Prevalence of Leaf Parasitism by Insects and Fungi in Wild Plant Communities: Implications for Community Assembly

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Keywords: plant community process, fungal disease, insect pest, host susceptibility, zero-inflated binomial regression, plant-parasite dynamics, suburban landscape, epidemiological triangle

Abstract

Parasitism by infectious diseases and insect pests significantly shapes wild plant communities by stabilizing them through suppressing dominant species and destabilizing them by suppressing minor species. However, the dynamics of parasitism in wild ecosystems remain understudied. This study aimed to determine whether parasites infect a wide range of host species or are plant-specific, assess the stabilizing and destabilizing effects of parasitism on plant community structure, and determine the influence of environmental and seasonal factors on parasitism. **Methods**: We conducted field surveys in herbaceous plant communities within a 1 km² area in the Tokyo metropolitan region, focusing on fungal diseases (rust-like and powdery mildew-like symptoms) and leaf-eating insect pests. Using zero-inflated binomial regression, we evaluated the symptom prevalence and intensity of parasitism across species, seasons, and environmental variables. **Results**: The results indicated that a few plant species were highly susceptible to parasitism, with rust-like infections tending to predominantly affect dominant species and leaf-eating insects targeting minor species. **Conclusion**: These findings highlight the contrasting roles of parasites in stabilizing and destabilizing plant communities and that both environmental and seasonal factors influence parasitism similar to cultivated ecosystems.

1 Introduction

Parasitism in plants, including fungal pathogens that reproduce on the host and cause disease, as well as insect pests that feed on plants, plays a crucial role in shaping plant community structure (Erizal and Koike, 2007; Konno & Seiwa, 2011; Wang et al., 2019; Halliday et al., 2020; Liu et al., 2020; Rohr et al., 2020; Kaishian et al., 2024). Fungal pathogens and insect pests are smaller than their host plants, and many individuals depend on a single host. Defensive host evolution has led to species-specific host-parasite relationships (Dobler et al., 1996; Ferreira et al., 2007), and plant species affect fungal community on leaves (Liu et al. 2021). In this study, both fungal pathogens and insect pests are considered forms of parasitism. Since insects often exhibit species preferences (Bernays and Chapman, 1994), and fungal pathogens are species-specific (Gilbert and Webb, 2007), it is unclear whether parasitism affects all plant species in a community equally or only impacts a subset of species. This suggests that parasitic effects may vary across communities, potentially influencing their composition and species diversity (Hatcher et al., 2006). Parasitism has a dual effect on plant communities (Gilbert & Webb, 2007; Gilbert et al., 2012; Forister et al., 2015; Fordyce, 2016), stabilizing wild plant communities through intensive infection of dominant species and destabilizing them by suppressing minor species (Mordecai, 2011). Although both infectious fungal diseases and insect pests are host-specific, they often differ in dispersal methods. Fungi disperse their spores passively via wind and water droplets (Lacey, 1996; Madden, 1997), whereas adult insects actively seek specific host plants to lay eggs (Mayhew, 1997). This suggests that insect pests may be more effective at spreading to rare hosts than fungi.

To understand the effect of parasitism on plant community assembly, two areas should be studied. First, we need to examine parasitism across the entire plant community, including its occurrence, intensity, host susceptibility, and environmental effects. Next, we must assess the damage parasitism causes to plant populations and species interactions represented as community-matrix (Kawatsu and Kondoh, 2018). This study focuses on the first step, with damage evaluation to be addressed in future studies.

This study examines the presence of visible symptoms associated with parasitism. The absence of such symptoms may indicate either the absence of parasites or conditions that are not conducive to symptom development. Plants previously not considered hosts can be infected without showing symptoms, and some hosts may exhibit symptoms only under certain conditions (Fondong et al., 2000; Bacon & Hill, 1996).

The epidemiological triangle (pathogen occurrence, host plant susceptibility, and environmental effects) posits that infection occurrence and intensity depend on interactions between the parasite, host, and environment (Stevens, 1960). Although we analyzed visible symptoms, the epidemiological triangle can serve as a framework to investigate the local occurrence of symptoms, host plant susceptibility, and the effects of the local environment. These factors are key drivers of outbreaks and play a crucial role in shaping plant community assembly through parasitism.

We investigated wild plant parasitism (specifically fungal infections and insect infestations) in herb layer plant communities across a 1 km^2 area. The main objectives of this study were to (1) determine whether parasites infect all plant host species evenly or target a few species, (2) assess the stabilization and destabilization effects by testing positive or negative correlations between plant dominance and parasitism, and (3) examine the effects of environmental and seasonal factors on parasitism. To our knowledge, this is the first study to simultaneously evaluate a kind of epidemiological triangle (symptom occurrence, host plant susceptibility, and environmental effects) in natural ecosystems.

2 Materials and methods

2.1 Research site

The study was conducted in a suburban 1 × 1 km landscape (latitude 35.473°, longitude 139.589°, and altitude 50 m) in Yokohama, Tokyo metropolitan area, Japan (Figure 1). Yokohama has a mean annual temperature of 16.3 °C and mean annual precipitation of 1687.5 mm (Japan Meteorological Agency, https://www.data.jma.go.jp), and falls within a warm-temperate moist forest biome (Miyawaki, 1986). The examined vegetation included seminatural grasslands, little-managed lawns, roadside verges, and forest floor vegetation of abandoned coppices and evergreen broad-leaved forests. Since vegetation types were continuous and difficult to classify by plant species composition, we used a principal component axis that represented the grassland-forest vegetation continuum. Fungicides, pesticides, and herbicides were not applied to any of the studied vegetation types.

