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

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The biodiversity of agricultural landscapes has been noticeably affected by rapid urbanization. 27Although many studies have examined species diversity per unit area (alpha diversity), knowledge 2829about the patterns of species turnover (beta diversity) in urban areas remains limited. Furthermore, 30 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 31urbanization is associated with decreases in the seasonal heterogeneity of species composition, 3233 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 3435averages (alpha diversity) and (2) the seasonal turnover of species composition (beta diversity) for 36 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 37 38 explanatory variables were urban areas within a 1-km radius of the center of each site. Increasing 39 urban area caused both the seasonal alpha and beta diversity of flowering plants and butterflies to 40 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 41 42studies 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. 43Ecologists and policy makers should focus on developing strategies to halt the loss of temporal 44 biological heterogeneity to maintain biodiversity. 45

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

49 Introduction

51	Land-use change reduces biodiversity in agricultural ecosystems globally (Sala et al., 2000;
52	Tilman et al., 2001; Foley et al., 2005). In recent decades, rapid urbanization has been one of the
53	main factors causing changes to biodiversity in agro-ecosystems (e.g., Blair & Johnson, 2008;
54	McKinney, 2008; Ushimaru, Kobayashi, & Dohzono, 2014). Biodiversity loss is partly the result
55	of reduced spatial and temporal heterogeneity in species composition (e.g., McKinney, 2006;
56	Smart et al., 2006; Tylianakis, Klein, & Tscharntke, 2005; Uchida & Ushimaru, 2015). Biotic
57	homogenization is a rapidly growing ecological issue worldwide, which is caused by the
58	combined effects of specialist and native species extinctions with invasions of generalist and
59	non-native species that are better able to adapt to anthropogenic changes in environmental
60	conditions (e.g., Olden, 2006; McKinney, 2006; Knop, 2016).
61	Most studies on biotic homogenization in urban areas have focused on spatial heterogeneity
62	(McKinney, 2006; Smart et al., 2006; Knop, 2016); however, changes in the temporal
63	heterogeneity of species composition due to urbanization are being overlooked (but see, La Sorte,
64	Tingley, & Hurlbert, 2014). Seasonal turnover in species composition shows how species share the
65	same habitat at different times of the year (Olesen et al., 2008; La Sorte, Tingley, & Hurlbert,
66	2014; Uchida & Ushimaru, 2015), and could be used as an indicator of biodiversity for deciding
67	where to implement conservation actions. Studies on biotic homogenization have confirmed that
68	seasonal heterogeneity in species composition, which is regulated by seasonal changes of weather
69	conditions, is fundamental for maintaining biodiversity (Benton, Vickery, & Wilson, 2003;
70	Tylianakis, Klein, & Tscharntke, 2005; Dalby et al., 2014). Seasonal turnover in species
71	composition is high in rainforest ecosystems, leading to greater biodiversity over the course of a
72	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).

78Globally, 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 > 7910 million people) are expected to have a negative effect on biodiversity, and are primarily located 80 81 in Asia (United Nations, 2014). Urbanization studies are common in Europe and North America, 82 but remain limited in Monsoon Asia, where extensive areas of semi-natural ecosystems (i.e., 83 agricultural lands and secondary forests) have been replaced by urban areas due to rapid economic 84 growth during the second half of the 20th century (Liu, Zhan, & Deng, 2005; Saizen, Mizuno, & 85 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; 86 87 Uematsu et al., 2010; Tsuji et al., 2011; Uchida & Ushimaru, 2014); however, urbanization may 88 have caused species pools to diminish due to increased anthropogenic impacts (Olden & Rooney, 89 2006; Qian et al., 2006; Tsuji et al., 2011; Ramírez-Restrepo & MacGregor-Fors, 2017). Therefore, 90 a better understanding of how urbanization impacts semi-natural ecosystems surrounding megacities in East Asia is required. 91Here, we focus on investigating the average seasonal species richness and temporal turnover of 92

93 species composition over the course of a year. Most previous studies have indicated that high

94 anthropogenic impact causes biological heterogeneity to decline (e.g., Vellend et al., 2007; Ekroos,

- 95 Heliölä, & Kuussaari, 2010; Uchida & Ushimaru, 2015). Furthermore, the spatial and temporal
- 96 heterogeneity of species composition may not necessarily be correlated. Plant and insect species

97 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, 98 99 we hypothesized that the loss of seasonal specialists and a prevalence of seasonal generalists cause 100 the temporal turnover of species composition to decline with increasing urbanization. The 101 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 102alpha and high beta diversity result in high gamma diversity over the course of a year. Temporal 103 104 dissimilarities in flowering plant composition were used to examine phenological variation in 105flowering activity, which approach is possible because the richness of flowering species is 106 significantly correlated with total plant species richness (including species that do and do not 107 flower) in this study region (Uchida & Ushimaru, 2015).

108 In this study, we tested changes in biodiversity along an urban-rural gradient, including 109 changes from extensive to intensive management practices in semi-natural grasslands. We 110examined the average seasonal species richness (alpha diversity) and two components of the 111 temporal turnover of species composition (beta diversity) to investigate whether biotic 112homogenization occurs in semi-natural ecosystems surrounding paddy fields along the urban-rural 113gradient of the Osaka-Kobe megacity, Japan. In this study area, urbanization has caused the cover 114of paddy fields to decrease more rapidly than that of forested areas over the last century (see 115Appendix 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 116 117diversity loss and within-year seasonal biotic homogenization (declines in β -diversity); (2) gamma 118 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 119results in biotic homogenization. 120

- 122
- 123 Materials and methods
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- 125 Study area and plots
- 126

