoned plots and lower than that in intensive plots (Fig. S3-1).

Landscape variables

I calculated the areas of abandoned, traditional, and intensive terraces and of secondary forest and residential land within a 1-km radius from the centre of each terrace using ArcGIS Spatial Analyst 9.3 (ESRI) with a land-use map (Geospatial Information Authority of Japan) and aerial photographs from Google maps (Google 2013).

I conducted a principal components analysis (PCA) of the five resulting area-variable data sets to reduce landscape variables for the following diversity analyses. I found that two primary axes explained 77.3% of the total variance. PCA axis-1 values increased with the area of secondary forest and decreased with the areas of abandoned and intensive terraces and residential land; thus, negative values along this axis indicate large land-use changes around the terraces (Fig. S3-2). PCA axis-2 values increased with the area of intensive terrace and residential land and decreased with the area of traditional and abandoned terraces; thus, high positive values along this axis indicate the occurrence of anthropogenic impact around the terraces (Fig. S3-2). I also measured the extent to which the grassland area of each plot was bordered by secondary forest (i.e. forest edge length within the study plot) and calculated the total forest edge length (m) for each paddy terrace.

Plant survey

I surveyed the plant community in each study plot monthly from late April to late September in 2011 and 2012 (six times per year). During each survey, I walked along the plots and recorded all vascular plant species and flower abundance (number of flowers) for all flowering species, except for wind-pollinated species. In October 2011, I conducted an intensive vegetation survey during which all vascular plants were recorded within each plot. I used total plant species richness throughout the year to calculate spatial β-diversity, and flowering species richness in each terrace to calculate temporal β-diversity (see *Statistical analyses*). Flowering plant richness was used to examine phenological variation in plant activity. Total richness of flowering species was significantly correlated with total plant species richness year round ($P < 0.01$, $r = 0.86$ and 0.87 in 2011 and 2012, respectively; Fig. S3-3).

Herbivorous insect survey

On the same days that monthly vegetation surveys were conducted, butterfly species identity and abundance in each plot were recorded using the standardised transect count method (Pollard & Yetes 1994). The butterfly survey was implemented for 15 min per plot (60 min per terrace) under sunny and warm conditions. Hesperioidea (skippers) and Papilionoidea (butterflies) species were defined as butterflies in this study.

Orthopteran species identity and abundance were surveyed using a sweep-net (42-cm diameter) with 200 sweeps per plot. To minimise the effects of differences in vegetation height among plots, I swept from the bottom to the top of the leaf layer during a single sweep. Orthopteran surveys were conducted twice (between mid-August and early October) per year for each plot in 2011 and 2012. Sweeping is considered a good method for estimating richness and abundance of orthopterans in grassland vegetation (Joern 2005). I identified species abundance after field collection.

Statistical analyses

Additive partitioning and Whittaker's multiplicative partitioning of species richness

First, I examined the additive partitioning of species richness as β-diversity (β_{add}) of plants and herbivores (Lande 1996; Veech *et al.* 2002; Crist *et al.* 2003). The spatial and temporal β_{add} for each terrace was calculated as follows:

$$\beta_{ad} = \frac{1}{N}\sum_{i=1}^{N}(\gamma - \alpha_i \quad ,$$

where N is number of plots (i.e. four for plants and herbivores) or monthly surveys (i.e. six for flowering plant species and butterflies and two for orthopterans), α_i is the number of species for plot i or survey i and γ is the total number of species for each terrace. High spatial and temporal β_{add} values indicate large spatio-temporal variation in species occurrence (Tylianakis, Klein & Tscharntke 2005, Clough *et al.* 2007; Flohre *et al.* 2011).

I next examined the multiplicative partitioning of species richness as β-diversity (β_{w}) (Whittaker 1960). The spatial and temporal β_{w} for each terrace were calculated as follows:

$$\beta_w = \frac{\gamma}{\bar{\alpha}},$$

where $\bar{\alpha}$ is the average number of species per plot or the average number of species per survey for each terrace. An increase in β_{w} indicates an increased ratio of variation in community composition (Whittaker 1960; Abadie *et al.* 2011; Anderson *et al.* 2011).

Relationship between β-diversity and land-use type

A general linear model (GLM, Gaussian error and identity link) was used to examine differences in spatial and temporal β_{add} and β_{w} of plants, butterflies, and orthopterans among the three land-use types. The response and explanatory variables were each diversity index and land-use type (abandoned, traditional and intensive), respectively. I evaluated the significance of the partial regression coefficients of the explanatory variables using a Wald test. The 2011 and 2012 data sets were examined separately. Because the spatial and temporal β_{add} of plants and herbivores differed substantially among land-use types (see *Results*), I further examined which factors influenced β_{add} in the following analyses.

Relationships between plant β-diversity indices and disturbance and landscape variables

I examined the relationships between spatial and temporal plant β_{add} and disturbance regime (mowing frequency), landscape variables (forest edge length and PCA axis-1 and -2 values), and the inter-year variation of these indices, using a GLM. The intermediate disturbance hypothesis (IDH) predicts that species richness will peak at intermediate mowing frequencies. Here, the intermediate disturbance hypothesis might predict that β-diversity decreases monotonically with changes in mowing frequency, because a lack of disturbance or an intensified level of disturbance can lead to homogenisation, represented by dominance of very competitive or disturbance-tolerant species, respectively. The landscape-change hypothesis predicts significant effects of the landscape variables on diversity. In the full GLMs, mowing frequency and its square, forest edge length, PCA axis-1 and -2 values, and study year (2011 = 0; 2012 = 1) were used as the explanatory variables and the spatial or temporal β_{add} of plants was the response variable. To evaluate the significance of the effects of the explanatory variables on each β_{add}, I used a model-selection procedure based on Akaike's information criterion (AIC): the model with the smallest AIC was considered the best model (Johnson & Omland 2004). The significance levels of the estimated partial regression coefficients of the explanatory variables in the best GLM model were examined by determining whether the 95% confidence intervals (CIs) of the estimated coefficients included zero.

Relationships between β-diversity indices of herbivorous insects and plant β-diversity, disturbance, and landscape variables

I examined the relationships between spatial and temporal β_{add} of herbivores and plant β_{add}, disturbance regime, and landscape variables using a GLM. The plant-decline hypothesis predicts significant positive relationships between plant and herbivore *β-diversity*. In the full models, the explanatory variables were plant spatial or temporal β_{add}, mowing frequency and its square, all landscape variables, and study year. The response variable was the spatial or temporal β_{add} of butterflies or orthopterans. Model selection was conducted based on AIC. The significance levels of the estimated partial regression coefficients of the explanatory variables were examined by determining whether the 95% confidence intervals (CIs) of the estimated coefficients included zero. All statistical analyses were performed using the software R (version 2.13.1).

Results

In total, 477 plant species, 61 butterfly species (3713 individuals), and 33 orthopteran species (4232 individuals) were recorded in 2011. In 2012, 468 plant species, 58 butterfly species (2902 individuals), and 28 orthopteran species (1957 individuals) were recorded.

Differences in β-diversity and land-use type

Traditional terraces had significantly higher spatial and temporal β_{add} of plants, butterflies and orthopterans than both abandoned and intensive terraces in 2011 and 2012 (Fig. 3-1). In contrast, the spatial and temporal β_{w} values of plants in traditional terraces were significantly lower than those of plants in abandoned terraces in both years, and values did not differ from those of plants in intensive terraces, except for temporal β_{w} in 2011 (Fig. 3-1). The spatial and temporal β_{w} of butterflies did not differ between traditional or abandoned and intensive terraces, except for spatial β_{w} in 2012 (Fig. 3-1). The spatial and temporal β_{w} values of orthopterans in traditional terraces were significantly lower than those of orthopterans in abandoned terraces in both years, except for tempral β_{w} in 2011 (Fig. 3-1), and the values did not differ significantly from those in intensive terraces in either year (Fig. 3-1).

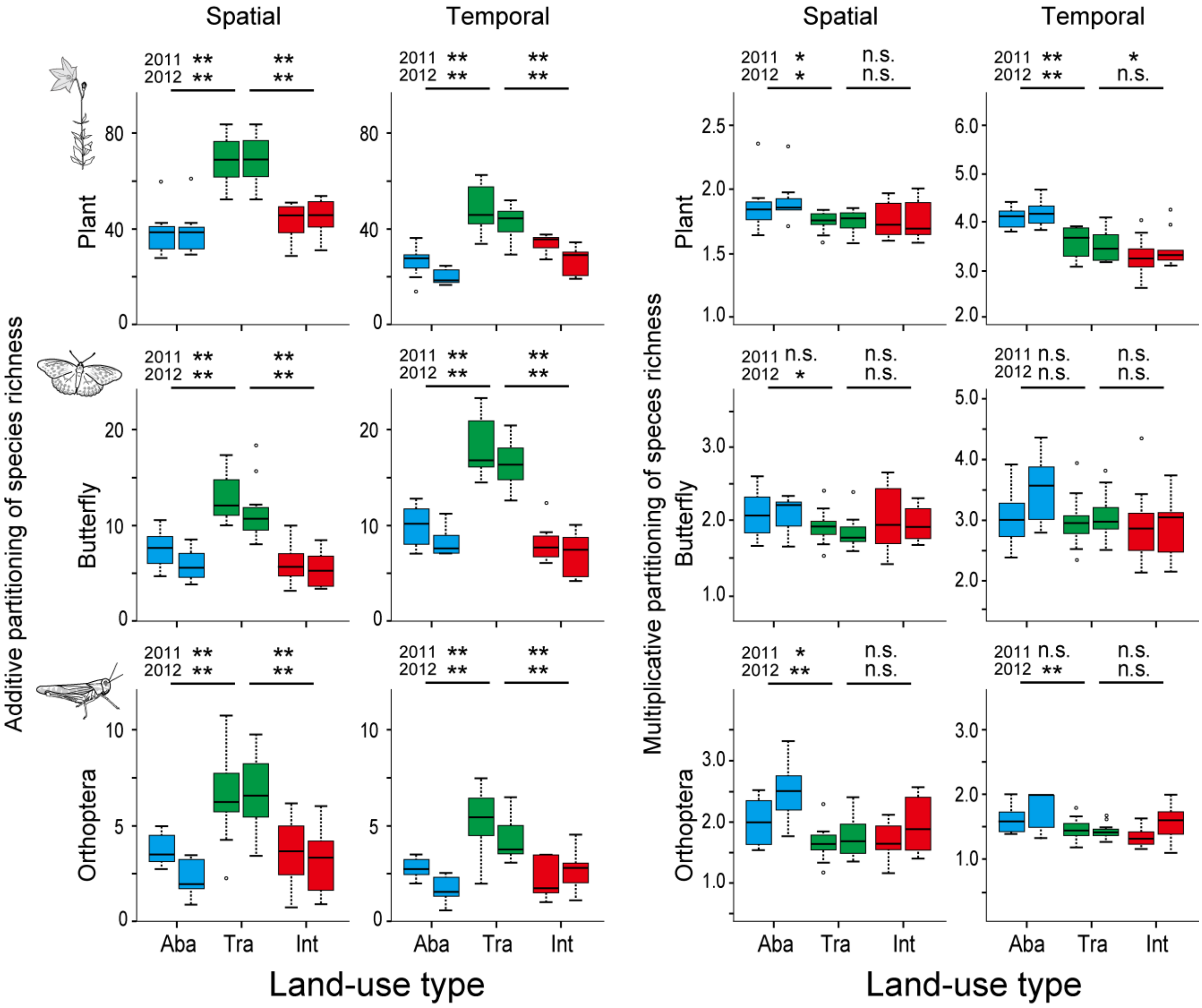


Fig. 3-1. Comparisons of additive and multiplicative partitioning of species richness of plant, butterfly and orthoptera among abandoned (Aba), traditional (Tra) and intensive (Int) plots (left box, 2011; right box, 2012). Box plots represent medians (bold black horizontal line), and first and third quartiles (box perimeters). $^{**}P < 0.01$, $^{*}P < 0.05$, n.s. not significant.

Relationships between β-diversity and disturbance and landscape variables

Both spatial and temporal plant β_{add} exhibited a significant unimodal relationship with mowing frequency in 2011 and 2012 (Table 3-1, Fig. 3-2). The estimated spatial and temporal β_{add} per terrace were maximised with a mowing frequency of 2–3 events per year (Fig. 3-2). Both spatial and temporal plant β_{add} increased with length of forest edge and PCA axis-1 values in one or both study years (Table 3-1, Fig. 3-2), but the values did not vary significantly with PCA axis 2. These results indicate that an increase in neighbouring secondary forest might increase plant β_{add}. Temporal plant β_{add} was significantly lower in 2012 than in 2011 (Table 3-1, Fig. 3-2).

Table 3-1. Estimated coefficients of explanatory parameters (mowing frequency, landscape variables and inter-year variation) in the best general linear models for plant additive partitioning of species richness (β_{add}). Bold typeface indicates that the 95% confidence interval for the partial regression coefficient did not include zero. AIC, Akaike's information criterion

	Mowing frequency		Land-scape variables				AIC value	
βadd	primary	quadric	forest edge length	pca axis 1 value	pca axis 2 value	Inter-year variation	best	full
Plant								
Spatial	**13.76**	**- 3.02**	**0.33**	**3.97**			472.8	476.7
Temporal	**9.80**	**- 2.01**		**2.75**		**- 6.27**	437.9	440.7

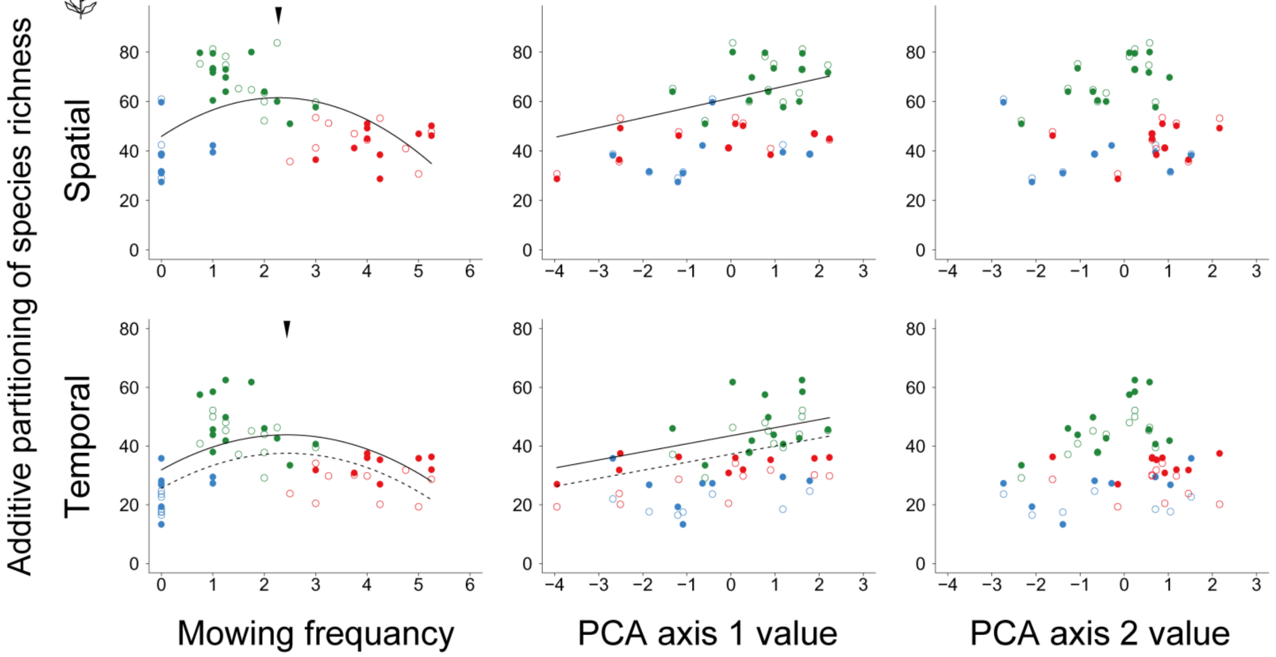


Fig. 3-2. Relationships between plant additive partitioning of species richness (β_{add}), and mowing frequency and PCA axis-1 or -2 values. PCA axis-1 values increasing area of secondary forest and decreased with areas of abandoned and intensive terraces and residential land, PCA axis-2 values increased with the area of both intensive terrace and residential land and decreased with the area of both traditional and abandoned terraces. Closed and open circles represent the β_{add} values in 2011 and 2012, respectively (blue, abandoned; green, traditional; red, intensive). Bold (2011) and dashed (2012) lines represent the estimated β_{add} from the best GLM (see Table 3-1 for details). Upside-down closed triangles indicate the mowing frequency at which the estimated β_{add} was the highest in 2011 and 2012, respectively (see Table 3-1 for details). The regression line for each predictor was drawn using fixed values (i.e., the means) for the other predictors.