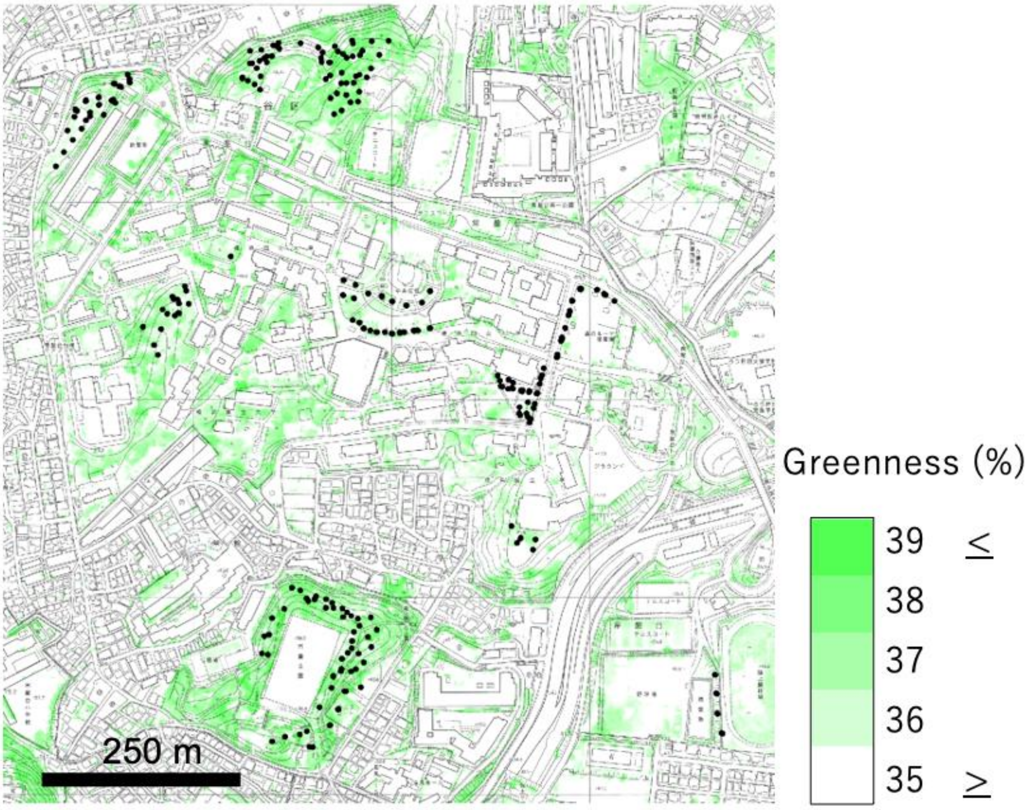

Figure 1. Map of the research site. The depth of the green color represents the greenness of the aerial photograph, green/(red + green + blue). The black dots represent research plots.

2.2 Symptoms and pests

We visually assessed symptom types according to Rottstock et al. (2014), focusing on easily observed powdery mildew-like visible external mycelia and rust-like visible external sporulation structures. Plant diseases that cause spots, lots, and breechings are sometimes difficult to distinguish from mineral deficiency, mineral toxicity, sunburn, or leaf aging without detailed information on each plant species. Several fungal taxa occur even in a disease spot (Tao et al. 2021) and molecular identification of symptoms is difficult. Consequently, in this study, to avoid including non-infectious symptoms, we excluded these and did not use molecular identification, as it was impractical to analyze all leaves this way.

During the examination of plant pests, we focused on insect pests, including leafminers (larvae of moths, sawflies, and flies), sap-sucking insects (aphids, whiteflies, and scale insects), and leaf-eating insects (mainly lepidopteran larvae and leaf beetles). We did not record scars without insects. These insects are major plant pests that affect young plant shoots.

2.3 Epidemic surveys

We established 365 circular plots, each 2 m in diameter, within the vegetated areas (Figure 1) during the growing seasons of spring (April–June), summer (July–August), and autumn (October–November) from October 2019 to November 2021. The surveys were conducted on sunny days between 9:00 and 14:00 to ensure sufficient lighting. The plots were spaced at least 20 m apart. The same vegetation was examined multiple times across different seasons.

All seed plants less than 2 m in height were examined. The height and plant coverage (%) of each plant species were measured. Coverage was estimated as the percentage of ground area within each 2m diameter circular plot occupied by the vertical projection of the foliage of each plant species. Specifically, within each plot, we visually estimated the foliage-covered area of each species and calculated its proportion relative to the total plot area. We carefully examined the fungal diseases and insect pests of each host species within the plot. A portable optical microscope with 60–120×magnification (Kenko, STV-120M) was used in the field to observe leaf lesions. When diseases or pests were found, we examined individual leaves (usually up to 100 leaves) and recorded the number of damaged or infected leaves. We did not count the leaves if parasitism was not detected because counting healthy leaves is labor-intensive. Hemispherical photographs were taken from the plot center to measure the upper canopy cover above the herb layer.

2.4 Analysis

We distinguished between endemic occurrence (in the epidemiological sense rather than biogeography) and outbreak intensity (Figure 2). Endemic occurrence refers to parasitism symptom occurring predominantly in plots where the host species exist, although the environment can influence it and might not necessarily affect all leaves within a plot. In contrast, outbreak intensity reflects the proportion of infected leaves within a plot and is similarly influenced by the environment.

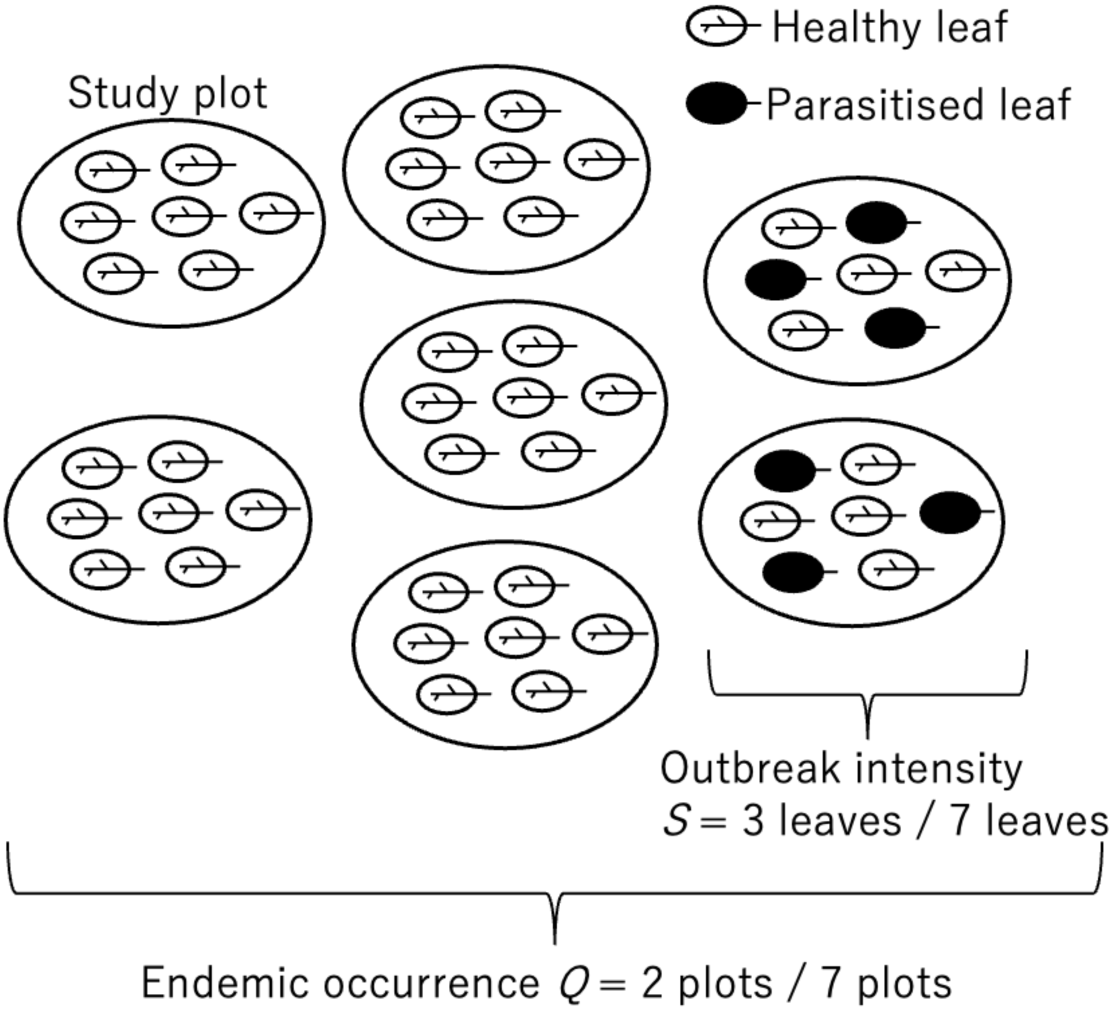

Figure 2. Simplified visual representation of endemic occurrence and outbreak intensity. Endemic occurrence represents the ratio of plots with parasitism, and outbreak intensity represents the average infected leaf ratio in plots with parasitism.

