Urbanization Effects on Plant Parasitism: A Multi-Regional Comparison of Endemic Occurrence and Outbreak Intensity

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Abstract

Microbial and insect parasitism plays a crucial role in shaping plant communities. The urban stress hypothesis posits that urbanization increases parasitism owing to the physiological environment, whereas the habitat fragmentation hypothesis suggests that habitat fragmentation in urban areas suppresses disease transmission. In the epidemiological triangle (comprising pathogen occurrence, environment, and host susceptibility as determinants of outbreak intensity), the habitat fragmentation hypothesis primarily influences parasitism occurrence, whereas the urban stress hypothesis mainly affects outbreak intensity. In this study, we aimed to distinguish between these two hypotheses by formulating an epidemiological triangle using zero-inflated binomial regression based on surveys of herb layer plant communities along urban-rural gradients in Japan and China. In general, urbanization enhanced parasitism. Strong seasonal signatures found in natural ecosystems were generally the same as those in cultivated crops. When all types of parasitism (powdery mildew-like, rust-like, spot-forming diseases, leaf-eating, and other insects) were combined, urbanization enhanced outbreak intensity, supporting the urban stress hypothesis, and suppressed endemic occurrence, supporting the habitat fragmentation hypothesis. Notable exceptions included a significantly high endemic occurrence in powdery mildew-like diseases and in the combined analysis of all insect pests. This may be because ruderal host plant habitats are fragmented in forest-dominated landscapes. Additionally, rich nitrogen deposition in urban areas may explain the generally higher outbreak intensity, although reducing hyperparasites and carnivorous species can cause complicated effects. These findings provide the new ecological consequences of urbanization, offering a framework for understanding plant-parasite dynamics in cross-regional perspective and informing strategies for sustainable urban planning.

1 Introduction

Land-use change and urbanization greatly affect ecological communities by altering habitat structure, species interactions, and the abiotic environment (Faeth et al., 2011; Seto et al., 2012; Rohr et al., 2020). Urban environments create unique conditions that can considerably influence various organisms (Aronson et al., 2017), and potentially affect parasitism by fungi and herbivorous insects (Meineke et al., 2013; Piekarska-Boniecka et al., 2022).

Several hypotheses have emerged regarding the effects of urbanization on plant-parasite interactions. The urban stress hypothesis posits that multiple urban stressors (e.g., heat, drought, and pollution) may compromise plant defense mechanisms, thereby increasing susceptibility to parasites (Dale and Frank, 2014; Youngsteadt et al., 2015). Conversely, the habitat fragmentation hypothesis suggests that reduced connectivity between plant populations in urban areas may impede parasite spread (Hanski, 2011), as indicated by the dispersal mechanisms of fungal spores and insects (Willocquet et al., 2008; Franke et al., 2009).

In our previous study, we adopted an epidemiological triangle (Fig. 1) to examine fungal and insect leaf parasitism within suburban herb-layer plant communities (Wang et al., 2025). The epidemiological triangle, comprising disease occurrence, host plant susceptibility, and environmental factors, posits that infection incidence and intensity are determined by interactions between the parasite, host, and environment (Stevens, 1960). We applied zero-inflated binomial regression and the Bayesian method to estimate the effects of environmental factors on parasitism occurrence and outbreak intensity. Within this framework, the habitat fragmentation hypothesis primarily affects the occurrence of parasitism, whereas the urban stress hypothesis primarily impacts outbreak intensity (Fig. 1).

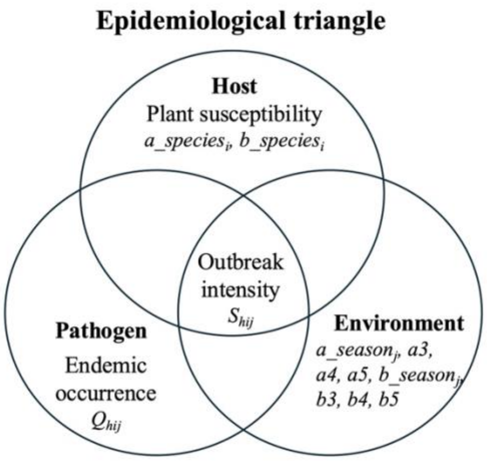


Fig. 1 Epidemic triangle (Stevens, 1960) and parameters of the zero-inflated binomial regression model used in this research. Italicized parameters are in Eq. 1 to Eq. 4. The diagram in Wang et al. (2025, preprint) was modified to adapt environmental parameters in this research. The parameters $a3$ and $b3$ correspond to urbanization, $a4$ and $b4$ to annual temperature, $a5$ and $b5$ to annual precipitation. The prefix a in parameter names indicates the effect to endemic occurrence, while b indicates the effect to outbreak intensity. For suffixes, h denotes the study plots, i represents the species, and j refers to the seasons

In this study, we aimed to evaluate the urban stress and habitat fragmentation hypotheses by assessing the impact of urbanization on parasitism occurrence and intensity. This is the first multi-regional epidemiological study examining these hypotheses and obtaining general patterns of parasitism in urban-rural gradient by quantifying the epidemiological triangle model.