The study was conducted in the Osaka-Kobe megacity, western Japan ($\sim 30 \times 40 \text{ km}^2$, $34^{\circ}43'$ -12757' N, 135°03'–25' E). The urban areas (residential, commercial, and industrial) were delineated in 128ArcGIS Spatial Analyst 9.3 (ESRI, Redlands, CA, USA) using land-use maps from 1896 to 1914 129("Kasei-Chikeizu" from the Imperial Japanese Army, Meiji era) and using high-resolution aerial 130131photographs from the Geospatial Information Authority of Japan and Google Maps in 2012. In the 132Osaka-Kobe megacity area, paddy fields and secondary forests have decreased due to urbanization 133since the 1980s. Approximately 100 years ago, the study area was composed of 7.2% urban area, 13420.4% agricultural land, and 61.9% forest. In contrast, by 2012, the study area was composed of 13526.4% urban area, 14.1% agricultural land, and 52.3% forest (see Appendix A: Fig. 1 and Table 1). 136 From ca.1910 to 2012, paddy fields significantly decreased by 31%, whereas urban areas 137significantly increased by 368% (see Appendix A: Fig. 1 and Table 1). In the study area, 138semi-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 139serrata), by periodic mowing (Uchida & Ushimaru, 2014). Although the map from ca. 1910 was 140141used to illustrate the process of urbanization over the last century and to calculate changes in 142urban 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 143plots per site) along the rural-urban gradient based on the prepared geographic maps (Fig. 1). The 144

145	rural-urban gradient was based on the extent of urban area surrounding each site, and is shown in
146	Fig.1. We then calculated the extent of the urban area within 500-m and 1-km radii of the center of
147	each site for the statistical analyses (see Appendix A: Fig. 2). We identified a significant
148	correlation between the urban areas within the 500-m and the 1-km radii ($R^2 = 0.92$, $p < 0.01$; R^2
149	value was calculated by Pearson's correlation and p value was tested by generalized linear model
150	(GLM) with the Wald test); thus, we used the 1-km radius model in this study. The 20 sites were
151	separated from one another by varying distances (Fig. 1), with a minimum distance of 1.2 km to
152	avoid pseudoreplication. The three plots in each site were selected depending on area of
153	continuous unfragmented habitat. Correlations between the distances of the three plots at each site
154	and the urban gradient were not significant ($p > 0.1$; GLM with the Wald test). In addition,
155	analysis of the landscape within a 1-km radius allowed us to compare our results with those of
156	previous studies, which also examined the alpha diversity of grassland butterflies in similarly
157	sized areas (Collinge, Prudic, & Oliver, 2003), including our previous reports on the alpha and
158	beta diversity of semi-natural grasslands around paddy fields (Uchida & Ushimaru, 2014, 2015).
159	
160	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

169	semi-natural grasslands but were used a few times a year on crops at all sites. In most cases, the
170	same farmer managed the semi-natural grasslands at each paddy site. We examined water content
171	to represent soil environmental variables in the 60 plots. We collected three soil core (5 cm
172	diameter, 5 cm depth) samples from three locations in each plot in mid-September. First, we mixed
173	the three fresh soil samples from each plot into a single sample and weighed the sample. Then, the
174	soil samples from all 60 plots were oven-dried at 70 °C for 72 h, weighed again and sieved (< 2
175	mm). We then calculated the soil water content using the fresh and dry weights of each soil sample
176	(Nagata & Ushimaru, 2016). The disturbance frequency increased with increasing urban area
177	within the 1-km radius of the center of each site (see Appendix A: Fig. 3, $R^2 = 0.14$, $P < 0.05$,
178	according to Pearson's correlation and GLM with Wald test). Correlations between environmental
179	factors (focal habitat area and soil water content) and urban area within the 1-km radius of the
180	center of each site were not significant (see Appendix A: Fig. 3, $P > 0.1$, GLM with the Wald test).
181	Although we detected a significant correlation between disturbance frequency and urbanization,
182	previous studies implied that many unexpected variables (e.g., climatic fluctuation due to
183	urbanization) could negatively affect biodiversity. Therefore, we used the urban gradient as an
184	indicator of anthropogenic activity, including disturbance frequency, in this study.
185	
186	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

193	in each plot were recorded (three 3×20 m plots in each site). We recorded names of flowering
194	plant species and counted number of flowering individuals of each species in each plot (entire 3 \times
195	20 m plot area). Butterflies were observed for 15 min per plot (45 min per site) under sunny and
196	warm condition. All butterflies were counted within the plots, and some of them were caught
197	using a sweep-net to be identified and released, if necessary (Pollard & Yates, 1994; Uchida &
198	Ushimaru, 2014). We spent the enough time (15 min per plot) to survey the butterfly species and
199	to avoid double counting for preventing effect of survey methods on the diversity metrics.
200	Based on the data collected from the surveys, lists of flowering plant and butterfly species
201	were prepared for each plot in each of the four time-periods (late April, early June, mid-July, and
202	mid-September 2014). In total, we identified 295 flowering plant species, and 43 butterfly species
203	(875 individuals).
204	We distinguished the seasonality of flowering plant and butterfly species by separating them
205	into three groups based on classifications in field guides (see Appendix B; Hayashi, 1989; Satake
206	et al., 1999; Shirouzu, 2006; Japan Butterfly Conservation Society, 2012): short flowering
207	period/short flight period (i.e., the species is found in a particular season (one or two months) over
208	the course of a year), intermediate flowering period/ intermediate flight period (i.e., found in two
209	seasons (three or four months) over the course of a year), and long flowering period/ long flight
210	period (i.e., found any time (more than five months) over the course of a year).
211	In addition, we classified plants and butterflies with different life-history traits based on their
212	response to the rural-urban gradient. Plant species were divided into two groups: annual and
213	perennial plants. Butterfly species were divided based on their life history traits, i.e., uni- and
214	multi-voltinism (see Appendix B). Because not all species respond equally to land-use changes in
215	semi-natural grasslands, it is essential to address the different responses of species and/or
216	ecological trait groups to understand the mechanisms that drive species loss (Pykälä, 2005; Uchida

217 & Ushimaru, 2014; Knop, 2016).

218

219 Statistical analyses

220

221 Calculations of alpha diversity and two components of beta diversity

The alpha diversity of plants and butterflies was calculated as average species richness per 222each survey in each site. Next, we calculated two different beta diversity indices in each site to 223224examine changes in species composition due to urbanization. Additive partitioning of species 225richness (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., 2262272002; Veech & Crist, 2010). The turnover components of Jaccard dissimilarity (β_{tu}) utilize species 228composition to assess whether changes in beta diversity are caused by a loss of species 229replacement (Baselga, 2012).

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

231
$$\beta_{add} = \frac{1}{N} \sum_{i=1}^{N} (\gamma - \alpha_i),$$

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).

