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都市化與鄰近植物對紫背草屬植物雌全同株繁殖特徵的影響

Exploring the influence of urbanization and neighborhood composition on gynomonoecy in *Emilia* Species

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中文摘要

植物發展出多種性別分化系統利用不同繁殖策略適應環境變異。雌全同株的性別分化系統，提供植物更多繁殖策略上的彈性，因應環境中各種生態因子的變化。雌全同株的植物能夠在同個花序中產生兩性花(雌雄同花)與雌性花，雌性花的比例影響該植物適應環境變化的能力。此研究旨在了解在環境變遷的過程，是否會對雌全同株的紫背草屬(*Emilia*)植物，其雌性花的比例產生影響。都市化已被證實對生態系統造成諸多影響，包括對生物相組成的改變。生物相的組成亦會受到生物間交互作用的影響。本研究欲探討在大尺度都市化進程，與小尺度鄰近物種組成的影響下，是否會對動植物關係中種子傳播前的種子植食者與授粉者的生物相造成改變，因應環境壓力的變化紫背草屬植物雌性花比例是否會間接地受到影響。本研究在臺北市內選取 13 個樣點，並對其地景結構進行量化，以不透水面積的佔比作為大尺度都市化的指標，並在每個樣點內利用樣框量化小尺度植物的組成，進行成熟花序的取樣與授粉者調查。本研究使用臺灣原生種紫背草 (*E. sonchifolia*) 和外來種粉黃纓絨花 (*E. praetermissa*) 作為研究物種檢驗上述內容。我們的結果支持雌全同株的紫背草屬植物，其雌性花比例有所變化以適應環境，且外來種的粉黃纓絨花相較於原生種紫背草，雌性花的佔比較高。我們發現小尺度植物組成差異會對雌性花的比例與生物相造成改變，但大尺度地景結構的影響並不顯著。異種鄰近植物的存在提高雌性花的佔比，但隨著異種植物花序密度的增加，雌性花的比例會隨之下降，顯示雌全同株植物採取分擔風險(bet-hedging)的繁殖策略。異種鄰近植物的存在提高種子傳播前種子被捕食的情形，且授粉者密度與種子傳播前的植食者數量存在顯著正相關，表示兩者在生態系統中可能受到相同的因子影響，但該因子未被納入我們研究系統。

關鍵字：雌全同株、雌性花比例、都市化、鄰近植物的組成、動植物交互關係

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ABSTRACT

Plants have developed various sexual system to adapt to environmental variations using different reproductive strategies. The gynomonoecy is a plant sexual system providing plants with greater flexibility in reproductive strategies to response to changes in various ecological factors. Gynomonoecious plants can produce both bisexual flowers (hermaphroditic) and female flowers within the same capitulum, with the female floret ratio influencing the ability of plants to adapt to environmental stresses. This study aims to understand whether changes in ecological conditions affect the female floret ratio in gynomonoecious *Emilia* plant species. Urbanization has been proven to impact ecosystems in many ways, including changes in biota composition. The composition of biotic communities is also influenced by biotic interactions. This study explores whether large-scale urbanization and fine-scale neighboring plant composition affect the pre-dispersal seed predator and pollinator communities, and indirectly influence the female floret ratio in *Emilia*. We selected 13 study sites in Taipei City and quantified their landscape structures, using the impervious surface ratio as an indicator of large-scale urbanization gradient. We also quantified fine-scale plant neighborhood composition at each site using quadrats in which mature capitulum collection and pollinator surveys were carried out. This study used the native *E. sonchifolia* and the exotic *E. praetermissa* as study species. Our results support the hypothesis that the female floret ratio in gynomonoecious *Emilia* species varies in response to different ecological conditions. The exotic *E. praetermissa* had higher female floret ratio compared to the native *E. sonchifolia*. We found that fine-scale neighborhood composition affected both the female floret ratio and biotic factors, while the influence of large-scale urbanization was not significant. The presence of

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heterospecific neighbors increased the female floret ratio, but it decreased with increasing density of heterospecific capitulum, indicating a bet-hedging reproductive strategy by gynomonoecious plant species. The presence of heterospecific neighbors also increase pre-dispersal seed predation rate, and there was a significant positive correlation between pollinator density and pre-dispersal seed predators, suggesting that both may be influenced by the same factors not included in our study system.

