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Urbanization promotes the loss of seasonal dynamics in the semi-natural grasslands of an East Asian megacity

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Abstract

The biodiversity of agricultural landscapes has been noticeably affected by rapid urbanization. Although many studies have examined species diversity per unit area (alpha diversity), knowledge about the patterns of species turnover (beta diversity) in urban areas remains limited. Furthermore, most beta diversity studies have focused on spatial heterogeneity; however, losses of temporal heterogeneity resulting from urbanization remain limited. In this study, we examined how urbanization is associated with decreases in the seasonal heterogeneity of species composition, which could be used as an indicator of the loss of seasonality by ecologists and policy makers aiming to conserve biodiversity. We investigated (1) changes in species richness based on seasonal averages (alpha diversity) and (2) the seasonal turnover of species composition (beta diversity) for flowering plants and butterflies along a rural-urban gradient in semi-natural grasslands. The response variables were alpha and beta diversity for flowering plants and butterflies, and the explanatory variables were urban areas within a 1-km radius of the center of each site. Increasing urban area caused both the seasonal alpha and beta diversity of flowering plants and butterflies to decline. These results supported the homogenization hypothesis for the seasonality of plants and butterflies in semi-natural grasslands surrounding dominant urban areas in East Asia. Future studies should focus on investigating how urbanization is causing both declines in seasonality and changes in the spatial heterogeneity of species composition and associated biodiversity loss. Ecologists and policy makers should focus on developing strategies to halt the loss of temporal biological heterogeneity to maintain biodiversity.

Keywords: additive partitioning; agricultural lands; beta diversity; land-use change; species turnover

Introduction

Land-use change reduces biodiversity in agricultural ecosystems globally (Sala et al., 2000; Tilman et al., 2001; Foley et al., 2005). In recent decades, rapid urbanization has been one of the main factors causing changes to biodiversity in agro-ecosystems (e.g., Blair & Johnson, 2008; McKinney, 2008; Ushimaru, Kobayashi, & Dohzono, 2014). Biodiversity loss is partly the result of reduced spatial and temporal heterogeneity in species composition (e.g., McKinney, 2006; Smart et al., 2006; Tylianakis, Klein, & Tscharntke, 2005; Uchida & Ushimaru, 2015). Biotic homogenization is a rapidly growing ecological issue worldwide, which is caused by the combined effects of specialist and native species extinctions with invasions of generalist and non-native species that are better able to adapt to anthropogenic changes in environmental conditions (e.g., Olden, 2006; McKinney, 2006; Knop, 2016).

Most studies on biotic homogenization in urban areas have focused on spatial heterogeneity (McKinney, 2006; Smart et al., 2006; Knop, 2016); however, changes in the temporal heterogeneity of species composition due to urbanization are being overlooked (but see, La Sorte, Tingley, & Hurlbert, 2014). Seasonal turnover in species composition shows how species share the same habitat at different times of the year (Olesen et al., 2008; La Sorte, Tingley, & Hurlbert, 2014; Uchida & Ushimaru, 2015), and could be used as an indicator of biodiversity for deciding where to implement conservation actions. Studies on biotic homogenization have confirmed that seasonal heterogeneity in species composition, which is regulated by seasonal changes of weather conditions, is fundamental for maintaining biodiversity (Benton, Vickery, & Wilson, 2003; Tylianakis, Klein, & Tscharntke, 2005; Dalby et al., 2014). Seasonal turnover in species composition is high in rainforest ecosystems, leading to greater biodiversity over the course of a year, despite anthropogenic disturbances, which reduce temporal heterogeneity (Tylianakis, Klein,

& Tscharntke, 2005). Increased anthropogenic disturbance due to land-use changes might cause the number of some species to increase, particularly seasonal generalist species. On the other hand, disturbances might cause the reproductive success of seasonal specialist species to decline due to their life history traits (e.g., Soga & Koike, 2012; Huston & Wolverton, 2012; Nakahama et al., 2016).

Globally, 54% of the human population resided in urban areas in 2014, with this percentage being expected to increase to 66% by 2050 (United Nations, 2014). Megacities (total population > 10 million people) are expected to have a negative effect on biodiversity, and are primarily located in Asia (United Nations, 2014). Urbanization studies are common in Europe and North America, but remain limited in Monsoon Asia, where extensive areas of semi-natural ecosystems (i.e., agricultural lands and secondary forests) have been replaced by urban areas due to rapid economic growth during the second half of the 20th century (Liu, Zhan, & Deng, 2005; Saizen, Mizuno, & Kobayashi, 2006; Tsuji et al., 2011). Traditionally, extensively managed agro-ecosystems have facilitated the persistence of high biodiversity in East Asia (Ishitani, Kotze, & Niemelä, 2003; Uematsu et al., 2010; Tsuji et al., 2011; Uchida & Ushimaru, 2014); however, urbanization may have caused species pools to diminish due to increased anthropogenic impacts (Olden & Rooney, 2006; Qian et al., 2006; Tsuji et al., 2011; Ramírez-Restrepo & MacGregor-Fors, 2017). Therefore, a better understanding of how urbanization impacts semi-natural ecosystems surrounding megacities in East Asia is required.

Here, we focus on investigating the average seasonal species richness and temporal turnover of species composition over the course of a year. Most previous studies have indicated that high anthropogenic impact causes biological heterogeneity to decline (e.g., Vellend et al., 2007; Ekroos, Heliölä, & Kuussaari, 2010; Uchida & Ushimaru, 2015). Furthermore, the spatial and temporal heterogeneity of species composition may not necessarily be correlated. Plant and insect species generally depend on the spatial heterogeneity of environmental factors (e.g., soil nutrients or climatic factors); however, some species do not necessarily exhibit seasonal specialization. Thus, we hypothesized that the loss of seasonal specialists and a prevalence of seasonal generalists cause the temporal turnover of species composition to decline with increasing urbanization. The temperate climatic zone, including Japan, exhibits clear seasonality, which contributes to a high temporal turnover in species composition. Therefore, it is important to assess whether both high alpha and high beta diversity result in high gamma diversity over the course of a year. Temporal dissimilarities in flowering plant composition were used to examine phenological variation in flowering activity, which approach is possible because the richness of flowering species is significantly correlated with total plant species richness (including species that do and do not flower) in this study region (Uchida & Ushimaru, 2015).

In this study, we tested changes in biodiversity along an urban-rural gradient, including changes from extensive to intensive management practices in semi-natural grasslands. We examined the average seasonal species richness (alpha diversity) and two components of the temporal turnover of species composition (beta diversity) to investigate whether biotic homogenization occurs in semi-natural ecosystems surrounding paddy fields along the urban-rural gradient of the Osaka-Kobe megacity, Japan. In this study area, urbanization has caused the cover of paddy fields to decrease more rapidly than that of forested areas over the last century (see Appendix A: Fig. 1, Table 1). We tested the effect of urbanization on the temporal alpha and beta diversity of plants and butterflies to determine whether: (1) urbanization causes both alpha diversity loss and within-year seasonal biotic homogenization (declines in β-diversity); (2) gamma diversity (representing biodiversity over the course of a year) depends on both alpha and beta diversity; and (3) the prevalence of seasonal generalists and/or the loss of seasonal specialists results in biotic homogenization.

Materials and methods

Study area and plots

The study was conducted in the Osaka-Kobe megacity, western Japan (~30 × 40 km^2, 34°43′–57′ N, 135°03′–25′ E). The urban areas (residential, commercial, and industrial) were delineated in ArcGIS Spatial Analyst 9.3 (ESRI, Redlands, CA, USA) using land-use maps from 1896 to 1914 (“Kasei-Chikeizu” from the Imperial Japanese Army, Meiji era) and using high-resolution aerial photographs from the Geospatial Information Authority of Japan and Google Maps in 2012. In the Osaka-Kobe megacity area, paddy fields and secondary forests have decreased due to urbanization since the 1980s. Approximately 100 years ago, the study area was composed of 7.2% urban area, 20.4% agricultural land, and 61.9% forest. In contrast, by 2012, the study area was composed of 26.4% urban area, 14.1% agricultural land, and 52.3% forest (see Appendix A: Fig. 1 and Table 1). From ca.1910 to 2012, paddy fields significantly decreased by 31%, whereas urban areas significantly increased by 368% (see Appendix A: Fig. 1 and Table 1). In the study area, semi-natural grasslands were maintained on the levees of paddy fields and irrigation ponds, and at the edges of paddy fields and secondary forests (dominated by *Pinus densiflora* and *Quercus serrata*), by periodic mowing (Uchida & Ushimaru, 2014). Although the map from ca. 1910 was used to illustrate the process of urbanization over the last century and to calculate changes in urban areas, information from this map was not included in the subsequent analyses.

We selected 60 plots located on semi-natural grasslands across 20 paddy sites (three 3 × 20 m plots per site) along the rural-urban gradient based on the prepared geographic maps (Fig. 1). The rural-urban gradient was based on the extent of urban area surrounding each site, and is shown in Fig.1. We then calculated the extent of the urban area within 500-m and 1-km radii of the center of each site for the statistical analyses (see Appendix A: Fig. 2). We identified a significant correlation between the urban areas within the 500-m and the 1-km radii ($R^2 = 0.92$, $p < 0.01$; R^2 value was calculated by Pearson's correlation and p value was tested by generalized linear model (GLM) with the Wald test); thus, we used the 1-km radius model in this study. The 20 sites were separated from one another by varying distances (Fig. 1), with a minimum distance of 1.2 km to avoid pseudoreplication. The three plots in each site were selected depending on area of continuous unfragmented habitat. Correlations between the distances of the three plots at each site and the urban gradient were not significant ($p > 0.1$; GLM with the Wald test). In addition, analysis of the landscape within a 1-km radius allowed us to compare our results with those of previous studies, which also examined the alpha diversity of grassland butterflies in similarly sized areas (Collinge, Prudic, & Oliver, 2003), including our previous reports on the alpha and beta diversity of semi-natural grasslands around paddy fields (Uchida & Ushimaru, 2014, 2015).

Relationships between environmental factors and urbanization

We calculated area of continuous unfragmented habitat including surveyed site within a 1-km radius and environmental factors (i.e., disturbance frequency and soil water content) to examine which environmental factors were correlated with the urban-rural gradient. To determine the disturbance frequency in 2014, we recorded the number of mowing events and herbicide applications in each plot during the agricultural season (April to October). We found that herbicides were applied once a year to semi-natural grasslands at only two of the 60 plots. Interviews with farmers at the study sites indicated that insecticides were not used in semi-natural grasslands but were used a few times a year on crops at all sites. In most cases, the same farmer managed the semi-natural grasslands at each paddy site. We examined water content to represent soil environmental variables in the 60 plots. We collected three soil core (5 cm diameter, 5 cm depth) samples from three locations in each plot in mid-September. First, we mixed the three fresh soil samples from each plot into a single sample and weighed the sample. Then, the soil samples from all 60 plots were oven-dried at 70 °C for 72 h, weighed again and sieved (< 2 mm). We then calculated the soil water content using the fresh and dry weights of each soil sample (Nagata & Ushimaru, 2016). The disturbance frequency increased with increasing urban area within the 1-km radius of the center of each site (see Appendix A: Fig. 3, $R^2 = 0.14$, $P < 0.05$, according to Pearson's correlation and GLM with Wald test). Correlations between environmental factors (focal habitat area and soil water content) and urban area within the 1-km radius of the center of each site were not significant (see Appendix A: Fig. 3, $P > 0.1$, GLM with the Wald test). Although we detected a significant correlation between disturbance frequency and urbanization, previous studies implied that many unexpected variables (e.g., climatic fluctuation due to urbanization) could negatively affect biodiversity. Therefore, we used the urban gradient as an indicator of anthropogenic activity, including disturbance frequency, in this study.