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

237
$$\beta_{tu} = \frac{2\left[\sum_{i < j} \min(b_{ij}, b_{ji})\right]}{\left[\sum_{i} S_{i} - S_{T}\right] + 2\left[\sum_{i < j} \min(b_{ij}, b_{ji})\right]},$$

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.

245

246 *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 247248and the two components of beta diversity in plant and butterfly communities at each site along the 249rural-urban gradient. The response variables were alpha-, β_{add} -, and β_{tu} - diversity in plants 250(Gaussian error and identity link) and butterflies (Gaussian error and identity link). The 251explanatory variable was the extent of urban area within a 1-km radius at each site. We identified 252whether sites occurred in coastal or valley areas (Fig. 1), and used this designation as a random 253term, because the study sites were spread over a broad geographic range; therefore, we nested 254variation in site location to analyze the GLMM. Note, we could not examine the relationships 255between the species traits of butterflies and the rural-urban gradient, because there was insufficient 256statistical 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 257gamma diversity (i.e., total diversity over the course of a year). In the GLMM, the response 258259variable 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 260regression coefficients of the explanatory variables was determined using the Wald-test and R² 261

values (Nakagawa & Schielzeth, 2013).

263

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

266The 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 267the extent of urban gradient. The response variable was the proportion of seasonal types (short, 268intermediate, and long) to total plant and butterfly species richness in each plot. The explanatory 269270variable 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 271272sites occurred in coastal or valley areas (Fig. 1), and used this designation as a random term, 273because the study sites were spread over a broad geographic range; therefore, we nested variation 274in 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 R² values 275276(Nakagawa & Schielzeth, 2013). In addition, we examined the relationships between seasonal type 277and species life history traits for all species (plant: annual and perennial; butterfly: voltinism) 278using 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 R² values of the GLM and GLMM.

283

284

285 **Results**

286 *Alpha, two components of beta, and gamma diversity*

287	The alpha and beta diversity of flowering plants and butterflies (average species richness per
288	each survey, β_{add} , and β_{tu}) decreased with increasing extent of urban area (Fig. 2; see Appendix A:
289	Table 3). The diversity of alpha and β_{add} for plant and butterfly species were strongly positively
290	correlated with total diversity over the course of a year (i.e., gamma diversity), and butterfly β_{tu}
291	was positively correlated with gamma diversity (Table 1).
292	
293	Relationships between the proportion of seasonal type of plants and butterflies and the
294	rural-urban gradient
295	Short-flowering plant species significantly decreased with increasing extent of urban area (Fig.
296	3A, see Appendix A: Table 4), whereas long-flowering species significantly increased with
297	increasing extent of urban area (Fig. 3C, see Appendix A: Table 4). For butterfly species, short and
298	intermediate flight period species significantly and marginally significantly decreased with
299	increasing urban area, respectively (Fig. 3D, see Appendix A: Table 4), whereas long flight period
300	species significantly increased with increasing extent of urban area (Fig. 3F, see Appendix A:
301	Table 4). Annual species had significantly longer flowering period than perennial species (see
302	Appendix A: Fig. 4), and uni-voltine butterfly species had significantly shorter flight period than
303	multi-voltine species (see Appendix A: Fig. 4).
304	
305	
306	Discussion
307	
308	Biodiversity loss in the megacity
309	

310 The present study supported the hypothesis that losses of average species richness per each 311 survey and seasonal turnover of species composition are caused by increasing anthropogenic 312activities via urbanization. Many studies have shown that total and native species diversity 313 decreases with increasing habitat fragmentation and human population density (e.g., Clark, Reed, 314 & Chew, 2007; Fischer & Lindenmayer, 2007; Ramalho et al., 2014; Schmiedel, Bergmeier, & 315Culmsee, 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, & 316 317 Tothmeresz, 2010; Turrini & Knop, 2016). Discrepancies among studies could be explained by 318 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 319 larval host plants) are often abundant in urbanized environments, such as amenity plants along 320 321 roadside verges and private gardens (Salisbury et al., 2015). Second, other urban studies might 322underestimate the effect of urban extent on biodiversity. For example, although grassland quality 323 strongly influences butterfly richness and abundance, the extent of urban development (5–30%) 324surrounding grasslands is not related to species richness (Collinge, Prudic, & Oliver, 2003). And 325the relationship between human population presence and species richness (vertebrate and plant) 326 may be explained by scale dependence (Pautasso, 2007). Fine scale studies (sample unit is smaller 327 than ca. 1 km) tend to show that biodiversity is negatively collated with human presence. In the 328 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 329 330 urban extent. Future studies should investigate the gradient of urban extent/human populations and 331 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 332surrounding rural areas (Turini & Knop, 2016), which may be prevalent in agricultural landscapes 333

334	subject to intensive farming management (e. g., use of pesticides, disturbance from farm
335	machinery, or clear-cuts after harvesting). The present study supported the explanation that
336	arthropod diversity in more extensively managed agricultural areas, rather than in intensively
337	managed landscapes, exceeded that of urban diversity (Turini & Knop, 2016). We focused on the
338	Osaka-Kobe megacity, which was the world's seventh largest urban agglomeration in 2014
339	(United Nations, 2014). Our study suggests that semi-natural grasslands in the urban-dominated
340	landscapes have low average richness in a given season, as well as low temporal species turnover,
341	due to high anthropogenic effects on biodiversity at the local scale.
342	Although we detected a significant correlation between disturbance frequency and
343	urbanization, previous studies indicated that the examined environmental factors might not be
344	enough to explain decreases in species diversity. The urban area includes many unexpected
345	variables (e.g., climatic fluctuation) that could negatively affect biodiversity. Although high
346	diversity is exhibited in unique environments, such as nutrient-poor areas (Kleijn et al., 2009;
347	Uematsu & Ushimaru, 2013) and heterogeneous landscapes (Tscharntke et al., 2005; Uchida &
348	Ushimaru, 2015), all such species are negatively affected by anthropogenic activities. Further
349	studies are required to determine the mechanisms of biodiversity loss using other potential
350	variables of anthropogenic activities, especially when elucidating the relationship between
351	biodiversity and urbanization.
352	
353	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