Keywords: Gynomonoecy; Female floret ratio; Urbanization; Neighborhood composition; plant-animal interaction

CONTENTS

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Chapter 1 Introduction

There is a variety of plant sexual systems in the plant kingdom, which have evolved to adapt to different environmental conditions (Barrett, 2002). Some plants develop both stamens and pistils within the same flower, while others produce only one of these floral structures in the same flower in order to avoid inbreeding (Pannell, 2018). Gynomonoecy represents a transitional plant sexual system between hermaphroditism and monoecy and is characterized by the presence of both female and bisexual (hermaphroditic) flowers on the same individual (Yampolsky & Yampolsky, 1922). However, the adaptive value of developing gynomonoecy in plants remains unexplored. This sexual system provides flexibility for plants to adapt to varying environments (Bertin & Gwisc, 2002). The variation in sex expression under different environment circumstances confers a selective advantage to gynomonoecious plants by enabling them to response to diverse selection pressure (Casimiro-Soriguer et al., 2016).

Entomophilous plants must balance the selection pressure between the benefits of attracting pollinators and the drawbacks of attracting potential herbivores, which influencing their floral reproductive traits (Cariveau et al., 2004). Pre-dispersal seed predation, a type of herbivory pressure, reduces fitness and population growth rates, thereby triggering the development of defensive mechanism in plants (Lewis & Gripenberg, 2008). Increased pre-dispersal seed predation rates lead to higher proportion of female florets due to fewer pollens act as signal for pre-dispersal seed predators (Aguirrebengoa & González-Megías, 2021). Producing more female florets also increases the chance for gynomonoecious plants to prevent inbreeding depression (Mamut et al., 2022). In some gynomonoecious plant species, floral structures differ between bisexual and female florets, leading to varying attractiveness for pollinators.

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For instance, the *Senecio vulgaris* has ray (female) and disc (bisexual) florets, and a higher proportion of ray florets increases the attractiveness to visiting insects, thereby enhancing the chances of outcrossing (Mani & Saravanan, 1999).

The composition of the biota can be influenced by both large-scale and fine-scale ecological conditions (Måsviken et al., 2023). Landscape structure, which indicates the composition of different land-use types, influences biota composition, and the pattern depends on the scale relevant to different species (Pan et al., 2022). Rapid Changes in landscape structure due to urbanization happening worldwide reduce the habitats, leading to a decrease in pre-dispersal seed predators or pollinators (Xiao, 2016). However, urbanization can also increase the pre-dispersal seed predators or pollinators through the luxury effect, where areas of higher socioeconomic status areas with more resources support greater biodiversity (Silva et al., 2021).

The composition of neighboring plants also plays an important role in determining the biota composition of pre-dispersal seed predators and pollinators, known as the neighbor effect (Hubbell, 1980; Lázaro et al., 2009). In plant ecology, the neighbor effect can be considered in terms of two aspects: the presence of heterospecific neighbors and their floral density (Hegland et al., 2009). The presence of heterospecific plant species provides more attraction to both pre-dispersal seed predators and pollinators (Ghazoul, 2006; Rand, 1999). However, in some cases, heterospecific neighboring plant species disrupt trophic interactions by releasing volatile compounds or altering chemical complexity of the habitat (Bezemer et al., 2014).

The floral densities of conspecific and heterospecific neighboring plants can have complex and sometimes contradictory effects on pre-dispersal seed predation and pollination (Underwood et al., 2014; Brückman et al., 2019). For example, increased floral densities of conspecific neighboring plants might attract more pre-dispersal seed predators but could also dilute pre-dispersal seed predation if floral densities are

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sufficiently high (Otway et al., 2005; Barbosa et al., 2009). Similar contradictory effects can be observed in pollination. Increased floral densities of conspecific or heterospecific neighboring plants may act as magnets, attracting more pollinators and facilitating outcrossing rates of focal plants (Moeller, 2004). Conversely, increased floral densities of conspecific or heterospecific neighboring plants may negatively impact pollination due to intraspecific or interspecific plant competition for pollinators (Brown et al., 2002).