Plant and butterfly data

Plant and butterfly diversity in each plot were surveyed four times across 2014 (late April, early June, mid-July, and mid-September). The four survey periods reflected different climatic conditions in the study area (see Appendix A: Table 2). These periods also corresponded to the peak flowering and butterfly flight in the study area (Uchida & Ushimaru, 2014). During each survey, the richness of all flowering plant species and richness and abundance of butterfly species in each plot were recorded (three 3 × 20 m plots in each site). We recorded names of flowering plant species and counted number of flowering individuals of each species in each plot (entire 3 × 20 m plot area). Butterflies were observed for 15 min per plot (45 min per site) under sunny and warm condition. All butterflies were counted within the plots, and some of them were caught using a sweep-net to be identified and released, if necessary (Pollard & Yates, 1994; Uchida & Ushimaru, 2014). We spent the enough time (15 min per plot) to survey the butterfly species and to avoid double counting for preventing effect of survey methods on the diversity metrics.

Based on the data collected from the surveys, lists of flowering plant and butterfly species were prepared for each plot in each of the four time-periods (late April, early June, mid-July, and mid-September 2014). In total, we identified 295 flowering plant species, and 43 butterfly species (875 individuals).

We distinguished the seasonality of flowering plant and butterfly species by separating them into three groups based on classifications in field guides (see Appendix B; Hayashi, 1989; Satake et al., 1999; Shirouzu, 2006; Japan Butterfly Conservation Society, 2012): short flowering period/short flight period (i.e., the species is found in a particular season (one or two months) over the course of a year), intermediate flowering period/ intermediate flight period (i.e., found in two seasons (three or four months) over the course of a year), and long flowering period/ long flight period (i.e., found any time (more than five months) over the course of a year).

In addition, we classified plants and butterflies with different life-history traits based on their response to the rural-urban gradient. Plant species were divided into two groups: annual and perennial plants. Butterfly species were divided based on their life history traits, i.e., uni- and multi-voltinism (see Appendix B). Because not all species respond equally to land-use changes in semi-natural grasslands, it is essential to address the different responses of species and/or ecological trait groups to understand the mechanisms that drive species loss (Pykälä, 2005; Uchida

& Ushimaru, 2014; Knop, 2016).

Statistical analyses

Calculations of alpha diversity and two components of beta diversity

The alpha diversity of plants and butterflies was calculated as average species richness per each survey in each site. Next, we calculated two different beta diversity indices in each site to examine changes in species composition due to urbanization. Additive partitioning of species richness (β_{add}) is frequently examined in biotic homogenization studies, even though low values of this index indicate both low species turnover and low gamma diversity (Lande, 1996; Veech et al., 2002; Veech & Crist, 2010). The turnover components of Jaccard dissimilarity (β_{tu}) utilize species composition to assess whether changes in beta diversity are caused by a loss of species replacement (Baselga, 2012).

The β_{add} was calculated for each site as follows (Lande, 1996; Veech et al., 2002):

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

where N is the number of the survey period (i.e., four) for flowering plants and butterflies, α_i is the number of species for survey i, and γ is the total number of species for each site. High temporal β_{add} values indicate large temporal variation in species occurrence and increased variation in community composition (Uchida & Ushimaru, 2015).

The β_{tu} was calculated for each site as follows (Baselga, 2012):

$$\beta_{\text{tu}} = \frac{2\left[\sum_{i<j}\min(b_{ij}, b_{ji})\right]}{\left[\sum_{i} S_i - S_T\right] + 2\left[\sum_{i<j}\min(b_{ij}, b_{ji})\right]},$$

where S_i is the total number of species in survey i, S_T is the total number of species in each site, and b_{ij} and b_{ji} are the number of species found exclusively in surveys i and j, respectively. High β_{tu} values indicate high temporal species replacement structure in species composition among each survey period (Baselga, 2012). Temporal heterogeneity of flowering plants and flying butterflies between each survey period was calculated by the value of two beta diversity (β_{add} and β_{tu}). These metrics were used to examine phenological variation in flowering plants and flying butterflies activity.

Changes in alpha diversity and the two components of beta diversity

A generalized linear mixed model (GLMM) was used to identify differences in alpha diversity and the two components of beta diversity in plant and butterfly communities at each site along the rural-urban gradient. The response variables were alpha-, β_{add}-, and β_{tu}- diversity in plants (Gaussian error and identity link) and butterflies (Gaussian error and identity link). The explanatory variable was the extent of urban area within a 1-km radius at each site. We identified whether sites occurred in coastal or valley areas (Fig. 1), and used this designation as a random term, because the study sites were spread over a broad geographic range; therefore, we nested variation in site location to analyze the GLMM. Note, we could not examine the relationships between the species traits of butterflies and the rural-urban gradient, because there was insufficient statistical power, due to the low richness and abundance in semi-natural grasslands surrounding major urban areas. We then tested whether the alpha and two beta diversity indices result in gamma diversity (i.e., total diversity over the course of a year). In the GLMM, the response variable was gamma diversity (Poisson error and log link) in each site, whereas the explanatory variables were alpha-, β_{add}-, and β_{tu}- diversity in each site. The significance of the estimated partial regression coefficients of the explanatory variables was determined using the Wald-test and R^2

values (Nakagawa & Schielzeth, 2013).

Relationships between variation in the seasonality of species richness and the rural-urban gradient

The GLMM was used to examine the proportion of seasonal types (short, intermediate, and long) to total plant and butterfly species richness in each plot (Binomial error and logit link) and the extent of urban gradient. The response variable was the proportion of seasonal types (short, intermediate, and long) to total plant and butterfly species richness in each plot. The explanatory variable was the extent of urban area within a 1-km radius at each plot. To avoid pseudoreplication, the site identity (i.e., three plots in each site) was used as a random term. We identified whether sites occurred in coastal or valley areas (Fig. 1), and used this designation as a random term, because the study sites were spread over a broad geographic range; therefore, we nested variation in site location to analyze the GLMM. The significance of the estimated partial regression coefficients of the explanatory variables was determined using the Wald-test and R^2 values (Nakagawa & Schielzeth, 2013). In addition, we examined the relationships between seasonal type and species life history traits for all species (plant: annual and perennial; butterfly: voltinism) using Fisher's exact test.

All statistical analyses were performed using the software R for Statistical Computing (version 3.3.2; R Development Core Team). We used the following packages for statistical analyses: *betaper* to calculate beta diversity, *lme4* to use the GLMM, and *r2glmm* to calculate the R^2 values of the GLM and GLMM.

Results

Alpha, two components of beta, and gamma diversity

The alpha and beta diversity of flowering plants and butterflies (average species richness per each survey, β_{add}, and β_{tu}) decreased with increasing extent of urban area (Fig. 2; see Appendix A: Table 3). The diversity of alpha and β_{add} for plant and butterfly species were strongly positively correlated with total diversity over the course of a year (i.e., gamma diversity), and butterfly β_{tu} was positively correlated with gamma diversity (Table 1).

Relationships between the proportion of seasonal type of plants and butterflies and the rural-urban gradient

Short-flowering plant species significantly decreased with increasing extent of urban area (Fig. 3A, see Appendix A: Table 4), whereas long-flowering species significantly increased with increasing extent of urban area (Fig. 3C, see Appendix A: Table 4). For butterfly species, short and intermediate flight period species significantly and marginally significantly decreased with increasing urban area, respectively (Fig. 3D, see Appendix A: Table 4), whereas long flight period species significantly increased with increasing extent of urban area (Fig. 3F, see Appendix A: Table 4). Annual species had significantly longer flowering period than perennial species (see Appendix A: Fig. 4), and uni-voltine butterfly species had significantly shorter flight period than multi-voltine species (see Appendix A: Fig. 4).

Discussion

Biodiversity loss in the megacity

The present study supported the hypothesis that losses of average species richness per each survey and seasonal turnover of species composition are caused by increasing anthropogenic activities via urbanization. Many studies have shown that total and native species diversity decreases with increasing habitat fragmentation and human population density (e.g., Clark, Reed, & Chew, 2007; Fischer & Lindenmayer, 2007; Ramalho et al., 2014; Schmiedel, Bergmeier, & Culmsee, 2015). In contrast, some studies have reported that biodiversity in urban ecosystems is sometimes similar to, or even higher than, that documented in rural ecosystems (Magura, Lovei, & Tothmeresz, 2010; Turrini & Knop, 2016). Discrepancies among studies could be explained by three factors. First, higher biodiversity in urban areas, compared to rural ones, could be explained by resource complementarity. For example, resources for pollinators (nectar producing flowers or larval host plants) are often abundant in urbanized environments, such as amenity plants along roadside verges and private gardens (Salisbury et al., 2015). Second, other urban studies might underestimate the effect of urban extent on biodiversity. For example, although grassland quality strongly influences butterfly richness and abundance, the extent of urban development (5–30%) surrounding grasslands is not related to species richness (Collinge, Prudic, & Oliver, 2003). And the relationship between human population presence and species richness (vertebrate and plant) may be explained by scale dependence (Pautasso, 2007). Fine scale studies (sample unit is smaller than ca. 1 km) tend to show that biodiversity is negatively collated with human presence. In the present study, we focused on a wide range of urban area extent (1–91%) and found that the loss of species diversity in semi-natural grasslands surrounded by major urban areas varied according to urban extent. Future studies should investigate the gradient of urban extent/human populations and consider scale dependence surrounding study sites. Finally, some rural ecosystems are highly degraded. For example, cities in Switzerland have greater or similar insect diversity than the surrounding rural areas (Turini & Knop, 2016), which may be prevalent in agricultural landscapes subject to intensive farming management (e. g., use of pesticides, disturbance from farm machinery, or clear-cuts after harvesting). The present study supported the explanation that arthropod diversity in more extensively managed agricultural areas, rather than in intensively managed landscapes, exceeded that of urban diversity (Turini & Knop, 2016). We focused on the Osaka-Kobe megacity, which was the world's seventh largest urban agglomeration in 2014 (United Nations, 2014). Our study suggests that semi-natural grasslands in the urban-dominated landscapes have low average richness in a given season, as well as low temporal species turnover, due to high anthropogenic effects on biodiversity at the local scale.