We used zero-inflated binomial regression with a stochastic modeling system (RStan by Stan Development Team 2023) to evaluate the effects of three major factors: endemic parasite occurrence on host plants, outbreak susceptibility of host plants, and the environment (Supporting Information). In the zero-inflated binomial regression, endemic parasitism (the number of plots with detected parasites /number of examined plots) and outbreak intensity (the number of infected leaves/number of examined leaves in a plot) were evaluated (Figure 2).

Outbreak intensity was evaluated as the probability S of parasitism on a leaf (Figure 2). When inspecting m leaves and identifying n positive leaves, the probability followed a binomial distribution with the number of trials m, successes n, and success probability S:

$$Prob\ (positive\ n\ leaves\ in\ examined\ m\ leaves) = binomial\ (n, m, S)$$

$$for\ n > 0 \qquad Eq\ (1),$$

where the logit of S is the linear combination of environment and outbreak susceptibility of plants aslogit(S) = ln(S/(1-S)),

$$\text{Logit}(S) = b0 + \text{species} + \text{season} + b3\ \text{topographic radiation} + b4\ \text{topographic wetness} + b5\ \text{topographic wind} + b6\ \text{greenness} + b7\ \text{distanceto road} + b8\ \text{canopy openness} + \text{year} \quad \text{Eq (2)},$$

where b0 is the intercept; b3 to b8 are regression coefficients; and species, season, and year arequalitative variables. For example, each plant species has an outbreak susceptibility value, and the average of all species is fixed at zero to avoid redundancy to b0 and other variables. All quantitative environmental variables were standardized before analysis using the mean and standard deviation.

The obtained regression coefficients represent the effects of the focal variable after adjusting other effects. Host plant susceptibility is determined after adjusting for seasonal and environmental effects.Conversely, the obtained seasonal effect value is determined after adjusting for host susceptibility.

The endemic occurrence of pathogens and parasitic insects was evaluated as the presence/absence probability Q, where at least one infected/infested leaf of a host species existed in a plot (Figure 2). The calculation is not a straightforward ratio of present plots to the total number of plots (present + absent plots). Instead, we accounted for the probability that parasitism exists in the plot but might go undetected, especially when only a few leaves exist. The observed probability that parasitism was not detected (R) is the sum of the probability that parasitism was truly absent (1−Q) and that parasitism existed (Q) but was undetected:

$$R = (1 - Q) + Q \times \text{binomial}\,(0, k, S) \qquad \text{Eq (3)},$$

where k is the assumed number of examined foliage, with the assumption that the occurrence of parasitism was examined at a precision of 1% plant cover (with the 10 cm radius circle of foliage being the unit coverage). The logit of Q is the linear combination of environment and endemic susceptibility of plants, as logit(Q)=ln(Q/(1-Q)):

$$\text{Logit}(Q) = a0 + \text{species} + \text{season} + a3\ \text{topographic radiation} + a4\ \text{topographic wetness} + a5\ \text{topographic wind} + a6\ \text{greenness} + a7\ \text{distance to road} + a8\ \text{canopy openness} + \text{year} \quad \text{Eq (4)},$$

where a0 is the intercept; a3 to a8 are regression coefficients; and species, season, and year are qualitative variables. For example, each species has its own value representing endemic susceptibility, and the average of all species is fixed to zero to avoid redundancy to a0 and other variables. All environmental variables are the same as those in Equation 2.

As described above, we assumed that endemic occurrence (probability of presence Q) and outbreak intensity (infection probability of leaves S) are functions of host species (qualitative variable representing susceptibility). The regression provides spai for endemic susceptibility (Eq 2) and spbi for outbreak susceptibility of species i (Eq 4). If no infection is found in any plot, Q should be zero; however, S cannot be determined. We assumed Q and S to be close to zero by introducing the difference, spai - spbi, which follows a normal distribution with a mean of zero. Both spai and spbi are values that drive Q and S towards zero.

The other factors studied included season (qualitative variables such as spring, summer, and autumn representing seasonal differences in temperature, humidity, radiation, and rainfall), distance from roads (using digital national land information https://nlftp.mlit.go.jp/ksj/gmlold/datalist/gmlold_KsjTmplt-N01.html and QGIS Ver.3.30, QGIS Development Team 2023), canopy openness (measured using hemispherical photographs), greenness (pixel brightness of green/red + green + blue) on a 3 m resolution aerial photograph taken during the growing season), and topographical environments (slope radiation, wetness as a log-specific catchment area, and wind by the width of unobstructed direction calculated, from a digital elevation model with 5 m horizontal resolution, https://fgd.gsi.go.jp/download/menu.php, following Koike 2022). All topographical environments were averaged over a 10 m radius. The survey year was considered a qualitative variable to eliminate the effect of year-to-year differences. Highly correlated environmental variables were excluded from the analysis to avoid multicollinearity.

To determine whether parasites infected all plant host species evenly or only a few limited species within a community, the frequency distribution of susceptibility among host plants was tested based on the skewness of spai and spbi using RStan.

To assess the stabilization and destabilization effects of parasitism on plant communities, we examined the positive or negative correlations between plant dominance and parasitism. Pearson's correlation coefficients were calculated for plant species susceptibility and plant host abundance. Plant occurrence (number of plots where the plant was found divided by all plots) and log-transformed plant species cover (average log-transformed cover in detected plots) were considered measures of plant host abundance.

Finally, the relation between susceptibility and plant position along the forest-grassland vegetation gradient was examined using principal component analysis (PCA) based on plot plant composition.

3 Results

We identified 169 plant species in 365 plots and focused our analysis on 49 species present in more than nine plots (Supporting information 2). Among them, seven forest-community species and three grassland-community species, as classified by Miyawaki (1986), were present in more than 50 plots. The forest-community species included Aphananthe aspera (Thunb.) Planch., Aucuba japonica Thunb. var. japonica, Machilus thunbergii Siebold et Zucc., Ligustrum lucidum Aiton, Trachycarpus fortunei (Hook.) H.Wendl., Quercus myrsinifolia Blume, and Houttuynia cordata Thunb. The grassland-community species included Pleioblastus chino (Franch. et Sav.) Makino., Causonis japonica (Thunb.) Raf, and Erigeron philadelphicus L. In the PCA of plot plant composition, forest plants were positively associated with the first principal component, whereas grassland plants were generally negatively associated (Table 1, Supporting Information 3). The environmental variable "topographic wind" was removed from the analysis because of a high correlation with "topographic wetness" and "greenness." After removing "topographic wind," mutual correlation among analyzed environmental variables was r2 < 0.14. Zero-inflated binomial regression did not provide a converged solution for leaf miners and sap-sucking insects because of their low total occurrences; therefore, it was excluded from the subsequent results.