358	specialists of flowering plant and butterfly species (i.e., species with short flowering/flight period)
359	decreased along the rural-urban gradient (Fig. 3). We showed that most values of beta diversity
360	were significantly correlated with total diversity over the course of a year (i.e., gamma diversity).
361	Recently, conceptual and empirical studies emphasized that beta diversity was not necessarily
362	correlated gamma diversity (Olden, 2006; Naaf & Wulf, 2010; Uchida & Ushimaru, 2015). These
363	studies suggested that community similarity between sites often increased with the increasing
364	species richness of each site (Naaf & Wulf, 2010). In other words, even if low beta diversity of
365	between season was observed in the given region, high alpha diversity resulted in high gamma
366	diversity. Our results indicated that both high alpha and high beta diversity of each survey season
367	contributes total diversity over the course of a year. To our knowledge, this study is the first to
368	demonstrate that the temporal heterogeneity of species composition is essential for the
369	conservation of biodiversity across two-trophic levels in the urban environment.
370	The present study supported the hypothesis that anthropogenic activities causes beta diversity
371	loss (e.g., Vellend et al., 2007; Ekroos, Heliölä, & Kuussaari, 2010; Uchida & Ushimaru, 2015). A
372	previous study on spatial heterogeneity suggested that a higher species turnover in rural areas than
373	in urban areas was driven by specialist species rather than generalist species (Knop, 2016).
374	Urbanization leads to the local extinctions of infrequent and specialist butterfly species, including
375	temporal specialists (Clark, Reed, & Chew, 2007; Soga & Koike, 2012; Ramírez-Restrepo &
376	MacGregor-Fors, 2017). We suggest that seasonal generalist species with short generation times
377	favor urbanized environmental conditions (e.g., plants, Albrecht & Haider, 2013; butterflies,
378	Takami et al., 2004). According to the r/K species concept (Pianka, 1970), species with rapid
379	regeneration times tolerate a high frequency or magnitude of disturbance. Declines in the temporal
380	heterogeneity of flowering plant species along the rural-urban gradient may have been caused by
381	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 388 period of each species (short, intermediate, and long). In the present study, we noted that 68% of 389 short flowering period plants (64 species) and 100% of short flight period butterflies (five species) 390 were categorized in seasonal species of spring to early summer (March to early July) according to 391field guides (Hayashi, 1989; Satake et al., 1999; Shirouzu, 2006; Japan Butterfly Conservation 392 393 Society, 2012). These results indicate that researchers and policy makers should pay attention to 394 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 395396 periods caused negative effects on reproductive success of grassland plant species. Although 397 recent studies emphasized that seasonal variation of species diversity was one of significant issues 398 in ecology (La Sorte, Tingley, & Hurlbert, 2014; Uchida & Ushimaru 2015; Graves et al. 2016), 399 very few studies have shown that human activities exert clear negative impacts on seasonal 400 variation of species diversity. This lack of information remains major issues for biodiversity 401 conservation.

402

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

406	Previous studies have indicated the importance of maintaining spatio-temporal heterogeneity
407	in semi-natural biodiversity conservation (Benton, Vickery, & Wilson, 2003; Tscharntke et al.,
408	2005; Uchida & Ushimaru, 2015). The loss of temporal variability in resource availability may
409	limit the seasonal distribution of species from higher-trophic levels. For instance, species that
410	provide pollination services are enhanced by the seasonality of plant activity (Tylianakis, Klein, &
411	Tscharntke, 2005; Diaz et al., 2007; Kremen et al., 2007; Ushimaru, Kobayashi, & Dohzono,
412	2014). In addition, some relationships between biodiversity and cultural ecosystem services (e.g.,
413	people interested in wild flower viewing) stem from these temporal dynamics (Graves, Pearson, &
414	Turner, 2017). Furthermore, temperate countries in Monsoon Asia, including Japan, exhibit four
415	distinct seasons, in which the temporal turnover of biological activities has been fostered by
416	certain aspects of the local cultures (Ministry of the Environment of Japan, 2016).
417	In East Asia and globally, high biodiversity has been maintained in semi-natural ecosystems,
418	supporting many endangered species, despite several types of land-use changes causing rapid
419	decreases in diversity in recent decades (Foley et al., 2005; Kleijn et al., 2011; Koyanagi &
420	Furukawa, 2013; Uematsu & Ushimaru, 2013; Uchida & Ushimaru, 2014). The use of extensive
421	traditional management systems has been largely abandoned due to agricultural intensification and
422	rapid urbanization in the mega-cities of Monsoon Asia, and globally. However, data on
423	biodiversity in megacities remain limited worldwide; thus, more focused research is needed to
424	study how urbanization affects biodiversity. In conclusion, future studies need to test whether
425	temporal biological heterogeneity affects total biodiversity over the course of a year along the
426	rural-urban gradient at a global scale.
427	

- 428

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400

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435	
436	Appendix A. Supplementary data
437	Supplementary data associated with this article can be found, in the online version, at
438	https://doi.org/XXXXX
439	
440	
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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

600 component of Jaccard dissimilarity). The significance of the explanatory variables was estimated using the Wald-test and calculated R^2

601 values.

602

					Gamma diversity						
			Plants		Butterflies						
Response variables	Estimated coefficient	t-value	Р	R^2	Estimated coefficient	t-value	Р	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			

603

605 Figure legends

607	Fig. 1. The study was conducted in the south-eastern part of Hyogo Prefecture, Japan ($\sim 25 \times 30 \text{ km}^2$,
608	34°48'-57' N, 135°03'-24' E). In the study area, semi-natural grasslands were maintained by
609	periodic mowing on the levees of paddy fields and ponds and at the edges between paddy fields
610	and secondary forests (paddy fields: blue; secondary forests and grassland: light green; residential
611	lands and artificial lands: grey). The number in the circle represents the site's rank along the
612	rural-urban gradient, with site 01 having the lowest extent of urban area in the surrounding habitat
613	(1-km radius). Sites 01 to 13 were located in a valley area, whereas sites 14 to 20 were located in a
614	coastal area. This information was used for analyses (see Material and methods section).
615	
616	Fig. 2. Relationships between diversity components (average species richness per each survey at each
617	site, beta diversity of additive partitioning of species richness, and beta diversity of turnover
618	component of Jaccard dissimilarity) of flowering plant and butterfly species in each site along the
619	rural-urban gradient. Solid lines represent significant coefficients at $P < 0.05$ estimated by the
620	Wald-test (see Appendix A: Table 3).
621	
622	Fig. 3. Relationships between the proportion of seasonal type (short, intermediate, and long
623	flowering/flight period) to total plant and butterfly species richness in each plot along the rural-urban
624	gradient. Solid lines represent significant coefficients at $P < 0.05$, the dashed line represents
625	marginally significant coefficients at $P < 0.1$ estimated by the Wald-test (see Appendix A: Table 4).
626	