2 Materials and Methods

2.1 Research sites

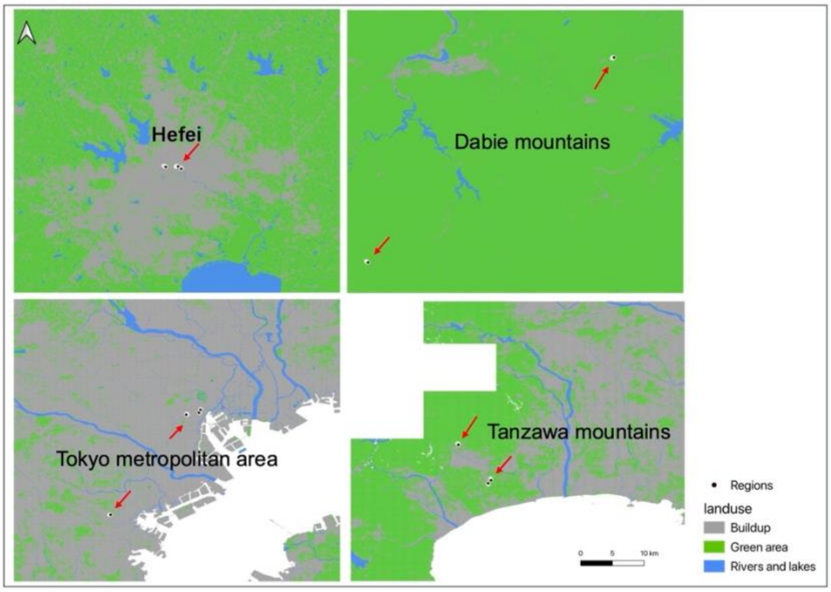


Fig. 2 Map showing the locations of the eleven study regions in Japan and China

This study was conducted across 11 regions in Japan and China, encompassing varying degrees of urbanization within similar evergreen broad-leaf forest zone climates (Fig. 2). Sites were selected in both the Tokyo metropolitan area (the most populated area in Japan) and Hefei City (the 18th most populous city in China), alongside their corresponding foothill rural areas in the Tanzawa and Dabie Mountains, respectively. All regions experienced similar overall climatic patterns (Supporting Information, Figure S1).

Urbanization levels were quantified using the proportion of built-up areas within a 1000-m radius of the center of each region using QGIS 3.22. Built-up areas included buildings, roads, railways, and industrial spaces, while green areas comprised forests, grasslands, agricultural lands, and recreational green spaces (Supporting Information Table S1). Land-use classification was based on the National Land Information Platform for Japanese sites (https://nlftp.mlit.go.jp/ksj) and Remote Sensing Land Use Data 2023 for Chinese sites (https://www.resdc.cn/DOI/DOI.aspx?DOIID=54). The 11 regions exhibited a clear urban-rural gradient, with built-up area proportions ranging from 92.78% at the most urbanized site (JP-C1) to 1.15% at the most rural site (CN-R3). Preliminary analysis revealed a strong negative correlation between built-up areas and the extent of forests, grasslands, and agricultural land, leading to the use of built-up areas as an indicator of the urban-rural gradient.

2.2 Disease Symptoms and Pest Identification

2.2.1 Fungal Diseases

We focused on three diseases, powdery mildew-like and rust-like symptoms and leaf spots, which could be reliably identified through visual assessment. Disease symptoms were verified using a portable optical microscope (Kenko, STV-120M) at 60–120× magnification. For each host species within a plot, the number of examined and symptomatic leaves were recorded following our established criteria.

Powdery mildew-like symptoms were characterized by white or grayish-white powdery mycelial growth on the leaf surfaces. These mycelial mats typically resist removal by simple rubbing, distinguishing them from sooty mold or whitefly-induced wax. Rust-like symptoms were identified by visible sporulation structures on the leaf underside, manifesting as rust-colored lesions or layered spots. Infected areas often exhibit concentric rings or layers of sporulation structures and clear boundaries between healthy and infected tissues, distinguishing these symptoms from physiological damage.