Relationships among herbivore β-diversity and plant β-diversity, disturbance and landscape variables

Spatial and temporal butterfly and orthopteran β_{add} values increased significantly with plant spatial and temporal β_{add}, respectively (Table 3-2, Fig. 3-3). Spatial and temporal butterfly β_{add} values exhibited a significant unimodal relationship with mowing frequency (Table 3-2, Fig. 3-3), whereas values for orthopterans did not (Table 3-2, Fig. 3-3). No landscape variables significantly affected both butterfly and orthopteran β_{add} (Table 3-2, Fig. 3-3).

Table 3-2. Estimated coefficients of explanatory parameters (additive partitioning of species richness (β_{add}) of plant, mowing frequency, landscape variables and inter-year variation) in the best general linear models for β_{add} of butterfly and orthoptera. Bold typeface indicates that the 95% confidence interval for the partial regression coefficient did not include zero. AIC, Akaike's information criterion

		Mowing frequency		Land-scape variables				AIC value	
β_{add}	Plant β_{add}	primary	quadric	forest edge length	pca axis 1 value	pca axis 2 value	Inter-year variation	best	full
Butterfly									
Spatial	**0.11**	**1.65**	**- 0.44**				**- 1.59**	294.8	296.3
Temporal	**0.27**	**2.09**	**- 0.62**	0.06				316.0	319.3
Orthoptera									
Spatial	**0.12**				- 0.31			243.6	250.1
Temporal	**0.11**	0.23	- 0.08		- 0.22	- 0.24		195.0	196.4

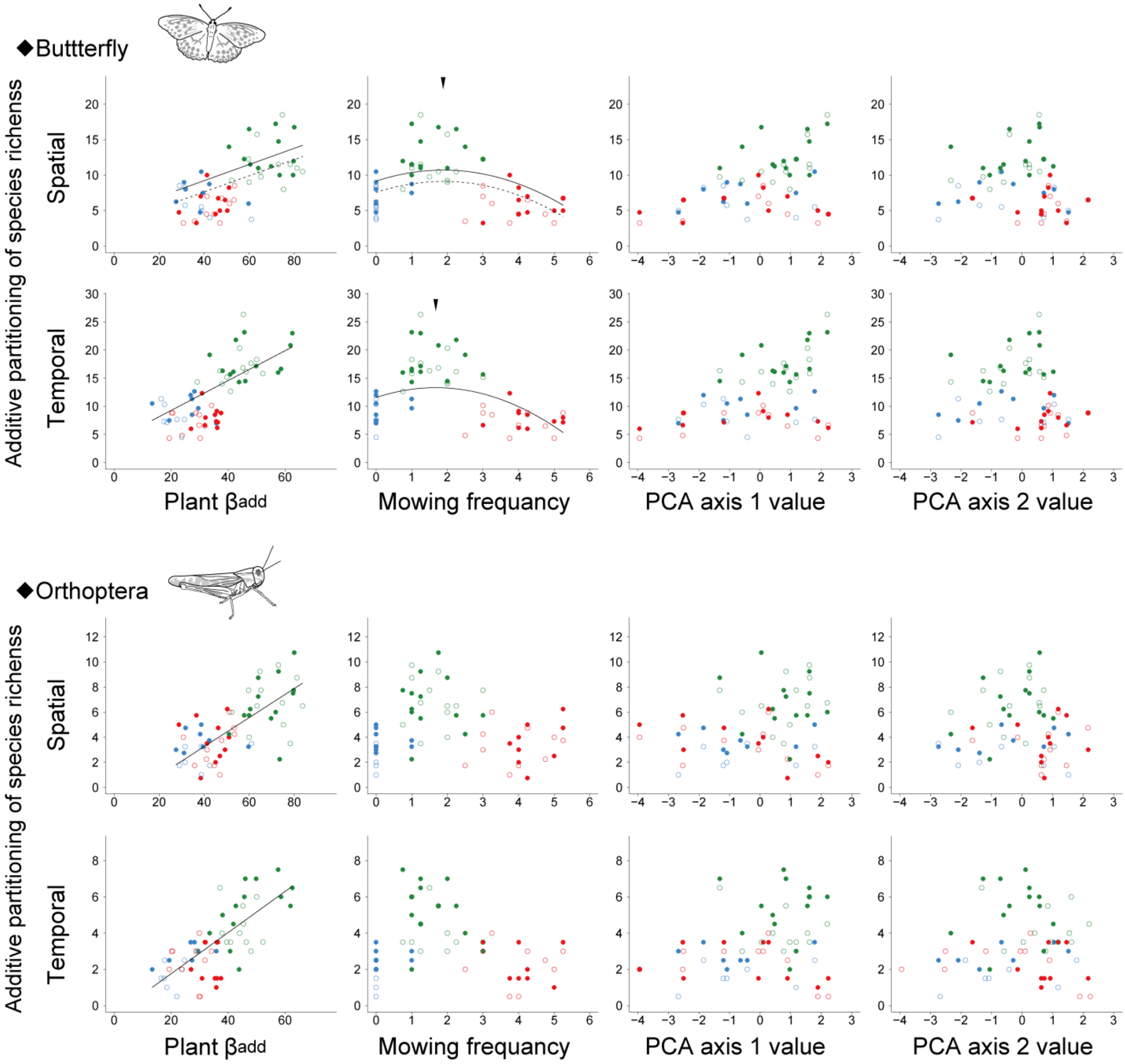


Fig. 3-3. Relationships between butterfly and orthopteran additive partitioning of species richness (β_{add}), and β_{add} of plant, mowing frequency and PCA axis-1 or -2 values. Closed and open circles represent the β_{add} in 2011 and 2012, respectively (blue, abandoned; green, traditional; red, intensive). Bold (2011) and dashed (2012) lines represent the estimated β_{add} from the best GLM (see Table 3-2 for details). Upside-down closed triangles indicate the mowing frequency at which the estimated β_{add} was the highest in 2011 and 2012, respectively (see Table 3-2 for details). The regression line for each predictor was drawn using fixed values (i.e., the means) for the other predictors.

Discussion

My results demonstrated that bidirectional land-use changes (land abandonment and intensification) caused a loss of β-diversity in plants and herbivorous insects at both spatial and temporal scales in paddy terraces, with a particular effect on the additive partitioning (β_{add}) of species richness (Fig. 3-1). Spatial and temporal β_{add} made a strong contribution to the percentage of overall γ-diversity of plants and herbivores (plants: spatial β_{add} 42–47 %, temporal β_{add} 70–76 %; butterflies: spatial β_{add} 45–51 %, temporal β_{add} 64–71 %; orthopterans: spatial β_{add} 39–59 %, temporal β_{add} 25–41 %; Fig. S3-4). These results suggest that bidirectional land-use changes largely reduced the species pool by diminishing heterogeneity in species occurrence within terraces. Although previous studies have found that land-use intensification does not decrease β-diversity at small spatial scales (Tylianakis, Klein & Tscharntke 2005; Karp *et al.* 2012), I documented spatial and temporal β-diversity declines at the within-field scale, similar to studies conducted at larger spatial scales (Clough *et al.* 2007; Flohre *et al.* 2011).

In contrast, another index of β-diversity, the β_{w} of plants and orthopterans, was significantly higher in abandoned than in traditional terraces, but equal in intensive and traditional terraces, at both spatial and temporal scales. Meanwhile, spatial and temporal butterfly β-diversity did not vary with land-use type. This discrepancy between additive and multiplicative partitioning results is further discussed in the following section. Spatial and temporal β_{add} of plants was influenced by mowing frequency and landscape variables, whereas β_{add} values for herbivores were affected by plant β_{add} and/or by mowing frequency. These results suggest that declines in spatial and temporal herbivore β-diversity were both directly and indirectly caused by changes in anthropogenic disturbance regimes and surrounding landscapes. Overall, my findings suggest that bidirectional land-use changes reduced plant, butterfly, and orthopteran species richness at the plot scale and reduced among-plot variation in species occurrence, leading to a decline in the species pool in paddy terraces (Figs.3-1 and S3-5).

Difference in land-use and β-diversity relationships between additive and multiplicative partitioning

High values of additive partitioning β-diversity indicate that most of the total (γ) diversity in a terrace is found among rather than within plots, whereas high multiplicative partitioning values indicate a high ratio of infrequently observed species to total number of species. Here, data from 52 plots in 13 traditional terraces revealed that ~73% of plant species, 65–70% of butterfly species, and 48–64% of orthopteran species were observed in < 13 plots in 2011 and 2012. These results indicate that most plant and herbivore species were found in < 1 plot for each traditional terrace (hereafter, infrequently observed species). This limited distribution may have been a result of habitat and host-plant preferences or low species abundance (Uematsu *et al*. 2010; Uematsu & Ushimaru 2013; Uchida & Ushimaru 2014). These plants and insects tended to be present or active during only certain survey periods. My β_{add} results suggest that land-use changes caused large declines of such infrequently observed plant and herbivore species (Uematsu *et al.* 2010; Uchida & Ushimaru 2014). In contrast to the additive partitioning results, I found no evidence for β-diversity declines (environmental homogenisation) due to land-use changes in terms of the multiplicative partitioning of species richness. Previous studies have often discussed the homogenisation of community composition resulting from agricultural intensification by comparing only the additive partitioning of species richness (Gabriel *et al.* 2006; Flohre *et al.* 2011). My results make clear, however, that caution should be exerted when discussing homogenisation using only one index (see also Ekroos, Heliölä & Kuussaari 2010). My findings suggest that land-use changes caused large declines in the infrequently observed species, which in turn diminished β_{add} diversity but did not cause spatial and temporal homogenisation of habitat conditions (Fig. 3-1). Thus, to clarify the mechanisms of β-diversity declines in relation to land-use changes, the use of both additive and multiplicative partitioning of diversity is optimal.

Effects of changes in plant β-diversity, disturbance regime, and the surrounding landscape on herbivore β-diversity

My results support the idea that declines in herbivorous insect β_{add} occurred in conjunction with declines in plant β_{add} (Fig. 3-3). Generally, different butterfly and orthopteran species depend on different plant species for their life cycles; therefore, a decline in plant diversity due to land-use change strongly affects herbivore diversity (e.g., Joern 2005; Öckinger & Smith 2007; Pöyry *et al.* 2009; Uchida & Ushimaru 2014). Although butterflies and orthopterans can move among plots within a terrace, their movements might be influenced by their host plants, the distribution of which is non-uniform and dependent on anthropogenic activity and on the presence of forest edge (Uematsu *et al.* 2010; Uematsu & Ushimaru 2013; this study). Most butterflies and some orthopterans use particular plant species as larval and/or adult hosts (Joern 1979; Shirouzu 2006;

EIEla, EISayed & Nakamura *et al*. 2010; Yoshioka *et al*. 2010). In the study terraces, many infrequently observed butterfly species foraged for nectar predominately on *Cirsium japonicum* or *Eupatorium lindleyanum* flowers (Uchida & Ushimaru unpublished data), which were not uniformly distributed among plots within terraces (Uematsu *et al.* 2010, Uematsu and Ushimaru 2013). Thus, my findings suggest that many butterfly and orthopteran species were limited in distribution within terraces in accordance with their host distribution, although these trends could be an artefact of incomplete sampling.

In contrast, only butterfly β_{add} decreased significantly with bidirectional changes in mowing frequency, and landscape variables had no significant effect on declines in β_{add} of either butterflies or orthopterans (Fig. 3-3). Changes in mowing frequency caused the reductions in plant β_{add} (Table 3-1, Fig. 3-2). Plant β_{add} was maximised at intermediate levels of mowing frequency (2–3 events per year), a frequency commonly practiced in traditional terraces. This intermediate level of disturbance enhanced butterfly and orthopteran β-diversity directly or indirectly by increasing plant β-diversity. Thus, the intermediate disturbance hypothesis can explain the declines in the additive partitioning of plant and herbivorous insect diversity in my abandoned and intensified agricultural paddy fields. These patterns are consistent with previous suggestions that semi-natural diversity would be maintained by traditional extensive agricultural practices (Tsharntke *et al.* 2005; Pöyry *et al.* 2006; Kleijn *et al.* 2011, Uchida and Ushimaru 2014). Considering the large contributions of spatial and temporal β_{add} to γ-diversity, overly frequent anthropogenic disturbance or the absence of disturbance could limit the species pool at the within-field scale. Plant β_{add} decreased with land-use changes in the surrounding landscape, whereas herbivore β_{add} was not directly affected by human impacts on the surrounding landscape. Changes in the landscape surrounding agricultural areas can lead to declines in herbivorous insect populations (Bergman *et al.* 2004; Tscharntke *et al.* 2005), although many exceptions have been reported (Collinge 2003; Kuussaari *et al.* 2007; Pöyry *et al.* 2009). Plant β_{add} was enhanced by the presence of surrounding secondary forest (Table 3-1, Fig. 3-2), suggesting positive effects of forest edge on the species pool of semi-natural grasslands, which in turn could enhance herbivore diversity within terraces.

Conclusions and implications for conservation

Because agricultural land occupies ~40% of total terrestrial area worldwide, maintaining biodiversity in semi-natural ecosystems is crucial for biological conservation (Tilman *et al.* 2001; Forey *et al.* 2005). In Japan, paddy fields comprise 6.5% of the total land area (Ministry of Agriculture, Forestry and Fisheries 2005). In 2005, ~10% of the total area of paddy fields had been abandoned (Ministry of Agriculture, Forestry and Fisheries 2005), and ~75% of Japanese paddy fields had been consolidated (Himiyama & Kikuchi 2007), indicating that abandoned and consolidated paddy areas are prevalent throughout Japan (Uematsu *et al.* 2010; Uematsu & Ushimaru 2013). My study demonstrates that these land-use changes have diminished the species pool within certain paddy areas. Traditional management practices such as extensive mowing enhance the spatial and temporal β_{add} of plants and herbivorous insects, but these management approaches have rapidly been abandoned due to agricultural intensification and the depopulation and ageing of farmers in rural areas.