Gynomonoecy is well developed in the family Asteraceae, with approximately 96% of gynomonoecious species belonging to this family (Yampolsky & Yampolsky, 1922). In northern Taiwan, two plant species from the small Genus *Emilia* Cassini in the family Asteraceae are present. These include the native *Emilia sonchifolia* (L.) DC. and the exotic *Emilia praetermissa* Milne-Redhead.

E. sonchifolia is an annual herb widely distributed in the South Pacific Island from Indonesia to eastern Polynesia, Japan, China, as well as Africa, and is a native weed in East Asian, occurring throughout lowland Taiwan, flowering and fruiting almost year-round in adequately wet soils. *E. praetermissa* is also an annual herb, but it is an exotic species naturalized in Taiwan, originating from West Africa, similarly flowers and fruits year-round in Taiwan. Both *E. sonchifolia* and *E. praetermissa* are congeneric species with similar plant traits, except for their floret color. *E. sonchifolia* possesses pink or purplish disc florets, while *E. praetermissa* has yellowish disc florets.

The variation in the female floret ratio is a potentially important floral reproductive trait for gynomonoecious plant species in adapting to environmental changes. However, this trait has received limited attention in research, and few studies took into account the influence of biotic factors on this floral reproductive trait underlying different ecological conditions. Hence this study asked the following questions: 1) whether the variation in the female floret ratio occur in response to the presence of pre-dispersal

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seed predators, and different pollinator density level, and 2) whether these biotic factors can be influenced by ecological condition, including the urbanization effect and two aspects of neighbor effect: the presence of heterospecific, and conspecific and heterospecific capitulum density effect (Fig. 1). To address these questions, we conducted mature capitula collection and pollinator surveys in the fields for both *Emilia* species at 13 study sites along an urbanization gradient in Taipei City. We quantified the landscape structure of each site to estimate the large-scale ecological effect from urbanization on biotic factors. In each site, we used sampling quadrats to estimate the fine-scale ecological effect from neighboring plants on biotic factors. We identified the quadrat type and recorded capitulum densities of both *Emilia* species within each sampling quadrats in which the mature capitula collection and pollinator surveys were carried out to quantify two terms of neighbor effect.

Chapter 2 Methods

2.1 Study system

To investigate the responses of floral reproductive trait plasticity in gynomonoecious plant species to biotic factors underlying different ecological conditions, we selected *E. sonchifolia and E. praetermissa* as our study species (Fig. 2a, 2b). *Emilia* species utilize pump mechanism of secondary pollen presentation during pollination process to prevent autogamy and promote outcrossing (Medabalimi et al., 2017). This mechanism involves the controlled release of pollen to visiting pollinators from specialized floral structure, thereby increasing effective cross-pollen transfer and reducing self-pollen contact. However, this mechanism cannot completely prevent geitogamous or autogamous selfing, as *Emilia* species are self-compatible, and their florets might receive self-pollen through visiting pollinator. Consequently, their florets might set achenes through both self-pollination and cross-pollination (Medabalimi et al., 2017).

The native *E. sonchifolia* and exotic *E. praetermissa* are sympatric and likely share common pollinators, as evidenced by the observation of natural hybrid in northern Taiwan (Wang & Wang, 2018). Both *Emilia* species possess two types of florets: 1) the outer circle female florets of a capitulum produce red and brown achenes, and 2) the inner hermaphroditic florets of a capitulum produce off-white achenes (Marks & Akosim, 1984, Fig. 2c, 2d). We calculated the female floret ratios of both *Emilia* species by calculating the proportion of red and brown achenes among the total achenes using the following formula.

$$\text{female floret ratio} = \frac{\text{the number of red and brown achenes}}{\text{the number of overall achenes}}$$

2.2 Study sites

We conducted mature capitula collection and pollinator surveys at 13 sites across an urbanization gradient in Taipei City (25˚00’ - 25˚05’N, 121˚30’ - 121˚35’E), where *E. sonchifolia* and *E. praetermissa* occur sympatrically. We collected mature capitula from each site to calculate female floret ratios, and pre-dispersal seed predation rates. Additionally, we conducted pollinator surveys at each site to estimate pollinator densities. Both capitulum collection and pollinator survey were carried out with arbitrarily selected 2m x 2m quadrats to assess neighbor effect.