For leaf spots, we recorded only leaf spot symptoms distinguishable from physiological disorders or mechanical damage, following the classification criteria set by the Phytopathological Society of Japan (https://www.ppsj.org/wp-content/uploads/mokuroku202408.pdf). These symptoms typically present as elliptical spots with clearly discolored edges and characteristic lesion patterns.

2.2.2 Insect pests

Two primary categories of insect parasitism were recorded. Leaf-eating insect damage was recorded only when herbivorous insects were observed within 2 m of affected leaves. The primary leaf-eating insects were lepidopteran larvae and leaf beetles. This criterion helped distinguish active herbivory from mechanical damage or old feeding scars.

The category of “other leaf-parasitic insects” included leaf miners (primarily Lepidoptera and Diptera larvae), which created distinctive tunnels within leaves; insects that formed leaf galls or rolls (e.g., various microlepidoptera); Geometridae larvae and other insects that utilized leaves for shelter; and ovipositing insects that reduced photosynthetic efficiency via egg deposition in leaf tissue (e.g., Tortricidae moths that induce leaf folding or rolling).

2.3 Survey Methods

Following a preliminary survey in the spring of 2023 (April–June) to establish and refine our methodology, intensive field surveys were conducted during the summer of 2023 (July–August), autumn of 2023 (October–November), and spring of 2024 (April–June). Within each region, we established circular plots (2 m in diameter) at 20-m intervals. The number of plots varied by region according to the accessible vegetation area, ranging from 30 to 90 (Supporting Information Table S2). All surveys were conducted on sunny days between 9:00 and 14:00 to ensure consistent lighting conditions and facilitate optimal observation of symptoms. All seed plant leaves less than 2 m in height were examined within each plot.

2.4 Statistical Analysis

We employed zero-inflated binomial regression using CmdStanR (Stan Development Team, 2023) to analyze both “endemic occurrence,” which denotes the occurrence probability of parasitism in the plot, and “outbreak intensity,” which indicates the occurrence probability of parasitism on individual leaves. The model builds upon our previous framework (Wang et al., 2025). Most plant leaves in plots with disease exhibited infection, while numerous plots remained completely disease-free. This uneven distribution is often caused by the absence of parasites within specific plots, as outlined in the epidemiological triangle. We assessed the extent of prevalence plots, which we termed “endemic occurrence,” using zero-inflated binomial regression. This was evaluated independently from the “outbreak intensity,” which denoted the ratio of positive leaves observed in plots where the disease was present. The probability of endemic occurrence (Q_{hij}) of plant species *i* at plot *h* in region *l* in season *j* was modeled as follows:

$$\text{Logit}(Q_{hij}) = a0 + a\_season_j + a\_species_i + a3 \times Urbanization_l + a4 \times annualTenperature_l + a5 \times annualPrecipitation_l \qquad Eq\ (1)$$

where *a0* is the intercept; *a3* is the urbanization effect; and *urbanization* is the standardized proportion of built-up area around region *l*. The species ($a\_species_i$) and season (a_season_j) terms are categorical variables with their means constrained to zero to avoid redundancy with the intercept term. Despite minor climatic differences among regions, annual temperature and precipitation were analyzed to mitigate climatic differences among regions and assess the impact of urbanization. We considered the effect of the country (China or Japan) as a qualitative variable in the preliminary analysis; however, the model did not converge and was subsequently excluded from the analysis.

Outbreak intensity (S_{hij}) was modeled similarly:

$$\text{Logit}(S_{hij}) = b0 + b\_season_j + b\_species_i + b3 \times Urbanization_l + b4 \times annualTenperature_l + b5 \times annualPrecipitation_l \qquad Eq\ (2)$$

For plots with detected parasitism (*n* positive leaves in *m* examined leaves), the probability followed a binomial distribution.

$$\text{Prob(positive } n \text{ leaves in examined } m \text{ leaves)} = \text{binomial}(n, m, S_{hij}) \text{ for } n > 0 \qquad Eq(3)$$

The probability of undetected parasitism (R_{hij}) in a plot was the sum of true absence ($1 - Q_{hij}$) and presence but undetected cases:

$$R_{hij} = (1 - Q_{hij}) + Q_{hij} \times \text{binomial}(0, k, S_{hij}) \qquad Eq(4)$$

where *k* is the assumed number of examined foliage units calculated based on 1% plant cover. The details of the analysis are provided in our previous paper (Wang et al., 2025).