- 692

- 1 Appendix A.
- $\mathbf{2}$
- 3 **Table 1.** Comparisons of area by land use (forests, paddy fields, urban areads, and others) between ca. 1910 and 2012.
- 4

		ca. 1910		2012	% of	
	area (km ²)	% of study area	area (km ²)	% of study area	maintaining areas	
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	

- 7 **Table 2.** Monthly values of temperature, humidity, and rainfall for April, June, July, and September
- 8 2014 in the study area.
- 9

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

11 parameters (average species richness per each survey, beta diversity of additive partitioning of species richness, and beta diversity of turnover

- 12 component of Jaccard dissimilarity). The significance of explanatory variables was estimated using the Wald-test and calculated R² values.

					Urban gradient						
	Plants				Butterflies						
Response variables	Estimated coefficient	t-value	Р	R ²	Estimated coefficient	t-value	Р	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 response18parameters of the proportion of seasonality type (short, intermediate, and long flowering/flight period) of total plant or butterfly species19richness in each plot along the rural-urban gradient. The significance of the explanatory variables were estimated using the Wald-test and20calculated R^2 values.

							Urban	gradient
	Plants						В	utterflies
Response variables	Estimated coefficient	t-value	Р	R^2	Estimated coefficient	t-value	Р	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



33 Fig. 1. Changes in the urban, paddy and forest areas from ca. 1910 to 2012 in the study area

(south-eastern Hyogo Prefecture, Japan, $\sim 30 \times 40$ km²). 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).



58 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 % (0.39km²). We surveyed semi-natural

60 grasslands surrounding agricultural lands. Blue: paddy fields, light green: secondary forests, grey:

61 residential lands and artificial lands, and white and yellow: other.

- 62
- 63
- 64
- 65
- 66
- 67
- 0.7
- 68





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.

- 1 Appendix B.
- $\mathbf{2}$
- 3 Table 1. This table shows the category of flowering period and months of appearance at each species in the present study. We investigated
- 4 flowering period using field guides as follows.
- $\mathbf{5}$
- 6 Satake, Y., Ooi, J., Kitamura, S., Watari, S., Tominari, T. 1999. Wild flowers of Japan Herbaceous Plants I, II, and III. Heibonsha, Tokyo,
- 7 Japan. (in Japanese)
- 8 Hayashi, Y. 1989. Wild flowers of Japan; Plains, seaside and hills. Yama-Kei publishers, Tokyo, Japan. (in Japanese)
- 9

Family name	Species name	Category of seasonality	Mon appearar stu	ths of nce in the 1dy	Life-history form
Acanthaceae	Justicia procumbens L. var. procumbens	М		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	<i>Cyclospermum leptophyllum</i> (Pers.) Sprague ex Britton et P.Wilson	NA	5		annual
Apiaceae	Sium ninsi L.	S		9	perennial
Apiaceae	Torilis japonica (Houtt.) DC.	Μ	6	7	annual

Apocynaceae	Vincetoxicum glabrum (Nakai) Kitag.	М				9	perennial
Apocynaceae	Vincetoxicum pycnostelma Kitag.	S		6	7	9	perennial
Aquifoliaceae	Ilex serrata Thunb.	М		6			woody
Araceae	Pinellia ternata (Thunb.) Breitenb.	М	5				perennial
Araliaceae	Hydrocotyle ramiflora Maxim.	М		6	7		perennial
Asteraceae	Achillea millefolium L.	М		6			perennial
Asteraceae	<i>Artemisia indica</i> Willd. var. <i>maximowiczii</i> (Nakai) H.Hara	S				9	perennial
Asteraceae	Artemisia japonica Thunb.	Μ			7		perennial
Asteraceae	Aster ageratoides Turcz. subsp. amplexifolius Kitam., excl. syn.	М				9	perennial
Asteraceae	Aster rugulosus Maxim.	М				9	perennial
Asteraceae	Aster scaber Thunb.	М				9	perennial
Asteraceae	Aster yomena (Kitam.) Honda	М				9	perennial
Asteraceae	Atractylodes japonica Koidz. ex Kitam.	S				9	perennial
Asteraceae	Bidens frondosa L.	S				9	annual
Asteraceae	Bidens pilosa L. var. pilosa	М				9	annual
Asteraceae	Cirsium japonicum Fisch. ex DC.	М	5	6	7	9	perennial
Asteraceae	Cirsium sieboldii Miq.	S				9	perennial
Asteraceae	Conyza canadensis (L.) Cronquist	М				9	annual
Asteraceae	Coreopsis lanceolata L.	М		6	7		perennial
Asteraceae	Crassocephalum crepidioides (Benth.) S.Moore	М				9	annual
Asteraceae	Eclipta alba (L.) Hassk.	М				9	annual
Asteraceae	Eclipta thermalis Bunge	М				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.	М			7	9	perennial
Asteraceae	Eupatorium makinoi T.Kawahara et Yahara	М				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	М	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.	Μ			7		perennial
Asteraceae	Ixeridium dentatum (Thunb.) Tzvelev subsp. dentatum	М	5	6	7		perennial
Asteraceae	Ixeris japonica (Burm.f.) Nakai	Μ	5	6			perennial
Asteraceae	Lactuca indica L. var. laciniata (Houtt.) H.Hara	Μ				9	annual
Asteraceae	<i>Lapsanastrum apogonoides</i> (Maxim.) J.H.Pak et K.Bremer	М	5	6			annual
Asteraceae	<i>Lapsanastrum humile</i> (Thunb.) J.H.Pak et K.Bremer	М	5	6	7		annual
Asteraceae	Leibnitzia anandria (L.) Turcz.	L	5				perennial
Asteraceae	<i>Picris hieracioides</i> L. subsp. <i>japonica</i> (Thunb.) Krylov	L		6	7		annual
Asteraceae	Senecio vulgaris L.	L		6			annual
Asteraceae	<i>Solidago virgaurea</i> L. subsp. <i>asiatica</i> (Nakai ex H.Hara) Kitam. ex H.Hara	М				9	perennial
Asteraceae	Sonchus asper (L.) Hill	L	5				annual
Asteraceae	Sonchus oleraceus L.	L	5	6			annual
Asteraceae	<i>Synurus palmatopinnatifidus</i> (Makino) Kitam. var. <i>palmatopinnatifidus</i>	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	<i>Tephroseris integrifolia</i> (L.) Holub subsp. <i>kirilowii</i> (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	<i>Trigonotis peduncularis</i> (Trevir.) Benth. ex Hemsl.	Μ	5	6			annual
Brassicaceae	Capsella bursa-pastoris (L.) Medik.	М	5			9	annual