Although we detected a significant correlation between disturbance frequency and urbanization, previous studies indicated that the examined environmental factors might not be enough to explain decreases in species diversity. The urban area includes many unexpected variables (e.g., climatic fluctuation) that could negatively affect biodiversity. Although high diversity is exhibited in unique environments, such as nutrient-poor areas (Kleijn et al., 2009; Uematsu & Ushimaru, 2013) and heterogeneous landscapes (Tscharntke et al., 2005; Uchida & Ushimaru, 2015), all such species are negatively affected by anthropogenic activities. Further studies are required to determine the mechanisms of biodiversity loss using other potential variables of anthropogenic activities, especially when elucidating the relationship between biodiversity and urbanization.

Decreases in the temporal turnover of species composition in a megacity

The results of this study indicated that the decline in the seasonal heterogeneity of species composition (from April to September) in the megacity was caused by an increase in the seasonal generalists of both flowering plant and butterfly species. In contrast, the number of seasonal specialists of flowering plant and butterfly species (i.e., species with short flowering/flight period) decreased along the rural-urban gradient (Fig. 3). We showed that most values of beta diversity were significantly correlated with total diversity over the course of a year (i.e., gamma diversity). Recently, conceptual and empirical studies emphasized that beta diversity was not necessarily correlated gamma diversity (Olden, 2006; Naaf &Wulf, 2010; Uchida & Ushimaru, 2015). These studies suggested that community similarity between sites often increased with the increasing species richness of each site (Naaf & Wulf, 2010). In other words, even if low beta diversity of between season was observed in the given region, high alpha diversity resulted in high gamma diversity. Our results indicated that both high alpha and high beta diversity of each survey season contributes total diversity over the course of a year. To our knowledge, this study is the first to demonstrate that the temporal heterogeneity of species composition is essential for the conservation of biodiversity across two-trophic levels in the urban environment.

The present study supported the hypothesis that anthropogenic activities causes beta diversity loss (e.g., Vellend et al., 2007; Ekroos, Heliölä, & Kuussaari, 2010; Uchida & Ushimaru, 2015). A previous study on spatial heterogeneity suggested that a higher species turnover in rural areas than in urban areas was driven by specialist species rather than generalist species (Knop, 2016). Urbanization leads to the local extinctions of infrequent and specialist butterfly species, including temporal specialists (Clark, Reed, & Chew, 2007; Soga & Koike, 2012; Ramírez-Restrepo & MacGregor-Fors, 2017). We suggest that seasonal generalist species with short generation times favor urbanized environmental conditions (e.g., plants, Albrecht & Haider, 2013; butterflies, Takami et al., 2004). According to the r/K species concept (Pianka, 1970), species with rapid regeneration times tolerate a high frequency or magnitude of disturbance. Declines in the temporal heterogeneity of flowering plant species along the rural-urban gradient may have been caused by increases in both the richness and abundance of annuals (e.g., *Rorippa indica*; *Stellaria uliginosa* *var. undulata*), which have long and overlapping flowering periods through the course of a year, in parallel to decreases in perennials (e.g., *Allium thunbergii*; *Taraxacum japonicum*; *Hemerocallis fulva var. kwanso*; *Iris ensata var. spontanea*) that have clear phenological patterns. In addition, we showed that the decrease in the temporal heterogeneity of butterflies was caused by an increase in the number of multivoltine species (e.g., *Pieris rapae*, *Pseudozizeeria maha*) and a decrease in the abundance of seasonal specialist species with clear phenological patterns.

This study focused on relationships between urbanization and durations of flowering/flight period of each species (short, intermediate, and long). In the present study, we noted that 68% of short flowering period plants (64 species) and 100% of short flight period butterflies (five species) were categorized in seasonal species of spring to early summer (March to early July) according to field guides (Hayashi, 1989; Satake et al., 1999; Shirouzu, 2006; Japan Butterfly Conservation Society, 2012). These results indicate that researchers and policy makers should pay attention to the loss of short flowering/ flight period species in spring and early summer due to urbanization. Nakahama et al. (2016) showed that timing of mowing events during the mid to late flowering periods caused negative effects on reproductive success of grassland plant species. Although recent studies emphasized that seasonal variation of species diversity was one of significant issues in ecology (La Sorte, Tingley, & Hurlbert, 2014; Uchida & Ushimaru 2015; Graves et al. 2016), very few studies have shown that human activities exert clear negative impacts on seasonal variation of species diversity. This lack of information remains major issues for biodiversity conservation.

Conclusions regarding the loss of seasonal heterogeneity in semi-natural grasslands due to increasing anthropogenic impacts

Previous studies have indicated the importance of maintaining spatio-temporal heterogeneity in semi-natural biodiversity conservation (Benton, Vickery, & Wilson, 2003; Tscharntke et al., 2005; Uchida & Ushimaru, 2015). The loss of temporal variability in resource availability may limit the seasonal distribution of species from higher-trophic levels. For instance, species that provide pollination services are enhanced by the seasonality of plant activity (Tylianakis, Klein, & Tscharntke, 2005; Diaz et al., 2007; Kremen et al., 2007; Ushimaru, Kobayashi, & Dohzono, 2014). In addition, some relationships between biodiversity and cultural ecosystem services (e.g., people interested in wild flower viewing) stem from these temporal dynamics (Graves, Pearson, & Turner, 2017). Furthermore, temperate countries in Monsoon Asia, including Japan, exhibit four distinct seasons, in which the temporal turnover of biological activities has been fostered by certain aspects of the local cultures (Ministry of the Environment of Japan, 2016).

In East Asia and globally, high biodiversity has been maintained in semi-natural ecosystems, supporting many endangered species, despite several types of land-use changes causing rapid decreases in diversity in recent decades (Foley et al., 2005; Kleijn et al., 2011; Koyanagi & Furukawa, 2013; Uematsu & Ushimaru, 2013; Uchida & Ushimaru, 2014). The use of extensive traditional management systems has been largely abandoned due to agricultural intensification and rapid urbanization in the mega-cities of Monsoon Asia, and globally. However, data on biodiversity in megacities remain limited worldwide; thus, more focused research is needed to study how urbanization affects biodiversity. In conclusion, future studies need to test whether temporal biological heterogeneity affects total biodiversity over the course of a year along the rural-urban gradient at a global scale.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/XXXXX

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Table 1. Estimated partial coefficients of the explanatory parameter (gamma diversity) in generalized linear models for response parameters (average species richness per each survey, beta diversity of additive partitioning of species richness, and beta diversity of turnover component of Jaccard dissimilarity). The significance of the explanatory variables was estimated using the Wald-test and calculated R^2 values.

	Gamma diversity							
	Plants				Butterflies			
Response variables	Estimated coefficient	t-value	*P*	R^2	Estimated coefficient	t-value	*P*	R^2
Average species richness per each survey	0.30	14.02	< **0.01**	0.92	0.41	14.62	< **0.01**	0.92
Beta diversity (Additive partitioning of species richness)	0.70	32.07	< **0.01**	0.98	0.61	20.01	< **0.01**	0.96
Beta diversity (Turnover component of Jaccard dissimilarity)	0.01	1.13	0.27	0.07	0.01	2.39	**0.03**	0.24

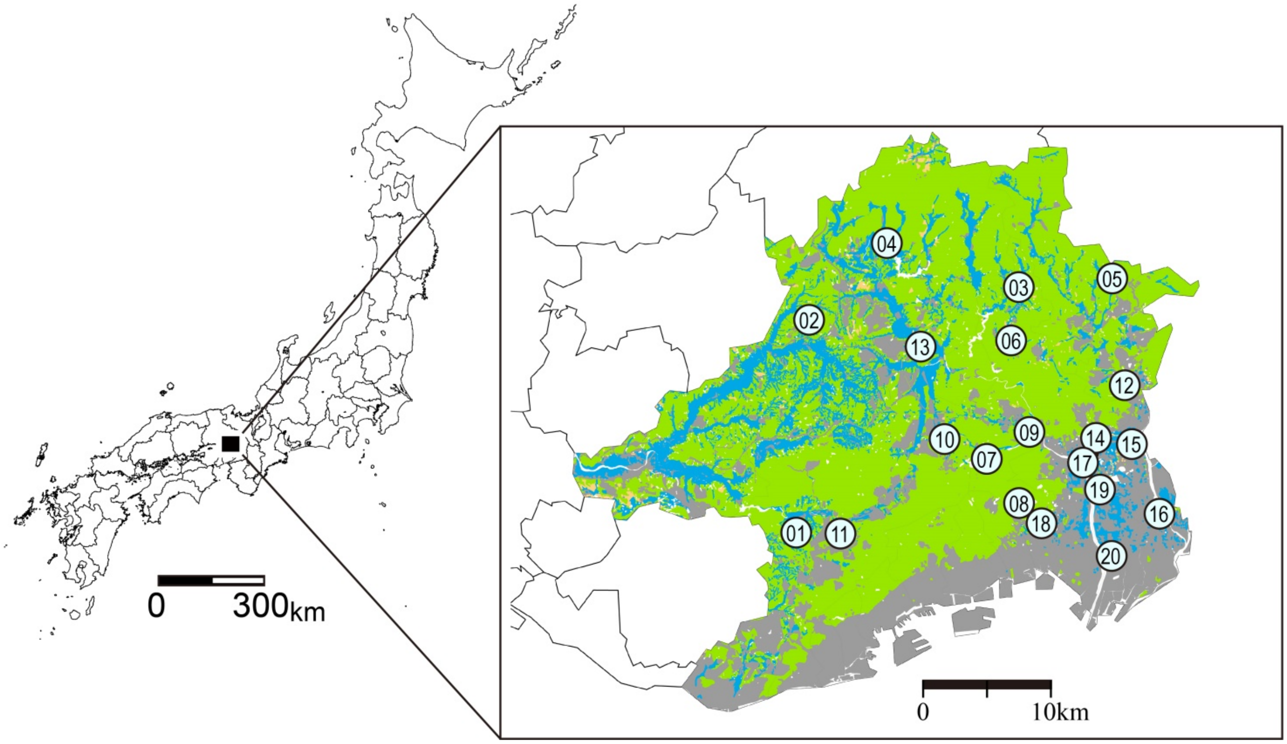
Figure legends

Fig. 1. The study was conducted in the south-eastern part of Hyogo Prefecture, Japan (~25 × 30 km^2, 34°48′–57′ N, 135°03′–24′ E). In the study area, semi-natural grasslands were maintained by periodic mowing on the levees of paddy fields and ponds and at the edges between paddy fields and secondary forests (paddy fields: blue; secondary forests and grassland: light green; residential lands and artificial lands: grey). The number in the circle represents the site's rank along the rural-urban gradient, with site 01 having the lowest extent of urban area in the surrounding habitat (1-km radius). Sites 01 to 13 were located in a valley area, whereas sites 14 to 20 were located in a coastal area. This information was used for analyses (see Material and methods section).