Table 1. Pearson's correlation coefficient between plant host dominance (occurrence and log-transformed cover), preference in a grassland–forest gradient (plant community PCA), and susceptibility of 49 host plants

Parasite types	Regional plant host occurrence	Log-transformed local plant cover	Grassland–forest community gradient
Endemic susceptibility			
Leaf-eating insects	0.069	-0.523 **	0.209
Powdery mildew-like diseases	-0.073	-0.183	0.061
Rust-like diseases	0.268 +	-0.151	0.190
Outbreak susceptibility			
Leaf-eating insects	-0.165	-0.376 **	-0.162
Powdery mildew-like diseases	-0.040	-0.238	0.049
Rust-like diseases	0.227	-0.191	0.172

+$p < 0.10$, *$p < 0.05$, **$p < 0.01$

3.1 Susceptibility of host plant species

The plants most susceptible to endemic occurrence in our study were Plantago asiatica L. to leaf-eating insects, Celtis sinensis Pers. to powdery mildew, and Quercus myrsinifolia Blume to rust. The skewness of endemic (0.65, p=0.023) and outbreak (0.91, p=0.007) susceptibilities was significantly positive in rust-like diseases. Plants that are susceptible to rust-like diseases were limited (Figure 3). The skewness values were 0.43 (p=0.077) for endemic and 0.89 (p=0.067) for outbreak susceptibilities, which was positive in powdery mildew-like diseases with limited susceptible plants

(Figure 3). Endemic (-0.16, p=0.73) and outbreak (-0.11, p=0.62) susceptibilities for leaf-eating insects were not positively skewed.

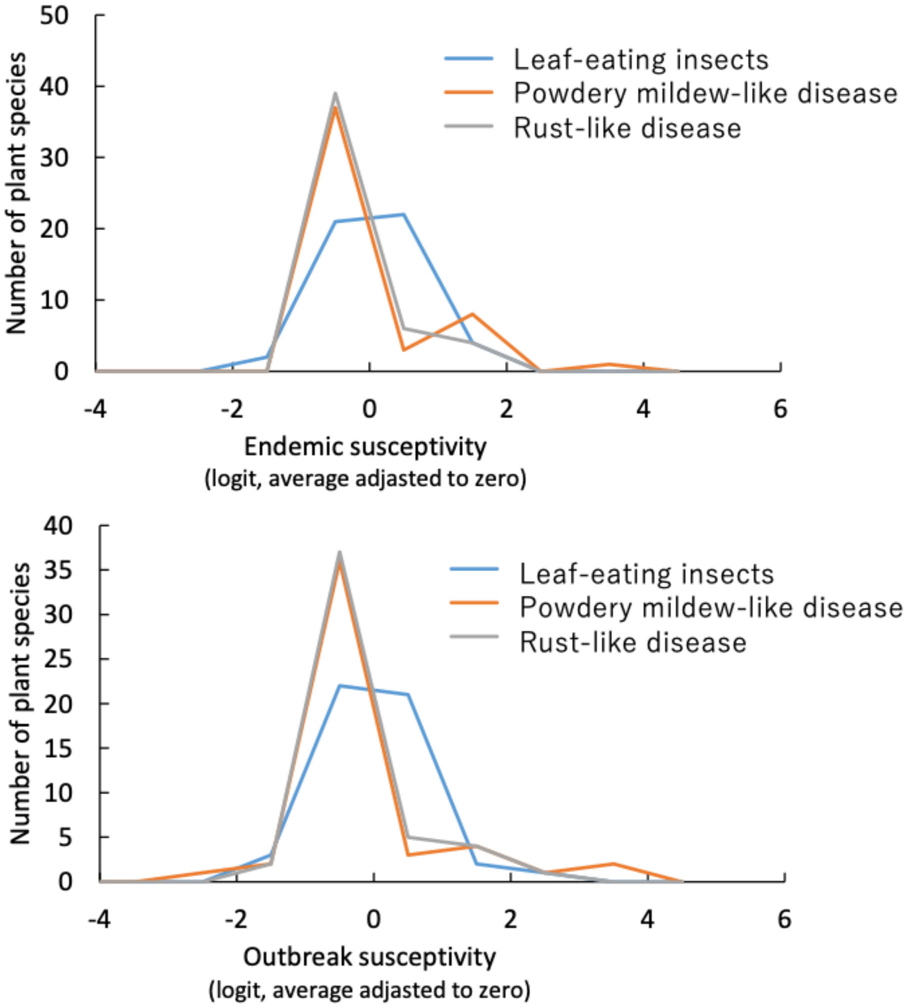

Figure 3. Effect size of host plant species on endemic parasitism occurrence (Q) and outbreak intensity (S), based on zero-inflated binomial regression.

3.2 Host abundance and susceptibility

Host plant occurrence (the ratio of plots where a host plant was found) showed a weak positive correlation with endemic susceptibility to rust-like diseases, although the significance level was low (Table 1). This suggests that commonly found plant hosts may be more frequently infected. In contrast, plant species with greater cover were less susceptible to leaf-eating insects in terms of both endemic and outbreak susceptibilities (Table 1), indicating that locally dominant plant hosts were both less frequently and less intensively infected. The plant susceptibilities did not correlate with plant position along the forest-grassland gradient (Table 1).

3.3 Seasonality and plot environments

Parasitism by leaf-eating insects was frequent (endemism) and intense (outbreak) in spring (Figure 4). Fungal diseases, specifically powdery mildew-like and rust-like diseases, were intensely parasitic in autumn, and powdery mildew-like diseases were intensely parasitic in spring. In general, the studied insects parasitized earlier in the growing season, whereas the studied diseases were more prevalent later in the growing season.

