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RESEARCH ARTICLE

Urbanised landscape and microhabitat differences can influence flowering phenology and synchrony in an annual herb

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Abstract

1. Flowering phenology, a crucial determinant of plant reproductive success and biotic interactions, is susceptible to urbanisation. Numerous studies have shown the impact of urbanised landscapes on flowering phenology based on comparisons along urban–rural gradients. Phenological patterns among microenvironments in the urban ecosystem have received less attention, although they often offer unique habitats with varying artificial influences, such as roadsides, drainage ditches and vacant lots. If differences in microenvironments diversify flowering phenology, the urban matrix might reduce flowering synchrony with neighbouring populations, limiting outcrossing opportunities and therefore reducing reproductive success.
2. We investigated the flowering phenology and synchrony of the native annual herb *Commelina communis* in approximately 250 populations at two rural and two urban sites over 3 years. To determine the effect of microhabitat differences, we categorised the microhabitats of *C. communis* populations into five types: drains, roadsides, vacant land, farmland and forest edge. In some study populations, we investigated reproductive success (seed set) to estimate the degree of outcross pollination limitation.
3. Our findings revealed that populations in urban sites exhibited earlier flowering onset and longer flowering duration compared to rural locations. Besides, we did not detect consistent patterns of flowering onset, peak and duration among the different microhabitat types. For flowering synchrony, we found that the population in urban sites, growing in drain habitats, and with artificial disturbances exhibited relatively lower interpopulation flowering synchrony, suggesting their phenology differed from neighbouring populations within the same landscape. Additionally, populations in urban sites, especially those growing in drain and roadside habitats, suffered severe outcross pollen limitation compared to those in rural landscapes.
4. *Synthesis and applications*. In conclusion, our results indicate that in addition to landscape changes associated with urbanisation, variations in local microhabitats also influence the flowering phenology and synchrony of *C. communis* populations. Urbanised landscapes and differences in microhabitats could contribute to the diversification of phenological patterns between populations,

potentially having a negative impact on the reproductive success of native plant species. These findings highlight the need to consider not only spatial but also temporal fragmentation from diversified flowering phenology when addressing conservation in the urban matrix.

KEYWORDS
artificial disturbance, *Commelina*, drainage ditches, flowering synchrony, roadside, ruderal plants, temporal fragmentation, urban ecology

1 | INTRODUCTION

The increase in human activity associated with urbanisation has considerably changed the landscape and local environments, and these changes are expected to intensify in the coming decades (McKinney, 2002; UN DESA, 2018). In addition to changes in physical conditions, such as an increase in temperature and atmospheric CO_2 concentrations, there have been changes in biotic conditions, represented by habitat loss and fragmentation of native species (Dobbs et al., 2017; Liu et al., 2016). Urban environments have received much attention from ecologists and evolutionary biologists in recent years because they are considered new ecosystems in themselves and provide a good opportunity to understand human impacts on ecosystems (Fukano et al., 2023; Johnson & Munshi-South, 2017; Yakub & Tiffin, 2017).

The flowering phenology of plant species, a key trait that responds to fluctuating environments, is considered to diversify in urban ecosystems (Fotiou et al., 2011; Roetzer et al., 2000). Neil and Wu (2006) reported that plants blooming in spring generally flower earlier in urban areas compared to nonurban habitats. A recent study showed that the urban environment drives the evolutionary change of later flowering, as well as the plastic response, in the annual *Trifolium repens* (Santangelo et al., 2020). In particular, elevated temperatures in urban environments (i.e. urban heat islands) are known to accelerate the flowering phenology, while various other factors, such as reduced soil moisture, increased CO_2 concentration and artificial light pollution, have also been shown to influence flowering phenology (Christmann et al., 2023; Luo et al., 2007; Meng et al., 2020; Wohlfahrt et al., 2019). Flowering phenology is considered to be an important factor for understanding urban ecosystems because changes in flowering phenology cause seasonal mismatches between plants and pollinators, which likely have negative effects on the viabilities of native plant and pollinator species (Bishop et al., 2024; Gérard et al., 2020; Kudo & Cooper, 2019). Such phenological mismatches are expected to increase globally with the future progress of urbanisation and climate change (Fisogni et al., 2020; Gordo & Sanz, 2005; Kudo & Ida, 2013; Manincor et al., 2023).

While there have been many studies on differences in plant phenology between rural areas, suburbs and urban centres (i.e. rural–urban gradients; Jia et al., 2021; Li et al., 2017; Neil et al., 2014), the differences between microhabitats in urban ecosystems have not been investigated (Neil & Wu, 2006). Although differences in phenology between microhabitats have rarely been studied in general, a previous study focusing on monocultural *Spartina alterniflora* in salt marshes reported that fine-scale microspatial differences in soil temperature influence its phenology (O'Connell et al., 2020). Urban ecosystems consist of various local microenvironments with different degrees of human impact, such as parks, roadsides and drains, providing new and unique habitats for both native and invasive plant species (Forman, 2014; Lundholm & Marlin, 2006; Taichi & Ushimaru, 2024). Among these microhabitats, if flowering phenology corresponds to fine-scale differences in physical environments and disturbance levels, this can lead to diversification of the flowering phenology of plant species living in them. Diversification between microhabitats could then reduce outcrossing opportunities and reproductive success due to phenological mismatches, not only with pollinators, but also with individuals and populations in close proximity. Therefore, reduced interpopulation synchrony between microhabitats may be an important determinant of plant population persistence in urban ecosystems.

In this study, we investigated the flowering phenology of the native annual herb *Commelina communis* and compared the populations growing in different microhabitats in rural and urban areas. *Commelina communis* is an ideal subject for this study because it is widely distributed in rural and urban environments and often grows in habitats that are heavily impacted by human activity, such as urban roadsides (Taichi & Ushimaru, 2024; Ushimaru et al., 2014). The flowering phenology of *C. communis*, which exhibits a long flowering duration from summer to autumn, is also characteristic of ruderal plants that grow in environments with high disturbance pressure. Here, we conducted 3 years of continuous surveys to detect robust patterns. We address the following questions: (1) Do the populations in different types of landscape (rural and urban) exhibit different flowering phenologies? (2) Do the populations in different microhabitat types exhibit different flowering phenologies? (3) Does the synchrony of flowering phenology within and between populations differ among landscapes and/or microhabitat types? (4) Does reproductive success differ among landscape and/or microhabitat types? We evaluated population reproductive success as the limitation of the outcrossing opportunities to examine its relationship with flowering synchrony. Based on these questions, we discuss the diversification of flowering phenology and its potential impact on population reproductive success, with the conservation and management of urban ecosystems.