Cardamine flexuosa With.	М	5			9	annual
Lepidium virginicum L.	S	5	6			annual
Rorippa indica (L.) Hiern	L	5	6	7	9	annual
Rorippa palustris (L.) Besser	Μ	5	6	7		annual
<i>Thlaspi arvense</i> L.	Μ			7		annual
Adenophora triphylla (Thunb.) A.DC. subsp. aperticampanulata Kitam.	М				9	perennial
Campanula punctata Lam. var. punctata	S			7		perennial
Platycodon grandiflorus (Jacq.) A.DC.	S				9	perennial
Triodanis perfoliata (L.) Nieuwl.	S		6			annual
Cerastium fontanum Baumg. subsp. vulgare						
(Hartm.) Greuter et Burdet var. <i>angustifolium</i> (Franch.) H.Hara	S	5	6	7		perennial
Cerastium glomeratum Thuill.	S	5				annual
Dianthus superbus L. var. longicalycinus (Maxim.) F.N.Williams	М			7	9	perennial
Sagina japonica (Sw.) Ohwi	L	5	6			annual
Stellaria aquatica (L.) Scop.	L		6			perennial
Stellaria neglecta Weihe	L	5	6		9	annual
<i>Stellaria uliginosa</i> Murray var. <i>undulata</i> (Thunb.) Fenzl	L	5				annual
Commelina communis L.	Μ		6	7	9	annual
Tradescantia reflexa Raf.	NA		6			annual
Calystegia pubescens Lindl. f. major (Makino) Yonek.	S		6	7		perennial
Ipomoea lacunosa L.	NA				9	annual
Sedum bulbiferum Makino	S		6			annual
Carex arenicola F.Schmidt	S	5	6			perennial
Carex biwensis Franch.	Μ	5				perennial
Carex capillacea Boott	Μ	5				perennial
Carex dickinsii Franch. et Sav.	S			7		perennial
	Cardamine flexuosa With. Lepidium virginicum L. Rorippa indica (L.) Hiern Rorippa palustris (L.) Besser Thlaspi arvense L. Adenophora triphylla (Thunb.) A.DC. subsp. aperticampanulata Kitam. Campanula punctata Lam. var. punctata Platycodon grandiflorus (Jacq.) A.DC. Triodanis perfoliata (L.) Nieuwl. Cerastium fontanum Baumg. subsp. vulgare (Hartm.) Greuter et Burdet var. angustifolium (Franch.) H.Hara Cerastium glomeratum Thuill. Dianthus superbus L. var. longicalycinus (Maxim.) F.N.Williams Sagina japonica (Sw.) Ohwi Stellaria aquatica (L.) Scop. Stellaria neglecta Weihe Stellaria uliginosa Murray var. undulata (Thunb.) Fenzl Commelina communis L. Tradescantia reflexa Raf. Calystegia pubescens Lindl. f. major (Makino) Yonek. Ipomoea lacunosa L. Sedum bulbiferum Makino Carex arenicola F.Schmidt Carex biwensis Franch. Carex dickinsii Franch. et Sav.	Cardamine flexuosa With.MLepidium virginicum L.SRorippa indica (L.) HiernLRorippa palustris (L.) BesserMThlaspi arvense L.MAdenophora triphylla (Thunb.) A.DC. subsp. aperticampanulata Kitam.MCampanula punctata Lam. var. punctataSPlatycodon grandiflorus (Jacq.) A.DC.STriodanis perfoliata (L.) Nieuwl.SCerastium fontanum Baumg. subsp. vulgareS(Hartm.) Greuter et Burdet var. angustifoliumSCerastium glomeratum Thuill.SDianthus superbus L. var. longicalycinusM(Maxim.) F.N.WilliamsMStellaria aquatica (L.) Scop.LStellaria neglecta WeiheLStellaria uliginosa Murray var. undulata (Thunb.)LFenzlCCommelina communis L.MTradescantia reflexa Raf.NACalystegia pubescens Lindl. f. major (Makino) Yonek.SCarex arenicola F.SchmidtSCarex dickinsii Franch. et Sav.S	Cardamine flexuosa With.M5Lepidium virginicum L.S5Rorippa indica (L.) HiernL5Rorippa palustris (L.) BesserM5Thlaspi arvense L.M4Adenophora triphylla (Thunb.) A.DC. subsp. aperticampanulata Kitam.MCampanula punctata Lam. var. punctataSPlatycodon grandiflorus (Jacq.) A.DC.STriodanis perfoliata (L.) Nieuwl.SCerastium fontanum Baumg. subsp. vulgare(Hartm.) Greuter et Burdet var. angustifolium(Hartm.) Greuter et Burdet var. angustifoliumSSigina japonica (Sw.) OhwiLSitellaria aquatica (L.) Scop.LStellaria aquatica (L.) Scop.LStellaria neglecta WeiheLCommelina communis L.MTradescantia reflexa Raf.NACalystegia pubsecens Lindl. f. major (Makino) Yonek.SIpomoea lacunosa L.NASedum bulbiferum MakinoSCarex arenicola F.SchmidtSScarex arenicola F.SchmidtMSedur bulbiferum Stranch.MSedur bulbiferum Stranch.MSedur bulbiferum MakinoSCarex dickinsii Franch. et Sav.S	Cardamine flexuosa With.M5Lepidium virginicum L.S56Rorippa indica (L.) HiernL56Rorippa palustris (L.) BesserM56Thlaspi arvense L.M56Adenophora triphylla (Thunb.) A.DC. subsp.M5aperticampanulata Kitam.M5Campanula punctata Lam. var. punctataS7Platycodon grandiflorus (Jacq.) A.DC.S6Cerastium fontanum Baumg. subsp. vulgare6(Hartm.) Greuter et Burdet var. angustifoliumS5Dianthus superbus L. var. longicalycinusM(Maxim.) F.N.WilliamsMSagina japonica (Sw.) OhwiL56Stellaria aquatica (L.) Scop.L56Stellaria neglecta WeiheL56Commelina communis L.M66Ipomoea lacunosa L.NA6Carex arenicola F.SchmidtS56Carex dickinsii Franch.M56Carex dickinsii Franch.M56	$\begin{array}{c c c c c c c c c c c c c c c c c c c $	Cardamine flexuosa With.M59Lepidium virginicum L.S567Rorippa indica (L.) HiernL567Rorippa palustris (L.) BesserM567Inlaspi arvense L.M77Adenophora triphylla (Thunb.) A.DC. subsp. aperticampanulata Kitam.M7Campanula punctata Lam. var. punctataS7Platycodon grandiflorus (Jacq.) A.DC.S6Cerastium fontanum Baumg. subsp. vulgare9Triodanis perfoliata (L.) Nieuwl.S6Cerastium fontanum Baumg. subsp. vulgare79(Hartm.) Greuter et Burdet var. angustifoliumS56Cerastium glomeratum Thuill.S56Sagina japonica (Sw.) OhwiL56Stellaria aquatica (L.) Scop.L6Stellaria aquatica (Sw.) OhwiL56Stellaria aquatica (L.) Scop.L56Stellaria neglecta WeiheL56Commelina communis L.M67Mandescantia reflexa Raf.NA6Carbystegia pubescens Lindl. f. major (Makino) Yonek.S6Sedum bulbiferum MakinoS67Carex arenicola F.SchmidtS56Carex tariencia a BoottM55Carex dickinstii Franch. et Sav.S7