The present study provides a unified explanation for declines in β-diversity resulting from abandonment and land-use intensification, two issues that have often been examined separately. The decline in spatial and temporal β-diversity of herbivorous insects due to land-use changes can be explained by multiple factors, including reductions in plant β-diversity and bidirectional changes in disturbance frequency and the surrounding environment. Changes in the disturbance regime resulted in a direct decline in the β_{add} of butterflies and indirectly affected butterfly and orthopteran β_{add} through diminished plant β_{add}. Surrounding land-use changes had an indirect negative effect on herbivore diversity, suggesting that many of the studied herbivores utilised a limited habitat range within a terrace. These results suggest that enhancing plant β-diversity by maintaining traditional mowing practices is essential for conserving herbivore β-diversity. Because only a limited number of traditionally managed paddy fields remain as refuges for many semi-natural grassland species, maintaining traditional practices in these fields is essential. Furthermore, I recommend a reduction in mowing frequency in consolidated paddy terraces and the reintroduction of mowing management in abandoned fields for biodiversity restoration. To generalise my finding that land-use changes will cause a loss of plant and herbivore β_{add} at relatively small spatial scales, future studies should examine different paddy systems in other regions of monsoonal Asia and different types of agricultural lands in other global regions.

Supporting information

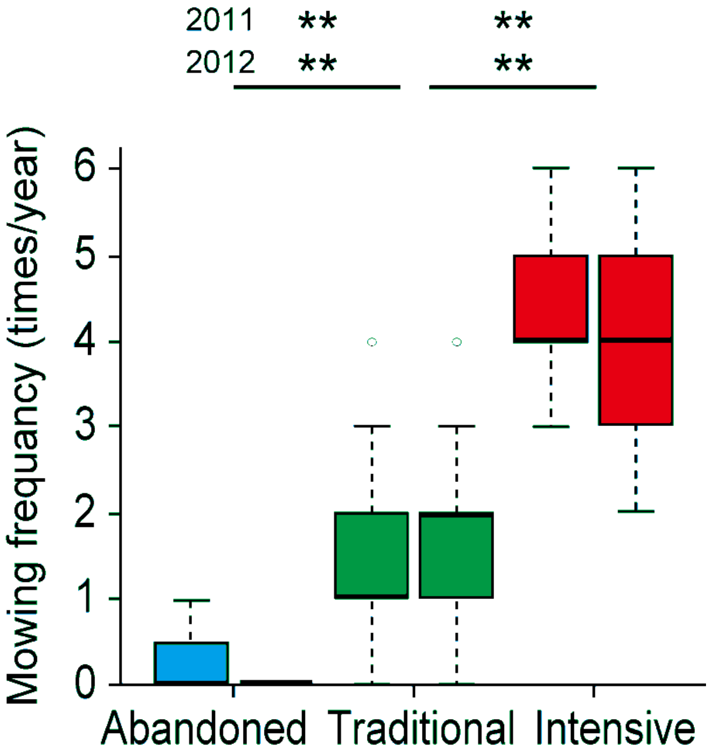
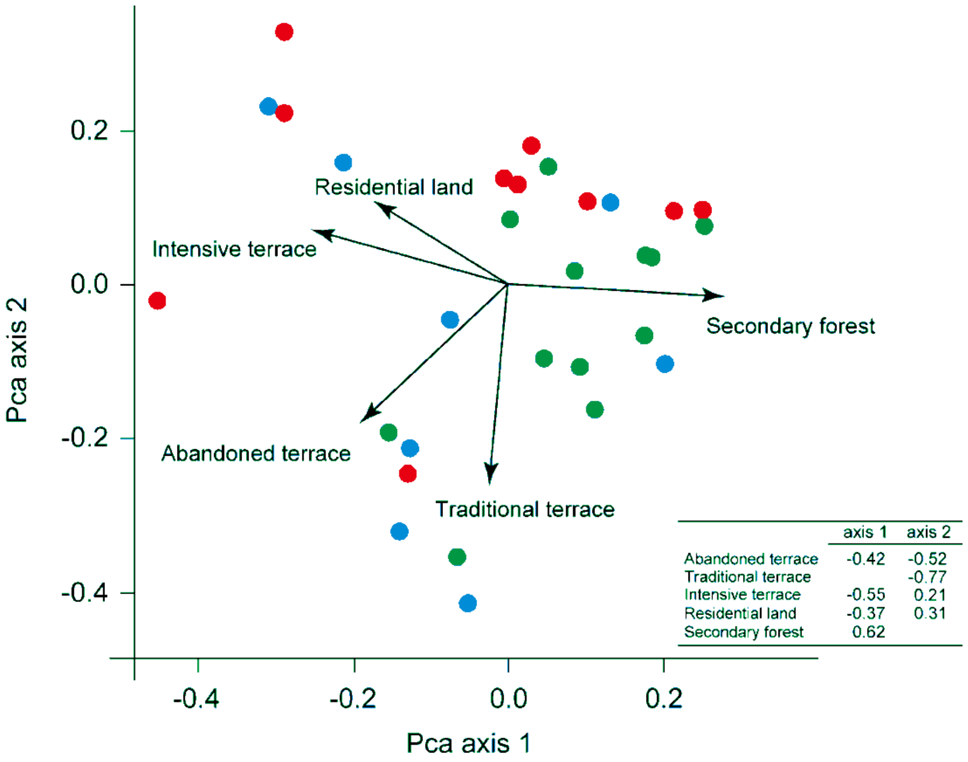


Fig. S3-1. Comparisons of mowing frequency among land-use types in 2011 and 2012 (left box, 2011; right box, 2012; blue, abandoned; green, traditional; red, intensive). $**P < 0.01$.



	axis 1	axis 2
Abandoned terrace	-0.42	-0.52
Traditional terrace		-0.77
Intensive terrace	-0.55	0.21
Residential land	-0.37	0.31
Secondary forest	0.62	

Fig. S3-2. Biplot showed the first two PCA axis of surrounding landscape variables (five environment types, intensive terrace area, traditional terrace area, abandoned terrace area, residential land area and secondary forest area) that explain 77.3% of the total variance (axis 1: 49.2%, axis 2: 28.1%). The PCA axis 1 increased with secondary forest area and decreased with areas of intensive and abandoned terrace and residential lands. Meanwhile the PCA axis 2 increased with areas of intensive terrace and residential lands and decreased with areas of traditional and abandoned terrace.

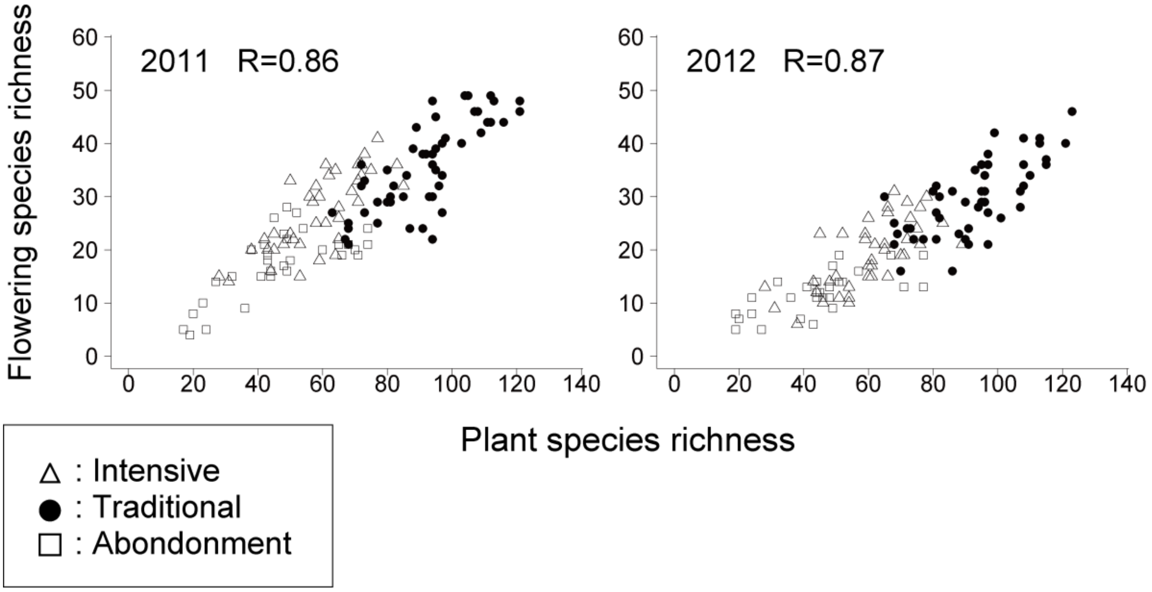


Fig. S3-3. Relationships between plant species richness and flowering species richness in 2011 and 2012. *Note*: $P < 0.01$ in 2011 and 2012.

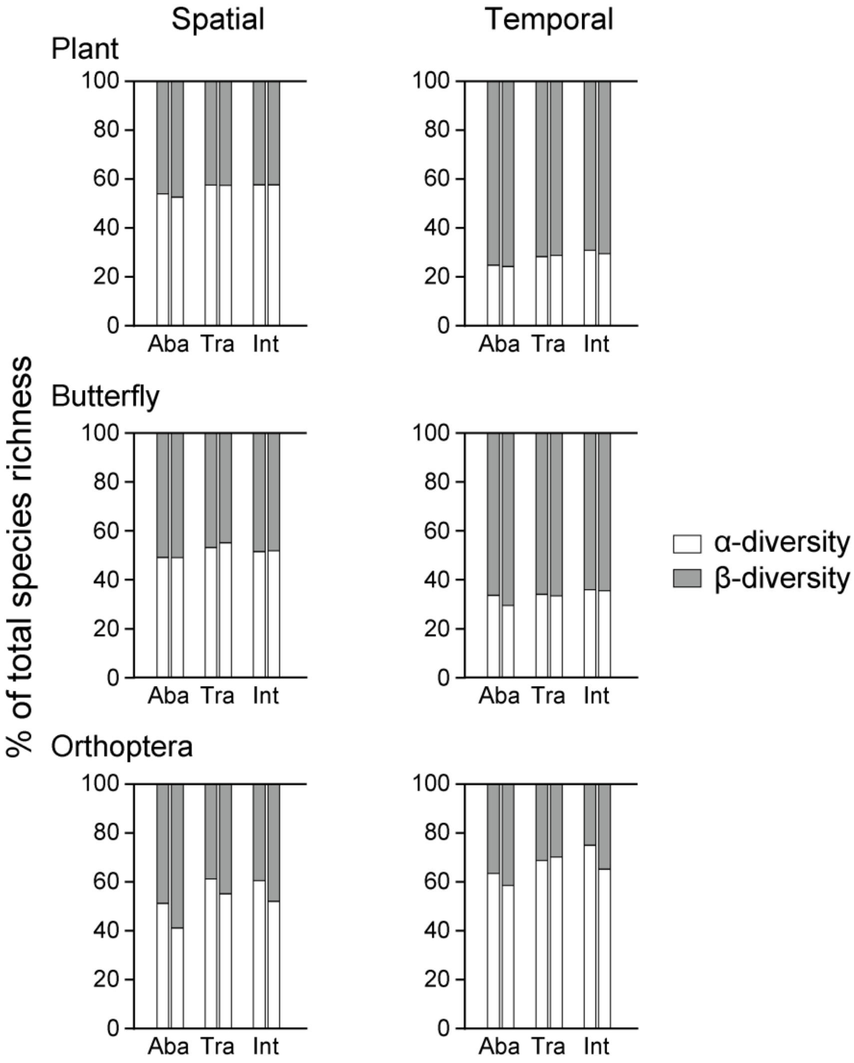


Fig. S3-4. Relative contributions in the percentage of the mean species richness per plot or season (α-diversity) and additive partitioning of species richness (β-diversity) to total species richness per terrace (γ-diversity) for plant and herbivorous insects in 2011 (left bar-plot) and 2012 (right bar-plot).

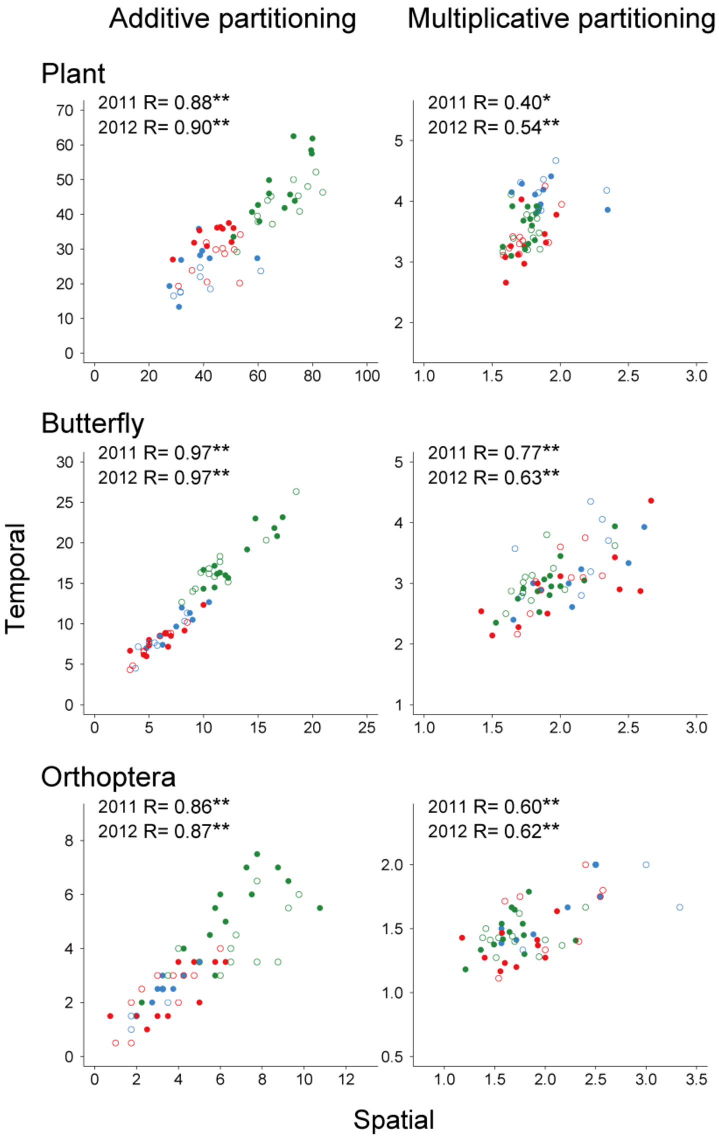


Fig. S3-5. Relationships between spatial and temporal of additive and multiplicative partitioning of species richness for plant and herbivorous insects in 2011 and 2012. *Note*: $**P < 0.01$, $*P < 0.05$.

Chapter 4.