2.2.1 Urbanization effect

To investigate the effect of different landscape structure which refers to the composition of land-use types on gynomonoecious *Emilia* plant species, we examined 13 sites across an urbanization gradient in Taipei City (Fig. 3; 25˚00’ - 25˚05’N, 121˚30’ - 121˚35’E). Each site was located at least approximately 1 km apart from any other site to ensure the independence of sampling. Urbanization is typically characterized by impervious surface ratio which is the proportion of land areas covered by surfaces that prevent water penetration, including roads, buildings, or asphalt (Xian et al., 2012). We defined the urbanization gradient using the impervious surface ratio within 500 m radius range of each site, as the effective foraging range for pollinators is approximately 500 m (Gathmann, 2002). We classified the land-use types into five categories: water, grass, forest, asphalt, and building. The impervious surface ratio refers to the proportion of asphalt and building areas in our study system, while the green surface ratio indicates the proportion of grass and forest areas within the 500 m radius of each site (Table 1, Fig. 4). We obtained land-use data using remote sensing satellite data (30 m resolution) from Landsat 8, provided by the US Geology Survey. We processed this data with supervised classification method with ENVI software.

2.2.2 Neighbor effect

We considered two terms of neighbor effect in this study system: the presence of heterospecific neighbor and capitulum densities of conspecifics and heterospecifics. To quantify neighboring plants composition, we arbitrarily selected 2m x 2m quadrats at each study site from open grass areas where only *Emilia* species were in bloom for mature capitula collection and pollinator surveys (Fig. 5c, 5d). Within each quadrat, we recorded the number of capitula for both *Emilia* species present, as the capitulum is the floral unit that attracts pre-dispersal seed predators and pollinators. Sampling quadrats were categorized into two types: ‘pure’ quadrat type and ‘mixed’ quadrat type. The ‘pure’ quadrat type indicates patches containing only the native *E. sonchifolia* or exotic *E. praetermissa*, and the ‘mixed’ quadrat type refers to patches where the native *E. sonchifolia* co-occurred with the *E. praetermissa*. Each sampling quadrat was situated at least 10 m apart from each other. The ‘pure’ quadrat type indicates the absence of heterospecific neighboring plants while the ‘mixed’ quadrat type indicates the presence of heterospecific neighboring plants.

2.3 Mature capitulum collection

In each quadrat, we arbitrarily collected one mature capitulum from an arbitrarily selected individual in the fields at each site on a sunny day during April to July 2023. We obtained a minimum of three replicates of both *Emilia* species from two quadrat types, except where suitable quadrats were unavailable. Two mature capitula were collected in mixed quadrat type: one from an individual of *E. sonchifolia*, and another from an individual of *E. praetermissa*. Collected capitula were inspected for estimating female floret ratios and pre-dispersal seed predation rates. We count the number of two

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types of seed: red or brown seeds produced from female florets, and off-white seeds produced from bisexual florets (Fig. 5a). The larva of fruit fly is the main pre-dispersal seed predator of *Emilia* species, and their eggs appears inside the capitulum during the flowering phase of flower reclosure to pappus appearance. Inspected capitula were then classified into two groups: intact capitula with no pre-dispersal seed predator inside, and damaged capitula whose achenes appeared to be chipped or bitten by pre-dispersal seed predators (Fig. 4b).

2.4 Pollinator survey

We conducted pollinator surveys with 30 arbitrarily selected 2m x 2m quadrats located in the 500 m radius range of each study site on sunny day in March 2023. Each sampling quadrat was at least 10 m apart from each other. We observed visiting insect pollinators for 5 minutes at each sampling quadrat during 9:00 a.m. to 16:00 p.m. at which the active duration for most insect pollinators of *Emilia* species (Medabalimi et al., 2017). The visiting insect pollinators were identified to family level and the total observation time was 2.5 hours for each site. We also identified the quadrat type (pure *E. sonchifolia*, pure *E. praetermissa*, and mixed) and recorded the capitulum densities of both *Emilia* species at each sampling quadrat.