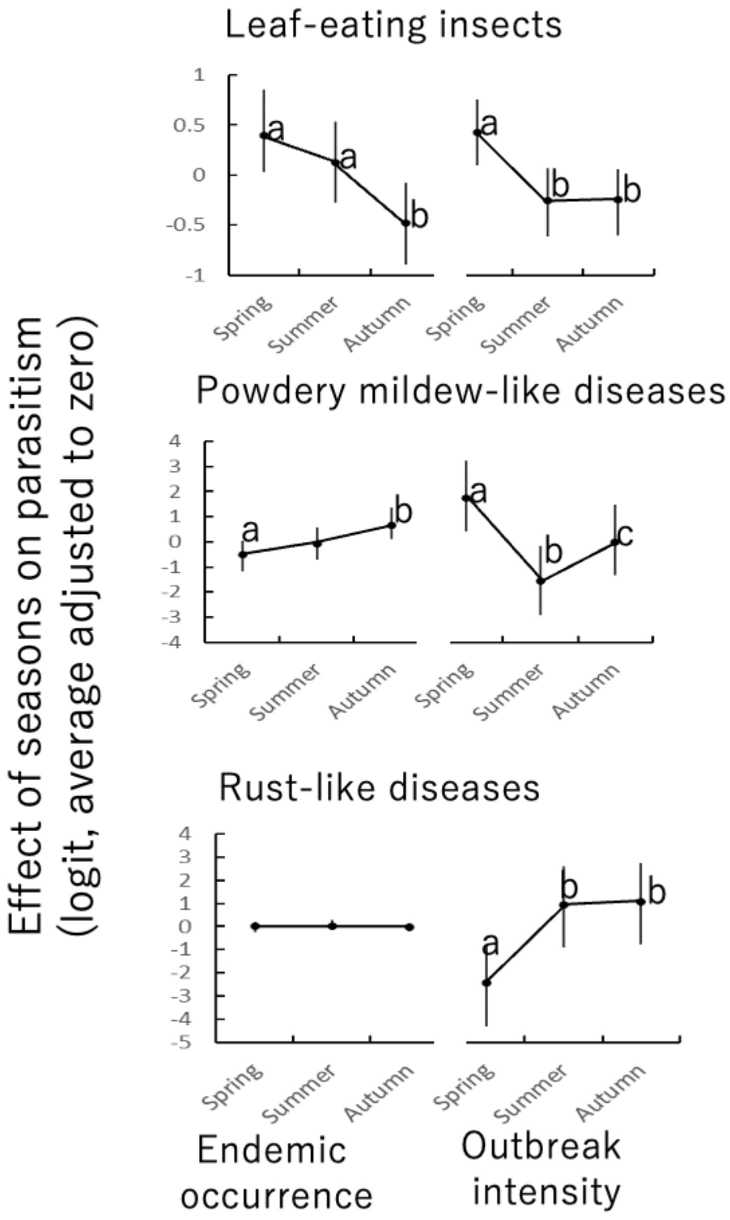

Figure 4. Effect sizes of seasons (categorical variable) based on zero-inflated binomial regression (Eqs 2 and 4).

Leaf-eating insects preferred topographically wet sites that were distant from the road (Figure 5). Powdery mildew-like diseases favored areas with strong radiation, wet topography, and proximity to roads. Rust-like diseases thrived in well-vegetative areas (aerial photograph greenness) with locally open canopy. Environmental effects on endemism were generally weak (Supporting Information 4).

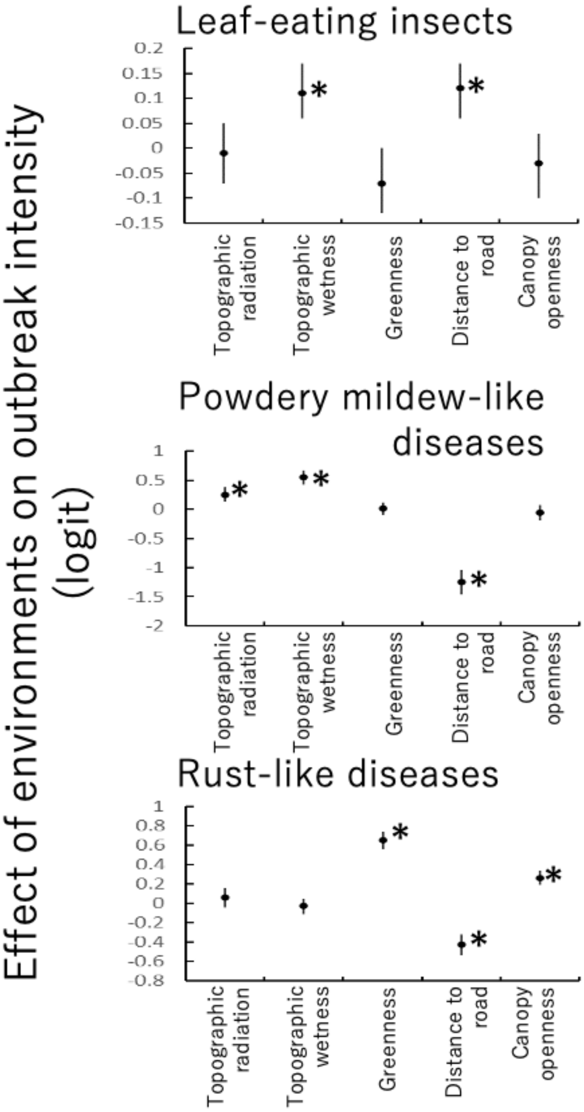

Figure 5. Effect sizes of environmental variables of research plots on parasitism intensity (outbreak) based on zero-inflated binomial regression (Eq 4). Environmental variables were standardized before analysis.

4 DISCUSSION

4.1 Implications on plant community assembly

The presence/absence of symptoms reflects both the existence of the pathogen and the conditions that lead to symptom development, while an outbreak signifies potential widespread damage. Some pathogen-host combinations show symptoms without significant damage, whereas others correlate strongly with damage. However, the exact nature of these interactions remains unclear. The results showed that only a limited number of species from the regional plant pool experienced damage from fungal diseases, suggesting that parasites might suppress plants unevenly with regard to community assembly processes, at least in fungal diseases.

Selective infection of minor hosts causes a destabilization effect, with minor host species experiencing more suppression than dominant host species because of positive feedback (Mordecai, 2011). In this study, damage by leaf-eating insects was higher in minor host species than in dominant host species. This suggests that leaf-eating insects may contribute to the destabilization of plant communities.

Plant leaf consumption by leaf-eating insects increases with the growth of individual caterpillars in the case of lepidopterans. Therefore, a small plant patch searched out by a mother may be completely consumed by a few large caterpillar individuals, whereas large plant patches remain unconsumed. Notably, strong density-controlling mechanisms for caterpillars driven by higher-trophic level predators and parasites (insects, microorganisms, and viruses) prevent caterpillars from causing widespread damage to dominant plant species (Myers & Cory, 2016), except in the case of some alien caterpillars.

In contrast, intensive parasitism of dominant plants can establish a negative feedback loop in host dominance, resulting in a community-stabilizing effect (Mordecai, 2011). We observed a weak stabilizing mechanism by rust-like diseases (Table 1), with regionally common hosts being susceptible to the parasites, as reported by Mitchell et al. (2002). Plant hosts are considered habitat patches for parasites and are a type of metapopulation (Thrall & Burdon, 1997). Habitat density (host plant) is crucial for the persistence and spread of focal parasitic species and involves a threshold habitat (host) density (Komuro & Koike, 2005). In this study, rust-like diseases exhibited a stabilizing effect; however, alien white pine blister rust catastrophically damages dominant pines in North America (Tomback & Achuff, 2010); therefore, the “stabilization effect” alone does not imply safety in quarantine.

4.2 Season and landscape environment

The effects of seasons and environment factors observed in this study generally align with well-known phenomena in cultivated crops in the research area (Yamaoka, 2014; Takamatsu & Miyamoto, 2019). Leaf-eating insect pest outbreaks were observed in spring. This can be attributed to active plant shoot growth during spring in temperate climates that provide soft tissues rich in nutrients for insects (Awmack & Leather, 2002). In contrast, fungal leaf disease outbreaks were generally observed in autumn (powdery mildew-like and rust-like diseases) and spring (powdery mildew-like diseases), which is consistent with the seasonality patterns observed in agricultural crops in the study area (Yamaoka, 2014; Takamatsu & Miyamoto, 2019).

Topographic wetness, such as valleys, caused parasitic outbreaks, except for rust-like diseases. Large canopy openness enhanced the intensity of rust-like diseases. Typically, sites with active plant growth and humid air conditions promote parasite outbreaks (Awmack & Leather, 2002; Yamaoka, 2014; Takamatsu & Miyamoto, 2019). Topographic radiation, as experienced by south-facing slopes, creates a dry environment and is a positive factor for powdery mildew-like diseases (Takamatsu & Miyamoto, 2019). The roads act as a wind corridor in urban landscapes (Cao et al., 2015), likely facilitating wind dispersal of fungal spores, leading to the outbreak of two fungal diseases at sites close to the road. However, proximity to roads suppressed leaf-eating insects.