Declines of inter-site beta diversity of regional scales due to land abandonment and intensification of agricultural lands

Introduction

As agricultural lands occupy approximately 40% of all terrestrial area (Ramankutty & Foley 1999), conservation of semi-natural ecosystems around agricultural fields is crucial for maintaining future biodiversity (Tilman *et al.* 2001; Forey *et al.* 2005). Despite the importance of biodiversity conservation, biodiversity losses due to land-use changes in agro-ecosystems have accelerated worldwide in recent decades (e.g., Krebs *et al*. 1999; Tilman *et al*. 2001; Benton, Vickery & Wilson 2003; Billeter *et al*. 2008). Although high plant and animal diversity in semi-natural ecosystems has been maintained by traditional management practices, such as low-intensity grazing and mowing (Tscharntke *et al*. 2005; Kleijn *et al*. 2011; Uchida & Ushimaru 2014), recent land abandonment and intensification have caused rapid declines in biodiversity through habitat loss, nitrogen input, and changes to the disturbance regime (Kruess & Tscharntke 2002; Öckinger & Smith 2007; Pöyry *et al*. 2009; Kleijn *et al*. 2011; Uematsu and Ushimaru 2013; Uchida & Ushimaru 2014). A few studies have demonstrated declines in among-plot and among-site diversity (β-diversity) consequent reductions in the local and regional species pool (γ-diversity) due to land-use changes in agricultural lands (Clough *et al.* 2007; Ekroos, Heliölä & Kuussaari 2010; Flohre *et al.* 2011; Karp *et al.* 2012). However, little is known about the underlying processes by which land abandonment and intensification have reduced the local and/or regional species pool (e.g., Abadie *et al*. 2011).

The process of local (and regional) species pool reduction due to land-use changes may be explained by one of two main hypotheses. First, the biotic homogenization hypothesis predicts few increasing species (winners) that can adapt to anthropogenically altered environments and many declining species (losers), leading to lower species richness and the homogenization of species composition among communities at both local and regional scales (Mackinly & Lockwood 1999; Olden & Rooney 2006; Tabarelli, Peres & Melo 2012). Second, the random loss hypothesis predicts species declines through the random loss of individuals, leading to local extinction of many rare species (Rajaniemi 2002; Stevens & Carson 2002; Suding *et al*. 2005; Uchida & Ushimaru 2014). According to this hypothesis, rare species are at greater risk of loss due to their smaller populations (Stevens & Carson 1999; Rajaniemi 2002; Suding *et al*. 2005). This hypothesis was first applied to plant species loss after anthropogenic N inputs, which intensify among-plant competition for light; however, further application to semi-natural biodiversity declines due to land-use changes has been limited (e.g., Stevens & Carson 1999; Rajaniemi 2002; Suding *et al*. 2005; Hautier *et al*. 2009). Although the random loss hypothesis also predicts species declines due to the local over-abundance of some species and lack of others, it does not always predict increased community similarity among agricultural lands experiencing similar land-use changes. This is because winners and losers will be randomly selected in different sites after land-use changes.

To test the above two hypotheses on biodiversity loss in agro-ecosystems, several indicators of β-diversity must be examined together, as the two hypotheses may predict different β-diversity patterns. Thus, whereas previous studies have often addressed biotic homogenization due to land use changes in agricultural lands using a given indicator of β-diversity (Gabriel *et al.* 2006; Smart *et al*. 2006; Vellend *et al*. 2007; Ekroos, Heliölä & Kuussaari 2010; Flohre *et al.*

2011), β-diversity indicators based on both species number and composition should be examined together.

In this study, I examined γ- and β-diversity declines in plant, butterfly, and orthopteran species caused by land abandonment and intensification at the local scale, and tested the above two hypotheses as explanations of local species pool decline. I compared the γ-diversity and three β-diversity measures (additive partitioning of species richness and Jaccard's and the Bray-Curtis dissimilarity indices) of plants, butterflies, and orthoptera in semi-natural grasslands within paddy terraces among three land-use types: abandoned, traditional, and intensive paddy terraces (see *Materials and Methods*: *Study area, paddy terraces, and plots*). I addressed the following specific questions. (1) Are γ- and additive partitioning of species richness significantly lower around abandoned and intensified paddy terraces than around those within traditional terraces? (2) Is community similarity significantly higher in land-use-changed terraces than in traditional terraces? (3) Are there common winners in abandoned and intensified paddy terraces? Based on the answers to these questions, I discuss the ability of the biotic homogenization and random loss hypotheses to explain local species pool declines in agricultural ecosystems.

Materials and Methods

Study area, paddy terraces and study plots

This study was conducted in 29 paddy terraces in southeastern Hyogo Prefecture, western Japan (ca. 19 × 30 km, 34°48’–57’ N, 135°03’–24’ E), which were examined in my previous study (Uchida & Ushimaru 2014). The mean annual temperature was 13.8°C, with a minimum monthly average of –2.4°C in January and a maximum monthly average of 31.6°C in August. The mean annual precipitation was 1,239.9 mm over the period 1981–2010. Meteorological data were recorded by a nearby automated meteorological data acquisition system (34°53.7’ N, 135°12.7’ E, 150 m alt.) by the Japan Meteorological Agency.

In the study area, semi-natural grasslands have been maintained on the levees of paddy fields and irrigation ponds and on the borders between paddy fields and secondary forests (dominated by *Pinus densiflora* and *Quercus serrata*) by periodic mowing (Uematsu *et al*. 2010). I consider mowing to be an agent of disturbance for plants and herbivores, and its frequency varied among study terraces depending on land-use type (Uchida & Ushimaru 2014). Semi-natural grasslands around paddy fields comprise approximately 30% of the total area of paddy terraces in Japan (Tabata 1997).

Paddy terraces were categorized into three land-use types (Uchida & Ushimaru 2014): abandoned terraces, where farmers had ceased rice cropping and mowing the semi-natural grasslands 3–15 (mean 9.75) years ago; traditional terraces, which are paddy terraces that have been managed traditionally for at least 100 years; and intensive terraces, characterized as land-consolidated paddy terraces that underwent land-consolidation 12–31 (mean 20) years ago. Paddy terrace abandonment initiates succession from semi-natural grassland to secondary forest and decreases grassland-specific plant diversity within a few years (Uematsu *et al*. 2010). In contrast, paddy consolidation, which converts small, irregular, and poorly drained paddy fields into large, quadrangular, well-drained fields to improve productivity and to allow mechanized farming (Uematsu *et al*. 2010; Matsumura & Takeda 2010), results in limited recovery of grassland plant species richness even after >20 years.

I studied seven abandoned, 12 traditional, and 10 intensive terraces (29 terraces in total) in 2011 and 2012. I established a four-plot transect (each 5 × 50 m, for a total of 5 × 200 m or 0.1 ha) in semi-natural grassland on each study terrace. The distance between each abandoned or intensive terrace and traditional terraces in the study varied from 0.10 to 25.55 km (mean 12.33 km) and from 0.11 to 33.57 km (mean 14.18 km) for abandoned and intensive terraces, respectively (Fig. S4-1). I interviewed all farmers, who indicated that they used little or no insecticide for paddy crops and did not apply insecticides to semi-natural grasslands. In most cases, the same farmer managed each individual terrace.

Anthropogenic disturbance

I recorded the number of mowing events in each terrace during my survey period to determine the disturbance frequency in 2011 and 2012. The mowing frequency in traditional plots was significantly higher and lower than that in abandoned and intensive plots, respectively (Fig. S4-2, Uchida & Ushimaru 2014).

Plant and herbivorous insect survey

For the plant survey, I established 24 plots of 0.5 × 0.5 m, each further divided into four 0.25 × 0.25-m subplots, along a belt plot in each study terrace (96 subplots per terrace). In all, I set 696 plots (2784 subplots). I recorded all vascular plant species in each subplot (0.25 × 0.25 m) in October 2011 and estimated the abundance of each plant species as the total number of subplots in which the species was found for each study terrace.

I conducted butterfly surveys approximately monthly (six times per year, from late April to mid-September). For each terrace on each study date, butterfly species and abundance (the number of individuals) in a belt plot (5 × 200 m) were recorded using the standardized transect count method (Pollard & Yates 1994; Uchida & Ushimaru 2014). The butterfly survey was conducted for 60 min per terrace under sunny and warm conditions. I included Hesperioidea (skippers) and Papilionoidea (butterflies) species in this study.

Orthoptera surveys were conducted twice (between mid-August and early October) per year for each belt plot in 2011 and 2012. Orthoptera species and abundance were surveyed using a sweep-net (42- cm- diameter) with 800 sweeps per belt plot. To minimize the effects of differences in vegetation height among the belt plots, I swept from the bottom to the top of the leaf layer (Uchida & Ushimaru 2014). After collecting orthopterans in the field, I identified them to species and counted them.

γ-diversity and additive partitioning of species richness

Based on the species data, I calculated γ-diversity (total species number) and additive partitioning of species richness (β_{add}-diversity) of plants, butterflies, and orthopterans for all possible terrace pairs of each land-use type (abandoned terrace: n = 21 pairs, traditional terrace: n = 66 pairs, intensive terrace: n = 45 pairs). The β_{add}-diversity was calculated as

$$\frac{1}{N}\sum_{i=1}^{N}(\gamma-\alpha_i),$$

where N is the number of plots (i.e., 2) and γ and α_i are the total number of species in the two terraces and in plot i, respectively.

Jaccard's and the Bray-Curtis dissimilarity indices

I also estimated β-diversity based on species composition using qualitative (Jaccard's dissimilarity index, JacI; Jaccard 1912, Koleff *et al.* 2003) and quantitative (Bray-Curtis dissimilarity index, BCI; Bray and Curtis 1957) dissimilarity indices of plant, butterfly, and orthopteran species for all terrace pairs of each land-use type.

To examine species composition dissimilarity among all study terraces, I also conducted an unconstrained metric multi-dimensional scaling (MDS) ordination based on JacI and BCI. The metric MDS can be based on any distance or dissimilarity measure, including ecologically meaningful measures such as JacI and BCI (Field *et al.* 1982, Minchin 1987). The method has been demonstrated as a particularly robust and useful unconstrained ordination procedure in ecology (Faith *et al.* 1987).

Statistical analyses

Differences in γ- and β-diversity indices between traditional and land-use changed terraces

I compared γ-diversity, additive partitioning of species richness, JacI, and BCI among traditional, abandoned, and intensive terraces, using a GLM (Gaussian error and identity link). I used geographic distance as a covariate (Fig. S4-1) because this parameter can affect the response variables such that the difference in species composition which will increase with distance between terraces. In the full GLM models, land-use types, geographic distance between terraces, and the interaction between these were used as the explanatory variables, and the respective diversity variable (γ-diversity, β_{add}-diversity, JacI, or BCI) was the response variable. To evaluate the significance of the effects of the explanatory variables, I conducted a randomization test (10,000 permutation runs). The significance levels of the partial regression coefficients of the explanatory variables were examined based on the 95 or 99% confidence intervals (CIs) of the estimated coefficients.

Rarefaction curves for γ-diversity

For each land-use type, I calculated species rarefaction curves by plotting the total species richness for a given number of terraces for plant, butterfly, and orthopteran species (Colwell, Mao & Chang 2004). This method provides a measure of the accumulation rate of different species as the sample size increases (Colwell, Mao & Chang 2004). The analysis incorporates the number of species and their identities, and the slope of each curve represents the increases in γ-diversity across all study scales.

Relationships between species and species loss, decline, and increase

To assess whether there were common winners in abandoned and intensified terraces, I conducted a null model analysis (Bell 2000, Hubbell 2001). I pooled all traditional terrace data from 2011 and 2012 and examined the rank-abundance relationships for plant, butterfly, and orthopteran species as an original (traditional) species pool. Then, I calculated the expected range (95%, from the lower 2.5% to upper 97.5%) of abundance for each plant, butterfly, and orthopteran species in the averaged traditional terrace, whose total abundance was calculated as the mean abundance of traditional terraces (Fig. 4-3). For the expected abundance calculations, I developed a null model assuming neutrality among individuals (Uchida & Ushimaru 2014). For example, in the butterfly model trial, 4446 (here I use the average number of butterfly individuals per traditional terrace) individuals were assigned to randomly selected species in proportion to the relative abundance of each species within all traditional terraces (Uchida & Ushimaru 2014). For the plant models, I used the sum of traditional subplots in which the respective species were found as total plant abundance. Based on model results, I divided species into two categories: those whose expected range of abundance did (rare species) and those whose expected range did not include zero (common species) in the averaged traditional terrace. I then counted the number of species in each category for all study terraces.

To examine whether there are common winners in land-use-changed terraces, I also examined whether the observed abundance of each species in each terrace was out of the expected range using the same null model approach and the observed total abundance for each study terrace.

All statistical analyses were performed in R (version 2.13.1; R Development Core Team).

Results

In total, 278 plant species (9, 360 cumulative subplots), 63 butterfly species (6,345 individuals), and 33 orthopteran species (5,894 individuals) were recorded during the study period.

Differences in γ- and β-diversity indices between traditional and land-use changed terraces

Traditional terrace pairs had the highest γ- and β_{add}-diversity among the three land-use types, except for orthopteran β_{add}-diversity (Fig. 4-1, Table S4-1). Plant JacI and BCI for abandoned and intensive terrace pairs were significantly higher than and did not differ from those for traditional terrace pairs, respectively (Fig. 4-1, Table S4-1). For butterfly species composition, JacI did not differ among land-use types, whereas the BCI was significantly higher for abandoned terrace pairs than for traditional terrace pairs (Fig. 4-1, Table S4-1). Orthoptera JacIs for abandoned and intensive terrace pairs were significantly higher than those for traditional terraces, whereas the BCI was significantly higher for abandoned terrace pairs than for traditional terrace pairs (Fig. 4-1, Table S4-1). Metric-MDS analyses showed that the species composition of plants, butterflies, and orthopterans in both abandoned and intensive terraces were clustered differently from those in traditional terraces (Fig. S4-3).

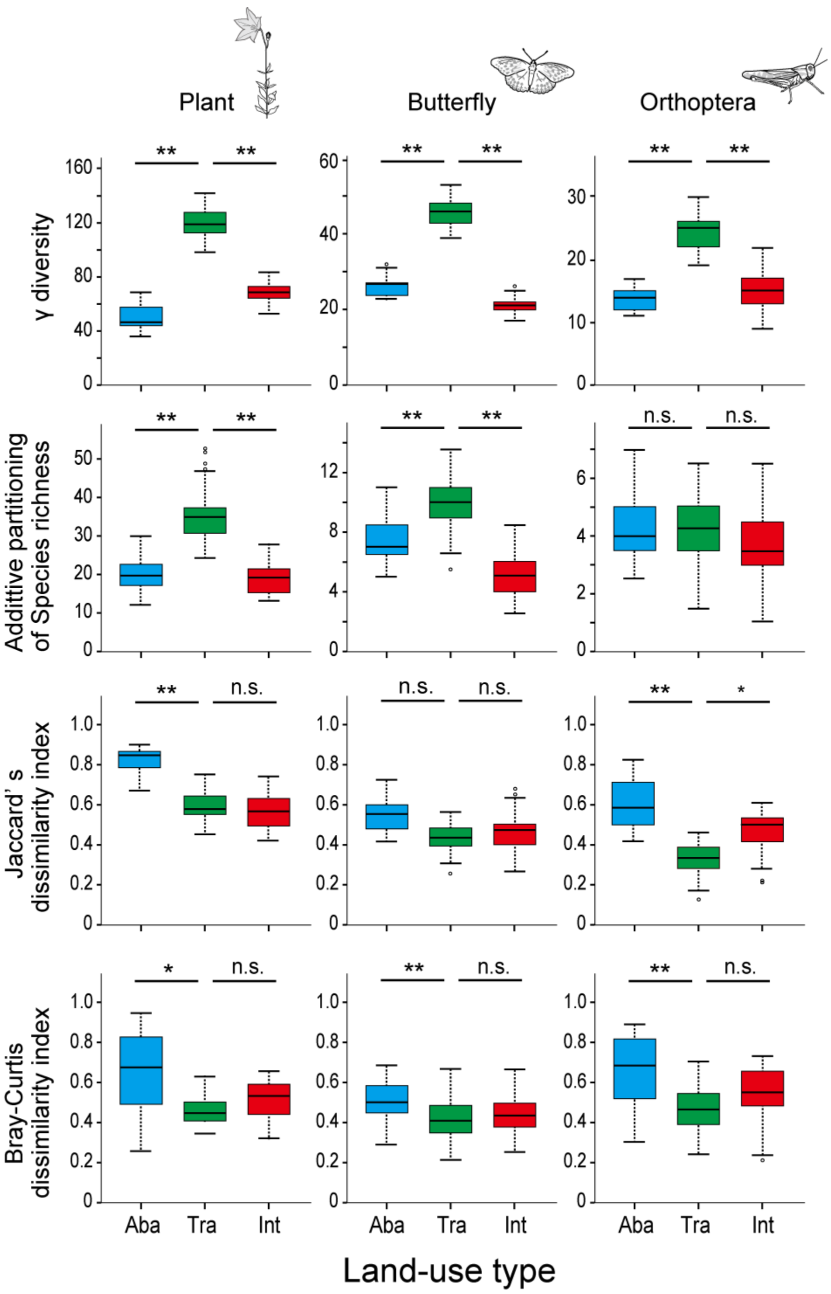


Fig 4-1. Comparisons of γ- and β-diversity and Jaccard's and the Bray-Curtis dissimilarity indices of plant, butterfly, and orthopteran species among abandoned, traditional, and intensive terraces. Box plots represent medians (bold black horizontal line) and first and third quartiles (box perimeters). ** = $P < 0.01$, * $P < 0.05$, n.s. not significant. See Table S4-1 for details.