2 | MATERIALS AND METHODS

2.1 | Study species

Commelina communis is an annual andromonoecious herb that grows near roadsides and rice fields in northeast Asia. An individual plant has many inflorescences, usually with three to five flowers and typically flowers from late June to October. A single flower opens daily from sunrise to noon. It exhibits self-compatibility and can be fertilised via autonomous self-pollination (Katsuhara & Ushimaru, 2019). Seed dispersal is by gravity (barochory). Some characteristics of this species, such as a mixed-mating system, one-day flower longevity and an extended flowering period from early summer to autumn, are typical of annual herbs growing in urban and semi-urban ecosystems, especially on agricultural grasslands and along roadsides (Baker, 1974; Gaba et al., 2017; Nagahama & Yahara, 2019). Species that often grow sympatrically with *C. communis* in Japan, such as *Persicaria thunbergii* (Polygonaceae), *Oxalis corniculata* (Oxalidaceae) and *Ipomoea coccinea* (Convolvulaceae), also exhibit similar reproductive characteristics and flowering phenology.

The flower is nectarless, providing pollen as a reward, and is visited by various pollinator taxa, such as bumblebees and syrphid flies (Morita & Nigorikawa, 1999; Ushimaru et al., 2009). It exhibits heteranthery with three types of stamen: two long brown stamens, one medium-length yellow stamen and three short yellow stamens; for a total of six stamens within a flower (Murakami et al., 2022). The long stamens, which are similar in length to the pistil, primarily contribute to pollination, while the medium and short stamens mainly function to provide pollen as a reward and to visually attract pollinators, respectively (Murakami et al., 2022; Ushimaru et al., 2007). Heteranthery, attractive blue petals, and the presence of a staminate flower suggest that pollinator-mediated outcrossing is important for this species (Murakami et al., 2022; Ushimaru et al., 2007).

In a study along a rural–urban gradient in the Osaka–Kobe metropolitan area, Japan, Ushimaru et al. (2014) showed that several urban populations of *C. communis* were visited relatively less frequently by pollinator insects and their flowers exhibit more self-pollination-like floral traits (lower stigma height and less separation between stigma and anther of a long stamen) compared to the rural population.

2.2 | Study sites

To examine the differences in phenological patterns between urban and rural environments, we established two rural (R1: 34° 77′83″ N, 133° 83′96′ E; R2: 34° 74′32′ N, 133° 87′67′ E) and two urban (U1: 34° 66′37′ N, 133° 89′80′ E; U2: 34° 64′79′ N, 133° 91′11′ E) sites in Okayama Prefecture, Japan (Figure 1). The location of these sites was carefully selected through examination of aerial photographs and preliminary investigation of surrounding areas to represent urban and rural landscapes in our region. The study areas were $0.5 \times 0.5\,\mathrm{km}^2$ and $0.5 \times 1.0\,\mathrm{km}^2$ for the rural and urban sites, respectively. The proportions of developed land area in each study site were calculated using QGIS based on land-use and land-cover

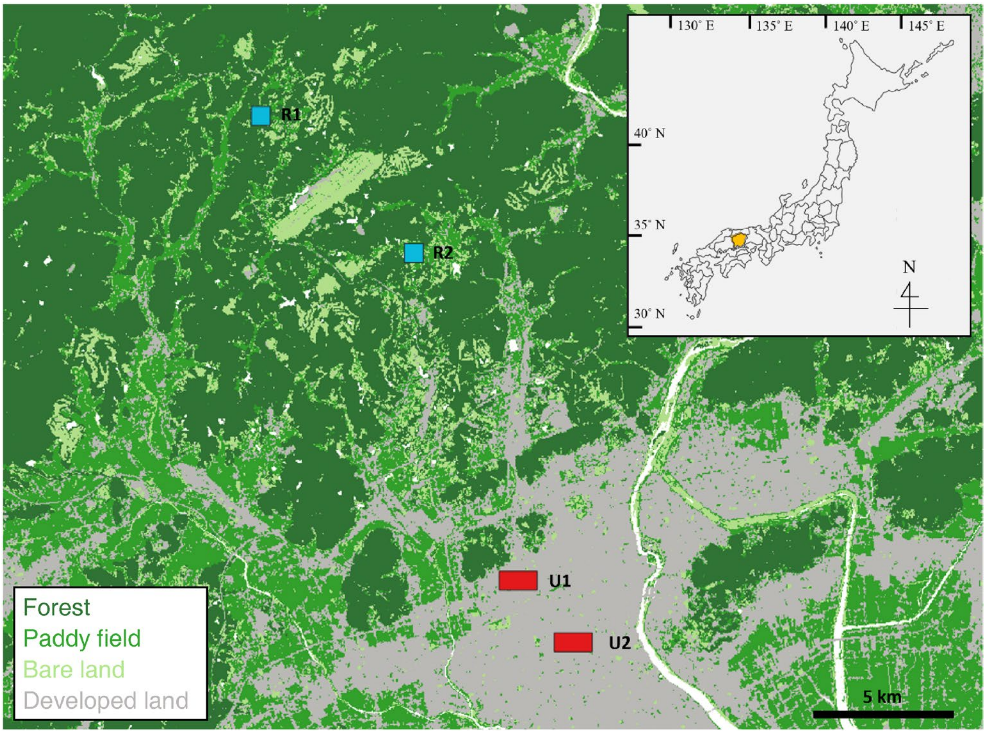

FIGURE 1 Map of the four study sites (R1, R2, U1 and U2) in southern Okayama Prefecture, Japan (orange area in the upper right panels). R1 and R2 represent rural study sites (blue squares), and U1 and U2 represent urban study sites (red rectangles). On the map in the background, dark green represents forest; green represents paddy field; light green represents bare land; grey represents developed land.

map with ca. 10×10 m^2 mesh (see Table S1 for detail: R1, 0.06; R2, 0.04; U1, 0.94; U2, 0.97). During this process, we used the JAXA high-resolution land-use and land-cover data for Japan, which were derived from Earth observations data made by the Advanced Land Observing Satellite (ALOS; Analysis of ALOS raw data by the Geospatial Information Authority of Japan, Japan Aerospace Exploration Agency, Ministry of Economy, Trade and Industry). The developed land includes residential, commercial and industrial land uses and areas for public facilities, as in a previous study (Taichi & Ushimaru, 2024; Ushimaru et al., 2014). In our study, we define 'urban' sites as those with more than 90% developed land area and 'rural' sites as those with less than 10%.