The findings of this study (Table 1) are not consistent with those of Dobson and Crawley (1994), who reported higher susceptibility in early successional vegetation. The discrepancy is likely attributed to the fact that, while the studied grasslands were secondary vegetation, they represented stable traditional seminatural grasslands rather than rapidly successional grasslands where early species are suppressed by late-successional species.

4.3 Limitation of the study

This is the first step of the study to understand the effect of parasitism on plant community assembly, and we examined parasitism across the entire plant community, including its occurrence, intensity, host susceptibility, and environmental effects. We analyzed the correlation between dominance and plant susceptibility. However, in the next study, we must assess the damage to plant population parameters and species interactions represented as community-matrices (Kawatsu and Kondoh, 2018) to clarify the quantitative effect on plant community assembly.

We surveyed visible symptoms. Molecular approaches will make exact identification of symptoms and pathogen existence possible. In the case of our research, we had 2011 plot x host samples for fungal occurrence analysis, and 3465 positive leaves for symptom identification (Supporting Information 2). Development of further cost-effective methods is necessary for plant-community x fungal-community studies using molecular approach, although our three objectives; (1) uneven effect on plant community, (2) assessing the stabilization and destabilization effects, and (3) evaluating environmental and seasonal factors, were possible to be examined by our approach.

This study focused on suburban landscapes in a warm-temperate climate. Expanding the research to include diverse climates, ranging from tropical to boreal, across various landscapes (from wilderness areas of primary vegetation to urban landscapes) and conducting surveys over several years with different weather trends would enhance the generalizability of the findings on community assembly mechanisms. The research approach outlined in this paper can be applied in the design of feasible landscape-scale organic farming systems (Tscharntke et al., 2021) following simultaneous evaluation of the effects of a kind of epidemiological triangle (occurrence of symptoms, host susceptibility, and environmental factors) across various cultivars and surrounding wild ecosystems.

5 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.

6 Author Contributions

FK and XW contributed to the study design, data analysis, and manuscript drafting; XW, fieldwork; KH, biological discussion on plant diseases. All the authors have read and approved the manuscript.

7 Funding

This study was supported by Project C of the Graduate School of Environment and Information Sciences, Yokohama National University.

8 Acknowledgments

We sincerely thank Professor Sasaki Takehiro for his guidance and support throughout this research and to Professor Kagami Maiko for her detailed advice on plant disease epidemiology. We also appreciate the valuable input and support from faculty and colleagues at Yokohama National University. Additionally, the financial support provided by the Takayama International Education Foundation was crucial to this work.

9 References

Awmack, C.S., and Leather, S. (2002). Host plant quality and fecundity in herbivorous insects. Annu. Rev. Entomol. 47, 817-844. https://doi.org/10.1146/annurev.ento.47.091201.145300

Bacon, C.W., and Hill, N.S. (1996). Symptomless grass endophytes: products of coevolutionary symbioses and their role in the ecological adaptations of grasses. In Redkin, S. C. & Carris, L. M. (Eds.), *Endophytic Fungi in Grasses and Woody Plants* (pp. 155–178). Springer. doi: 10.1007/978-3-319-66541-2_1

Cao, A., Li, Q., and Meng, Q. (2015). Effects of orientation of urban roads on the local thermal environment in Guangzhou City. Procedia Engineering. 121, 2075-2082. https://doi.org/10.1016/j.proeng.2015.09.209

Dobler, S., Mardulyn, P., Pasteels, J.M., Rowell-Rahier, M. (1996). Host-plant switches and the evolution of chemical defense and life history in the leaf beetle genus Oreina. Evolution. 50, 2373-2386. https://doi.org/10.2307/2410706

Dobson, A., and Crawley, M. (1994). Pathogens and the structure of plant communities. Trends Ecol. Evol. 9, 393-398. https://doi.org/10.1016/0169-5347(94)90062-0

Erizal, M., and Koike, F. (2007). Dispersal and survival of juveniles of dominant tree species in a tropical rain forest of West Sumatra. Tropics. 16, 205-214. https://doi.org/10.3759/tropics.16.205

Ferreira, R.B., Monteiro, S., Freitas, R., Santos, C. N., Chen, Z., Batista, L.M., et al. (2006). Fungal pathogens: the battle for plant infection. Crit. Rev. Plant Sci. 25, 505-524. https://doi.org/10.1080/07352680601054610

Fondong, V.N., Pita, J.S., Rey, M.E., de Kochko, A., Beachy, R.N., and Fauquet, C.M. (2000). Co-infection of cassava mosaic geminiviruses in *Nicotiana benthamiana* results in synergism or suppression of symptoms depending on the host plant genotype. Front. Ecol. Evol. https://doi.org/10.3389/fevo.2020.12345

Fordyce, J.A., Nice, C.C., Hamm, C.A., and Forister, M.L. (2016). Quantifying diet breadth through ordination of host association. Ecology. 97, 842-849. https://doi.org/10.1890/15-0093.1

Forister, M.L., Novotny, V., Panorska, A.K., Baje, L., Basset, Y., Butterill, P.T., et al. (2015). The global distribution of diet breadth in insect herbivores. Proc. Natl. Acad. Sci. U S A. 12. 442-447. https://doi.org/10.1073/pnas.1423042112

Gilbert, G. S., and Webb, C. O. (2007). Phylogenetic signal in plant pathogen–host range. Proc. Natl. Acad. Sci. U S A. 104, 4979-4983. https://doi.org/10.1073/pnas.0607968104

Gilbert, G.S., Magarey, R., Suiter, K., and Webb, C.O. (2012). Evolutionary tools for phytosanitary risk analysis: phylogenetic signal as a predictor of host range of plant pests and pathogens. Evol. Appl. 5, 869-878. https://doi.org/10.1111/j.1752-4571.2012.00265.x

Halliday, F.W., Rohr, J.R., and Laine, A.L. (2020). Biodiversity loss underlies the dilution effect of biodiversity. Ecol. Lett. 23, 1611-1622. https://doi.org/10.1111/ele.13590

Kawatsu, K., and Kondoh, M. (2018). Density-dependent interspecific interactions and the complexity–stability relationship. Proc. R. Soc. B. 285, 20180698. https://doi.org/10.1098/rspb.2018.0698

Koike, F. (2022). Minna de GIS: spatial information processing system for education, research, and environmental assessment by citizens. Available at: https://www.minnagis.com [Accessed October 2, 2023].

Kolmer, J.A., Ordonez, M.E., and Groth, J.V. (2001). The Rust Fungi. John Wiley & Sons. https://doi.org/10.1002/9780470015902.a0021264.

Komuro, T., and Koike, F. (2005). Colonization by woody plants in fragmented habitats of a suburban landscape. Ecol. Appl. 15, 662-673. https://doi.org/10.1890/03-5232

Konno, M., and Seiwa, K. (2011). The validity of the Janzen-Connell model in the maintenance of tree species diversity. Jpn. J. Ecol. 61, 319-328. https://doi.org/10.18960/seitai.61.3_319

Lacey, J. (1996). Spore dispersal — its role in ecology and disease: the British contribution to fungal aerobiology. Mycol Res. 100, 641-660. https://doi.org/10.1016/S0953-7562(96)80194-8.