Species rarefaction curves for γ-diversity

Rarefaction curves indicated that the *γ-diversity* of plant, butterfly, and orthopteran species in traditional terraces was consistently and significantly higher than those in abandoned and intensive terraces, irrespective of sample number (Fig. 4-2).

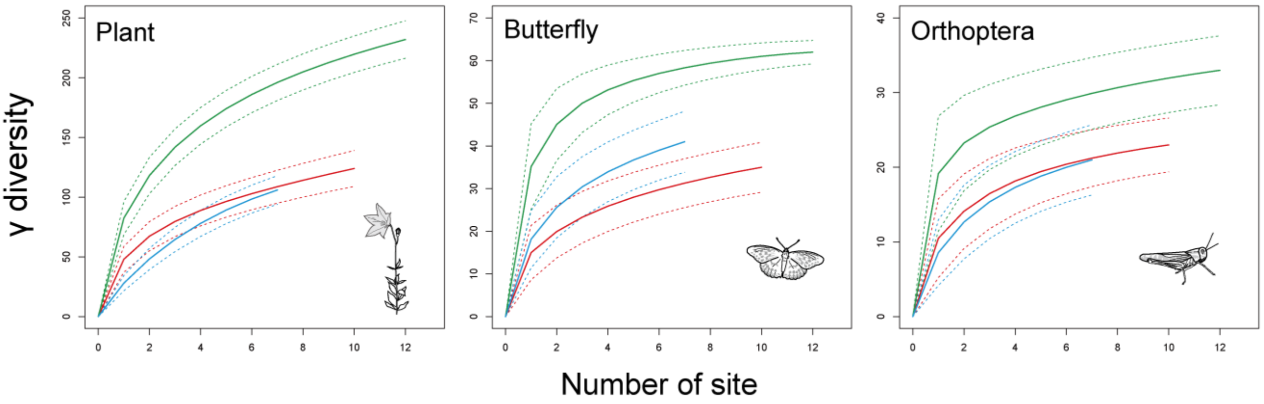


Fig 4-2. Species rarefaction curves for abandoned, traditional, and intensive terraces. Bold curves represent estimated species richness at sites, and dashed lines represent 95% confidence intervals for the estimated regression coefficient.

Relationships between species extirpation, decline, and increase in terraces with altered land-use

My null model analyses revealed that the expected range of abundance for plant species of rank ≤39, butterfly species of rank ≤16, and orthopteran species of rank ≤18 did not include zero in the averaged traditional terrace (Figs. 4-3–4-5). My results indicate that these species are potentially seen in any traditional terrace (common species), whereas others (rare species) cannot always be found. Both common and rare species richness in abandoned terraces were lower than those in traditional terraces, whereas only rare plant species richness in intensive terraces was lower than that in traditional terraces (Fig. 4-3). I also found some plant species absent from traditional terraces in both abandoned and intensive terraces (Fig. 4-3). The patterns for common and rare butterflies and orthopterans were very similar to those for plant species (Figs. 4-3–4-5).

Winners in abandoned and intensive terraces

For both plants and herbivores, winners and losers were not always consistent among traditional terraces (Figs. 4-3–4-5). Only plant species of rank 3 had significantly higher abundance than expected in >50% (i.e., >4) of abandoned terraces, whereas plant species of ranks 18, 74, 83, 148, 162, and 165 were all more numerous in >50% (i.e., >5) of intensive terraces (Fig. 4-3). In contrast, several herbivores were more numerous than expected in abandoned and intensive terraces (Figs. 4-3–4-5): butterflies of ranks 3 and 4 in abandoned terraces and those of ranks 1, 3, 6, 9, and 10 in intensive terraces, as well as orthopterans of rank 16 in abandoned terraces and of ranks 1 and 7 in intensive terraces.

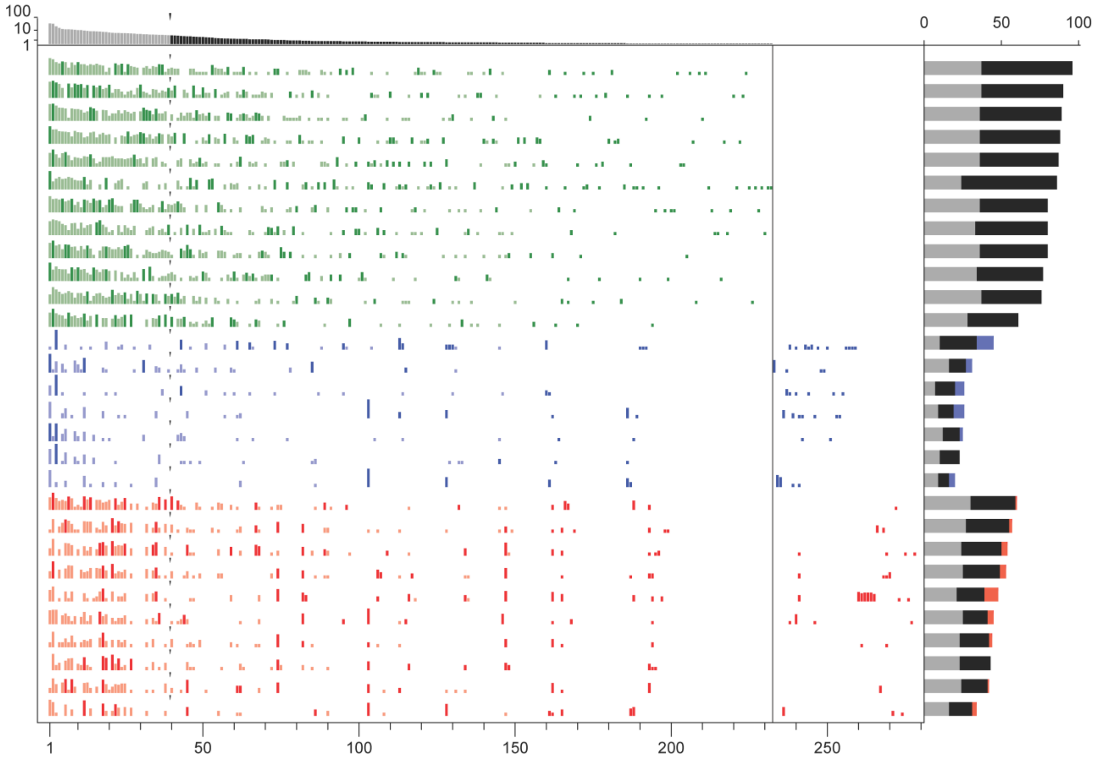


Fig. 4-3. The upper histogram represents the species rank for each species of individuals ($\log_{10}$) of mean number in traditional terraces from null model analysis (see *Materials and methods* for details). Species rank is given according to the order of abundance in traditional terraces. Gray bar plots show species whose expected range did not included zero, and black bar plots show species whose expected range included zero. The right histogram shows the richness of species whose expected ranges included (black) or did not include (gray) zero for all sites. The number of individuals of each plant species at each site ($\log_{10}$) are given for traditional (green), abandoned (blue), and intensive (red) terraces. Dark colors represent greater than expected abundance (upper 97.5% and lower 2.5%) calculated from the rank-abundance relationship of traditional terraces and the plant abundance for each land-use type (see *Statistical analyses* for details).

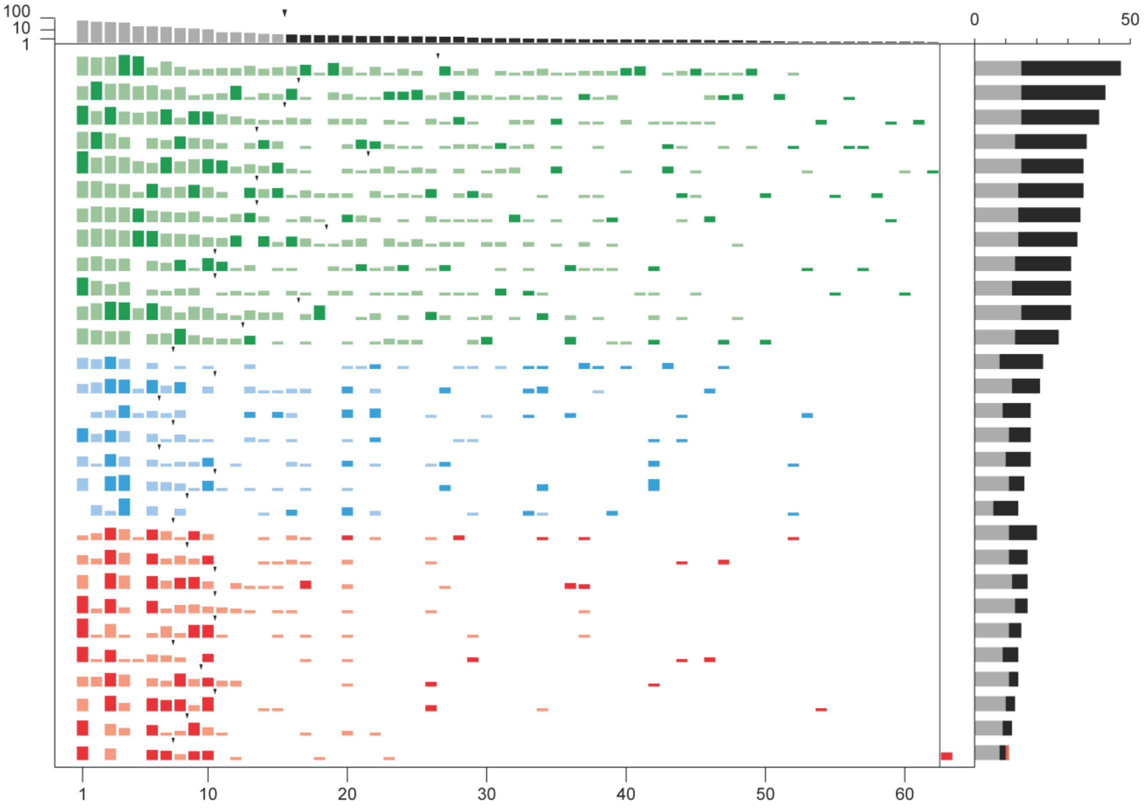


Fig. 4-4. The upper histogram represents the species rank for each species of individuals ($\log_{10}$) of mean number in traditional terraces from null model analysis (see *Materials and methods* for details). Species rank is given according to the order of abundance in traditional terraces. Gray bar plots show species whose expected range did not included zero, and black bar plots show species whose expected range included zero. The right histogram shows the richness of species whose expected ranges included (black) or did not include (gray) zero for all sites. The number of individuals of each butterflyt species at each site ($\log_{10}$) are given for traditional (green), abandoned (blue), and intensive (red) terraces. Dark colors represent greater than expected abundance (upper 97.5% and lower 2.5%) calculated from the rank-abundance relationship of traditional terraces and the plant abundance for each land-use type (see *Statistical analyses* for details).

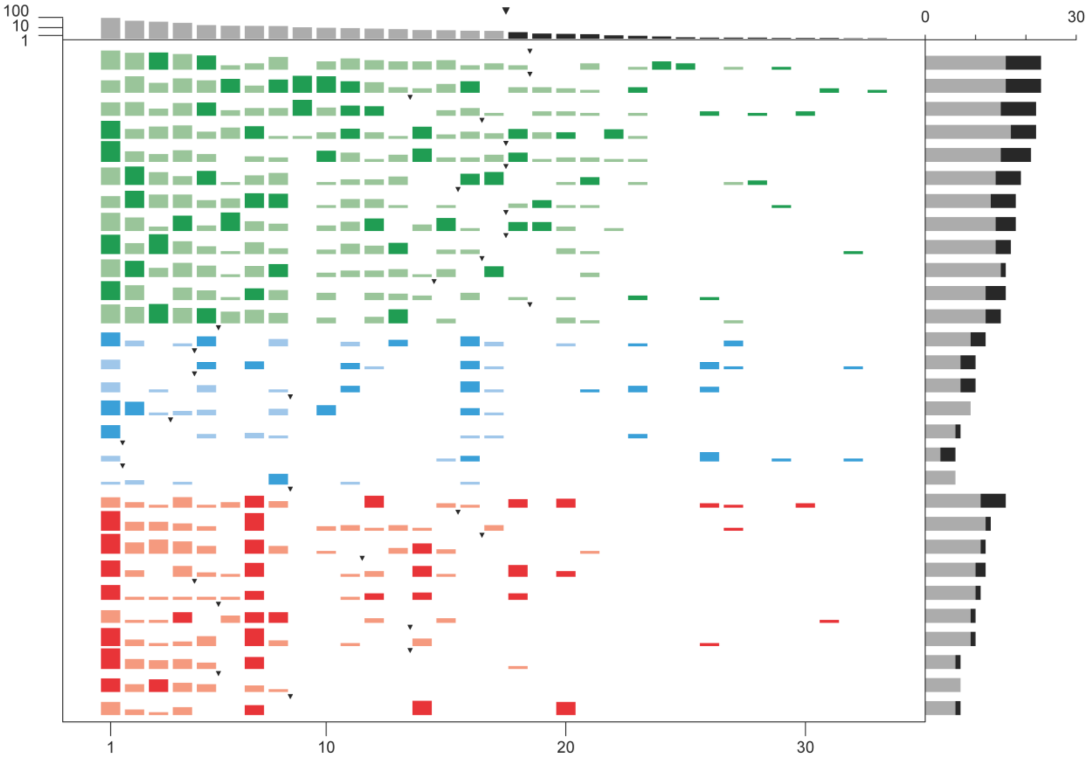


Fig. 4-5. The upper histogram represents the species rank for each species of individuals ($\log_{10}$) of mean number in traditional terraces from null model analysis (see *Materials and methods* for details). Species rank is given according to the order of abundance in traditional terraces. Gray bar plots show species whose expected range did not included zero, and black bar plots show species whose expected range included zero. The right histogram shows the richness of species whose expected ranges included (black) or did not include (gray) zero for all sites. The number of individuals of each orthopteran species at each site ($\log_{10}$) are given for traditional (green), abandoned (blue), and intensive (red) terraces. Dark colors represent greater than expected abundance (upper 97.5% and lower 2.5%) calculated from the rank-abundance relationship of traditional terraces and the plant abundance for each land-use type (see *Statistical analyses* for details).