2.3 | Field method

From 2021 to 2023, during the flowering period of *C. communis* from June to October, we conducted a field survey of flowering phenology at each study site. We have a caution when interpreting the annual variation of flowering phenology because the first survey date in 2021 (July 6th) was a little later than in 2022 (June 14th) and 2023 (June 13th). On the first visit to each study site in each year, we thoroughly surveyed all accessible parts of the study site, excluding restricted sections such as school and factory grounds, and, where necessary (e.g. farmland or car parks), we obtained permission from landowners to enter, on foot in groups of two or three and recorded the locations of *C. communis* populations. These surveys took about half a day to complete at each study site. Note that to compare the effects of local microhabitat on flowering phenology, we defined population as those discontinuously separated by differences in soil substrate (some populations are close enough to be expected to interact with each other via pollination and seed dispersal). The microhabitat types of each population were divided into five groups: drains, populations growing in roadside drainage ditches with or without cover; roadsides, populations growing in a crack of asphalt road or on a roadside; vacant land, populations growing in vacant land, parks and slope faces; farmland, populations growing on paddy ridges and fields, ploughed fields and fruit gardens; forest edge, populations growing on the edges of a forest or bush (Figure 2). The first two types were considered to experience high levels of artificial disturbance, whereas the last three types represented semi-natural environments. We excluded forest edge populations from the statistical analyses because they were observed only in rural sites

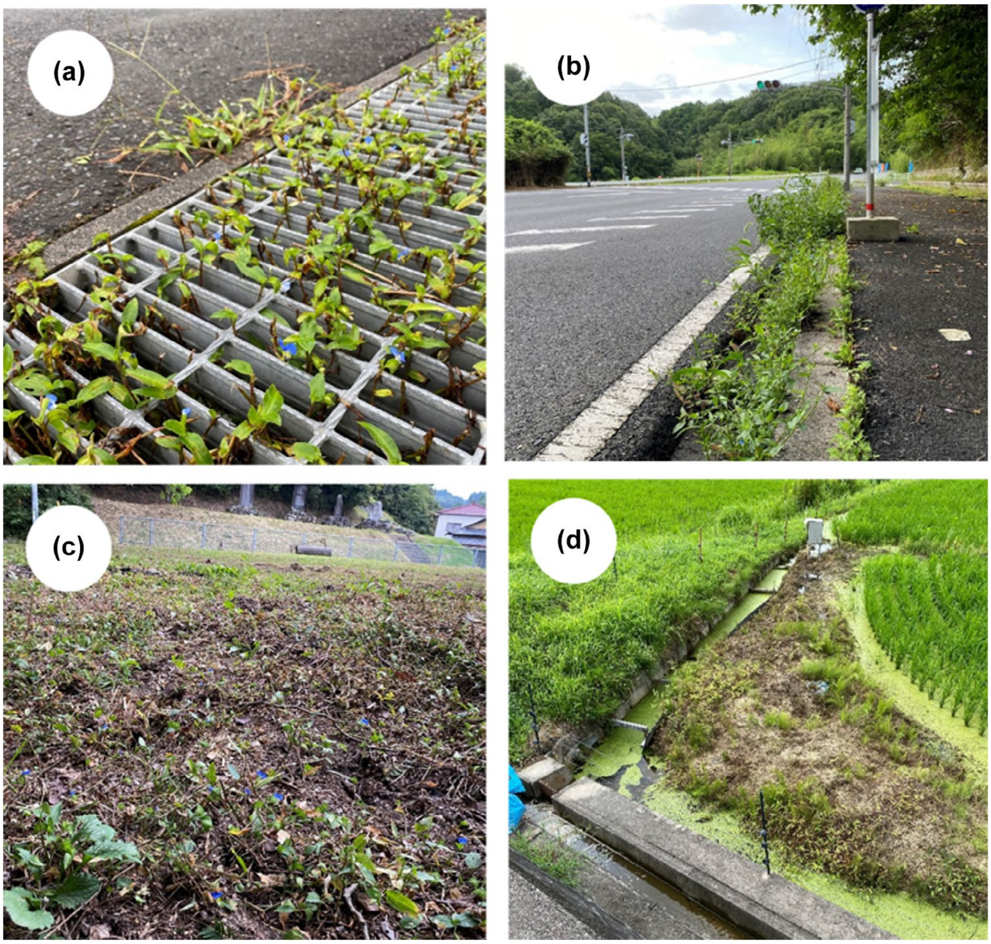

FIGURE 2 Examples of *Commelina communis* populations in different microhabitat types: (a) drain, (b) roadside, (c) vacant land and (d) farmland.

and accounted for only a small proportion of the total population (Table 1). The latitude and longitude of the centre point of each population were recorded using Google Maps. We visited one or two sites per day, each site being visited on 3–14-day intervals (in almost every case, with 7-day intervals: see Figure S1 for details), and recorded the number of flowers in all *C. communis* populations. Individual *C. communis* plants were sometimes mowed or removed by farmers or land managers. We also recorded any evidence of artificial disturbance (mainly mowing by landowners) in each population because this would have an effect on the population phenology indices. Because freshly cut plant material was either left behind or entirely removed after mowing, we could easily distinguish disturbed populations from those where plants had simply withered due to harsh conditions. However, cases of withering before the seed production period were very rare over the three-year study period. Accordingly, each population was further divided into two categories, indicating whether there was presence or absence of artificial disturbances during the survey.

In 2023, we examined the reproductive successes in five, five, three and four *C. communis* populations in R1, R2, U1 and U2, respectively, which are some of the populations we surveyed for the flowering phenology. We arbitrarily selected flowers from the population and conducted either hand- or open-pollination treatments. In the hand-pollination treatment, we applied pollen from another individual to the stigma on the focal flower. Then, we marked the inflorescences rather than the flower to reduce the difficulty of the procedure and removed the other flower buds in the inflorescence (usually one or two) to identify the treated flower. In the open-pollination treatment, we marked the inflorescences and removed the other flower buds in the inflorescences. We applied both treatments to either eight flowers per day for 3 days or 15 flowers per day for 2 days. Due to unexpected disturbances, some marked flowers could not be collected. After approximately 4 weeks, we counted the seeds in the treated flowers to calculate each treatment's seed set (the number of mature seeds divided by the ovule number). We calculated the index of outcross pollen limitation as the ratio of the difference between the seed set under hand-pollination and the seed set under open-pollination to the seed set under open-pollination (Eckert et al., 2010).

2.4 | Flowering phenology

Using the seasonal change in the number of flowers during the survey period, we calculated three phenology indices (flowering onset, peak and duration) for each population in which more than 10 flowers were recorded at least in a given year. The onset and peak of flowering were defined as the number of weeks from the base date (1 June) to the week in which flowering was first observed and to the week in which the maximum number of flowers was recorded, respectively. If two or more weeks had the same maximum number, the flowering peak was taken as the midpoint between those weeks, rounded to the nearest whole number. The duration of flowering was calculated as the difference between the onset of flowering and the offset of flowering, which was the number of weeks from the base date to the week when flowering was no longer observed. For 2021, on the final day of the survey, we observed flowering in only three populations in U2 and one population in R1 (the number of flowers was three or less in each population). The flowering offset for these three populations was treated as the number of weeks from the base date to the final survey week. Additionally, we calculated the natural logarithm of the number of flowers on the peak flowering date as an indicator of flowering abundance in each population.