All environmental variables were standardized prior to analysis using their means and standard deviations. The model was implemented using the provided Stan code, which accounted for both endemic occurrence and outbreak intensity while incorporating urbanization effects. Model convergence was assessed using standard diagnostics (Gelman–Rubin statistic and effective sample sizes), with posterior predictive checks performed to evaluate the model fit.

3 Results

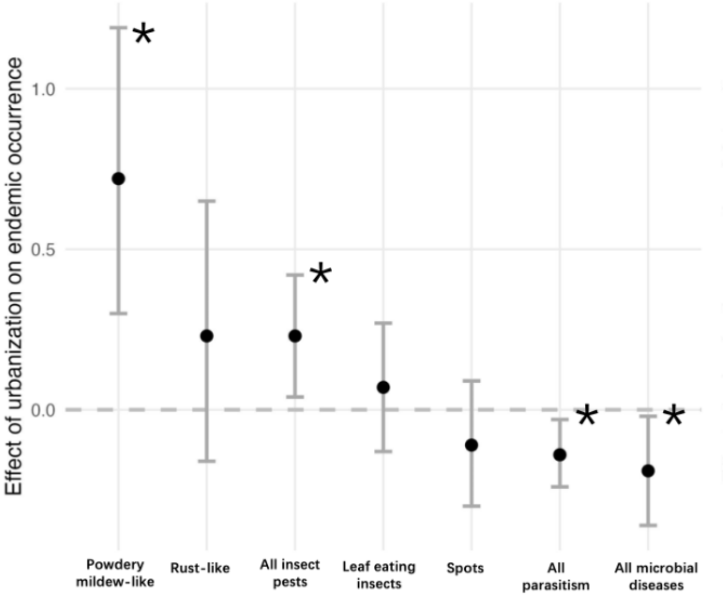
3.1 Host plants and parasitism

Across all regions, we recorded between 43 and 100 plant species per region. We analyzed 99 species that occurred in more than 10 plots. Each plant species in each plot was treated as a sample in the epidemiological survey. A total of 6,552 samples were analyzed, with the following counts of parasitized samples: 262, 163, 318, 618, and 373 for powdery mildew-like disease, rust-like disease, spot-forming disease, leaf-eating insects, and other leaf-parasitic insects, respectively. Supporting Information Table S2 presents the dominant plants and floristic overlaps among regions, highlighting the number of shared species. This information serves as a basis for analyzing cross-regional variations in infection rates among common hosts. The median species-overlap between the two regions was 16 species, with a quantile range of 14–21 species.

3.2 Effect of urbanization

The analysis failed to converge for the "other leaf-parasitic insects." The results of this type were not presented individually but the data were incorporated into a combined analysis categorized as "all insect pest" and "all parasitism."

Urbanization typically increased outbreak intensity and suppressed the endemic occurrence of parasitism ("all parasitism" in Fig. 3). A similar pattern with increased outbreak intensity was detected in rust-like diseases and in the combined analysis of all microbial diseases, although the endemic occurrence in rust-like diseases was not significant. Significantly high endemic occurrences of powdery mildew-like diseases were observed in urban areas, with the analysis combining all insect pests. The effects of leaf-eating insects and spot-forming diseases were not significant.