Discussion

This study demonstrated that land-use changes, including both abandonment and intensification, have driven declines of plant and herbivorous insect γ- and β_{add}- diversity around paddy terraces at the local scale (Fig. 4-1), supporting both the biotic homogenization and random loss hypotheses. In contrast, I either found no differences in plant and herbivore JacI or BCI between traditional and intensified terraces or found that they were significantly higher for abandoned than for traditional terraces (Fig. 4-1).

Species composition of plants and herbivores varied more among abandoned terraces than among traditional or intensified terraces in MDS space (Fig. S4-3). This result did not support the biotic homogenization hypothesis, which predicts greater community similarity after land-use changes. The numbers of infrequently observed plant and butterfly species were much lower in abandoned and intensified terraces than in traditional terraces, whereas those of common plants and butterflies were similar between traditional and land-use-changed terraces (Figs. 4-3 and 4-4). Both rare and common orthopteran species decreased with land-use changes (Fig. 4-5). Additionally, I found very few plant and herbivore winner species in abandoned and intensified terraces (Figs. 4-3–4-5).

Together, these results indicate that decline in the local species pool occurred via the loss of infrequently observed species richness due to land-use changes (e.g., Benton, Vickery & Wilson 2003), lending support to the random loss hypothesis.

Process of species declines: the biotic homogenization and random loss hypotheses

Land-use intensification at the regional scale is a major driver of β-diversity decline in agricultural lands (Tylianakis, Klein & Tscharntke 2005; Gabriel *et al*. 2006; Ekroos, Heliölä & Kuussaari 2010; Flohre *et al.* 2011; Karp *et al*. 2011). My results also demonstrate declines in biological heterogeneity in terms of additive partitioning of species richness in my 19 × 30-km study area. Although many studies have suggested that declines in β-diversity (heterogeneity among sites) indicate species composition homogenization caused by a few winners in a given study area (Tylianakis, Klein & Tscharntke 2005; Gabriel *et al*. 2006; Smart *et al*. 2006; Ekroos, Heliölä & Kuussaari 2010; Flohre *et al.* 2011; Karp *et al*. 2011), my results showed no obvious increases in community similarity or common "winners" in abandoned and intensified terraces. Furthermore, most dominant species in abandoned or intensified terraces were also dominant in traditional terraces. This trend may be explained by the random loss hypothesis (Rajaniemi 2002; Stevens & Carson 2002; Suding *et al*. 2005; Uchida & Ushimaru 2014).

Previous studies have often discussed biotic homogenisation by comparing a single index, such as the additive partitioning of species richness or the dissimilarity index (Tylianakis, Klein & Tscharntke 2005; Gabriel *et al.* 2006; Smart *et al.* 2006; Ekroos, Heliölä & Kuussaari 2010; Flohre *et al.* 2011). My results suggest that to clarify how β-diversity declines occur in agricultural lands, I have to examine β-diversity indices based on both species number and composition together. Although β-diversity declines due to human impacts are often attributed to biotic homogenization, random loss of individuals can result in similar diversity patterns.

Conclusion

This study demonstrated that declines in the local species pool, at least in my study area, cannot be explained by biotic homogenization, but may be explained by the random loss of plants and herbivore species due to paddy field abandonment and intensification. Some 12.4% of the total area of Japan is under cultivation, and in 2005, about 10% of this area had been abandoned (Ministry of Agriculture, Forestry and Fisheries 2005), and approximately 75% of Japanese paddy fields had been already consolidated (Himiyama and Kikuchi 2007). My study demonstrates that the species pool in a given area is significantly diminished by both land abandonment and intensification. Spatial heterogeneity (β-diversity) at local scales would enhance overall diversity at regional scales (Tylianakis, Klein & Tscharntke 2005; Clough *et al.* 2007; Ekroos, Heliölä & Kuussaari 2010; Flohre *et al.* 2011; Karp *et al.* 2011). Thus, to maintain local γ-diversity, conservation of traditional terraces will be essential, although they remain only in limited areas throughout Japan. Conservationists and policy makers should give high conservation priority to these areas as land abandonment and intensification continue to increase.

Supporting information

Table S4-1. Estimated coefficients of explanatory parameters: land-use types (1: Traditional land-use was used as a baseline), distance, and the interaction of distance and land-use types for four diversity indices of the response variables (γ-diversity, additive partitioning of species richness, Jaccard’s and the Bray-Curtis dissimilarity indices). ** $P < 0.01$, * $P < 0.05$, n.s. not significant.

Responsible		plant		Butterfly		Orthoptera	
	explanatory	Estimated coefficient	*P*	Estimated coefficient	*P*	Estimated coefficient	*P*
γ-diversity							
	Land use type						
	Traditional [1]						
	Abandoned	-67.94	**	-20.31	**	-10.51	**
	Intensive	-53.62	**	-23.98	**	-8.90	**
	Distance (km)	-0.03	n.s.	0.12	n.s.	0.09	n.s.
	Distance (km) × Abandoned	-0.21	n.s.	0.13	n.s.	0.02	n.s.
	Distance (km) × Intensive	0.19	n.s.	-0.10	n.s.	-0.03	n.s.
	Intercept	119.57	**	44.51	**	23.14	**
Additive partitioning of species richness							
	Land use type						
	Traditional [1]						
	Abandoned	-13.21	**	-3.88	**	0.75	n.s.
	Intensive	-16.93	**	-4.90	**	-0.40	n.s.
	Distance (km)	0.08	n.s.	0.00	n.s.	0.06	**
	Distance (km) × Abandoned	0.13	n.s.	0.15	n.s.	-0.06	n.s.
	Distance (km) × Intensive	-0.10	n.s.	0.00	n.s.	-0.01	n.s.
	Intercept	34.67	**	9.95	**	3.36	*
Jaccard's							
	Land use type						
	Traditional [1]						
	Abandoned	0.25	**	0.06	n.s.	0.36	**
	Intensive	-0.04	n.s.	0.04	n.s.	0.11	*
	Distance (km)	0.00	n.s.	0.00	n.s.	0.00	n.s.
	Distance (km) × Abandoned	0.00	n.s.	0.01	n.s.	-0.01	n.s.
	Distance (km) × Intensive	0.00	n.s.	0.00	n.s.	0.00	n.s.
	Intercept	0.58	n.s.	0.45	n.s.	0.29	**
Bray-Cutis							
	Land use type						
	Traditional [1]						
	Abandoned	0.15	*	0.12	**	0.30	**
	Intensive	0.02	n.s.	-0.03	n.s.	0.11	n.s.
	Distance (km)	0.00	n.s.	0.00	n.s.	0.00	*
	Distance (km) × Abandoned	0.00	n.s.	0.00	n.s.	-0.01	n.s.
	Distance (km) × Intensive	0.00	n.s.	0.00	n.s.	0.00	n.s.
	Intercept	0.45	*	0.40	n.s.	0.41	**

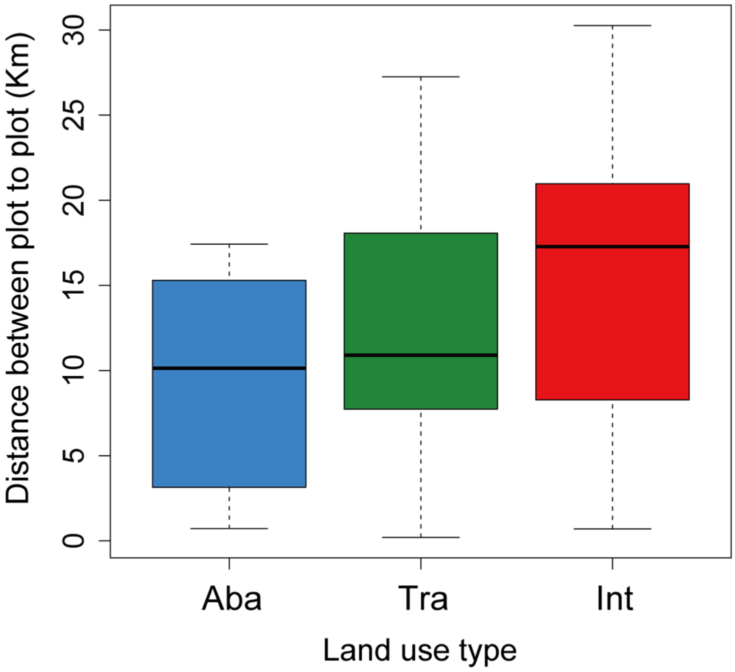


Fig. S4-1. Comparison of surrounding landscape variables (site slope angle; areas of abandoned, traditional, and intensive terraces; residential lands; and secondary forests within a 1-km radius of each terrace) among land-use types (blue = abandoned; green = traditional; red = intensive). Note: not statistically significant.

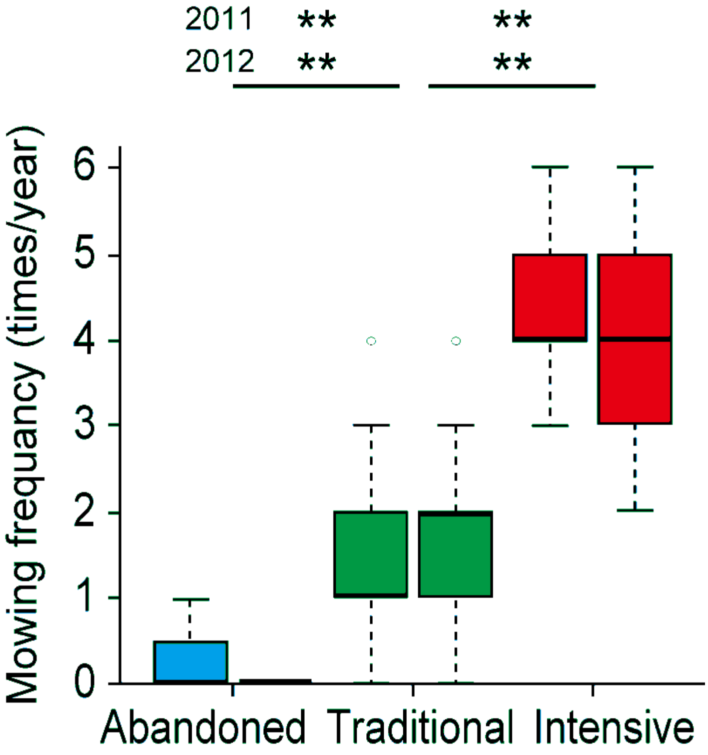


Fig. S4-2. Comparisons of mowing frequency among land-use types in 2011 and 2012 (left box, 2011; right box, 2012; blue, abandoned; green, traditional; red, intensive). **$P < 0.01$.

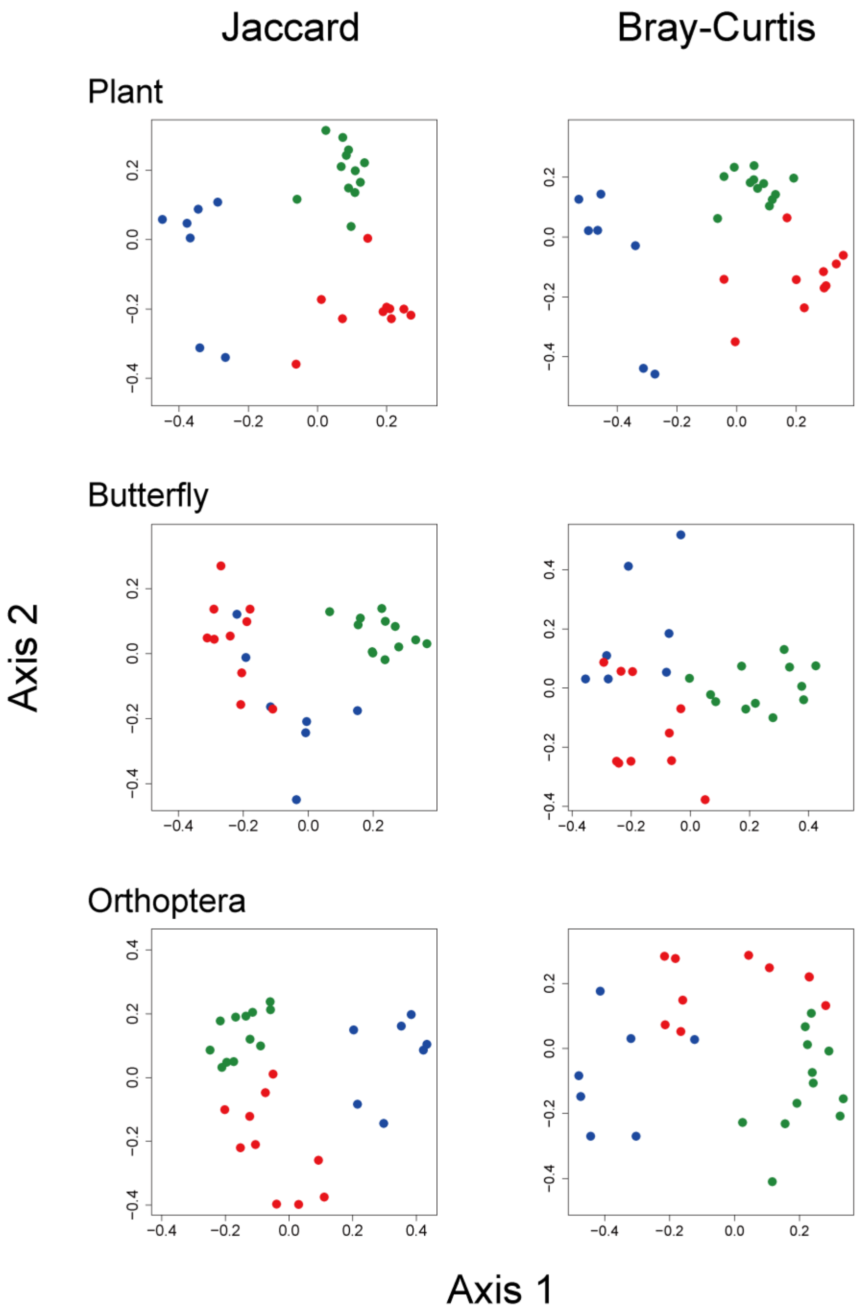


Fig. S4-3. Species composition in all terraces among three land use types (blue = abandoned; green = traditional; red = intensive) based on metric-MDS analysis.

Chapter 5.