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

Dioscoreaceae	Dioscorea japonica Thunb.	S			7		perennial
Droseraceae	<i>Drosera peltata</i> Thunb. var. <i>nipponica</i> (Masam.) Ohwi	S		6			perennial
Droseraceae	Drosera rotundifolia L.	М		6	7		perennial
Ericaceae	Rhododendron kaempferi Planch. var. kaempferi	М	5				woody
Ericaceae	Rhododendron macrosepalum Maxim.	S	5				woody
Euphorbiaceae	Acalypha australis L.	Μ				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	М				9	annual
Fabaceae	Astragalus sinicus L.	Μ	5				annual
Fabaceae	Desmodium paniculatum (L.) DC.	S				9	annual
Fabaceae	Desmodium podocarpum DC. subsp. oxyphyllum (DC.) H.Ohashi	М				9	perennial
Fabaceae	Dunbaria villosa (Thunb.) Makino	S				9	perennial
Fabaceae	<i>Glycine max</i> (L.) Merr. subsp. <i>soja</i> (Siebold et Zucc.) H.Ohashi	S				9	annual
Fabaceae	Indigofera pseudotinctoria Matsum.	Μ			7	9	woody
Fabaceae	Kummerowia striata (Thunb.) Schindl.	S				9	annual
Fabaceae	Lespedeza bicolor Turcz.	Μ			7	9	woody
Fabaceae	Lespedeza cuneata (Dum.Cours.) G.Don	Μ				9	perennial
Fabaceae	Lespedeza pilosa (Thunb.) Siebold et Zucc.	Μ				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.	Μ	5	6			annual
Fabaceae	Trifolium dubium Sibth.	Μ	5				annual
Fabaceae	Trifolium pratense L.	М		6			perennial

Fabaceae	Trifolium repens L.	L	5	6	7	9	perennial
Fabaceae	Vicia hirsuta (L.) Gray	М	5				annual
Fabaceae	Vicia sativa L. subsp. nigra (L.) Ehrh.	М	5	6			annual
Fabaceae	Vicia tetrasperma (L.) Schreb.	S	5				annual
Fumariaceae	Corydalis incisa (Thunb.) Pers.	М	5				annual
Gentianaceae	<i>Gentiana scabra</i> Bunge var. <i>buergeri</i> (Miq.) Maxim. ex Franch. et Sav.	М				9	perennial
Gentianaceae	Swertia japonica (Schult.) Makino	Μ				9	annual
Geraniaceae	Geranium carolinianum L.	М	5	6	7		annual
Geraniaceae	Geranium thunbergii Siebold ex Lindl. et Paxton	М				9	perennial
Haloragaceae	Haloragis micrantha (Thunb.) R.Br.	М				9	perennial
Hemerocallidacea e	<i>Hemerocallis citrina</i> Baroni var. <i>vespertina</i> (H.Hara) M.Hotta	М			7		perennial
Hemerocallidacea e	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.	М		6			woody
Hypericaceae	Hypericum erectum Thunb.	М			7	9	perennial
Hypericaceae	Hypericum laxum (Blume) Koidz.	М			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	М	5	6	7		perennial
Juncaceae	Luzula capitata (Miq.) Miq. ex Kom.	S	5	6			perennial
Juncaceae	Luzula multiflora (Ehrh.) Lejeune	М	5				perennial
Lamiaceae	Ajuga decumbens Thunb.	М	5	6	7		perennial
Lamiaceae	<i>Clinopodium chinense</i> (Benth.) Kuntze subsp. grandiflorum (Maxim.) H.Hara	S			7	9	perennial
Lamiaceae	Clinopodium gracile (Benth.) Kuntze	М	5	6	7	9	perennial