Liu, X., Chen, L., Liu, M., García-Guzmán, G., Gilbert, G.S., and Zhou, S. (2020). Dilution effect of plant diversity on infectious diseases: latitudinal trend and biological context dependence. Oikos. 129, 457-465. https://doi.org/10.1111/oik.07027

Liu, X., Jia, P., Cadotte, M.W. Chen Z, Xingfeng, S., Yunquan, W., Fei, C., Jihua, W., Shurong, Z. (2021) Host plant environmental filtering drives foliar fungal community assembly in symptomatic leaves. Oecologia. 195, 737–749. https://doi.org/10.1007/s00442-021-04849-3

Madden, L.V. (1997). Effects of rain on splash dispersal of fungal pathogens. Can. J. Plant Pathol. 19, 225-230. https://doi.org/10.1080/07060669709500557

Mitchell, C.E., Tilman, D., and Groth, J.V. (2002). Effects of grassland plant species diversity, abundance, and composition on foliar fungal disease. Ecology. 83, 1713-1726. https://doi.org/10.1890/0012-9658(2002)083[1713:EOGPSD]2.0.CO;2

Miyawaki, A. (1986). Vegetation of Japan: Kanto. Shibundo, Tokyo

Mordecai, E.A. (2011). Pathogen impacts on plant communities: unifying theory, concepts, and empirical work. Ecol. Monogr. 81, 429-441. https://doi.org/10.1890/10-2241.1

Mayhew, P.J. (1997). Adaptive patterns of host-plant selection by phytophagous insects. Oikos. 79, 417-428. https://doi.org/10.2307/3546884

Myers, J.H., and Cory, J.S. (2016). Ecology and evolution of pathogens in natural populations of Lepidoptera. Evol. Appl. 9, 231-247. https://doi.org/10.1111/eva.12328

QGIS Development Team (2023) QGIS Geographic Information System. Open Source Geospatial Foundation Project. https://qgis.osgeo.org [Accessed October 2, 2023].

Rohr, J. R., Civitello, D. J., Halliday, F. W., Hudson, P. J., Lafferty, K. D., Wood, C. L., & Mordecai, E. A., (2020). Towards common ground in the biodiversity–disease debate. Nat. Ecol. Evol. 4, 24-33. https://doi.org/10.1038/s41559-019-1060-6

Rottstock, T., Joshi, J., Kummer, V., and Fischer, M. (2014). Higher plant diversity promotes higher diversity of fungal pathogens, while it decreases pathogen infection per plant. Ecology. 95, 1907-1917. https://doi.org/10.1890/13-2317.1

Schnitzer, S.A., Klironomos, J.N., HilleRisLambers, J., Kinkel, L.L., Reich, P.B., Xiao, K., et al. (2011). Soil microbes drive the classic plant diversity–productivity pattern. Ecology. 92, 296-303. https://doi.org/10.1890/10-0773.1

Stan Development Team (2023). “RStan: the R interface to Stan.” R package version 2.21.8. https://mc-stan.org/ [Accessed: October 2, 2023].

Stevens, R.B. (1960) Cultural practices in disease control. In: JG Horsfall, AE Dimond, eds. Plant Pathology, An Advanced Treatise, Vol. III. New York, NY, USA: Academic Press, 357-429.

Takamatsu, S., and Miyamoto, T. (2019). Ecology and control of plant diseases caused by powdery mildew fungi. Plant Protection. 73, 53-58.

Tao, J., Cao, P., Xiao, Y., Wang, Z., Huang, Z., Jin, J., Liu, Y., Yin, H., Liu, T., Zhou, Z. (2021). Distribution of the potential pathogenic Alternaria on plant leaves determines foliar fungal communities around the disease spot. Environmental Research, 200: 111715. https://doi.org/10.1016/j.envres.2021.111715.

Thrall, P.H., and Burdon, J.J. (1997). Host-pathogen dynamics in a metapopulation context: the ecological and evolutionary consequences of being spatial. J. Ecol. 85, 743-753. https://doi.org/10.2307/2960598

Tomback, D.F., and Achuff, P. (2010). Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology. 40, 186-225. https://doi.org/10.1111/j.1439-0329.2010.00655.x

Tscharntke, T., Grass, I., Wanger, T.C., Westphal, C., Batáry, P. (2021). Beyond organic farming – harnessing biodiversity-friendly landscapes. Trends Ecol. Evol. 36, 919-930. https://doi.org/10.1016/j.tree.2021.06.010

Wang, Y.X.G., Matson, K.D., Prins, H.H.T., Gort, G., Awada, L., Huang, Z.Y.X., et al. (2019). Phylogenetic structure of wildlife assemblages shapes patterns of infectious livestock diseases in Africa. Funct. Ecol. 33, 1332-1341. https://doi.org/10.1111/1365-2435.13311

Yamaoka, Y. (2014). Recent outbreaks of rust diseases and the importance of basic biological research for controlling rusts. Japanese Journal of Phytopathology. 80, 40-48. https://doi.org/10.3186/jjphytopath.80.S40