2.5 Data analysis

2.5.1 Biotic factors and female floret ratio

To investigate the relationships between pre-dispersal seed predation and female floret ratio, we used two-way ANOVA to test their correlation. We obtained the predation rate of each site by calculating the proportion of collected mature capitulum with the presence of seed predators. The pre-dispersal seed predation rates of both *Emilia* species at each site were calculated with the formula below:

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$$\frac{\text{the number of collected mature capitula with the presence of pre} - \text{dispersal seed predator}}{\text{the number of all collected mature capitulua}}$$

We classified the sites into two groups: sites with the presence of pre-dispersal seed predators, and sites without the presence of pre-dispersal seed predators. The female floret ratio for each site was calculated with the formula below:

$$\frac{\text{the total number of red or brown achenes in each site}}{\text{the total number of all achenes in each site}}$$

We treated the female floret ratio of both *Emilia* species at each site as response variable, the plant species type (native/exotic), the presence of pre-dispersal seed predator (with/without) as explanatory variables, and site as random effect. The interaction between plant species type and the presence of pre-dispersal seed predator was considered in the two-way ANOVA model.

To investigate the relationship between pollinator density and female floret ratio at each site, the same approach mentioned above was applied. We obtained the pollinator density per site with 30 sampling quadrats, and used the female floret ratio aforementioned. The pollinator density at each site was classified into two groups by comparing to the overall mean pollinator density of both *Emilia* species at each site: high pollinator density level group, and low pollinator density level. We treated the female floret ratio of both *Emilia* species from each site as response variable, the plant species type (native/exotic), the pollinator density level (high/low) as explanatory variables, and site as random effect. The interaction between plant species type and the pollinator density level was considered in the two-way ANOVA. All analyses were performed in R 4.2.3 (R Core Team,2018) with function lmer from ‘lme4’ package (Bates et al., 2015)

2.5.2 The urbanization effect

We used GLMM to investigate the relationship between each biotic factor and the urbanization effect. The pre-dispersal seed predation rate and pollinator density of both *Emilia* species at each site was treated as response variable respectively. The full model was constructed for both biotic factors with continuous value of impervious surface ratio and the species type (categorical: native/exotic) as fixed effect, and site as random effect. We compared the full model with and without interaction first using likelihood ratios first, and then compared the full model with subsequent models. We used binomial distribution for the GLMM of pre-dispersal seed predation rate, and negative binomial for the GLMM of pollinator density in R 4.2.3 (R Core Team,2018) with function glmer and glm.nb from ‘lme4’ package (Bates et al., 2015).

2.5.3 The heterospecific presence effect

We used generalized linear mixed model (GLMM) to investigate the relationship between biotic factors and the presence of heterospecific neighbor. The pre-dispersal seed predation rate and pollinator density of both *Emilia* species from two quadrat types at each site was treated as response variable respectively. The full model was constructed for both biotic factors with quadrat type (categorical: pure/mixed) and the plant species type (categorical: native/exotic) as fixed effect, and site as random effect. We compared the full model considering with and without interaction first using likelihood ratios first, and then compared the full model with subsequent models. We used binomial distribution for the GLMM of pre-dispersal seed predation rate, and negative binomial for the GLMM of pollinator density in R 4.2.3 (R Core Team,2018) with function glmer from ‘lme4’ package (Bates et al., 2015).

2.5.4 Conspecific and heterospecific capitulum density effect

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To determine whether the floral quantity of neighboring plant species modified both biotic factors, we performed general additive mixed models (GAMM) because the expected responses to capitulum density are not necessarily linear. This approach is non-parametric, allowing the exploration of both linear and non-linear responses (Rathcke, 1983). We treated conspecific capitulum density, heterospecific capitulum density, species type as fixed effect, and site as random effect. The pre-dispersal seed predation rate and pollinator density of both *Emilia* species of two quadrat types at each site was treated as response variable respectively in R 4.2.3 (R Core Team,2018) with ‘gamm4’ package (Wood & Scheipl, 2021) to perform the analyses. Conspecific and heterospecific capitulum density were treated as fixed effect together in the same model to take into account their influence on each other, and they are both modeled as smooth terms considering potential non-linear effects.