Furthermore, we calculated intra- and interpopulation flowering synchrony for each population using the following procedures. For the intrapopulation flowering synchrony index (intra-FSI), we calculated the coefficient of variation (CV) of the flower number

TABLE 1 The number of *Commelina communis* populations with more than 10 recorded flowers. R1 and R2 represent rural study sites, and U1 and U2 represent urban study sites. Each study site included multiple populations. Please see the main text for definitions of microhabitat types (Habitat).

		Habitat					
Year	Site	Drain	Roadside	Vacant land	Farmland	Forest edge	Total number of populations
2021	R1	14 (13.7%)	45 (44.1%)	17 (16.7%)	18 (17.6%)	8 (7.8%)	102
	R2	7 (6.2%)	27 (23.9%)	21 (18.6%)	57 (50.4%)	1 (0.8%)	113
	U1	4 (23.5%)	3 (17.6%)	7 (41.2%)	3 (17.6%)	0 (0.0%)	17
	U2	2 (11.1%)	5 (27.8%)	8 (44.4%)	3 (16.7%)	0 (0.0%)	18
2022	R1	23 (19.3%)	49 (41.2%)	22 (18.5%)	17 (14.3%)	8 (6.7%)	119
	R2	11 (8.8%)	35 (28.0%)	22 (17.6%)	56 (44.8%)	1 (0.8%)	125
	U1	3 (21.4%)	2 (14.3%)	7 (50.0%)	2 (14.3%)	0 (0.0%)	14
	U2	1 (6.3%)	5 (31.3%)	7 (43.8%)	3 (18.8%)	0 (0.0%)	16
2023	R1	17 (15.7%)	46 (42.3%)	22 (20.4%)	16 (14.8%)	7 (6.5%)	108
	R2	13 (10.4%)	33 (26.4%)	21 (16.8%)	57 (45.6%)	1 (0.8%)	125
	U1	2 (16.7%)	1 (8.3%)	5 (41.7%)	4 (33.3%)	0 (0.0%)	12
	U2	4 (22.2%)	4 (22.2%)	7 (38.9%)	3 (16.7%)	0 (0.0%)	18

among survey days in each population. CV is the ratio between the standard deviation and the population mean, and it is commonly used to measure the extent of variability. Here, a higher intra-FSI represented a sharper-shaped peak of flower numbers, indicating higher intrapopulation synchrony. A lower intra-FSI indicates that flowering is more spread out during the season, leading to lower synchrony. For the interpopulation flowering synchrony index (inter-FSI), we first calculated the product of the flower number in the focal population and the sum of the flower numbers in all other populations on a given survey day. We repeated this calculation for all survey days and summed the resulting values to obtain the observed value. This observed value tends to be larger not only due to higher interpopulation synchrony but also because of a greater overall flowering number and survey frequency. To normalise the values to be independent of both flower numbers and survey frequency, we generated a null distribution by randomly shuffling the flowering numbers among survey days within each population and recalculating the sum of products 1000 times. We then computed the mean and standard deviation of this null distribution and used them to calculate the z score, which represents the inter-FSI. A higher inter-FSI indicates that the focal population had a larger flower number on days when other populations also had larger flower numbers. We confirmed inter-FSI's robustness to differences in the number of populations among sites via bootstrap sampling and provided it in the Supporting Information (Figure S2).

2.5 | Statistical analyses

2.5.1 | Flowering phenology

To examine the effects of urbanised landscapes and local microhabitat differences on flowering abundance and phenology indices, we conducted analyses using Bayesian generalised linear mixed models (GLMMs) implemented with the brm function in the brms package of R software (Bürkner, 2017; R Core Team, 2021). Models were constructed using data from 2021 to 2023 combined, with year included as an explanatory variable.

We examined six response variables: flowering abundance, three indices of flowering phenology (onset, peak, duration), and two indices for flowering synchrony (intra-FSI and inter-FSI). For each response variable, we constructed models with three key explanatory variables—Site (R1, R2, U1, U2), Habitat (i.e. microhabitat types; drain, roadside, vacant land, farmland) and Year (2021, 2022, 2023)—and evaluated the effects of including all possible two-way pairwise interactions. This resulted in a total of eight models for each response variable (one model without an interaction, three models with a single interaction, three models with two interactions and one model with three interaction terms; see Table S2). We compared these models using expected log predictive density (ELPD) estimated via leave-one-out cross-validation, implemented with the loo and loo_compare functions in the loo package (Vehtari et al., 2017, 2023). Additionally, all models included 'presence/absence of artificial disturbance' as an explanatory variable. For the models examining flowering phenology and synchrony indices, 'flowering abundance' was also included. Population identities were included as a random term in all models.

Since strong interaction effects were not detected (see Table S2 in the Supporting Information), we focused on models without interactions to assess the effects of the explanatory variables. For the categorical variables Site, Habitat and Year, we used emmeans and contrast functions from the emmeans package (Lenth, 2023) to compare levels and assess differences based on estimated marginal means (EMMs) and their 95% highest posterior density (HPD) intervals. We also calculated the difference in EMMs between the rural (R1, R2) and urban (U1, U2) populations to examine the effect of urbanised landscapes. A difference was considered credible if the 95% HPD interval of the EMM difference did not include zero.

To confirm whether populations that are spatially closer exhibit more similar flowering phenology, we conducted a Mantel test to examine the correlation between spatial distance and differences in flowering onset and peak among populations located within the same study sites. The analyses were performed using the mantel function from the vegan package (method = Spearman, number of permutations = 999; Oksanen, 2022). These results are shown in the Supporting Information (Table S3).

2.5.2 | Reproductive success

To compare the degree of pollen limitation between rural and urban landscapes and among microhabitats, we constructed a GLMM using the brm function. The response variable was the outcross pollen limitation, and the explanatory variables included Site (rural or urban), Habitat (drain, roadside, vacant land, farmland) and their interaction term. Since the U1 site lacked 'roadside' populations, we combined the two sites within each landscape type (R1, R2 for rural and U1, U2 for urban) and treated them as two levels (rural and urban) instead of four separate categories. We assessed urban–rural differences and separately compared microhabitat types between rural and urban landscapes, based on the EMMs calculated using the emmeans and contrast functions. A difference was considered credible if the 95% HPD interval did not include zero.

All Bayesian GLMMs were constructed using the brm function in the brms package with the following settings: four chains, each with 3000 iterations after 3000 warmup iterations: Gaussian family and identity link for flowering abundance, intra-FSI, inter-FSI and outcross pollen limitation, and Poisson family and log link for onset, peak and duration.