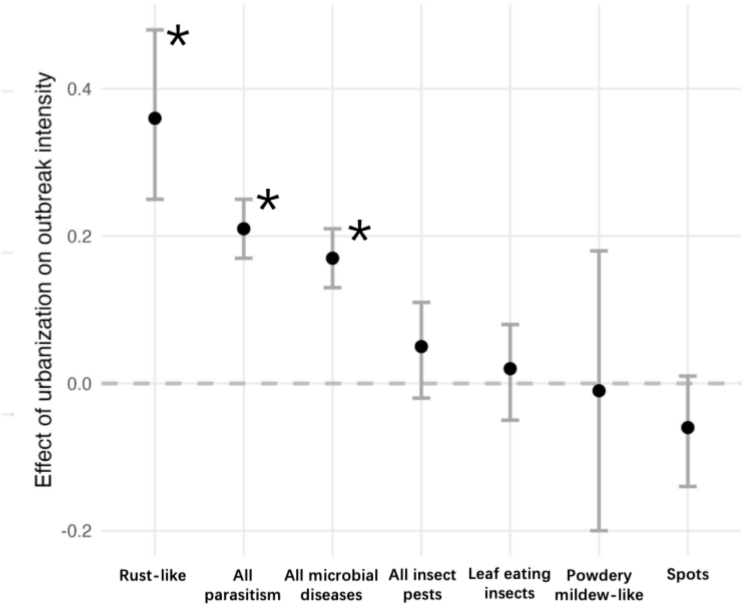
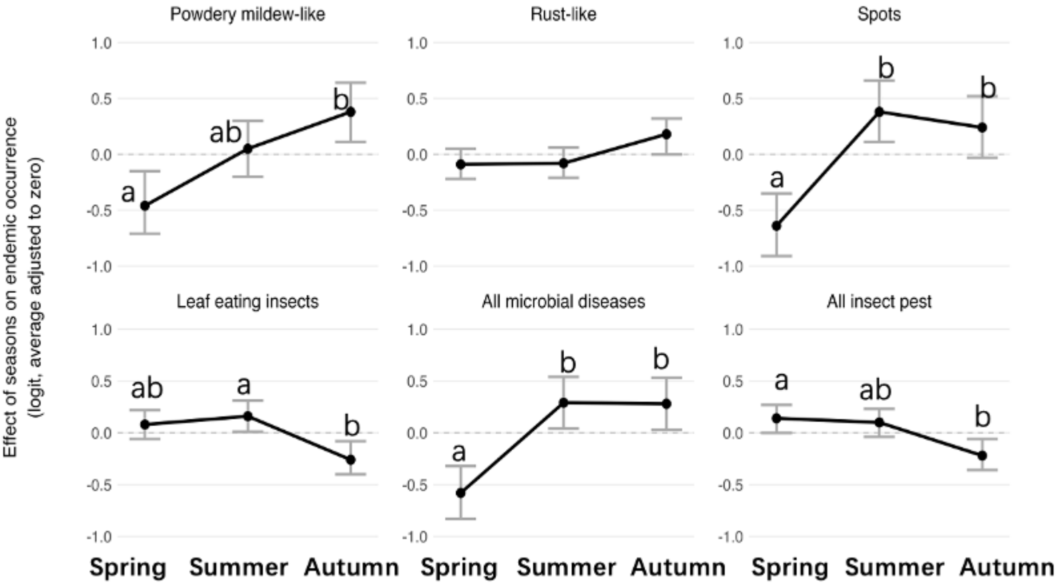


Fig. 3 Effect of urbanization (built-up area percentage) on parasitism metrics: *a*3 in Eq 1 as endemic occurrence (left) and *b*3 in Eq. 2 as outbreak intensity (right). The points show mean estimated effects with 95% credible intervals. Asterisks indicate significant effects ($p < 0.05$). The all insect pests category includes both leaf-eating insects and other leaf-parasitic insects (e.g., leaf miners and gall-formers). The all microbial diseases category includes powdery mildew-like, rust-like, and leaf spot diseases. The all parasitism category includes all the above insects and microbial parasitism on leaf surfaces

3.3 Effect of seasons

The effects of seasons (spring, summer, and autumn) on the endemic occurrence of powdery mildew-like, spot-forming, and all microbial diseases increased from spring to summer and autumn (Fig. 4). Conversely, it decreased in leaf-eating insects and in all insects combined. In outbreak intensity, all parasitism types followed a distinct “U-shaped” curve: higher levels in spring and autumn, with significant declines in summer; the only exception was a non-significant summer decline in spot-forming diseases (Fig. 4). Microbial diseases are generally more prevalent in autumn than in spring, whereas insect pests tend are more common in spring than in autumn.