Supporting information

STAN code for zero-inflated binomial regression
by Wang & Koike

```
data {
   int Ndata;                    //number of all data
   int Nyear;                    //number of years
   int Nseason;                  //number of considered seasons within a year
   int Npoint;                   //number of studied plot
   int Nsp;             //number of species considered
   int Year_index[Ndata];              //index of studied year for each data: 1,2,3...
   int Season_index[Ndata];    //index of studied season for each data: 1,2,3...
   int Point_index[Ndata];             //index of studied plot for each data: 1,2,3...
   int Species_index[Ndata];   //index of examined species for each data: 1,2,3...
   int N1_examined[Ndata];    //number of examined unit-foliage in the plot for endemic occurrence
   int N2_examined[Ndata];    //number of examined leaves in the plot for outbreak intensity
   int N2_positive[Ndata];             // number of infested leaves in the plot for outbreak intensity
   real Radiation[Ndata];        //radiation by digital elevation model
   real LnSpecificCatchmentArea[Ndata];      // log(specific catchment area) by digital elevation model
   real Green[Ndata];                     //greenness by aerial photograph
   real Distance_to_roadside[Ndata];      //distance from road
   real Light_transmittance[Ndata];        //Canopy openness
}


transformed data{
   int F1_positive[Ndata];
   int Ndata_species[Nsp];
   for (i in 1:Ndata) {
      if (N2_positive[i]==0) {
         F1_positive[i]=0;
         }
      else {
         F1_positive[i]=1;
         }
   }

   for (j in 1:Nsp) {Ndata_species[j]=0;}
   for (i in 1:Ndata) {
      Ndata_species[Species_index[i]]=Ndata_species[Species_index[i]]+1;
   }
}

parameters {
   real a_year[Nyear];
   real <lower=0> sd_a_year;
   real a_season[Nseason];
   real <lower=0> sd_a_season;
   real a_species[Nsp];
   real <lower=0> sd_a_species;
   real a_intercept;

   real f_year[Nyear];
   real <lower=0> sd_f_year;
   real f_season[Nseason];
   real <lower=0> sd_f_season;
```

```
  real f_species[Nsp];
  real <lower=0> sd_f_species;
  real f_intercept;
  real <lower=0> sd_difference_af;

  real a_Radiation;
  real a_LnSpecificCatchmentArea;
  real a_Green;
  real a_Distance_to_roadside;
  real a_Light_transmittance;

  real f_Radiation;
  real f_LnSpecificCatchmentArea;
  real f_Green;
  real f_Distance_to_roadside;
  real f_Light_transmittance;
}

transformed parameters{
  real a_logit[Ndata];
  real <upper=0> lnp_arrived[Ndata];
  real f_logit[Ndata];
  real <upper=0> lnp_infested[Ndata];
  for (i in 1:Ndata) {
    a_logit[i]=a_year[Year_index[i]]+a_season[Season_index[i]]+
    a_Radiation*Radiation[i]+
    a_LnSpecificCatchmentArea*LnSpecificCatchmentArea[i]+
    a_Green*Green[i]+
    a_Distance_to_roadside*Distance_to_roadside[i]+
    a_Light_transmittance*Light_transmittance[i]+
    a_species[Species_index[i]]+
    a_intercept;
    lnp_arrived[i]=a_logit[i]-log_sum_exp(0,a_logit[i]);
    f_logit[i]=f_year[Year_index[i]]+f_season[Season_index[i]]+
    f_Radiation*Radiation[i]+
    f_LnSpecificCatchmentArea*LnSpecificCatchmentArea[i]+
    f_Green*Green[i]+
    f_Distance_to_roadside*Distance_to_roadside[i]+
    f_Light_transmittance*Light_transmittance[i]+
    f_species[Species_index[i]]+
    f_intercept;
    lnp_infested[i]=f_logit[i]-log_sum_exp(0,f_logit[i]);
  }
}


model {

  for (j in 1:Nsp) {
    a_species[j]~normal(0, sd_a_species);
    f_species[j]~normal(0, sd_f_species);
    a_species[j]-f_species[j]~normal(0, sd_difference_af);
  }
  for (j in 1:Nyear) {a_year[j]~normal(0, sd_a_year);}
  for (j in 1:Nseason) {a_season[j]~normal(0, sd_a_season);}
  for (j in 1:Nyear) {f_year[j]~normal(0, sd_f_year);}
  for (j in 1:Nseason) {f_season[j]~normal(0, sd_f_season);}
```

```
//Zero Inflated Binomial
   for (i in 1:Ndata) {
      if(F1_positive[i]==0) {
         target += log_sum_exp(
                        bernoulli_lpmf(0|exp(lnp_arrived[i])),
                        bernoulli_lpmf(1|exp(lnp_arrived[i]))+
                        binomial_lpmf(0|N1_examined[i],exp(lnp_infested[i]))
                        );
         }
      else   {
         target += bernoulli_lpmf(1|exp(lnp_arrived[i]));
         target += binomial_lpmf(N2_positive[i]|N2_examined[i],exp(lnp_infested[i]));
         }
   }
// end of ZIB
}


generated quantities{
   real p_arrived[Nsp];
   real p_infested[Nsp];
   real sub_a_year[Nyear,Nyear];
   real sub_a_season[Nseason,Nseason];
   real sub_f_year[Nyear,Nyear];
   real sub_f_season[Nseason,Nseason];

   real a_sp_moment1;
   real a_sp_moment2;
   real a_sp_sd2;
   real a_sp_moment3;
   real a_sp_moment4;
   real a_sp_skewness;
   real a_sp_kurtosis;
   real f_sp_moment1;
   real f_sp_moment2;
   real f_sp_sd2;
   real f_sp_moment3;
   real f_sp_moment4;
   real f_sp_skewness;
   real f_sp_kurtosis;
   a_sp_moment1=0;
   a_sp_moment2=0;
   a_sp_moment3=0;
   a_sp_moment4=0;
   f_sp_moment1=0;
   f_sp_moment2=0;
   f_sp_moment3=0;
   f_sp_moment4=0;
   for (j in 1:Nsp) {
      a_sp_moment1=a_sp_moment1+a_species[j];
      f_sp_moment1=f_sp_moment1+f_species[j];
   }
   a_sp_moment1=a_sp_moment1/Nsp;
   f_sp_moment1=f_sp_moment1/Nsp;
   for (j in 1:Nsp) {
```

```
      a_sp_moment2=a_sp_moment2+(a_species[j]-a_sp_moment1)^2;
      a_sp_moment3=a_sp_moment3+(a_species[j]-a_sp_moment1)^3;
      a_sp_moment4=a_sp_moment4+(a_species[j]-a_sp_moment1)^4;
      f_sp_moment2=f_sp_moment2+(f_species[j]-f_sp_moment1)^2;
      f_sp_moment3=f_sp_moment3+(f_species[j]-f_sp_moment1)^3;
      f_sp_moment4=f_sp_moment4+(f_species[j]-f_sp_moment1)^4;
    }
    a_sp_moment2=a_sp_moment2/(Nsp-1);
    a_sp_sd2=sqrt(a_sp_moment2);
    a_sp_moment3=a_sp_moment3*Nsp/(Nsp-1)/(Nsp-2);
    a_sp_moment4=a_sp_moment4*Nsp*(Nsp+1)/(Nsp-1)/(Nsp-2)/(Nsp-3);
    f_sp_moment2=a_sp_moment2/(Nsp-1);
    f_sp_sd2=sqrt(a_sp_moment2);
    f_sp_moment3=f_sp_moment3*Nsp/(Nsp-1)/(Nsp-2);
    f_sp_moment4=f_sp_moment4*Nsp*(Nsp+1)/(Nsp-1)/(Nsp-2)/(Nsp-3);
    a_sp_skewness=a_sp_moment3/a_sp_sd2^3;
    a_sp_kurtosis=a_sp_moment4/a_sp_sd2^4-3*(Nsp-1)^2/(Nsp-2)/(Nsp-3);
    f_sp_skewness=f_sp_moment3/f_sp_sd2^3;
    f_sp_kurtosis=f_sp_moment4/f_sp_sd2^4-3*(Nsp-1)^2/(Nsp-2)/(Nsp-3);

    for (j in 1:Nsp) {
      p_arrived[j]=0;
      p_infested[j]=0;
    }
    for (i in 1:Ndata) {
      p_arrived[Species_index[i]]=p_arrived[Species_index[i]]+lnp_arrived[i];
      p_infested[Species_index[i]]=p_infested[Species_index[i]]+lnp_infested[i];
    }
    for (j in 1:Nsp) {
      p_arrived[j]=exp(p_arrived[j]/Ndata_species[j]);
      p_infested[j]=exp(p_infested[j]/Ndata_species[j]);
    }

    for (j1 in 1:Nyear) {
      for (j2 in 1:Nyear) {
        sub_a_year[j1,j2]=a_year[j1]-a_year[j2];
      }
    }
    for (j1 in 1:Nseason) {
      for (j2 in 1:Nseason) {
        sub_a_season[j1,j2]=a_season[j1]-a_season[j2];
      }
    }

    for (j1 in 1:Nyear) {
      for (j2 in 1:Nyear) {
        sub_f_year[j1,j2]=f_year[j1]-f_year[j2];
      }
    }
    for (j1 in 1:Nseason) {
      for (j2 in 1:Nseason) {
        sub_f_season[j1,j2]=f_season[j1]-f_season[j2];
      }
    }
  }
```