2.5.5 Piecewise structural equation model

To investigate possible relationships when consider all variables together in a system instead of examining separately, we aggregated all variables in piecewise structural equation model (piecewise SEM) in R 4.2.3 (R Core Team, 2018) with ‘piecewiseSEM’ package (Lefcheck, J. S., 2016). Based on our prediction, we regarded female floret ratios of both *Emilia* species to be influenced potentially by pre-dispersal seed predation rate and pollinator density. And hence we construct a GLMM with female floret ratio as response variable, species type, biotic factors as fixed effect, and site as random effect initially. To investigate the potential influence from large-scale and fine-scale ecological factors on biotic factors, we constructed GLMM and GLM for pre-dispersal seed predation rate and pollinator density respectively with species type, impervious surface ratio, quadrat type, conspecific and heterospecific capitulum density as fixed effect. Site was treated as random effect for pre-dispersal seed predation

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rate but not for pollinator density due to little variance in pollinator density between sites. We transformed categorical data of both *Emilia* species from two quadrat types at each site to numerical data to perform piecewise SEM, including species type (native=0/exotic=1), and quadrat type (pure=0/mixed=1). We used binomial distribution for female floret ratio and pre-dispersal seed predation rate, and we used negative binomial distribution for pollinator density.

Chapter 3 Results

3.1 Biotic factors and female floret ratio

3.1.1 Pre-dispersal seed predation

We collected 208 mature capitula from 13 study sites of both *Emilia* species: 107 of *E. sonchifolia*, and 101 of *E. praetermissa* (Appendix 1). We used 25 aggregated site data to perform the analysis, and the residuals of 25 data points fitted in the model followed normal distribution (Table 2, Appendix 2). The Shapiro-Wilk test was used to assess the normality of the residuals (W=0.98, df=25, *p*=0.81). There was no severe multicollinearity in the model (VIF value=3.015 for the presence of pre-dispersal seed predation, VIF value=1.411 for species type, and VIF value=3.702 for interaction term). The mean female floret ratio of the *Emilia* plants (exotic and native pooled) with the presence of pre-dispersal seed predator was 0.24 ± 0.02 [mean ± SE], which is significantly higher ($F_{7,18}$=6.30, *p*=0.033, Table 2) than that of the group without the presence of pre-dispersal seed predator (0.17 ± 0.03 [mean ± SE], Fig. 6). There was no difference in the female floret ratio for species type ($F_{7,18}$=1.95, *p*=0.196, Table 2) or the interaction term ($F_{7,18}$=2.32, *p*=0.162, Table 2). The female floret ratio of *E. sonchifolia* was 0.17 ± 0.02 [mean ± SE], which was not significant different from that of *E. praetermissa* (0.27 ± 0.01[mean ± SE]) considering difference between sites.

3.1.2 Pollinator density

We conducted pollinator surveys with 390 quadrats in 13 study sites: 109 quadrats from ‘pure *E. praetermissa*’, 230 quadrats from ‘pure *E. sonchifolia*’, and 51 quadrats from ‘mixed’ quadrat type. Fifty-five visiting pollinators were recorded from 7 insect families (17 Syrphidae, 11 Lycaenidae, 10 Apidae, 9 Tephritidae, 4 Pieridae, 2

Calliphoridae, and 2 Choreutidae). The overall mean pollinator density of both *Emilia* species was 1.88 pollinators per sites. We used 25 aggregated site data to perform the analysis (Appendix 3), and the residuals of 25 data points fitted in the model followed normal distribution (Appendix 4). The Shapiro-Wilk test was used to assess the normality of residuals (W=0.98, df=25, p=0.95). There was no severe multicollinearity in the model (VIF value=2.007 for pollinator density level, VIF value=2.787 for species type, and VIF value=3.919 for interaction term). The mean female floret ratio of *Emilia* plants (exotic and native pooled) with high pollinator density level was 0.19 ± 0.03 [mean ± SE], which was marginal decreased ($F_{10,15}$=4.56, p=0.061, Table 3) compared to the group with low pollinator density level (0.25 ± 0.02 [mean ± SE], Fig. 7). There was no difference in the female floret ratio for species type ($F_{10,15}$=2.67, p=0.137, Table 3) or in the interaction term ($F_{10,15}$=1.99, p=0.192, Table 3) considering difference between sites.