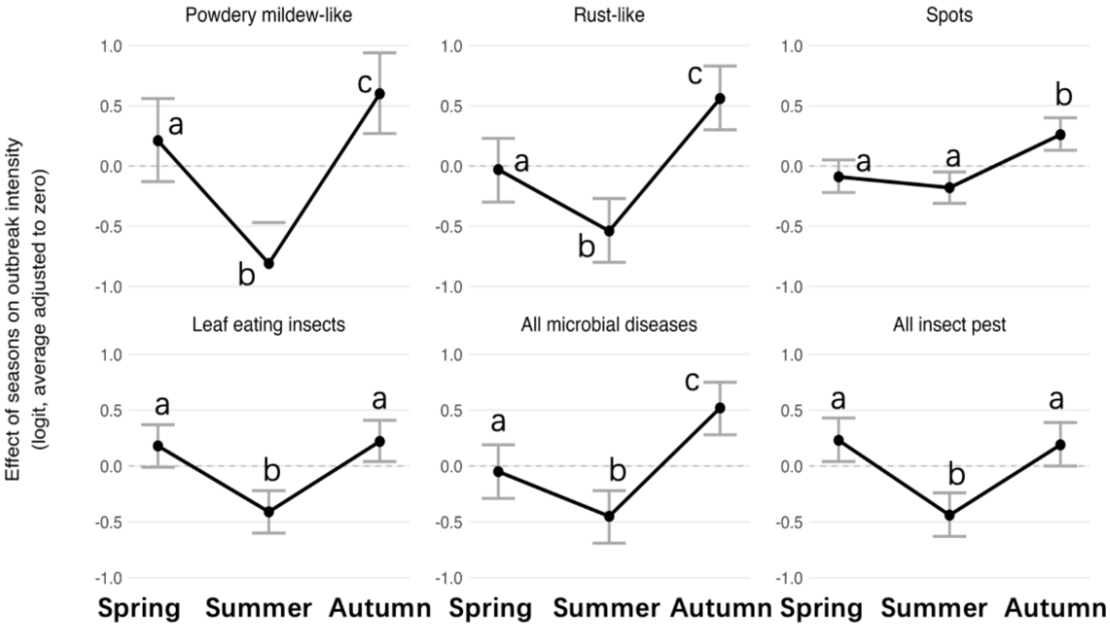


Fig. 4 Seasonal effects on endemic occurrence, a_season_j in Eq. 1, and outbreak intensity, b_season_j in Eq. 2, for five parasite categories. The vertical bars show the quartile ranges. Different letters indicate significant differences between seasons ($p < 0.05$)

4 Discussion

The strong seasonal signature was generally the same as that observed in our previous study in the Tokyo metropolitan area (Wang et al., 2025) and the general patterns in Japan (Takamatsu & Miyamoto, 2019) and China (Wang, 2023). This seasonal pattern may represent a common phenological phenomenon in East Asia.

The findings suggest that urbanization generally enhances the intensity of parasitism outbreaks, supporting the urban stress hypothesis, while simultaneously reducing endemic occurrence, in line with the habitat fragmentation hypothesis ("all parasitism" in Fig. 3). However, this trend is not observed for the endemic occurrence of powdery mildew and combined analysis of insect pests.

The heat-island effect has been identified as an important factor contributing to elevated outbreak intensity and increased parasitism in urban areas (Dale and Frank, 2014; Youngsteadt et al., 2015). However, we explicitly evaluated temperature in the model, suggesting that other factors are likely at play in our case.

Nitrogen deposition in urban areas is an important factor contributing to increased outbreak intensity. This deposition occurs through ammonia gas emissions and nitrogen oxides associated with urban pollution (Galloway et al., 2008), as well as through bird-mediated nutrient transport originating from urban waste sources (Fujita and Koike, 2007). Nitrogen often affects fungal diseases in wild plant communities (Liu et al., 2017, 2019). It also increases plant susceptibility to obligate parasites, such as powdery mildew and rust; however, it decreases susceptibility to facultative parasites, such as *Xanthomonas* spp. and *Alternaria* spp., some of which cause leaf spots (Dordas, 2008). Nitrogen deposition positively influences herbivorous insects by improving host plant nutrient status (Throop & Lerdau 2004), suggesting enhanced insect outbreak intensity in urban areas. These responses may align with our findings of a higher outbreak intensity in urban areas by rust and combined analyses, including microbial diseases (Fig. 3). Parasitoids, predator insects, and predator birds may decrease in urban areas (Corcos et al. 2019; Pena et al. 2021), potentially leading to an increase in herbivorous insects within urban areas, independent of the physiological environment.

The habitat fragmentation of plant parasites in urban areas results from the isolated distribution of host plants within the urban landscape. This mechanism results in the absence of parasites in some plots (Hanski 2011), and reduces endemic occurrence, even in the presence of high outbreak intensity where the parasite occurs, as demonstrated by our combined analyses of "all parasitism" and "all microbial diseases" (Fig. 3). Parasites of the dominant tree species in climax forests are suppressed in urban areas, probably due to habitat fragmentation (Schueller et al. 2019). Some microbial parasites are dispersed by plant debris, soil, and raindrop splashes (Schaad and White 1974), indicating a relatively short dispersal distance that can limit endemic occurrence.