Fig. 2. Relationships between diversity components (average species richness per each survey at each site, beta diversity of additive partitioning of species richness, and beta diversity of turnover component of Jaccard dissimilarity) of flowering plant and butterfly species in each site along the rural-urban gradient. Solid lines represent significant coefficients at $P < 0.05$ estimated by the Wald-test (see Appendix A: Table 3).

Fig. 3. Relationships between the proportion of seasonal type (short, intermediate, and long flowering/flight period) to total plant and butterfly species richness in each plot along the rural-urban gradient. Solid lines represent significant coefficients at $P < 0.05$, the dashed line represents marginally significant coefficients at $P < 0.1$ estimated by the Wald-test (see Appendix A: Table 4).

Fig. 1.


0
300km
04
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10km

Fig. 2.

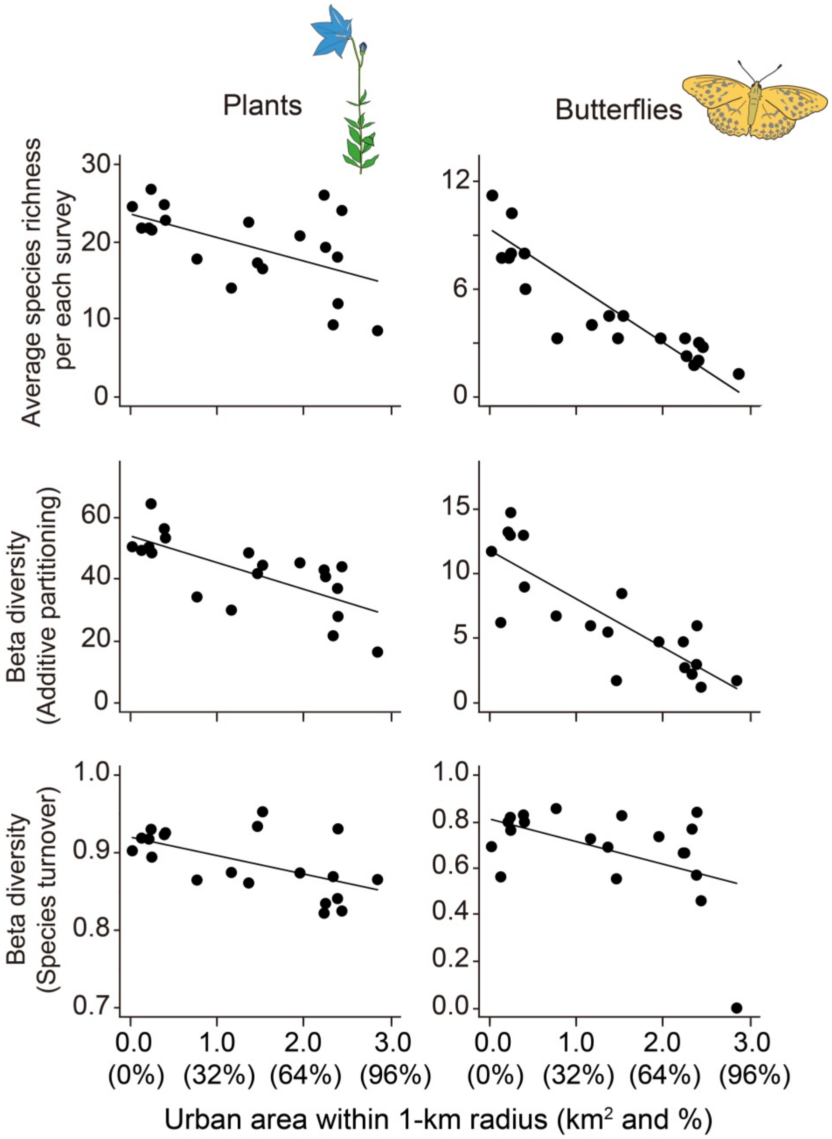
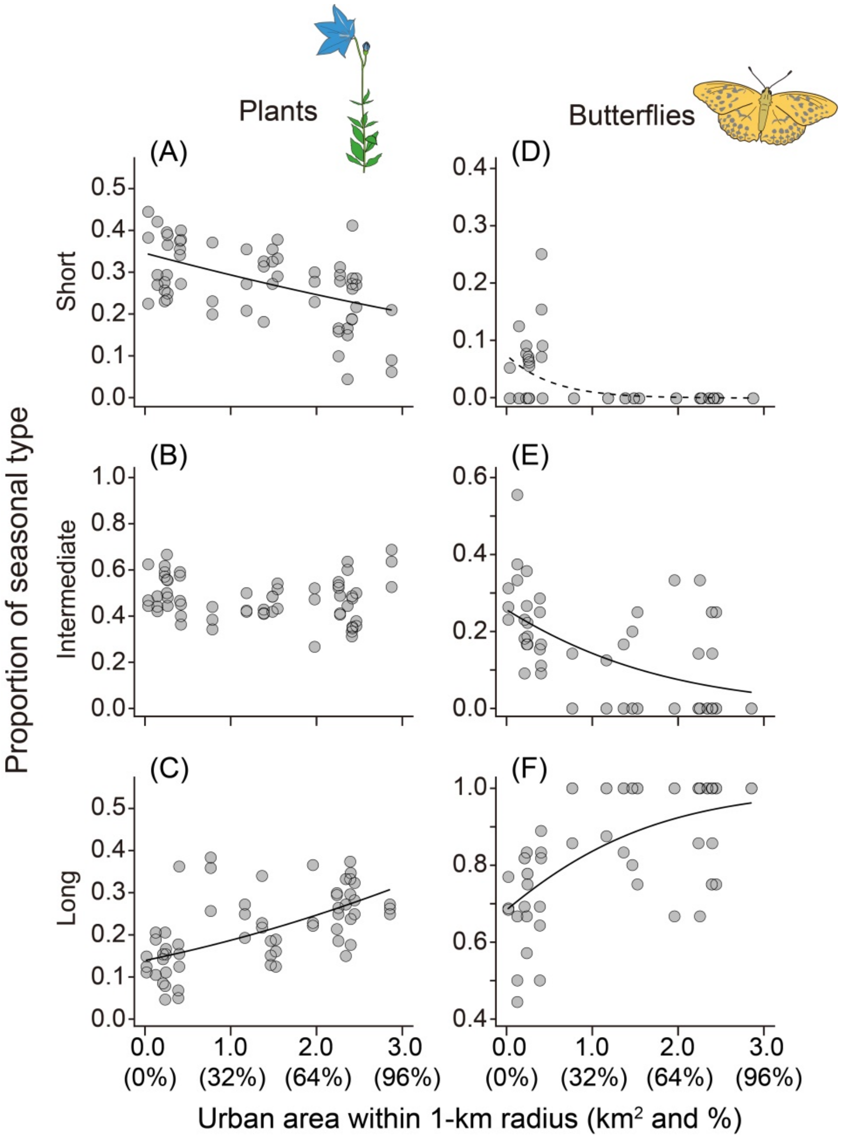

Plants
Butterflies
Average species richness per each survey
Beta diversity (Additive partitioning)
Beta diversity (Species turnover)
30
20
10
0
12
6
0
60
40
20
0
15
10
5
0
1.0
0.9
0.8
0.7
1.0
0.8
0.6
0.4
0.2
0.0
0.0 (0%)
1.0 (32%)
2.0 (64%)
3.0 (96%)
Urban area within 1-km radius (km^2 and %)

Fig. 3.



Plants
Butterflies
(A)
(B)
(C)
(D)
(E)
(F)
Proportion of seasonal type
Short
Intermediate
Long
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.8
1.0
0.0 (0%)
1.0 (32%)
2.0 (64%)
3.0 (96%)
Urban area within 1-km radius (km² and %)

Appendix A.

Table 1. Comparisons of area by land use (forests, paddy fields, urban areads, and others) between ca. 1910 and 2012.

	ca. 1910		2012		% of maintaining areas
	area (km^2)	% of study area	area (km^2)	% of study area	
Forests	744.76	61.86	645.37	52.34	84.61
Paddy Fields	245.84	20.42	173.57	14.08	68.95
Urban (residential and artificial lands)	86.32	7.17	325.04	26.36	367.64 (increase)
others	126.98	10.55	88.97	7.22	68.44

Table 2. Monthly values of temperature, humidity, and rainfall for April, June, July, and September 2014 in the study area.

Month	climate variables	Temperature	Humidity	Precipitation
April	Minimum	10.8		
	Mean	14.6	56.0	
	Maximum	18.8		
	Sum total			72.5
June	Minimum	21.2		
	Mean	23.8	67.5	
	Maximum	27.4		
	Sum total			45.5
July	Minimum	24.9		
	Mean	27.3	71.7	
	Maximum	30.6		
	Sum total			69.5
September	Minimum	21.3		
	Mean	24.4	60.7	
	Maximum	28.0		
	Sum total			127.0

Table 3. Estimated partial coefficients of the explanatory parameter (urban gradient) in generalized linear mixed models for response parameters (average species richness per each survey, beta diversity of additive partitioning of species richness, and beta diversity of turnover component of Jaccard dissimilarity). The significance of explanatory variables was estimated using the Wald-test and calculated R^2 values.

	Urban gradient							
	Plants				Butterflies			
Response variables	Estimated coefficient	t-value	*P*	R^2	Estimated coefficient	t-value	*P*	R^2
Average species richness per each survey	-3.03	-2.81	< **0.01**	0.29	-3.20	-6.68	< **0.01**	0.82
Beta diversity (Additive partitioning of species richness)	-8.60	-4.27	< **0.01**	0.49	-3.75	-6.43	< **0.01**	0.69
Beta diversity (Turnover component of Jaccard dissimilarity)	-0.02	-3.13	< **0.01**	0.34	-0.10	-2.33	**0.03**	0.22

Table 4. Estimated partial coefficients of the explanatory parameter (urban gradient) in generalized linear mixed models for response parameters of the proportion of seasonality type (short, intermediate, and long flowering/flight period) of total plant or butterfly species richness in each plot along the rural-urban gradient. The significance of the explanatory variables were estimated using the Wald-test and calculated R^2 values.