General discussion

General discussion

This thesis provides a unified explanation for biodiversity declines due to the abandonment and intensification of agricultural lands, which have typically been studied separately. I demonstrate that declines in herbivorous insects (butterfly and orthopteran species) due to land-use changes can be explained by multiple factors, such as declining plant richness, changes in anthropogenic disturbance (mowing) frequency, and increases in land-use changes and human impacts in the landscapes surrounding my study terraces. Changes in the mowing regime directly resulted in declines in the richness of plant, butterfly, and orthopteran species at both plot and terrace scales, and had additional indirect effects via diminishing plant richness. The loss of surrounding secondary forests directly reduced plant and, subsequently, herbivore richness. These plot- and terrace-level declines in plant and herbivore diversity may have reduced local β- and γ-diversity (species pool diversity). I briefly summarize the main findings of each chapter below and discuss how biodiversity declines due to land abandonment and intensification based on my results. Finally, I propose some approaches for biodiversity conservation in semi-natural grasslands.

Summary of main results

In Chapter 2, I report on my examination of how plant and herbivorous insect diversity declines due to land-use changes. The α- diversity of plant had a unimodal patterns with disturbance regime (mowing frequency) and decreased with the loss of surrounding secondary forests, whereas herbivorous insects decreased with declining plant diversity and also displayed a unimodal relationship with mowing frequency. Thus, I showed that the intermediate disturbance hypothesis effectively explained biodiversity declines due to land abandonment and intensification in my study area. I also demonstrated that perennial plant richness played a key role in maintaining overall butterfly and orthopteran richness. Surrounding land-use changes had only minor negative effects on herbivore diversity, suggesting that many of the herbivores had a limited foraging range. Furthermore, my results suggest that the number of individuals of most herbivorous species decreased randomly after the loss of plant richness.

In Chapter 3, I discuss a comparison of spatial and temporal additive (β_{add}) and multiplicative (β_{w}) partitionings of plant, butterfly, and orthpteran species richness among land use types and their dependence on mowing frequency and surrounding landscape attributes. Land-use changes decreased between-plot diversity (β-diversity) at the within-terrace scale, as well as plot-scale (α-) diversity in agricultural landscapes. The spatial and temporal β_{add} for plant, butterfly, and orthopteran species were highest in traditionally managed terraces. By contrast, the spatial and temporal β_{w} of plants and orthopterans in abandoned and intensive terraces were, respectively, significantly higher than and equal to those in traditional terraces, whereas spatial and temporal butterfly β_{w} did not vary with land-use type. Mowing frequency changes had direct negative effects on plant β_{add} and indirectly affected butterfly and orthopteran β_{add} through diminished plant β_{add}, in both abandoned and intensified terraces.

Chapter 4 reports results from my test of the biotic homogenization and random loss hypotheses as explanations of local β-diversity decline due to land abandonment and intensification. I compared β-diversity indices (additive partitioning of species richness (β_{add}) and

Jaccard's and the Bray-Curtis dissimilarity indices) for terrace pairs among three land-use (abandoned, traditional, and intensified) types. I demonstrated that β_{add} for traditional terrace pairs was significantly higher than that for land-use-changed terrace pairs, whereas Jaccard's and the Bray-Curtis dissimilarity indices for traditional terrace pairs were significantly lower than or did not differ from those for abandoned and/or intensified terrace pairs. My results did not support the biotic homogenization hypothesis but generally support the random loss hypothesis.

Biodiversity declines due to land abandonment and intensification

I demonstrated that both reduction and increase in human activities around paddy terraces alter the disturbance regime and reduce surrounding secondary forests, which, in turn, had negative impacts on α- and β-diversity within paddy terraces for plant, butterfly, and orthopteran species. Furthermore, these biodiversity declines may result in local species pool reduction; this decline appears best explained by the random loss of plants and herbivores due to land-use change, not by biotic homogenization. To my knowledge, this is the first research to demonstrate that the intermediate disturbance hypothesis explains declines in biodiversity due to a combination of land-use abandonment and intensification and to propose that within-terrace and local β-diversity is better explained by the random loss hypothesis than by the biotic homogenization hypothesis. My results suggest that land-use changes have caused rapid declines in rare species, leading to spatial and/or temporal homogenization within terraces and across the study area. Thus, land-use changes significantly reduced the local species pool by diminishing both the α-diversity and the within-terrace and local β-diversity of plant and herbivores.

My results also suggest that enhancing the α- and *β*-diversity of plants (particularly perennial plants) by maintaining traditional mowing practices is essential for conserving herbivore α- and *β*-diversity in semi-natural grasslands around paddy terraces. As only a limited number of traditionally managed paddy fields remain as refuges for semi-natural grassland species, maintaining traditional practices in these fields should be a priority for biodiversity conservation.

Future extension of the study

1. I believe that declines in herbivore diversity can be explained by random loss, as land abandonment and intensification together resulted in the loss of rare species in my study area. My results also suggest that plant richness lost to land abandonment and intensification reduces carrying capacity, affecting most herbivore species equally and causing those with low abundance to be randomly lost (Suding *et al.* 2005). However, this idea must be further developed by examining the effects of other species traits (e.g., reproductive traits, pollination and dispersal systems in plants, and mobility and overwintering stage and habitat in herbivores) on biodiversity, beyond those addressed here.
2. I also believe that most species loss can be explained by the random loss hypothesis. However, some species declined more in abandoned and intensive than in traditional terraces (e.g., various butterflies (*Polytremis pellucid*, *Minois dryas*) and orthopterans (*Conocephalus gladiatus*, *Conocephalus japonicus*, *Gastrimargus marmoratus*)), and it is important to clarify why land-use changes had stronger impacts on these species.
3. I found significantly lower local-scale additive partitioning values for plants and herbivores in

abandoned and intensive terraces than in traditional terraces, whereas Jaccard's and the Bray Curtis dissimilarity indices showed different trends. To examine whether the random loss hypothesis can fully explain these patterns, I need to test both the random loss and biotic homogenization hypotheses using a null-model analysis that assumes neutrality among species.

4. Because I demonstrated strong richness declines in both plants and herbivores, the impacts on ecosystem functions and services should be examined in the future.

Conclusions and implications for conservation practices

Overall, my findings suggest that land abandonment and intensification drive plant, butterfly, and orthopteran species diversity declines at the plot, within-terrace, and local scales around paddy terraces. Declines in plant richness and changes in mowing frequency more strongly contributed to the loss of butterflies and orthoptera than did changes to the surrounding landscape. Additionally, my results suggest that conservation priority should be given to rare species that are at greater risk from land-use abandonment and intensification. By conserving these rare species, α-diversity and within-terrace and local β-diversity (γ-diversity) will be maintained.

Agricultural lands comprise approximately 40% of Earth's terrestrial surface (Tilman *et al.* 2001; Forey *et al.* 2005). My study demonstrates that land-use changes such as land abandonment and intensification diminish the species pool in a given area. Traditional management practices such as extensive mowing (one or two mowing events during the growing season) would enhance the α-diversity and spatial and temporal β-diversity of plants and herbivorous insects, but these management approaches have been abandoned due to agricultural intensification and the depopulation and aging of farmers in rural areas. Thus, more species may go extinct as the area of abandoned and consolidated agricultural land increases (Uematsu *et al.* 2010, Uematsu and Ushimaru 2013).

Surrounding land-use changes had a direct negative effect on plant richness and an indirect negative effect on herbivore diversity. Positive edge effects, defined as changes in the density of an organism (or other response variable) near the boundary between two habitat types (Fagan, Cantrell & Cosner 1999; Ries & Sisk 2004, Reeve and Cronin 2010), have been reported from many ecosystems. This highlights the importance of conserving or restoring the ecological connection between paddy fields and surrounding secondary forests to maintain or enhance plant and herbivore richness.

Because my results indicate that rare species are more susceptible to land-use changes, terraces in which rare species are still present deserve conservation priority. As the habitat of rare species (including many endangered species) can be recognized easily on maps (Uematsu *et al.* 2010, Uematsu and Ushimaru 2013), it will be important to identify the hotspots of as many rare species as possible and to maintain traditional mowing practices in these areas.

Finally, the effects of land-use changes on semi-natural biodiversity have rarely been investigated in monsoon Asia. To generalize my findings and further validate the random loss hypothesis as an explanation for biodiversity loss due to land-use changes, future studies should examine different paddy systems in other regions of monsoon Asia and different types of agricultural land worldwide.

Acknowledgements

I sincerely appreciate Prof. Atushi Ushimaru and Prof. Yoshiaki Takeda for their advising me on the doctoral dissertation. I am grateful to supervisors for Assosiate Prof. Yasuoki Takami, Assosiate Prof. Shinji Sugiura, Prof. Kuniyoshi Ebina and Prof. Taira Enomoto.

I sincerely appreciate James T. Cronin, Michael A. Huston and Joseph A. Veech for detailed comments that greatly improved the doctoral dissertation. I thank also Debra L. Wohl, Tatsuya Amano, and Akira S. Mori for their helpful comments and discussions on draft of the thesis. I wish to thank Yuko Nagata, Sogo Takahashi, Toshiki Izumisawa, Kumiko Michimoto, Shiori Maihara, Masayoshi K. Hiraiwa, Chihiro Fukada, Kotaro Nakamoto, Tomoya Shiotani and Wataru Maruyama for their assistance in field surveys, and Takuma Nagai, Hiroki Fujimoto, and Kouki Katsuhara for their assistance on the manuscript.

This research was partly supported by grants-in-aid for Kei Uchida (No. 13J03127) and Atushi Ushimaru (No. 23570024) from the Japan society for the promotion of science, grant of Kansai Organization for Nature Conservation, and grant from Kinki branch of Ecological Society of Japan.

Finally, I am profoundly grateful for Emi Uchida, Kai Uchida, Kazunobu Uchida, Mari Uchida, and Shu Uchida assistance to my daily life and to study in Kobe University.

References

Aarssen, W. L. (2000) Why are most selfers annuals? A new hypothesis for the fitness benefit of selfing. *Oikos* 89:606-612.

Abadie, Jean-Claude, Machon, N., Muratet, A. & Porcher, E. (2011) Landscape disturbance causes small-scale functional homogenization, but limited taxonomic homogenization, in plant communities. *Journal of Ecology*, 99, 1134-1142.

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B., Stegen, J. C. & Swenson, N. G. (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters*, 14, 19-28.

Andreasen, C., Stryhn, H. & Streibig, J. C. (1996) Decline of the flora in Danish arable fields. *Journal of Applied Ecology*, 33, 619-626.

Baker, H.G. (1974) The evolution of weeds. *Annual Review of Ecology and Systematics* 5:1-24.

Begon, M., Townsend, R.C. & Harper, L. J. (2006) *Ecology*: From individuals to ecosystems. John Wiley & Sons.

Bell, G. (2000) The distribution of abundance in neutral communities. *The American Naturalist* 155:606–617.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F. & Nyström, M. (2003) Reserves, resilience and dynamic landscapes. *AMBIO: A Journal of the Human Environment*, 32.6, 389-396.

Bennett, A. F., Radford, Q. J., & Haslem, A. (2006) Properties of land mosaics: implications for nature conservation in agricultural environments. *Biological Conservation*, 133.2, 250-264.

Benton, T. G., Bryant, D. M., Cole, L. & Crick, H. Q. (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology*, 39: 673-687.

Benton, T. G., Vickery, J. A. & Wilson, J. D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, 18, 182-188.

Bergman, K., Askling, J., Ekberg, O., Ignell, H., Wahlman, H. & Milberg, P. (2004) Landscape effects on butterfly assemblages in an agricultural region. *Ecography*, 27, 619-628.

Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekötter, T., Dietz, H., Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, P. J., Opdam, P., Roubalova, M., Schermann, A., Schermann, N., Schmidt,T., Schweiger, O., Smulders, J. M. M., Speelmans, M., Simova, P., Verboom, J., Van Wingerden, K. R. E. W., Zobel, M. & Edwards, J. P. (2008) Indicators for biodiversity in agricultural landscapes: a pan-European study. *Journal of Applied Ecology*, 45:141-150.

Bray, J. R., & Curtis, T. J. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecological monographs*, 27.4, 325-349.

Chiari, C., Dinetti, M., Licciardello, C., Licitra, G., & Pautasso, M. (2010) Urbanization and the more-individuals hypothesis. *Journal of Animal Ecology*, 79:366-371.

Clausen, H. D., Holbeck, H. B., & Reddersen, J. (2001) Factors influencing abundance of butterflies and burnet moths in the uncultivated habitats of an organic farm in Denmark. *Biological Conservation*, 98.2, 167-178.

Clough, Y., Holzschuh, A., Gabriel, D., Purtauf, T., Kleijn, D., Kruess, A., Steffan-Dewenter, I. & Tscharntke, T. (2007) Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. *Journal of Applied Ecology*, 44, 804-812.

Collinge, S. K. (2003) Effects of local habitat characteristics and landscape context on grassland butterfly diversity. *Conservation Biology*, 17, 178-187.

Collins, S.L., Glenn, S. M. & Briggs, J. M. (2002) Effect of local and regional processes on plant species richness in tallgrass prairie. *Oikos*, 99, 571-579.

Colwell, K. R., Mao, X. C. & Chang, J. (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, 85.10, 2717-2727.

Connell, J. H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, 199, 1302-1310.

Conrad, F. K., Warrenb, S. M., Foxb, R., Mark, S., Parsons, S. M., Woiwoda, P. I. (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, 132, 279–291.

Crist, T. O., Veech, J. A., Gering, J. C. & Summerville, K. S. (2003) Partitioning species diversity across landscapes and regions: a hierarchical analysis of α, β, and γ diversity. *American Naturalist*, 162, 734-743

Davies, K. F., Margules, R. C., & Lawrence, F. J. (2000) Which traits of species predict population declines in experimental forest fragments? *Ecology* 81: 1450-1461.

Di Giulio, M. D., Edwards, J. P., & Meister, E. (2001) Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *Journal of Applied Ecology* 38:310-319.

Donald, P. & Evans, A. D. (2006) Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *Journal of Applied Ecology*, 43: 209-218.

Duffy, J. E., Richardson, P. J. & Canuel, A. E. (2003) Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecology Letters* 6:637-645.

EIEla, S. A., EISayed, W. & K. Nakamura. (2010) Mandibular structure, gut contents analysis and feeding group of orthopteran species collected from different habitas of Satoyama area within Kanazawa City, Japan. *Journal of Threatened Taxa* 2:849-857.

Ekroos, J., Heliölä, J. & Kuussaari, M. (2010) Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *Journal of Applied Ecology* 47:459-467.

Fagan, F. W., Cantrell, S. R. & Cosner, C. (1999) How habitat edges change species interactions. *The American Naturalist*, 153.2, 165-182.

Faith, P. D., Minchin, R. P. & Belbin, L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, 69.1-3, 57-68.

Field, J. G., Clarke, K. R. & Warwick R. M. (1982) A practical strategy for analysing multispecies distribution patterns. *Marine ecology progress series*, 8.1, 35-52

Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R., Ceryngier, P., Clement, L.W., Dennis, C., Eggers, S., Emmerson, M., Geiger, F., Guerrero, I., Hawro, V., Inchausti, P., Liira, J., Morales, M. B., Oñate, J. J., Pärt, T., Weisser, W.W., Winqvist, C., Thies, C. & Tscharntke, T. (2011) Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids, and birds. *Ecological Applications*, 21, 1722-1781.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., Snyder, P. K. (2005) Global consequences of land use. *Science*, 309, 570-574.

Fukamachi, K., Oku, H., & Miyake, A. (2005) The relationships between the structure of paddy levees and the plant species diversity in cultural landscapes on the west side of Lake Biwa, Shiga, Japan. *Landscape and Ecological Engineering*, 1.2, 191-199.