However, some exceptions exist. Abundant host plants and sufficient dispersal capabilities in urban landscapes may result in a higher endemic occurrence of powdery mildew and insects in urban areas than in rural areas (Fig. 3). Ruderal species inhabit fragmented environments in forest-dominated landscapes, whereas their habitats are more continuous and abundant in urban areas (Koike 2006) despite being separated by dozens of meters due to infrastructure and buildings in urban landscapes. Numerous host plants for powdery mildew exist in urban areas (Wang et al. 2005), including the saplings of the ruderal tree *Celtis sinensis* Pers. (Kimura et al. 2019) and various ornamental plants (Yeh 2021). Certain insects travel considerable distances by self-propulsion and being carried by the wind. Fungal diseases, such as powdery mildew, produce spores dispersed in the wind. Roads act as wind corridors in urban landscapes (Cao et al., 2015), potentially facilitating wind dispersal.

Because numerous effects on endemic occurrence were detected in this study, dealing with multi-regional comparisons (Fig. 3). Endemic occurrence is influenced by the dispersal distance (Franke et al. 2009; Hanski 2011), suggesting that the spatial scale for endemic occurrence is landscape-level and exceeds the spatial scale of outbreak intensity, which is determined by the local environment. In our previous study, which encompassed all plots within a 2 × 2 km area, numerous local environments were found to be significant for outbreak intensity, whereas only a limited number were significant for endemic occurrence (Wang et al. 2025).

The host-parasite system is complex. Herbivorous insects serve as prey for hyper-parasitic or predatory animals, and an increase in these animals decreases herbivorous insect populations through a top-down effect. Habitat fragmentation has both positive and negative effects on plant parasitism, depending on the specific trophic level involved. Parasitoids, predatory insects, and predatory birds generally decrease in urban areas (Corcos et al. 2019; Pena et al. 2021); however, flower plantations in urban areas can attract nectar-feeding parasitoid adults (Piekarska-Boniecka et al. 2022).

Host plant fragmentation primarily influences endemic occurrence; however, increased spore production resulting from high outbreak intensity promotes higher endemic occurrence through longer distance immigration caused by the increased number of arriving spores (Wingen et al. 2013).

4.1 Conclusion

Both the habitat fragmentation hypothesis and the urban stress hypothesis were supported by our findings. Urban settings generally increased parasitism intensity. However, habitat fragmentation may lead to complex outcomes, with both positive and negative effects of urbanization depending on the specific host-parasite systems. For sustainable urban planning, urban planners should pay closer attention to high plant susceptibility and clustered host distributions than is typically required in rural landscapes. Parasitism predominantly affects a limited subset of the regional flora (Wang et al., 2025), suggesting a potential decline in susceptible plants from urban plant communities. The effect of parasitism on the local plant extinction in urban-rural gradient should be studied in future.

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Statements and Declarations

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Author Contributions

FK and XW contributed to the study design, data analysis, and manuscript drafting. XW conducted the fieldwork. FK designed and analyzed the statistical models. All the authors have read and approved the manuscript.

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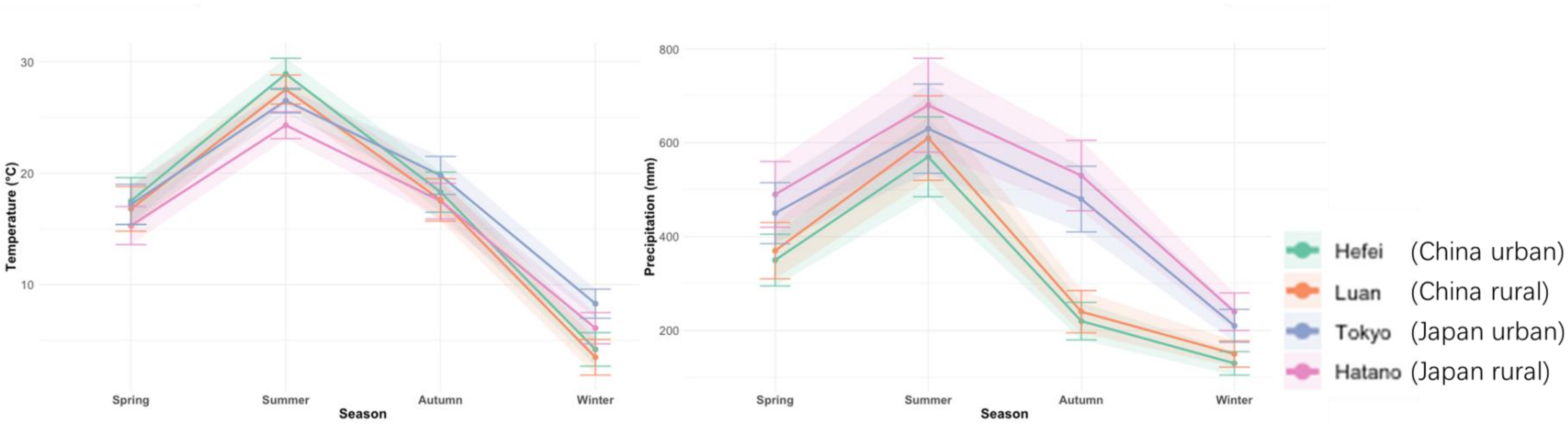
Supporting Information Table S1 Summary of land-use characteristics across the 11 study regions in Japan and China. The values show the percentage composition within a 1,000-m radius of each regional center, including built-up areas (buildings, roads, and railways), green spaces (forests and grasslands), agricultural lands, and water bodies. Region type (-C: urban/city; -R: rural) and geographic coordinates (WKT format) were provided for each site. The built-up area ranged from 1.15% (CN-R3) to 92.78% (JP-C1), representing a comprehensive urban-rural gradient