	Urban gradient							
	Plants				Butterflies			
Response variables	Estimated coefficient	t-value	*P*	R^2	Estimated coefficient	t-value	*P*	R^2
Short	-0.24	-4.18	< **0.01**	0.50	-2.03	-1.70	<u>0.09</u>	0.99
Intermediate	-0.06	-1.07	0.28	0.02	-0.73	-3.47	< **0.01**	0.44
Long	0.36	4.82	< **0.01**	0.48	0.86	4.04	< **0.01**	0.21

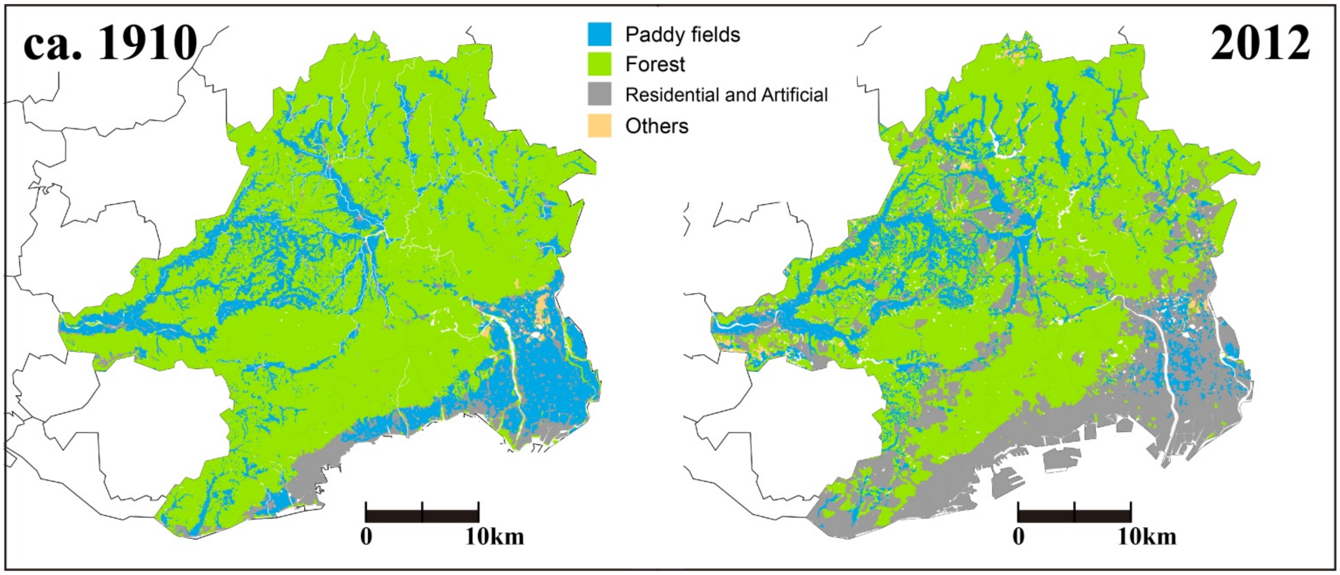


Fig. 1. Changes in the urban, paddy and forest areas from ca. 1910 to 2012 in the study area (south-eastern Hyogo Prefecture, Japan, ~30 × 40 km^2). The ca. 1910 map was constructed based on land-use maps of 1896–1914. Blue: paddy fields, Light green: secondary forests, Grey: residential lands and artificial lands, white and yellow: others. Urbanization drive rapidly declines paddy fields rather than forests (see Appendix A: Table 1).

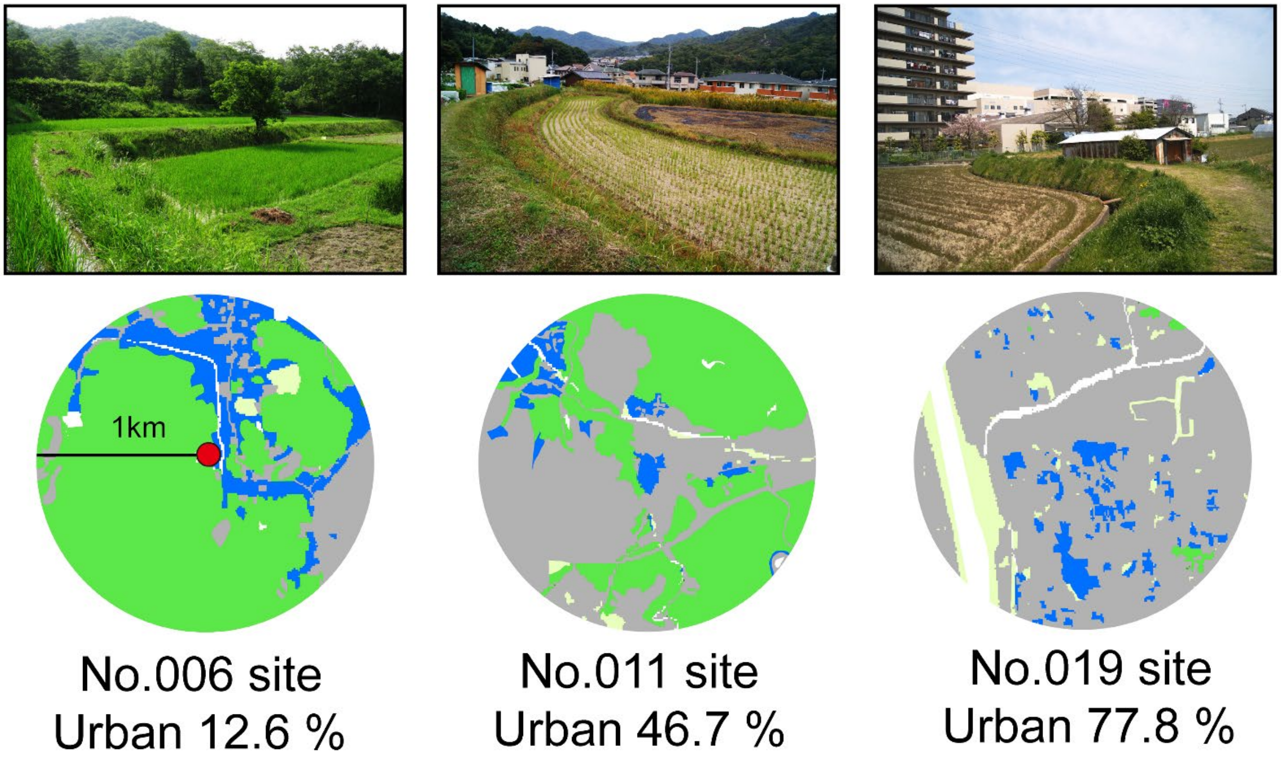


Fig. 2. We surveyed study sites along a rural-to-urban gradient. For example, the extent of urban area inside a 1km radius of the center of site No.006 was 12.6 % (0.39km^2). We surveyed semi-natural grasslands surrounding agricultural lands. Blue: paddy fields, light green: secondary forests, grey: residential lands and artificial lands, and white and yellow: other.

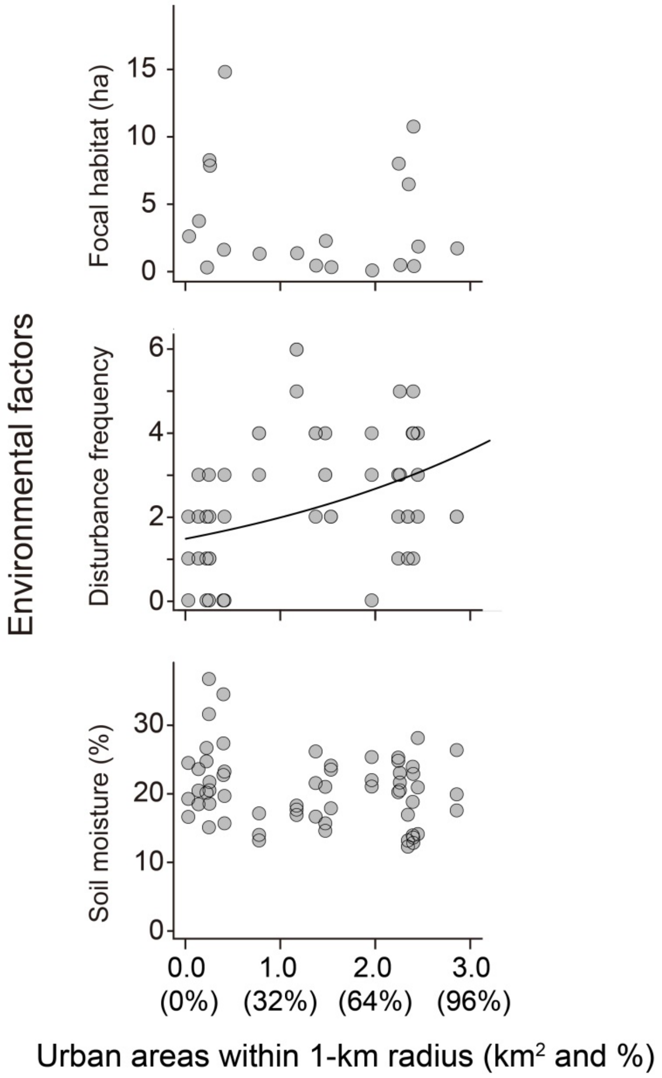


Fig. 3. Relationships between three environmental factors, such as focal habitat (area of continuous unfragmented habitat including survey site within a 1-km radius), disturbance frequency, and soil moisture, and the extent of urban area. Solid lines represent significant coefficients at $p < 0.05$ (*see* Materials and Methods section in detail).

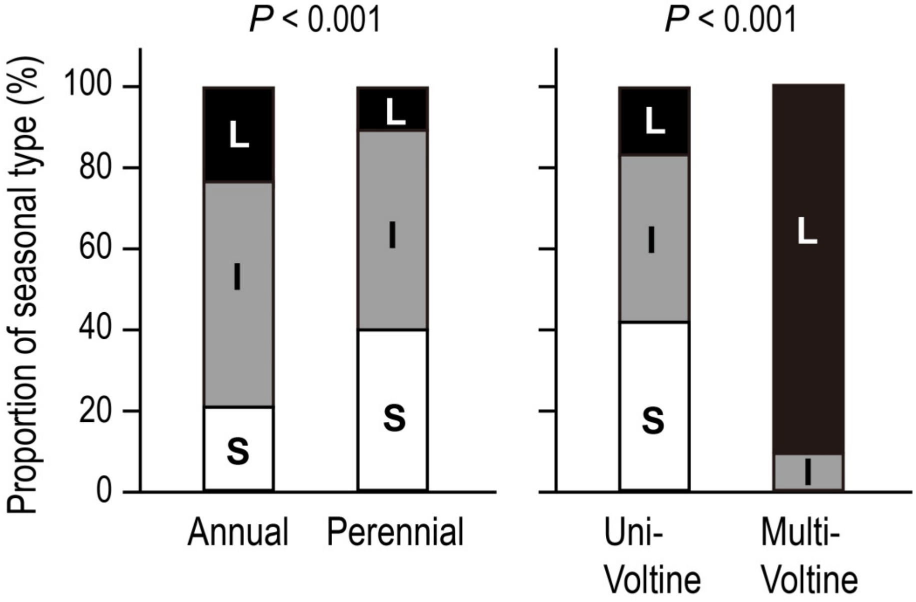


Fig. 4. Comparisons between seasonal type of each species and life-history trait (Plant: annual and perennial, butterfly: uni- and multi-voltine). The significance of the explanatory variables was estimated by fisher's exact test. S: short; I: intermediate; L: long, classifications are explained by Material and Methods section.

Appendix B.

Table 1. This table shows the category of flowering period and months of appearance at each species in the present study. We investigated flowering period using field guides as follows.