3 | RESULTS

We recorded 250, 274 and 263 *C. communis* populations for 2021, 2022 and 2023, respectively (Table 1). Although we observed flowering individuals in many populations throughout the 3 years, we found flowering individuals in some populations only in 1 year (19.0%) or 2 years (22.8%); for most cases in such a situation, there were no growing individuals at all. Populations at the forest edge were observed only at the two rural sites, and their percentage was less than 5% within all microhabitat types. In contrast, populations in all other microhabitat types were observed at all study sites (Table 1). Therefore, forest edge populations were excluded from the statistical analyses. Urban sites were characterised by a relatively high proportion of populations occurring in vacant land, with three-year mean proportions of 44.2% and 42.3% in U1 and U2, respectively. In both urban sites, the other three microhabitat types each accounted for approximately 20%, though there was some year-to-year variation. In rural sites, R1 and R2 had relatively higher proportions of roadside and farmland populations, with three-year mean proportions of 42.6% and 46.8%, respectively.

For the three phenological indices (onset, peak and duration) and the two synchrony indices (intra-FSI and inter-FSI), we found that some pairs of indices have correlations (Figure S3). Flowering onset and duration exhibited a strong negative correlation (Pearson correlation coefficient = −0.89), suggesting that earlier flowering populations tend to have a longer flowering duration. Intra-FSI was positively correlated with onset (0.52) and negatively correlated with duration (−0.62). Inter-FSI showed a positive correlation with peak (0.59), while its correlations with onset and duration were weak (0.13 and 0.06).

For Bayesian GLMMs, convergence was verified for all models based on standard diagnostic criteria, with Rhat values below 1.01 and effective sample sizes (ESS_bulk and ESS_tail) exceeding 400. Leave-one-out cross-validation indicated that models incorporating a Site × Year interaction term best explained all response variables, except for flowering abundance and intra-FSI. The best model for flowering abundance included Site × Habitat and Site × Year interaction terms. Additionally, the best model for intra-FSI included all possible pairwise interactions among Site, Habitat and Year. However, for all response variables, the ELPD of the model without interactions did not differ significantly from that of the best model, suggesting that interaction effects were small (Table S2). These results suggest that microhabitat type consistently influences flowering phenology and synchrony between urban and rural sites and vice versa. Furthermore, these effects may be in a consistent manner across years. Therefore, we evaluated the effect of each explanatory variable based on the results of the model without interaction terms. The raw data and results of the best models are shown in the Supporting Information (Figures S4 and S5).

3.1 | Effect of urbanised landscapes

Bayesian GLMM analyses showed no difference in flowering abundance between rural and urban populations (EMM and 95% HPD interval for the difference of rural minus urban populations: −0.008, −0.362 to 0.346; Figure 3). Flowering onset and peak were earlier in urban populations (EMM and 95% HPD interval: 0.278 [0.179–0.382] for onset and 0.069 [0.012–0.124] for peak; Figure 3). Additionally, flowering duration was longer in urban populations (EMM and 95% HPD interval: −0.154 [−0.234 to −0.075]; Figure 3). For flowering synchrony, both intra-FSI and inter-FSI were lower in urban populations (EMM and 95% HPD interval: 0.260 [0.140–0.377] for intra-FSI and 0.661 [0.376–0.933] for inter-FSI; Figure 4). The results for each site (R1, R2, U1, U2) rather than the difference of rural and urban populations were shown in Supporting Information (Table S4).

3.2 | Effect of local microhabitat differences

According to the Bayesian GLMM analyses, flowering abundance was larger in the following order: farmland, vacant land, roadside and drain populations (Figure 3; Table S4). In detail, credible differences were found between farmland and roadside/drain populations, as well as between vacant land and drain populations (Table S4). There were no credible differences among microhabitat types for flowering phenology indices (onset, peak and duration) (Figure 3; Table S4). Intra-FSI in farmland populations and inter-FSI in drain populations were credibly lower than those in the other three microhabitat types (Figure 4; Table S4).

3.3 | Annual variations

Bayesian GLMM analyses revealed that at least one of the 95% HPD intervals for the pairwise EMM difference between years did not include zero for all response variables, indicating that all response variables varied among years (Table S4). In summary, 2021 had greater flowering abundance and lower intra- and inter-FSI, 2022 had a later flowering peak and higher inter-FSI, and 2023 had an earlier flowering onset and a longer flowering duration (Figures 3 and 4; Table S4). It should be noted that the first survey date in 2021 (July 6th) was later than in 2022 (June 14th) and 2023 (June 13th), so the flowering onset and duration might be over- and underestimated, respectively.

3.4 | Effect of artificial disturbances

Artificial disturbances were often observed in *C. communis* populations. The degree of mowing ranged from only a part to the entire population. From 2021 to 2023, the mean proportions of populations where mowing was observed at least once during the survey period were 54.9%, 46.3%, 65.1% and 40.3% in R1, R2, U1 and U2, respectively. By microhabitat type, the proportions were 44.6%, 47.1%, 53.6% and 54.4% in drain, roadside, vacant land and farmland, respectively. Overall, the proportion of populations experiencing artificial disturbances was around 50% across study sites and microhabitat types, though it tended to be slightly higher in U1. We provided more detailed information in the Supporting Information (Table S5).