Gabrier, D., Roschewitz, I., Tscarntke, T. & Thies, C. (2006) Beta diversity at different spatial scales: plant communities in organic and conventional agriculture. *Ecological Applications*, 16, 2011-2021.

Grime, J. P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, 242, 344–347.

Haddad, N. M., Tilman, D., Haarstad, J., Ritchie, M. & Knops, M. H. J. (2001) Constrasting effects of plant diversity and composition on insect communities: a field experiment. *The American Naturalist* 158:17-35

Haddad, N. M., Crutsinger, M. G., Gross, K., Haarstad, J., Knops, M. H. J. & Tilman, D. (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* 12:1029-1039

Hambäck, P. A., Summerville, S. K., Dewenter, S. I., Krauss, J., Englund, G. & Crist, T. O. (2007)

Habitat specialization, body size, and family identity explain lepidopteran density-area relationships in a cross-continental comparison. *Proceedings of the National Academy of Sciences of the United States of America* 104:8368-8373.

Hambäck, P. A., Bergman, K., Bommarco, R., Krauss, J., Kuussaari, M., Pöyry, J. & Öckinger, E. (2010) Allometric density responses in butterflies: the response to small and large patches by small and large species. *Ecography* 33:1149-1156.

Hautier, Y., Niklaus, A. P. & Hector, A. (2009) Competition for light causes plant biodiversity loss after eutrophication. *Science*, 324:636-638.

Hawkins, B. A. & Poter, E. E. (2003) Does herbivore diversity depend on plant diversity? The case of California butterflies. *The American Naturalist* 161:40-49.

Hill, M. O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology* 54: 427–432.

Himiyama, Y. & Kikuchi, Y. (2007) Agricultural field improvement projects in Japan since 1980. *Reports of the Taisetsuzan Institute of Science*, 41, 9-12. (Japanese)

Holland, J. D., Fahrig, L. & Cappuccino, N. (2005) Body size affects the spatial scale of habitat-beetle interactions. *Oikos* 110:101-108.

Horn, H.S. (1975) Markovian properties of forest succession. *Ecology and Evolution of Communities*, Belknap Press, Cambridge, Massachusetts.

Hubbell, S.P. (2001) The Unified Neutral Theory of Biodiversity and Biogeography. *Princeton University Press*, Princeton, NJ.

Huston, M. (1979) A general hypothesis of species diversity. *The American Naturalist* 113:81-101.

Huston, M.A. (1994) Biological diversity: the coexistence of species in changing landscapes. *Cambridge University Press*.

Huston, M. (1999) Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos*, 86,393-401.

Huston, M. A. & Wolverton, S. (2011) Regulation of animal size by eNPP, Bergmann's rule, and related phenomena. *Ecological Monographs* 81: 349-405.

Ichikawa, A., Kano, Y., Kawai, M., Tominago, O. & Murai, T. (2006) Orthoptera of the Japanese Archipelago in Color. *Hokkaido University Press*: Hokkaido, Japan.

Isley, F.B. (1944) Correlation between mandibular morphology and food specificity in grasshoppers. *Annals of Entomological society of America* 37: 47-67

IPSI 2014, http://satoyama-initiative.org/en/about/

Jaccard, P. (1912) The distribution of the flora in the alpine zone. *New Phytologist*, 11, 37–50.

Joern, A. (1979) Feedingpatterns in Grasshoppers (Orthoptera: Acrididae): factors influencing diet specialization. *Oecologia*, 38, 325-347.

Joern, A. (2005) Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. *Ecology*, 86, 861-873.

Johnson, J. B. & Omland, K. S. (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution*, 19, 101-108.

Karp, D.S., Rominger, A. J., Zook, J., Ranganathan, J., Ehrlich, P. R. & Daily, G. C. (2012) Intensive agriculture erodes β-diversity at large scales. *Ecology Letters*, 15, 963-970.

Kells, A. R. & Goulson, D. (2003) Preferred nesting sites of bumblebee queens (Hymenoptera:

Apidae) in agroecosystems in the UK. *Biological conservation*, 109.2, 165-174.

Kleijn, D., Kohler, F., Báldi, A., Batáry, P., Concepción, E. D., Clough, Y., Díaz, M., Gabriel, D., Holzschuh, A., Knop, E., Kovács, A., Marshall, E. J. P., Tscharntke, T. & Verhulst, J. (2009) On the relationship between farmland biodiversity and land-use intensity in Europe. *Proceedings of the Royal Society Biological Sciences*, 276, 903-909.

Kleijn, D., Rundlöf, M., Scheper, J., Smith, H. G. & Tscharntke, T. (2011) Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology and Evolution*, 26, 474-481.

Knop, E., Kleijn, D., Herzog, F. & Schmid, B. (2006) Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. *Journal of Applied Ecology*, 43, 120–127.

Koleff, P., Gaston, J. K. & Lennon, J. J. (2003) Measuring beta diversity for presence–absence data. *Journal of Animal Ecology*, 72.3, 367-382.

Koyanagi, F. T. & Furukawa, T. (2013) Nation-wide agrarian depopulation threatens semi-natural grassland species in Japan: Sub-national application of the Red List Index. *Biological Conservation*, 167, 1-8.

Krebs, J. R., Wilson, D. J., Bradbury, B. R. & Siriwardena, M. G. (1999) The second silent spring? *Nature*, 400:611-612.

Kricheva, J., Mulder, P. H. C., Schmid, B., Joshi, J. & Huss-Danell, K. (2000) Numerical responses of different triphic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia* 125:271-282.

Kruess, A & Tscharntke, T. (1994) Habitat fragmentation, species loss, and biological control.

Science, 264:1581-1584.

Kruess, A. & Tscharntke, T. (2002) Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conservation Biology*, 16, 1570-1580.

Kuussaari, M., Heliölä, J., Luoto, M. & Pöyry, J. (2007) Determinants of local species richness of diurnal Lepidoptera in boreal agricultural landscapes. *Agriculture, Ecosystems & Environment* 122: 366-376

Lande, R. (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*, 76, 5-13.

Matsumura, T. & Takeda, Y. (2010) Relationship between species richness and spatial and temporal distance from seed source in semi-natural grassland. *Applied Vegetation Science* 13:336-345.

McNeely, J. A., Gadgil, M., Leveque, C., Padoch, C. & Redford, K. (1995) Human influences on biodiversity. V. H. Heywood, R. T. Watson, Editors. *Global Biodiversity Assessment*. Cambridge University Press 711-821.

McKinney, L. M., & Lockwood, L. J. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in ecology & evolution*, 14.11, 450-453.

Minchin, R. P. (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Theory and models in vegetation science*, 8, 89-107.

Öckinger, E. & Smith, H. G. (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, 44, 50-59.

Ogura, J. (2006) The transition of grassland area in Japan. *J Kyoto Seika Univ*, 30, 160-172.

(Japanese)

Olden, D. J. & Rooney, P. T. (2006) On defining and quantifying biotic homogenization. *Global Ecology and Biogeography*, 15.2, 113-120.

Pautasso, M. & Chiarucci, A. (2008) A Test of the Scale-dependence of the Species Abundance–People Correlation for Veteran Trees in Italy. *Annals of botany* 101:70-715.

Pereira, H. M., Daily, G. C. (2006) Modeling Biodiversity Dynamics in countryside landscapes, *Ecology*, 87: 1877-1885.

Petermann, J. S., M*ü*ller, B. C., Weigelt, A., Weisser, W. W. & Schmid, B. (2010) Effect of plant species loss on arphid-parasitoid communities. *Journal of Animal Ecology* 79: 709-720.

Petterson, B. D. (1984) Correlation between mandibular morphology and specific diet of some desert grassland Acrididae (Orthoptera). *American Midland Naturalist* 111:296-303.

Pimentel, D., Stachow, U., Takacs, A. D., Brubaker, W. H., Dumas, R. A., Meaney, J. J., O'Neil, A. S. J., Onsi, E. D. & Corzilius, B. D. (1992) Conserving biological diversity in agricultural/forestry systems. *BioScience*, 42, 354-362.

Pimm, S. L., Gareth, J. R., John, L. G., & Thomas, M. B. (1995) The Future of Biodiversity. *Science*, 269, 347-350.

Pimm, S. L. & Raven, P. (2000) Biodiversity: Extinction by numbers. *Nature*, 403, 843-845.

Pollard, E., & Yates, T. J. (1994) Monitoring butterflies for ecology and conservation: the British butterfly monitoring scheme. *Chapman and Hall.*

Pöyry, J., Luoto, M., Paukkunen, J., Pykälä, J., Raatikainen, K. & Kuussaari, M. (2006) Different responses of plants and herbivore insects to a gradient of vegetation height: an indicator of the vertebrate grazing intensity and successional age. *Oikos*, 115, 401-412.

Pöyry, J., Paukkunen, J., Heliölä, J. & Kuussaari, M. (2009) Relative contributions of local and regional factors to species richness and total density of butterflies and moths in semi-natural grasslands. *Oecologia*, 160, 577-587.

Pykälä, J. (2000) Mitigating human effects on European biodiversity through traditional animal husbandry. *Conservation Biology*, 14, 705–712.

Pykälä, J. (2005) Cattle grazing increases plant species richness of most species trait groups in mesic semi-natural grasslands. *Plant Ecology* 175:217-226.

Rajaniemi, K. T. (2002) Why does fertilization reduce plant species diversity? Testing three competition based hypotheses. *Journal of Ecology*, 90.2, 316-324.

Ramankutty, N. & Foley, A. J. (1999) Estimating historical changes in global land cover: Croplands from 1700 to 1992. *Global biogeochemical cycles*, 13, 997-1027.

Reeve, D. J., & Cronin, J. T. (2010) Edge behaviour in a minute parasitic wasp. *Journal of Animal Ecology*, 79.2, 483-490.

Ries, L., & Sisk, D. T. (2004) A predictive model of edge effects. *Ecology*, 85.11, 2917-2926.

Robinson, R. A., Sutherland, W. J. (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, 39, 157–176.

Rodriguez-Estrella, R. (2007) Land use changes affect distributional patterns of desert birds in the Baja California peninsula, Mexico. *Diversity and Distributions* 13:877-889.

Sala, O.E., Stuart, C.F., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N. L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, 287, 1770-1774.

Secretariat of the Conservation on Biological diversity 2010, *http://www.cbd.int/abs/*

Shirouzu, T. (2006) The butterflies of Japan in color. *Gakken Holdings*. (in Japanese)

Siemann, E., Tilman, D., Haarstad, J. & Ritchie, M. (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. *The American Naturalist*, 152:738-750.

Simpson, E. H. (1949) Measurement of species diversity. *Nature*, 163: 688.

Smart, M. S., Thompson, K., Marrs, H. R., Le Duc, G. M., Maskell, C. L. & Firbank G. L. (2006) Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, 273.1601, 2659-2665.

Sotherton, N. W. & Self, M. (2000) Changes in plant and arthropod biodiversity on lowland farmland: an overview. *Ecology and conservation of lowland farmland birds*, 26-35.

Srivastava, D. S. & Lawton, H. J. (1998) Why more productive sites have more species: An experimental test of theory using tree-hole communities. *American Naturalist*, 152:510-529.

Stevens, M.H.H. & Carson, P. W. (1999) Plant density determines species richness along an experimental fertility gradient. *Ecology*, 80, 455–465.

Stevens, M. H. H. & Carson, P. W. (2002) Resource quantity, not resource heterogeneity, maintains plant diversity. *Ecology Letters* 5:420-426.

Suding, K. N., Collins, L. S., Gough, L., Clark, C., Cleland, E. E., Gross, L. K., Milchnas, G. D. & Pennings ,S. (2005) Functional- and abundance- based mechanisms explain diversity loss due to N fertilization. *Proceeding of the National Academy of Sciences of the United States of*

America 102:4387-4392

Svensson, B., Lagerlöf, J., & Svensson, G. B. (2000) Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agriculture, ecosystems & environment*, 77, 247-255.

Tabarelli, M., Peres, A. C. & Melo, P. L. F. (2012) The 'few winners and many losers' paradigm revisited: Emerging prospects for tropical forest biodiversity. *Biological Conservation*, 155, 136-140.

Tabata, H. (1997) Satoyama and its conservation. *Hoikusya Publishing*. (Japanese)

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W. H., Simberloff, D. & Swackhamer, D. (2001) Forecasting agriculturally driven global environmental change. *Science*, 292, 281-284.

Thomas, D. C., Cameron, A., Green, E. R., Bakkenes, M., Beaumont, J. L., Collingham, C. Y., Erasmus, F. N. B., Ferreira de Siqueira, M., Grainger, A., Lee, H., Hughes, L., Huntley, B., Van Jaarsveld, S. A., Midgley, F. G., Miles, L., Ortega-Huerta, A. M., Peterson, T, A., Phillips, L. O. & Williams, E. S. (2004) Extinction risk from climate change. *Nature*, 427, 145-148.

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecology Letters*, 8, 857-874.

Tylianakis, J.M., Klein, A.M. & Tscharntke, T. (2005) Spatiotemporal variation in the diversity of hymenoptera across a tropical habitat gradient. *Ecology*, 86, 3296-3302.

Uchida, K. & Ushimaru, A. (2014) Biodiversity declines due to abandonment and intensification of agricultural lands: patterns and mechanisms. *Ecological Monographs*, http://dx.doi.org/10.1890/13-2170.1

Uematsu, Y., Koga, T., Mitsuhashi, H. & Ushimaru, A. (2010) Abandonment and intensified use of agricultural land decrease habitats of rare herbs in semi-natural grasslands. *Agriculture, Ecosystems and Environment*, 135, 304-309.

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

Veech, J. A., Summerville, K. S., Crist, T. O. & Gering, J. C. (2002) The additive partitioning of species diversity: recent revival of an old idea. *Oikos*, 99, 3-9.

Veech, J. A. & Crist, K. S. (2010) Toward a unified view of diversity partitioning. *Ecology*, 91, 1988-1992.

Vellend, M., Verheyen, K., Flinn, M. K., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., Graae, J. B., Bellemare, J., Honnay, O., Brunet, J., Wulf, M., Gerhard, F. & Hermy, M. (2007) Homogenization of forest plant communities and weakening of species–environment relationships via agricultural land use. *Journal of Ecology*, 95.3, 565-573.

Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D. B., Telfer, M. G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S. G., Greatorex-Davies, J. N., Moss, D. &Thomas, C. D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, 414: 65-69.

Wettstein, W. & Schmid, B. (1999) Conservation of arthropod diversity in montane wetlands:

effect of altitude, habitat quality and habitat fragmentation on butteries and grasshoppers. *Journal of Applied Ecology* 36:363-373.

Whittaker, R. H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30, 279-338.

Whittaker, R.H. (1975) Communities and Ecosystems, 2nd ed. Macmillan, London.

Wootton, J. T. (1998) Effects of disturbance on species diversity: a multitrophic perspective. *The Amrican Naturalist* 152:803-825.

Yee, D. A. & Juliano, A. S. (2007) Abundance matters: a field experiment testing the more individuals hypothesis for richness-productivity relationships. *Oecologia* 153:153-162.

Yoshioka, A., Kadoya, T., Suda, S. & Washitani. I. (2010) Invasion of weeping lovegrass reduces native food and habitat resource of Eusphingonotus japonics (Saussure). *Biological Invasions*, 12, 2789-2796.

Young, T. P., Petersen, D. A. & Clary, J. J. (2005) The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecology Letters*, 8.6, 662-673.