Satake, Y., Ooi, J., Kitamura, S., Watari, S., Tominari, T. 1999. Wild flowers of Japan Herbaceous Plants I, II, and III. Heibonsha, Tokyo, Japan. (in Japanese)

Hayashi, Y. 1989. Wild flowers of Japan; Plains, seaside and hills. Yama-Kei publishers, Tokyo, Japan. (in Japanese)

Family name	Species name	Category of seasonality	Months of appearance in the study	Life-history form
Acanthaceae	*Justicia procumbens* L. var. *procumbens*	M	9	annual
Alliaceae	*Allium macrostemon* Bunge	S	5 9	perennial
Alliaceae	*Allium thunbergii* G.Don	S	9	perennial
Amaranthaceae	*Achyranthes bidentata* Blume var. *japonica* Miq.	S	9	perennial
Amaryllidaceae	*Lycoris radiata* (L'Hér.) Herb.	S	9	perennial
Apiaceae	*Cyclospermum leptophyllum* (Pers.) Sprague ex Britton et P.Wilson	NA	5	annual
Apiaceae	*Sium ninsi* L.	S	9	perennial
Apiaceae	*Torilis japonica* (Houtt.) DC.	M	6 7	annual

Apocynaceae	*Vincetoxicum glabrum* (Nakai) Kitag.	M				9	perennial
Apocynaceae	*Vincetoxicum pycnostelma* Kitag.	S		6	7	9	perennial
Aquifoliaceae	*Ilex serrata* Thunb.	M		6			woody
Araceae	*Pinellia ternata* (Thunb.) Breitenb.	M	5				perennial
Araliaceae	*Hydrocotyle ramiflora* Maxim.	M		6	7		perennial
Asteraceae	*Achillea millefolium* L.	M		6			perennial
Asteraceae	*Artemisia indica* Willd. var. *maximowiczii* (Nakai) H.Hara	S				9	perennial
Asteraceae	*Artemisia japonica* Thunb.	M			7		perennial
Asteraceae	*Aster ageratoides* Turcz. subsp. *amplexifolius* Kitam., excl. syn.	M				9	perennial
Asteraceae	*Aster rugulosus* Maxim.	M				9	perennial
Asteraceae	*Aster scaber* Thunb.	M				9	perennial
Asteraceae	*Aster yomena* (Kitam.) Honda	M				9	perennial
Asteraceae	*Atractylodes japonica* Koidz. ex Kitam.	S				9	perennial
Asteraceae	*Bidens frondosa* L.	S				9	annual
Asteraceae	*Bidens pilosa* L. var. *pilosa*	M				9	annual
Asteraceae	*Cirsium japonicum* Fisch. ex DC.	M	5	6	7	9	perennial
Asteraceae	*Cirsium sieboldii* Miq.	S				9	perennial
Asteraceae	*Conyza canadensis* (L.) Cronquist	M				9	annual
Asteraceae	*Coreopsis lanceolata* L.	M		6	7		perennial
Asteraceae	*Crassocephalum crepidioides* (Benth.) S.Moore	M				9	annual
Asteraceae	*Eclipta alba* (L.) Hassk.	M				9	annual
Asteraceae	*Eclipta thermalis* Bunge	M				9	annual
Asteraceae	*Erigeron annuus* (L.) Pers.	L	5	6	7	9	annual
Asteraceae	*Erigeron philadelphicus* L.	L	5	6			annual
Asteraceae	*Eupatorium lindleyanum* DC.	M			7	9	perennial
Asteraceae	*Eupatorium makinoi* T.Kawahara et Yahara	M				9	perennial
Asteraceae	*Galinsoga quadriradiata* Ruiz et Pav.	L			7	9	annual
Asteraceae	*Gamochaeta coarctata* (Willd.) Kerguelen	L	5	6	7		perennial

Asteraceae	*Gnaphalium affine* D.Don	M	5	6	7		annual
Asteraceae	*Gnaphalium japonicum* Thunb.	L	5	6	7		perennial
Asteraceae	*Hypochaeris radicata* L.	L	5	6	7	9	perennial
Asteraceae	*Inula salicina* L. var. *asiatica* Kitam.	M			7		perennial
Asteraceae	*Ixeridium dentatum* (Thunb.) Tzvelev subsp. *dentatum*	M	5	6	7		perennial
Asteraceae	*Ixeris japonica* (Burm.f.) Nakai	M	5	6			perennial
Asteraceae	*Lactuca indica* L. var. *laciniata* (Houtt.) H.Hara	M				9	annual
Asteraceae	*Lapsanastrum apogonoides* (Maxim.) J.H.Pak et K.Bremer	M	5	6			annual
Asteraceae	*Lapsanastrum humile* (Thunb.) J.H.Pak et K.Bremer	M	5	6	7		annual
Asteraceae	*Leibnitzia anandria* (L.) Turcz.	L	5				perennial
Asteraceae	*Picris hieracioides* L. subsp. *japonica* (Thunb.) Krylov	L		6	7		annual
Asteraceae	*Senecio vulgaris* L.	L		6			annual
Asteraceae	*Solidago virgaurea* L. subsp. *asiatica* (Nakai ex H.Hara) Kitam. ex H.Hara	M				9	perennial
Asteraceae	*Sonchus asper* (L.) Hill	L	5				annual
Asteraceae	*Sonchus oleraceus* L.	L	5	6			annual
Asteraceae	*Synurus palmatopinnatifidus* (Makino) Kitam. var. *palmatopinnatifidus*	S				9	perennial
Asteraceae	*Taraxacum japonicum* Koidz.	S	5	6	7		perennial
Asteraceae	*Taraxacum officinale* Weber ex F.H.Wigg.	L	5	6	7	9	perennial
Asteraceae	*Tephroseris integrifolia* (L.) Holub subsp. *kirilowii* (Turcz. ex DC.) B.Nord.	S	5				perennial
Asteraceae	*Youngia japonica* (L.) DC.	L	5	6	7		annual
Boraginaceae	*Bothriospermum zeylanicum* (J.Jacq.) Druce	S			7	9	annual
Boraginaceae	*Trigonotis peduncularis* (Trevir.) Benth. ex Hemsl.	M	5	6			annual
Brassicaceae	*Capsella bursa-pastoris* (L.) Medik.	M	5			9	annual

Brassicaceae	*Cardamine flexuosa* With.	M	5			9	annual
Brassicaceae	*Lepidium virginicum* L.	S	5	6			annual
Brassicaceae	*Rorippa indica* (L.) Hiern	L	5	6	7	9	annual
Brassicaceae	*Rorippa palustris* (L.) Besser	M	5	6	7		annual
Brassicaceae	*Thlaspi arvense* L.	M			7		annual
Campanulaceae	*Adenophora triphylla* (Thunb.) A.DC. subsp. *aperticampanulata* Kitam.	M				9	perennial
Campanulaceae	*Campanula punctata* Lam. var. *punctata*	S			7		perennial
Campanulaceae	*Platycodon grandiflorus* (Jacq.) A.DC.	S				9	perennial
Campanulaceae	*Triodanis perfoliata* (L.) Nieuwl.	S		6			annual
Caryophyllaceae	*Cerastium fontanum* Baumg. subsp. *vulgare* (Hartm.) Greuter et Burdet var. *angustifolium* (Franch.) H.Hara	S	5	6	7		perennial
Caryophyllaceae	*Cerastium glomeratum* Thuill.	S	5				annual
Caryophyllaceae	*Dianthus superbus* L. var. *longicalycinus* (Maxim.) F.N.Williams	M			7	9	perennial
Caryophyllaceae	*Sagina japonica* (Sw.) Ohwi	L	5	6			annual
Caryophyllaceae	*Stellaria aquatica* (L.) Scop.	L		6			perennial
Caryophyllaceae	*Stellaria neglecta* Weihe	L	5	6		9	annual
Caryophyllaceae	*Stellaria uliginosa* Murray var. *undulata* (Thunb.) Fenzl	L	5				annual
Commelinaceae	*Commelina communis* L.	M		6	7	9	annual
Commelinaceae	*Tradescantia reflexa* Raf.	NA		6			annual
Convolvulaceae	*Calystegia pubescens* Lindl. f. major (Makino) Yonek.	S		6	7		perennial
Convolvulaceae	*Ipomoea lacunosa* L.	NA				9	annual
Crassulaceae	*Sedum bulbiferum* Makino	S		6			annual
Cyperaceae	*Carex arenicola* F.Schmidt	S	5	6			perennial
Cyperaceae	*Carex biwensis* Franch.	M	5				perennial
Cyperaceae	*Carex capillacea* Boott	M	5				perennial
Cyperaceae	*Carex dickinsii* Franch. et Sav.	S			7		perennial

Cyperaceae	*Carex dispalata* Boott	M	5				perennial
Cyperaceae	*Carex gibba* Wahlenb.	S		6			perennial
Cyperaceae	*Carex lanceolata* Boott	M	5				perennial
Cyperaceae	*Carex lenta* D.Don var. *lenta*	M				9	perennial
Cyperaceae	*Carex leucochlora* Bunge	M	5	6		9	perennial
Cyperaceae	*Carex maximowiczii* Miq.	S		6	7		perennial
Cyperaceae	*Carex phacota* Spreng.	S	5				perennial
Cyperaceae	*Carex rugata* Ohwi	S	5				perennial
Cyperaceae	*Carex spp. 1*	NA				9	NA
Cyperaceae	*Carex spp. 2*	NA	5				NA
Cyperaceae	*Carex thunbergii* Steud.	S	5				perennial
Cyperaceae	*Cyperus brevifolius* (Rottb.) Hassk. var. *leiolepis* (Franch. et Sav.) T.Koyama	M			7	9	perennial
Cyperaceae	*Cyperus difformis* L.	M				9	annual
Cyperaceae	*Cyperus iria* L.	M			7	9	annual
Cyperaceae	*Cyperus microiria* Steud.	M			7	9	annual
Cyperaceae	*Cyperus nipponicus* Franch. et Sav. var. *spiralis* Ohwi	M				9	annual
Cyperaceae	*Cyperus pygmaeus* Rottb.	M				9	annual
Cyperaceae	*Eleocharis congesta* D.Don var. *japonica* (Miq.) T.Koyama	L			7		annual
Cyperaceae	*Eleocharis wichurae* Boeck.	M			7	9	perennial
Cyperaceae	*Fimbristylis autumnalis* (L.) Roem. et Schult.	M				9	annual
Cyperaceae	*Fimbristylis complanata* (Retz.) Link f. exaltata T.Koyama	M		6	7	9	perennial
Cyperaceae	*Fimbristylis littoralis* Gaudich.	M				9	perennial
Cyperaceae	*Rhynchospora chinensis* auct. non Nees et Meyen	M				9	perennial
Cyperaceae	*Scirpus wichurae* Boeck. f. concolor (Maxim.) Ohwi	M			7	9	perennial
Cyperaceae	*Scleria parvula* Steud.	M				9	perennial