Lamiaceae	<i>Glechoma hederacea</i> L. subsp. <i>grandis</i> (A.Gray) H.Hara	S	5				perennial
Lamiaceae	Isodon inflexus (Thunb.) Kudô	S				9	perennial
Lamiaceae	Lamium amplexicaule L.	Μ	5				annual
Lamiaceae	Lamium purpureum L.	S	5				annual
Lamiaceae	Lycopus maackianus (Maxim. ex Herder) Makino	М				9	perennial
Lamiaceae	<i>Mentha canadensis</i> L. var. <i>piperascens</i> (Malinv. ex Holmes) H.Hara	М			7		perennial
Lamiaceae	<i>Prunella vulgaris</i> L. subsp. <i>asiatica</i> (Nakai) H.Hara	М		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	<i>Tricyrtis macropoda</i> Miq. subsp. <i>affinis</i> (Makino) Kitam.	М				9	perennial
Linderniaceae	Lindernia procumbens (Krock.) Borbás	М				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.	Μ			7		perennial
Nartheciaceae	Aletris spicata (Thunb.) Franch.	М		6	7		perennial
Onagraceae	Ludwigia epilobioides Maxim.	М				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	М		6	7		perennial
Orchidaceae	Platanthera minor (Miq.) Rchb.f.	S			7		perennial
Orchidaceae	Pogonia minor (Makino) Makino	Μ		6			perennial
Orchidaceae	Spiranthes sinensis (Pers.) Ames subsp. australis (R.Br.) Kitam., excl. basion.	L			7	9	perennial
Orobanchaceae	<i>Melampyrum roseum</i> Maxim. var. <i>japonicum</i> Franch. et Sav.	М		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.	Μ	5	6	7		annual
Plantaginaceae	Veronica arvensis L.	Μ	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	М	5	6	7		annual
Poaceae	Andropogon virginicus L.	Μ				9	perennial
Poaceae	Anthoxanthum odoratum L.	Μ		6			perennial
Poaceae	Arundinella hirta (Thunb.) Tanaka	М				9	perennial

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

Poaceae	Paspalum thunbergii Kunth ex Steud.	Μ		6	7	9	perennial
Poaceae	Paspalum urvillei Steud.	NA				9	perennial
Poaceae	Pennisetum alopecuroides (L.) Spreng.	Μ				9	perennial
Poaceae	Phragmites australis (Cav.) Trin. ex Steud.	Μ				9	perennial
Poaceae	Phragmites japonicus Steud.	Μ				9	perennial
Poaceae	Poa acroleuca Steud.	Μ	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	М				9	annual
Poaceae	Setaria faberi R.A.W.Herrm.	М			7	9	annual
Poaceae	Setaria glauca (L.) P.Beauv. var. pallidefusca (Schumach.) T.Koyama	Μ				9	annual
Poaceae	Setaria pumila (Poir.) Roem. et Schult.	М				9	annual
Poaceae	Setaria viridis (L.) P.Beauv.	М			7	9	annual
Poaceae	Sorghum halepense (L.) Pers.	М			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.	Μ	5	6			perennial
Polygonaceae	Persicaria longiseta (Bruijn) Kitag.	L	5		7	9	annual
Polygonaceae	Polygonum sieboldii	Μ				9	annual
Polygonaceae	<i>Rumex acetosa</i> L.	Μ	5	6			perennial
Polygonaceae	Rumex acetosella L. subsp. pyrenaicus (Pourret ex Lapeyr.) Akeroyd	М		6			perennial
Polygonaceae	Rumex japonicus Houtt.	М	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	<i>Ranunculus silerifolius</i> H.Lév. var. glaber (H.Boissieu) Tamura	L	5	6	7	9	perennial
Ranunculaceae	<i>Thalictrum minus</i> L. var. <i>hypoleucum</i> (Siebold et Zucc.) Miq.	М			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.	Μ		6	7		woody
Rosaceae	Sanguisorba officinalis L.	Μ				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	Μ	5		7	9	perennial
Salicaceae	Salix sieboldiana Blume	S	5				woody
Santalaceae	Thesium chinense Turcz.	Μ	5	6	7		perennial
Saururaceae	Houttuynia cordata Thunb.	S		6	7		perennial
Saxifragaceae	Astilbe microphylla Knoll	Μ			7		perennial
Saxifragaceae	Chrysosplenium grayanum Maxim.	S	5				perennial
Solanaceae	Solanum ptychanthum Dunal	L			7	9	annual
Thymelaeaceae	Diplomorpha trichotoma (Thunb.) Nakai	Μ				9	woody
Urticaceae	Boehmeria spicata (Thunb.) Thunb.	Μ			7	9	woody

Valerianaceae	Patrinia scabiosifolia Fisch. ex Trevir.	М	9	perennial
Valerianaceae	Valerianella locusta (L.) Laterr.	S	5	annual
Verbenaceae	Verbena brasiliensis Vell.	М	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.	М	7	perennial

12 **Table 2.** This table shows the category of flight period and months of appearance at each species in the present study. We investigated flight

13 period using field guides as follows.

14

- 15 Shirouzu, T. 2006. The butterflies of Japan in color. In Japanese. Gakken Holdings, Tokyo, Japan. (in Japanese)
- 16 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	app	Months of appearance in the study			Voltinism U: uni, M: multi
Papilionidae	Graphium sarpedon (Linnaeus, 1758)	L				9	М
Papilionidae	Papilio dehaanii C. & R. Felder, 1864	L	4				Μ
Papilionidae	Papilio helenus Linnaeus, 1758	Μ		6			М
Papilionidae	Papilio machaon Linnaeus, 1758	L	4	6		9	Μ
Papilionidae	Papilio protenor Cramer, 1775	L	4	6			М
Papilionidae	Papilio xuthus Linnaeus, 1767	L	4	6	7	9	Μ
Pieridae	Anthocharis scolymus Butler, 1866	S	4				U
Pieridae	Colias erate (Esper, 1805)	L	4	6	7	9	М
Pieridae	Eurema mandarina (de l'orza, 1869)	L	4	6	7	9	М
Pieridae	Pieris melete (Ménétriès, 1857)	L	4	6	7	9	М
Pieridae	Pieris rapae (Linnaeus, 1758)	L	4	6	7	9	М
Lycaenidae	Celastrina argiolus (Linnaeus, 1758)	L		6		9	М
Lycaenidae	Callophrys ferrea (Butler, 1866)	S	4				U

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

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