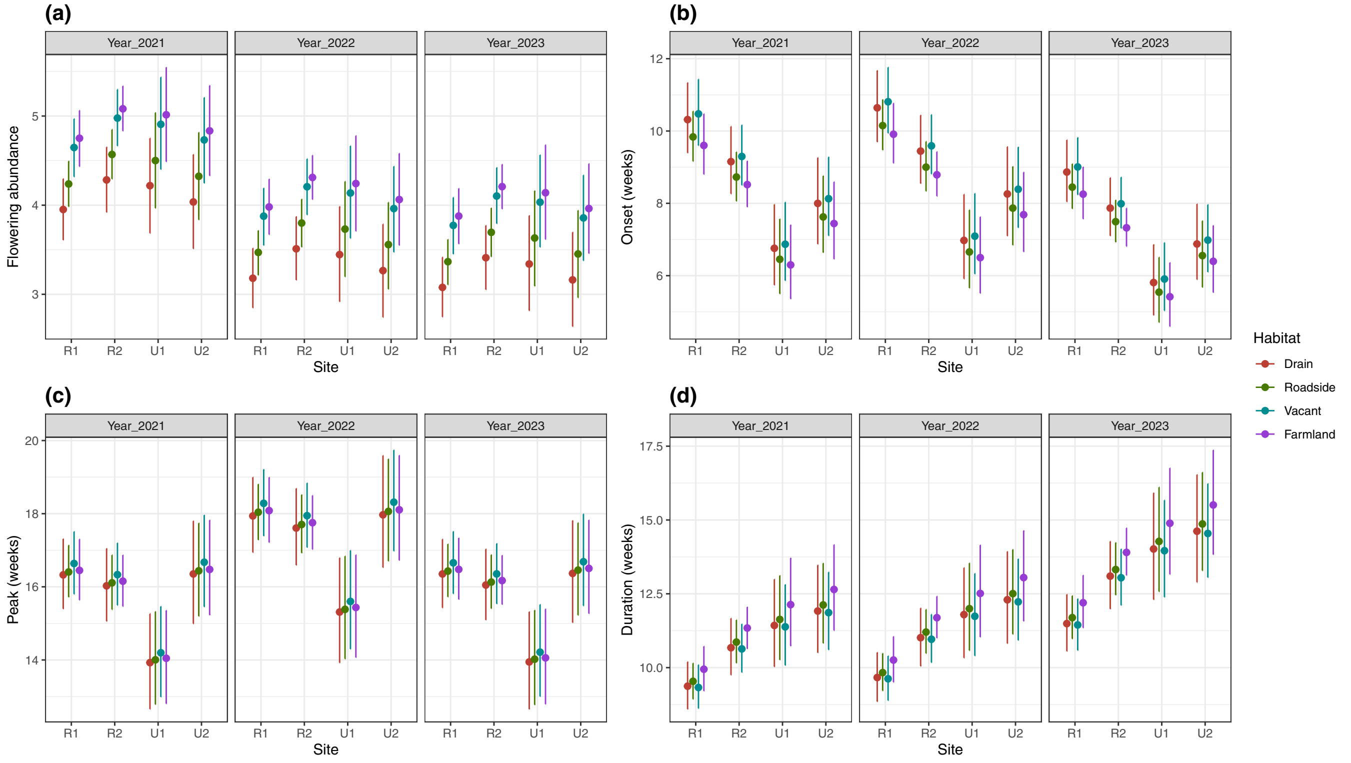

FIGURE 3 Comparison of flowering abundance and flowering phenology across four study sites (R1, R2, U1, U2), four microhabitat types (drain, roadside, vacant land, farmland) and years 2021–2023: (a) flowering abundance, (b) onset, (c) peak, (d) duration. The points represent estimated marginal means (EMMs), and error bars indicate 95% credible intervals (CIs). Predictions were obtained from a Bayesian generalised linear mixed model (GLMM) using the ggpredict function in the ggeffects package (Lüdecke, 2018).

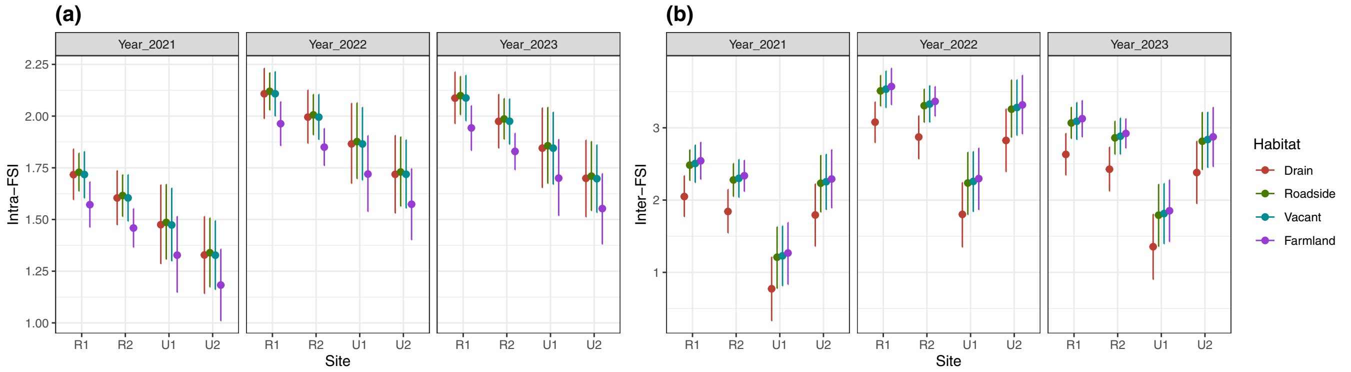

FIGURE 4 Comparison of flowering synchrony across four study sites (R1, R2, U1 and U2), four microhabitat types (drain, roadside, vacant land, farmland) and years 2021–2023: (a) Intra-FSI, (b) Inter-FSI. The points represent estimated marginal means (EMMs), and error bars indicate 95% credible intervals (CIs). Predictions were obtained from a Bayesian generalised linear mixed model (GLMM) using the ggpredict function in the ggeffects package (Lüdecke, 2018).

The estimated coefficients with 95% credible intervals (quantile-based) for the effect of disturbance on flowering onset and peak were −0.099 (−0.153 to −0.046) and −0.040 (−0.076 to −0.005), respectively, suggesting that disturbed populations had earlier flowering onset and peak than the undisturbed populations (Figure 5). Inter-FSI was credibly lower in disturbed populations than in undisturbed populations (estimated coefficient with 95% credible interval: −0.333, −0.494 to −0.169), while intra-FSI was comparable regardless of the presence or absence of artificial disturbance (0.048, −0.026 to 0.122) (Figure 5). There was no credible difference in flowering abundance (0.121, −0.059 to 0.302) or duration (0.035, −0.013 to 0.083) between disturbed and undisturbed populations (Figure 5).

3.5 | Relationship with flowering abundance

As expected, flowering abundance (i.e. natural logarithm of the number of flowers on the peak flowering date) showed credible

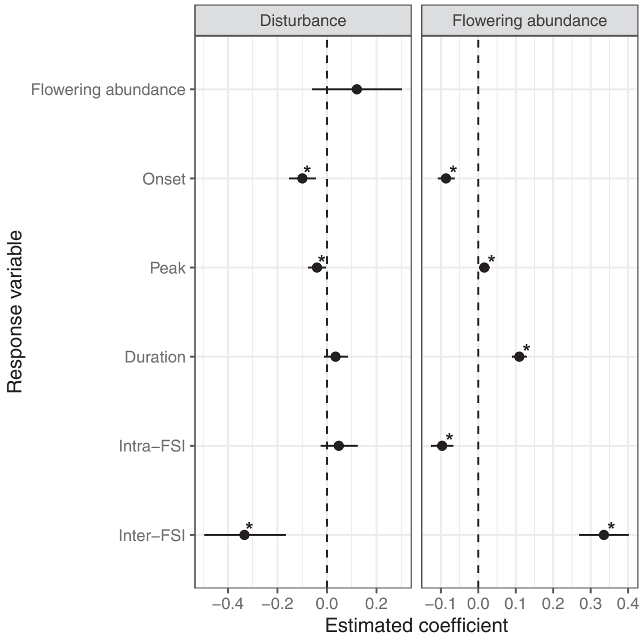

FIGURE 5 Estimated coefficients and their 95% credible intervals (CIs) of presence/absence of artificial disturbance and flowering abundance obtained from a Bayesian generalised linear mixed model (GLMM). An asterisk indicates a 95% CI does not include zero.