Dioscoreaceae	*Dioscorea japonica* Thunb.	S			7		perennial
Droseraceae	*Drosera peltata* Thunb. var. *nipponica* (Masam.) Ohwi	S		6			perennial
Droseraceae	*Drosera rotundifolia* L.	M		6	7		perennial
Ericaceae	*Rhododendron kaempferi* Planch. var. *kaempferi*	M	5				woody
Ericaceae	*Rhododendron macrosepalum* Maxim.	S	5				woody
Euphorbiaceae	*Acalypha australis* L.	M				9	annual
Euphorbiaceae	*Chamaesyce maculata* (L.) Small	L		6		9	annual
Euphorbiaceae	*Chamaesyce nutans* (Lag.) Small	L				9	annual
Fabaceae	*Amphicarpaea bracteata* (L.) Fernald subsp. *edgeworthii* (Benth.) H.Ohashi var. *japonica* (Oliv.) H.Ohashi	M				9	annual
Fabaceae	*Astragalus sinicus* L.	M	5				annual
Fabaceae	*Desmodium paniculatum* (L.) DC.	S				9	annual
Fabaceae	*Desmodium podocarpum* DC. subsp. *oxyphyllum* (DC.) H.Ohashi	M				9	perennial
Fabaceae	*Dunbaria villosa* (Thunb.) Makino	S				9	perennial
Fabaceae	*Glycine max* (L.) Merr. subsp. *soja* (Siebold et Zucc.) H.Ohashi	S				9	annual
Fabaceae	*Indigofera pseudotinctoria* Matsum.	M			7	9	woody
Fabaceae	*Kummerowia striata* (Thunb.) Schindl.	S				9	annual
Fabaceae	*Lespedeza bicolor* Turcz.	M			7	9	woody
Fabaceae	*Lespedeza cuneata* (Dum.Cours.) G.Don	M				9	perennial
Fabaceae	*Lespedeza pilosa* (Thunb.) Siebold et Zucc.	M				9	perennial
Fabaceae	*Lotus corniculatus* L. var. *corniculatus*	L		6			perennial
Fabaceae	*Lotus corniculatus* L. var. *japonicus* Regel	L		6	7	9	perennial
Fabaceae	*Sophora flavescens* Aiton	S		6			perennial
Fabaceae	*Medicago lupulina* L.	M	5	6			annual
Fabaceae	*Trifolium dubium* Sibth.	M	5				annual
Fabaceae	*Trifolium pratense* L.	M		6			perennial

Fabaceae	*Trifolium repens* L.	L	5	6	7	9	perennial
Fabaceae	*Vicia hirsuta* (L.) Gray	M	5				annual
Fabaceae	*Vicia sativa* L. subsp. *nigra* (L.) Ehrh.	M	5	6			annual
Fabaceae	*Vicia tetrasperma* (L.) Schreb.	S	5				annual
Fumariaceae	*Corydalis incisa* (Thunb.) Pers.	M	5				annual
Gentianaceae	*Gentiana scabra* Bunge var. *buergeri* (Miq.) Maxim. ex Franch. et Sav.	M				9	perennial
Gentianaceae	*Swertia japonica* (Schult.) Makino	M				9	annual
Geraniaceae	*Geranium carolinianum* L.	M	5	6	7		annual
Geraniaceae	*Geranium thunbergii* Siebold ex Lindl. et Paxton	M				9	perennial
Haloragaceae	*Haloragis micrantha* (Thunb.) R.Br.	M				9	perennial
Hemerocallidaceae	*Hemerocallis citrina* Baroni var. *vespertina* (H.Hara) M.Hotta	M			7		perennial
Hemerocallidaceae	*Hemerocallis fulva* L. var. *kwanso* Regel	S			7		perennial
Hyacinthaceae	*Barnardia japonica* (Thunb.) Schult. et Schult.f.	S				9	perennial
Hydrangeaceae	*Deutzia crenata* Siebold et Zucc.	M		6			woody
Hypericaceae	*Hypericum erectum* Thunb.	M			7	9	perennial
Hypericaceae	*Hypericum laxum* (Blume) Koidz.	M			7		annual
Iridaceae	*Crocus sativus* L.	NA				9	perennial
Iridaceae	*Iris ensata* Thunb. var. *spontanea* (Makino) Nakai ex Makino et Nemoto	S		6	7		perennial
Iridaceae	*Sisyrinchium rosulatum* E.P.Bicknell	S	5	6	7		perennial
Juncaceae	*Juncus decipiens* (Buchenau) Nakai	M	5	6	7		perennial
Juncaceae	*Luzula capitata* (Miq.) Miq. ex Kom.	S	5	6			perennial
Juncaceae	*Luzula multiflora* (Ehrh.) Lejeune	M	5				perennial
Lamiaceae	*Ajuga decumbens* Thunb.	M	5	6	7		perennial
Lamiaceae	*Clinopodium chinense* (Benth.) Kuntze subsp. *grandiflorum* (Maxim.) H.Hara	S			7	9	perennial
Lamiaceae	*Clinopodium gracile* (Benth.) Kuntze	M	5	6	7	9	perennial

Lamiaceae	*Glechoma hederacea* L. subsp. *grandis* (A.Gray) H.Hara	S	5				perennial
Lamiaceae	*Isodon inflexus* (Thunb.) Kudô	S				9	perennial
Lamiaceae	*Lamium amplexicaule* L.	M	5				annual
Lamiaceae	*Lamium purpureum* L.	S	5				annual
Lamiaceae	*Lycopus maackianus* (Maxim. ex Herder) Makino	M				9	perennial
Lamiaceae	*Mentha canadensis* L. var. *piperascens* (Malinv. ex Holmes) H.Hara	M			7		perennial
Lamiaceae	*Prunella vulgaris* L. subsp. *asiatica* (Nakai) H.Hara	M		6	7		perennial
Lamiaceae	*Salvia japonica* Thunb.	L			7	9	perennial
Lamiaceae	*Scutellaria indica* L.	S		6	7		perennial
Lauraceae	*Lindera umbellata* Thunb.	S	5				woody
Liliaceae	*Lilium japonicum* Houtt.	S		6			perennial
Liliaceae	*Tricyrtis macropoda* Miq. subsp. *affinis* (Makino) Kitam.	M				9	perennial
Linderniaceae	*Lindernia procumbens* (Krock.) Borbás	M				9	annual
Linnaeaceae	*Abelia spp.*	NA					woody
Lobeliaceae	*Lobelia chinensis* Lour.	L		6	7	9	perennial
Lythraceae	*Ammannia coccinea* Rottb.	L				9	annual
Lythraceae	*Lythrum anceps* (Koehne) Makino	S				9	perennial
Melanthiaceae	*Chionographis japonica* Maxim.	S		6			perennial
Melanthiaceae	*Helonias orientalis* (Thunb.) N.Tanaka	S	5				perennial
Myrsinaceae	*Lysimachia clethroides* Duby	S		6	7		perennial
Myrsinaceae	*Lysimachia fortunei* Maxim.	S			7	9	perennial
Myrsinaceae	*Lysimachia japonica* Thunb.	S	5	6	7	9	perennial
Nartheciaceae	*Aletris luteoviridis* (Maxim.) Franch.	M			7		perennial
Nartheciaceae	*Aletris spicata* (Thunb.) Franch.	M		6	7		perennial
Onagraceae	*Ludwigia epilobioides* Maxim.	M				9	annual
Onagraceae	*Oenothera biennis* L.	L			7	9	annual

Onagraceae	*Oenothera rosea* L'Hér. ex Aiton	L	5	6	7	9	perennial
Orchidaceae	*Bletilla striata* (Thunb.) Rchb.f.	S		6			perennial
Orchidaceae	*Epipactis thunbergii* A.Gray	M		6	7		perennial
Orchidaceae	*Platanthera minor* (Miq.) Rchb.f.	S			7		perennial
Orchidaceae	*Pogonia minor* (Makino) Makino	M		6			perennial
Orchidaceae	*Spiranthes sinensis* (Pers.) Ames subsp. *australis* (R.Br.) Kitam., excl. basion.	L			7	9	perennial
Orobanchaceae	*Melampyrum roseum* Maxim. var. *japonicum* Franch. et Sav.	M		6	7		annual
Orobanchaceae	*Monochasma sheareri* (S.Moore) Maxim.	S	5				annual
Oxalidaceae	*Oxalis corniculata* L.	L	5	6	7	9	perennial
Oxalidaceae	*Oxalis debilis* Kunth subsp. *corymbosa* (DC.) Lourteig	S	5	6	7		perennial
Oxalidaceae	*Oxalis dillenii* Jacq.	L	5	6	7	9	perennial
Phrymaceae	*Mazus miquelii* Makino	S	5				perennial
Phrymaceae	*Mazus pumilus* (Burm.f.) Steenis	L	5	6	7	9	annual
Plantaginaceae	*Nuttallanthus canadensis* (L.) D.A.Sutton	S	5	6			annual
Plantaginaceae	*Plantago asiatica* L.	L		6	7	9	perennial
Plantaginaceae	*Plantago virginica* L.	M	5	6	7		annual
Plantaginaceae	*Veronica arvensis* L.	M	5	6	7		annual
Plantaginaceae	*Veronica persica* Poir.	S	5	6			annual
Poaceae	*Agrostis canina* L.	NA		6			perennial
Poaceae	*Agrostis clavata* Trin. subsp. *matsumurae* (Hack. ex Honda) Tateoka	S	5	6			perennial
Poaceae	*Agrostis valvata* Steud.	S		6			perennial
Poaceae	*Alopecurus aequalis* Sobol. var. *amurensis* (Kom.) Ohwi	M	5	6	7		annual
Poaceae	*Andropogon virginicus* L.	M				9	perennial
Poaceae	*Anthoxanthum odoratum* L.	M		6			perennial
Poaceae	*Arundinella hirta* (Thunb.) Tanaka	M				9	perennial

Poaceae	*Beckmannia syzigachne* (Steud.) Fernald	S	5		7		annual
Poaceae	*Briza minor* L.	M		6			annual
Poaceae	*Bromus catharticus* Vahl	S	5	6	7		perennial
Poaceae	*Calamagrostis brachytricha* Steud.	M				9	perennial
Poaceae	*Cymbopogon tortilis* (J.Presl) Hitchc. var. *goeringii* (Steud.) Hand.-Mazz.	M				9	perennial
Poaceae	*Dactylis glomerata* L.	S		6			perennial
Poaceae	*Digitaria ciliaris* (Retz.) Koeler	L			7	9	annual
Poaceae	*Eccoilopus cotulifer* (Thunb.) A.Camus	S				9	perennial
Poaceae	*Echinochloa crus-galli* (L.) P.Beauv. var. *crus-galli*	M			7	9	annual
Poaceae	*Eleusine indica* (L.) Gaertn.	M			7	9	annual
Poaceae	*Elymus racemifer* (Steud.) Tzvelev	M		6	7		perennial
Poaceae	*Elymus tsukushiensis* Honda var. *transiens* (Hack.) Osada	M		6	7		perennial
Poaceae	*Eragrostis curvula* (Schrad.) Nees	L		6			perennial
Poaceae	*Festuca arundinacea* Schreb.	M	5	6	7		perennial
Poaceae	*Festuca ovina* L. subsp. *coreana* (St.Yves) E.B.Alexeev	M		6			perennial
Poaceae	*Festuca parvigluma* Steud.	S		6			perennial
Poaceae	*Imperata cylindrica* (L.) Raeusch. var. *koenigii* (Retz.) Pilg.	M		6			perennial
Poaceae	*Isachne globosa* (Thunb.) Kuntze	M			7		perennial
Poaceae	*Leptochloa chinensis* (L.) Nees	M				9	annual
Poaceae	*Lolium multiflorum* Lam.	M	5	6			annual
Poaceae	*Miscanthus sinensis* Andersson	M				9	perennial
Poaceae	*Moliniopsis japonica* (Hack.) Hayata	M				9	perennial
Poaceae	*Oplismenus undulatifolius* (Ard.) Roem. et Schult.	M				9	perennial
Poaceae	*Paspalum dilatatum* Poir.	M		6	7	9	perennial
Poaceae	*Paspalum distichum* L.	M			7		perennial