Region index	Region code	Longitude Latitude	Country	Built-up	Forest	Grassland	Agricultural	Water
1	CN-C1	117.292083 31.871277	China	87.78	0	8.8	0	3.42
2	CN-C2	117.274534 31.869838	China	84.62	0	11.2	0	4.18
3	JP-C1	139.749842 35.660607	Japan	92.78	7.22	0	0	0
4	JP-C2	139.725888 35.652768	Japan	91.68	4.9	3.42	0	0
5	JP-C3	139.589634 35.473789	Japan	84.74	5.63	3.2	6.43	0
6	CN-R1	116.588574 31.422752	China	15.55	19.58	55.78	8.97	0.12
7	CN-R2	116.194439 31.08858	China	2.38	23.19	74.43	0	0
8	CN-R3	116.60368 31.428318	China	1.15	0	57.8	41.05	0
9	JP-R1	139.240595 35.34534	Japan	38.19	29.84	0	31.97	0
10	JP-R2	139.183868 35.408588	Japan	8.5	43.73	20.46	27.31	0
11	JP-R3	139.236143 35.337726	Japan	4.79	56.46	0	38.75	0
Average				46.56	17.32	21.37	15.45	0.70

Supporting Information Table S2 Dominant plant species and interregional floristic similarities. The matrix shows the number of shared species between regional pairs, quantifying floristic overlap. The diagonal elements of the matrix denote the number of species in a region

Region index	Region code	Number of quadrat	Most dominant species	Second dominant species	Number of species found in both regions										
					CN-C1	CN-C2	JP-C1	JP-C2	JP-C3	CN-R1	CN-R2	CN-R3	JP-R1	JP-R2	JP-R3
1	CN-C1	90	*Liriope spicata*	*Alternanthera philoxeroides*	67	23	14	17	12	20	19	13	17	14	12
2	CN-C2	60	*Liriope spicata*	*Melia azedarach*	23	59	13	16	14	19	23	12	16	15	11
3	JP-C1	60	*Pleioblastus chino*	*Causonis japonica*	14	13	58	25	21	15	14	10	21	20	15
4	JP-C2	60	*Pleioblastus chino*	*Aphananthe aspera*	17	16	25	69	22	16	15	11	24	32	18
5	JP-C3	30	*Plantago lanceolata*	*Solidago canadensis*	12	14	21	22	54	13	15	11	16	17	25
6	CN-R1	60	*Erigeron annuus*	*Bidens pilosa*	20	19	15	16	13	100	44	25	20	17	13
7	CN-R2	60	*Conyza canadensis*	*Erigeron annuus*	19	23	14	15	15	44	81	26	19	16	14
8	CN-R3	30	*Eleusine indica*	*Digitaria sanguinalis*	13	12	10	11	11	25	26	43	14	12	15
9	JP-R1	60	*Digitaria sanguinalis*	*Taraxacum spp.*	17	16	21	24	16	20	19	14	98	37	21
10	JP-R2	60	*Bidens pilosa*	*Causonis japonica*	14	15	20	32	17	17	16	12	37	94	24
11	JP-R3	30	*Achyranthes aspera*	*Causonis japonica*	12	11	15	18	25	13	14	15	21	24	64



Supporting Information Figure S1 Seasonal temperature (°C) and precipitation (mm) patterns in the four representative regions of China (Hefei and Lu'an) and Japan (Tokyo and Hadano) in 2022. The data represent mean seasonal values with standard deviations covering both urban (CN-C, JP-C) and rural (CN-R, JP-R) sites. Data sources: China Meteorological Administration (CMA) and Japan Meteorological Agency (JMA)