correlations with both flowering phenology and synchrony. Specifically, it was negatively correlated with the flowering onset (estimated coefficient with 95% credible interval: −0.086, −0.108 to −0.065) and positively correlated with the flowering peak (0.016, 0.003–0.030) and duration (0.109, 0.090–0.128) (Figure 5). These results indicated that populations with higher flowering abundance tended to exhibit earlier and longer flowering with a slightly late flowering peak. The earlier and longer flowering duration could be explained by a larger population size, which is more likely to have an individual in bloom at any given time. Additionally, flowering abundance was negatively correlated with intra-FSI (−0.097, −0.125 to −0.068) and positively correlated with inter-FSI (0.335, 0.270–0.401) (Figure 5).

3.6 | Reproductive success

We obtained seed set data for a total of 357 hand-pollinated and 366 open-pollinated flowers, with an average of 21 and 21.5 flowers per population, respectively. According to the Bayesian GLMM results, outcross pollen limitation was greater in urban populations than in rural populations (EMM and 95% HPD interval for the difference: rural minus urban = −0.801, −1.160 to −0.463; Figure 6). A credible interaction between Site and Habitat was detected. In rural sites (R1, R2), there were no credible differences among microhabitat types (EMM and 95% HPD intervals: −0.187 [−0.666 to 0.287] for drain, 0.246 [−0.138 to 0.649] for roadside, −0.081 [−0.589 to 0.388] for vacant land and 0.099 [−0.291 to 0.495] for farmland populations).

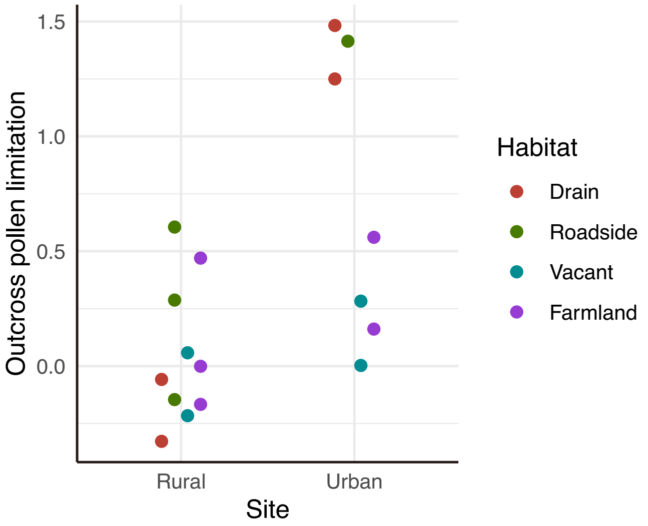

FIGURE 6 The index of outcross pollen limitation (the ratio of the difference between the seed set under hand-pollination and the seed set under open-pollination to the seed set under open-pollination) in studied *Commelina communis* populations. Rural and Urban on the x-axis contain the populations in both R1 and R2, and both U1 and U2, respectively.

In contrast, in urban sites (U1, U2), drain and roadside populations exhibited greater outcross pollen limitation than vacant land and farmland populations (EMM and 95% HPD intervals: 1.365 [0.884–1.866] for drain, 1.412 [0.743–2.126] for roadside, 0.139 [−0.338 to 0.632] for vacant land and 0.362 [−0.124 to 0.829] for farmland populations; Figure 6). Detailed results from the contrast function are provided in the Supporting Information (Table S6).

4 | DISCUSSION

The flowering phenology of *C. communis* populations was influenced by landscape-level changes associated with urbanisation and also variations in local microhabitats. First, our results showed that urban populations tended to exhibit earlier flowering onsets and longer flowering durations than rural populations. These are consistent with previous studies reporting that urbanisation promotes early flowering onset in various plant taxa (Li et al., 2021; Neil et al., 2010; Roetzer et al., 2000; Sexton et al., 2023). In contrast, we did not detect a consistent pattern of variation in flowering onset, peak and duration among different microhabitats. Second, populations in urban sites and those on drain habitats tended to display less simultaneous flowering with the neighbouring populations. This suggests that biotic or abiotic complexity within the urban matrix can produce variations in flowering phenology, accelerating temporal fragmentation among populations. In particular, the low interpopulation synchrony observed in drain populations, despite no apparent shift in average flowering timing, likely indicates that the effects of drain microhabitats are localised and context-dependent. Our analyses revealed that these differences remained robust after accounting for differences in flowering abundance, while all indices of flowering phenology and synchrony were correlated with flowering abundance (Figure 5).

Many studies have reported that warming temperatures in urban environments can advance plant flowering (Meng et al., 2020; Mimet et al., 2009; Ziska et al., 2003). In *C. communis*, earlier flowering onsets in urban populations could also be due to urban heat island effects. During the flowering season (1 June to 15 November) the mean air temperature was 21.5°C, 22.0°C and 22.4°C at the weather observation station near the rural sites (Nichiouji) and 23.3°C, 23.8°C and 24.2°C at the station near the urban sites (Okayama) in 2021, 2022 and 2023, respectively (Japan Meteorological Agency; https://www.jma.go.jp/jma/index.html: Table S7). High temperatures may also explain why 2023 exhibits the earliest flowering onset and longest flowering duration. It should be noted that, especially in urban sites, the microclimate in *C. communis* populations is likely to be strongly influenced by topography, soil substrate and surrounding structure. Moreover, it may be difficult to interpret the role of a single environmental factor in the divergence in flowering phenology. Some studies have suggested that limited soil moisture could affect flowering phenology; however, whether it advances or delays flowering phenology varies depending on the species' flowering period, life history and geographic distribution, as well as climate conditions (Christmann et al., 2023; Peñuelas et al., 2004; Wolf et al., 2017; Zhu et al., 2016). The unique conditions experienced by the drain populations, in which the surrounding asphalt maintains high temperatures and the limited soil substrate restricts water availability, could have complicated effects on the phenology of flowering. Our supplemental analysis showed that differences in flowering onset and peak were not correlated with the distance between populations in most cases, suggesting that microenvironmental factors played a more important role in determining flowering phenology than the peripheral environment (Table S3). In future studies, extensive monitoring of the microclimate conditions will be essential to identify which aspects of microhabitat variation are most impactful on flowering phenology in artificial ecosystems.