Poaceae	*Paspalum thunbergii* Kunth ex Steud.	M		6	7	9	perennial
Poaceae	*Paspalum urvillei* Steud.	NA				9	perennial
Poaceae	*Pennisetum alopecuroides* (L.) Spreng.	M				9	perennial
Poaceae	*Phragmites australis* (Cav.) Trin. ex Steud.	M				9	perennial
Poaceae	*Phragmites japonicus* Steud.	M				9	perennial
Poaceae	*Poa acroleuca* Steud.	M	5	6			annual
Poaceae	*Poa annua* L.	L	5	6	7	9	annual
Poaceae	*Poa chapmaniana* Scribn.	NA				9	annual
Poaceae	*Poa compressa* L.	NA	5				perennial
Poaceae	*Poa trivialis* L.	NA		6	7	9	perennial
Poaceae	*Sacciolepis spicata* (L.) Honda ex Masam. var. *spicata*	M				9	annual
Poaceae	*Setaria faberi* R.A.W.Herrm.	M			7	9	annual
Poaceae	*Setaria glauca* (L.) P.Beauv. var. *pallidefusca* (Schumach.) T.Koyama	M				9	annual
Poaceae	*Setaria pumila* (Poir.) Roem. et Schult.	M				9	annual
Poaceae	*Setaria viridis* (L.) P.Beauv.	M			7	9	annual
Poaceae	*Sorghum halepense* (L.) Pers.	M			7	9	perennial
Poaceae	*Themeda japonica* (Willd.) Tanaka	S				9	perennial
Poaceae	*Trisetum bifidum* (Thunb.) Ohwi	S	5	6	7		perennial
Poaceae	*Vulpia myuros* (L.) C.C.Gmel.	S		6			annual
Poaceae	*Zoysia japonica* Steud.	S		6	7		perennial
Polygalaceae	*Polygala japonica* Houtt.	M	5	6			perennial
Polygonaceae	*Persicaria longiseta* (Bruijn) Kitag.	L	5		7	9	annual
Polygonaceae	*Polygonum sieboldii*	M				9	annual
Polygonaceae	*Rumex acetosa* L.	M	5	6			perennial
Polygonaceae	*Rumex acetosella* L. subsp. *pyrenaicus* (Pourret ex Lapeyr.) Akeroyd	M		6			perennial
Polygonaceae	*Rumex japonicus* Houtt.	M	5	6	7	9	perennial
Ranunculaceae	*Clematis terniflora* DC.	S				9	perennial

Ranunculaceae	*Ranunculus japonicus* Thunb.	S	5	6			perennial
Ranunculaceae	*Ranunculus sceleratus* L.	S	5				annual
Ranunculaceae	*Ranunculus silerifolius* H.Lév. var. *glaber* (H.Boissieu) Tamura	L	5	6	7	9	perennial
Ranunculaceae	*Thalictrum minus* L. var. *hypoleucum* (Siebold et Zucc.) Miq.	M			7	9	perennial
Rosaceae	*Agrimonia pilosa* Ledeb. var. *viscidula* (Bunge) Kom.	S				9	perennial
Rosaceae	*Potentilla freyniana* Bornm.	S	5	6			perennial
Rosaceae	*Potentilla hebiichigo* Yonek. et H.Ohashi	S	5				perennial
Rosaceae	*Potentilla kleiniana* Wight et Arn. subsp. *anemonifolia* (Lehm.) Murata	S	5	6	7		perennial
Rosaceae	*Rubus parvifolius* L.	M		6	7		woody
Rosaceae	*Sanguisorba officinalis* L.	M				9	perennial
Rubiaceae	*Galium spurium* L. var. *echinospermon* (Wallr.) Hayek	S	5				annual
Rubiaceae	*Galium trachyspermum* A.Gray	S		6	7		perennial
Rubiaceae	*Gardenia jasminoides* Ellis	S			7		woody
Rubiaceae	*Neanotis hirsuta* (L.f.) W.H.Lewis var. *hirsuta*	S				9	annual
Rubiaceae	*Paederia scandens* (Lour.) Merr.	S			7	9	woody
Rubiaceae	*Sherardia arvensis* L.	L		6			annual
Ruscaceae	*Liriope minor* (Maxim.) Makino	M	5		7	9	perennial
Salicaceae	*Salix sieboldiana* Blume	S	5				woody
Santalaceae	*Thesium chinense* Turcz.	M	5	6	7		perennial
Saururaceae	*Houttuynia cordata* Thunb.	S		6	7		perennial
Saxifragaceae	*Astilbe microphylla* Knoll	M			7		perennial
Saxifragaceae	*Chrysosplenium grayanum* Maxim.	S	5				perennial
Solanaceae	*Solanum ptychanthum* Dunal	L			7	9	annual
Thymelaeaceae	*Diplomorpha trichotoma* (Thunb.) Nakai	M				9	woody
Urticaceae	*Boehmeria spicata* (Thunb.) Thunb.	M			7	9	woody

Valerianaceae	*Patrinia scabiosifolia* Fisch. ex Trevir.	M				9	perennial
Valerianaceae	*Valerianella locusta* (L.) Laterr.	S	5				annual
Verbenaceae	*Verbena brasiliensis* Vell.	M		6	7		perennial
Violaceae	*Viola grypoceras* A.Gray var. *grypoceras*	S	5				perennial
Violaceae	*Viola mandshurica* W.Becker	S	5				perennial
Violaceae	*Viola verecunda* A.Gray	S	5				perennial
Violaceae	*Viola violacea* Makino var. *violacea*	S	5				perennial
Vitaceae	*Cayratia japonica* (Thunb.) Gagnep.	M			7		perennial

Table 2. This table shows the category of flight period and months of appearance at each species in the present study. We investigated flight period using field guides as follows.

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

Japan Butterfly Conservation Society. 2012. Field guide to the butterflies of Japan. Seibundo-shinkosha, Tokyo, Japan. (in Japanese)

Family name	Species name	Category of seasonality	Months of appearance in the study	Voltinism U: uni, M: multi
Papilionidae	*Graphium sarpedon* (Linnaeus, 1758)	L	9	M
Papilionidae	*Papilio dehaanii* C. & R. Felder, 1864	L	4	M
Papilionidae	*Papilio helenus Linnaeus, 1758*	M	6	M
Papilionidae	*Papilio machaon* Linnaeus, 1758	L	4 6 9	M
Papilionidae	*Papilio protenor* Cramer, 1775	L	4 6	M
Papilionidae	*Papilio xuthus* Linnaeus, 1767	L	4 6 7 9	M
Pieridae	*Anthocharis scolymus* Butler, 1866	S	4	U
Pieridae	*Colias erate* (Esper, 1805)	L	4 6 7 9	M
Pieridae	*Eurema mandarina* (de l'orza, 1869)	L	4 6 7 9	M
Pieridae	*Pieris melete* (Ménétriès, 1857)	L	4 6 7 9	M
Pieridae	*Pieris rapae* (Linnaeus, 1758)	L	4 6 7 9	M
Lycaenidae	*Celastrina argiolus* (Linnaeus, 1758)	L	6 9	M
Lycaenidae	*Callophrys ferrea* (Butler, 1866)	S	4	U

Lycaenidae	*Curetis acuta* Moore, 1877	L		6	7		M
Lycaenidae	*Everes argiades* (Pallas, 1771)	L	4	6	7	9	M
Lycaenidae	*Japonica lutea (Hewitson, 1865)*	S		6			U
Lycaenidae	*Lycaena phlaeas* (Linnaeus, 1761)	L	4	6	7	9	M
Lycaenidae	*Zizeeria maha* (Kollar, 1844)	L	4	6	7	9	M
Nymphalidae	*Argynnis paphia* (Linnaeus, 1758)	M				9	U
Nymphalidae	*Argyreus hyperbius* (Linnaeus, 1763)	L		6	7	9	M
Nymphalidae	*Argyronome laodice* (Pallas, 1771)	M			7	9	U
Nymphalidae	*Damora sagana* (Doubleday, 1847)	M				9	U
Nymphalidae	*Ladoga glorifica* (Fruhstorfer, 1909)	L		6			M
Nymphalidae	*Lethe sicelis* (Hewitson, 1862)	L		6	7	9	M
Nymphalidae	*Libythea lepita* Moore,1858	L	4	6			U
Nymphalidae	*Minois dryas* (Scopoli, 1763)	M			7	9	U
Nymphalidae	*Mycalesis gotama* Moore, 1858	L		6		9	M
Nymphalidae	*Nephargynnis anadyomene* (C. & R. Felder, 1862)	L		6			U
Nymphalidae	*Neptis pryeri* Butler, 1871	L				9	M
Nymphalidae	*Neptis sappho* (Pallas, 1771)	L	4	6	7	9	M
Nymphalidae	*Nymphalis xanthomelas* (Esper, 1781)	S	4				U
Nymphalidae	*Polygonia c-aureum* (Linnaeus, 1758)	L		6		9	M
Nymphalidae	*Vanessa cardui* (Linnaeus, 1758)	L		6	7		M
Nymphalidae	*Vanessa indica* (Herbst, 1794)	L	4	6			M
Nymphalidae	*Ypthima argus* Butler, 1866	L	4	6	7	9	M
Hesperiidae	*Erynnis montanus* (Bremer, 1861)	S	4				U
Hesperiidae	*Isoteinon lamprospilus* C. & R. Felder, 1862	M			7		U
Hesperiidae	*Leptalina unicolor* (Bremer & Grey, 1852)	L				9	M
Hesperiidae	*Parnara guttata* (Bremer & Grey, 1852)	L		6		9	M

Hesperiidae	*Pelopidas mathias* (Fabricius, 1798)	L	6	7	9	M
Hesperiidae	*Polytremis pellucida* (Murray, 1875)	M	6	7	9	M
Hesperiidae	*Potanthus flavus* (Murray, 1875)	M		7	9	M
Hesperiidae	*Thoressa varia* (Murray, 1875)	L	6		9	M