Our results showed that artificial disturbances could affect the flowering phenology of the population, as some previous studies had reported (McDonnell & Hahs, 2015; Völler et al., 2017). First, we found that populations that experienced artificial disturbance exhibited advanced flowering phenology, that is an earlier onset and peak, than undisturbed populations (Figure 5). Adaptive evolution and plastic response could explain this shift, although our data cannot distinguish between these mechanisms. Some previous studies have suggested that artificial disturbances can lead to adaptive evolution because only individuals flowering before disturbance can leave seeds for the next generation (i.e. phenological escape strategy; Reisch & Poschlod, 2011; Völler et al., 2013; Völler et al., 2017). In terms of plastic responses, Liu et al. (2017) showed that mowing after anthesis in previous years prolonged the flowering onset by changing the accumulation of standing litter in alpine meadows. Regardless of whether the observed phenological shift results from adaptive evolution or plastic response, the timing of mowing could play a critical role in shaping flowering phenology (Johansen et al., 2019; Völler et al., 2013). Because some populations were mowed multiple times during the survey in the case of *C. communis*, considering the timing of mowing would have made the statistical model too complicated; therefore, it was not included in this study. Implementation of common garden experiments and analyses of the effect disturbance timing are required to clarify the underlying mechanism in future studies. Second, it should be noted that artificial disturbances did not affect the flowering abundance and durations. We often observed that the disturbed populations flowered again after a couple of days, even after mowing cut out almost all individuals. It is possible that cut stem fragments can flower immediately because this species has runner-like structures such as a stoloniferous stem with nodes allowing the emergence of roots; note that *C. communis* does not have a regenerable underground part and it usually takes 2 months or more for an individual to flower after seed germination (Wilson, 1981). This immediate population regeneration may depend on disturbance timing and may play an important role in enabling *C. communis* populations to colonise habitats that are susceptible to high levels of human pressure.

We found a notable pattern in reproductive success: outcrossing pollen limitation was pronounced in urban populations, especially in drain and roadside populations, while no significant difference among microhabitat types was detected in rural populations. This pattern might be partially explained by a sparser and more fragmented distribution of the populations in the urban landscapes (Andrieu et al., 2009; Rivkin et al., 2020). Although urban areas are generally considered to be pollen-limited environments, some studies, including those on *C. communis*, have reported relatively high reproductive success via autonomous self-pollination (Bennett et al., 2020; Spigler, 2018; Ushimaru et al., 2014). Moreover, it is widely recognised that populations in urban environments have limited gene flow due to habitat fragmentation (Andrieu et al., 2009; Honnay & Jacquemyn, 2007; Young et al., 1996). We found that the *C. communis* populations in urban sites, especially those growing in drain habitats, exhibited a low interpopulation flowering synchrony. This phenological mismatch with neighbouring populations might have a synergistic effect with habitat fragmentation on gene flow, possibly decreasing long-term population viability in urban ecosystems.

In this study, we demonstrated that not only landscape changes associated with urbanisation, but also local microhabitats and artificial disturbances determine the flowering phenology of *C. communis* populations. Our results showed that urbanised landscapes, growing in drain habitats and artificial disturbances lead to a decline in the flowering synchrony among populations, likely complicating population persistence via outcrossing pollen limitation. In recent years, with the continual acceleration of urbanisation, human activities have created a diverse array of unique and extreme microenvironments, especially in urban and semi-urban ecosystems. Although spatial fragmentation has been repeatedly noted as important in determining metapopulations' persistence in urban ecosystems, we emphasise that temporal fragmentation caused by diversification of flowering phenology in the urban matrix may also play a critical role. On the flip side, in the context of invasive or weedy species management, it may be useful to select mowing times and target populations in a way that disrupts flowering synchrony across populations. Indeed, *C. communis* is known to be invasive in North America and Europe and reported as a troublesome weed in northeast China, eastern United States and the Caribbean Islands (Aulakh, 2022; Fukuoka & Iwatsuki, 2016; Isaac et al., 2013). Besides, although variation of flowering phenology may create phenological mismatch among populations, it could also have the side effect of increasing the temporal availability of floral resources for pollinators within the urban landscape (Samuelson et al., 2022). In future studies, it will be important to determine the key factors that shape flowering phenology in artificial microenvironments and investigate how such variation affects long-term metapopulation viability and broader ecological interactions.

AUTHOR CONTRIBUTIONS

All authors conceived the ideas and designed the methodology. Hinata Fujiwara, Hiroto Yamaguchi and Koki R. Katsuhara collected and analysed the data. Hinata Fujiwara and Koki R. Katsuhara led the writing of the first draft, with advice from Kazuyoshi Nakata. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data and R code used during the current study are available in Zenodo (https://doi.org/10.5281/zenodo.15845435) (Fujiwara et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Percentage of land cover types within each study site.

Table S2. The results of comparisons among eight Bayesian generalized linear mixed models (GLMMs) with or without interaction terms.

Table S3. Results of the Mantel test for the correlation between spatial distance and differences in flowering onset and peak.

Table S4. Estimated marginal means (EMMs) and their 95% highest posterior density (HPD) intervals for each level of the three focal explanatory variables (Site, Habitat, and Year), obtained from the Bayesian GLMM analyses.

Table S5. The number of *Commelina communis* populations used in the statistical analyses.

Table S6. Pairwise differences in EMMs among habitat types and their 95% HPD intervals, obtained from the Bayesian GLMM analyses for outcross pollen limitation.

Table S7. Meteorological observation data from the weather observation stations near the study sites in rural (Nichiouji) and urban (Okayama) areas (https://www.jma.go.jp/jma/index.html).

Figure S1. The histogram of survey intervals (i.e. the number of days since the last visit to a given study site).

Figure S2. The relationship between the observed inter-FSI and the bootstrapped inter-FSI in rural sites (R1, R2).

Figure S3. The pairwise Pearson correlation coefficients for flowering abundance, onset, peak, duration, intra-FSI, and inter-FSI.

Figure S4. Boxplots of row data of flowering abundance, flowering phenology, and flowering synchrony across four study sites (R1, R2, U1, U2), four habitat types (drain, roadside, vacant land, farmland), and years 2021–2023: (a) flowering abundance (b) onset, (c) peak, (d) duration, (e) intra-FSI, (f) inter-FSI.

Figure S5. Comparison of flowering abundance, flowering phenology, and flowering synchrony across four study sites (R1, R2, U1, U2), four habitat types (drain, roadside, vacant land, farmland), and years 2021–2023 based on the best models: (a) flowering abundance (b) onset, (c) peak, (d) duration, (e) intra-FSI, (f) inter-FSI. The points represent estimated marginal means (EMMs), and error bars indicate 95% confidence intervals (CIs).

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