3.2 Ecological factors and pre-dispersal seed predation rate

3.2.1 The urbanization effect

We used 25 data points to perform GLMM featuring impervious surface ratio and species type as explanatory variables, sites as random effect for pre-dispersal seed predation rate (Appendix 5), and the full model without interaction was selected as final model (Table 4). The conditional R^2 for the final selected model was 0.11, and the marginal R^2 was 0.03. There was little correlation between these two predictors (VIF values=1.002 for impervious surface ratio, and VIF values=1.002 for species type). The final model did not have issues with overdispersion (x^2 =11.59, dispersion parameter=0.55, rdf=21, p=0.950). The effect from impervious surface ratio on pre-dispersal seed predation rate was not statistically significant (0.78 ± 1.14 [estimate ±

SE], *p*=0.491, Table 8, Fig. 8a), nor was the effect of species type on pre-dispersal seed predation rate (-0.57 ± 0.41 [estimate ± SE], *p*=0.170, Table 8, Fig. 8b). The variance for the random effect was 0.29 (SD=0.54), suggesting slight variation between sites (Appendix 8e).

3.2.2 The heterospecific presence effect

We used 47 data points to perform GLMM featuring the presence of heterospecific neighbor, species type as explanatory variables, sites as random effect on pre-dispersal seed predation rate (Appendix 6), and the full model without interaction was selected (Table 5). The conditional R^2 for the final selected model was 0.25, and the marginal R^2 was 0.16. There was little correlation between these two predictors (VIF values=1.002 for quadrat type, and VIF values=1.002 for species type). The final model showed slight under-dispersion (x^2 =32.86, dispersion parameter=0.76, rdf=43, *p*=0.869). The model comparison showed that the quadrat type had a strong significant effect (x^2=13.47, *p*=0.000, Table 5), and the final model indicated that the presence of heterospecific neighbor significantly increased pre-dispersal seed predation rate (-1.55 ± 0.44 [estimate ± SE], *p*=0.000, Table 9, Fig. 8b). The exotic *E. praetermissa* tended to have higher pre-dispersal seed predation rate, however the difference was not significant (-0.58 ± 0.43 [estimate ± SE], *p*=0.175, Table 8). The variance for random effect was 0.37 (SD=0.61), indicating some variability between sites (Appendix 8f).

3.2.3 Conspecific and heterospecific capitulum density effect

We used 47 data points to perform GAMM treating conspecific and heterospecific capitulum density as smooth term together in the same model, specific type as fixed effect, and site as random effect (Appendix 6, Table 9, Appendix 9). *E. sonchifolia* had a lower pre-dispersal seed predation rate on average compared to *E. praetermissa* (-

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0.11 ± 0.08 [estimate ± SE] for native species type, Table 9), but this difference was not statistically significant (p=0.158, Table 9). The smooth term for conspecific capitulum density was essentially linear but not significant (edf=1, p=0.116, Table 9, Fig. 8c), and the smooth term for heterospecific capitulum density showed non-linearity but was also not significant (edf=2.42, p=0.100, Table 9, Fig. 8d). The model explained about 19.7% of the variance in pre-dispersal seed predation rate (adjusted R^2=0.197).

3.3 Ecological factors and pollinator density

3.3.1 The urbanization effect

We used 25 data points to perform GLMM featuring impervious surface ratio and species type as explanatory variables (Appendix 3), site as random effect for pollinator density, and the full model without interaction was selected as final model (Table 6). The conditional R^2 for the final selected model was 0.20, and the marginal R^2 was also 0.20. There was little correlation between these two predictors (VIF values=1.046 for urbanization effect, and VIF values=1.046 for species type). The final model did not have issues with overdispersion (x^2=20.46, dispersion parameter=1.02, rdf=20, p=0.429). The urbanization effect on pollinator density demonstrated a marginally significant negative relationship (-1.89 ± 1.11 [estimate ± SE], p=0.09, Table 8, Fig. 9a). The effect from species type on pollinator density did not have significance (-0.03 ± 0.46 [estimate ± SE] for native species type, p=0.941, Table 8, Fig. 9b). The variance for the random effect was very small (3.596e-13), suggesting minimal impact of site-specific differences for pollinator density (Appendix 10e).

3.3.2 The heterospecific presence effect

We used 45 data points to perform GLMM featuring the presence of heterospecific

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neighbor, species type as explanatory variables, sites as random effect on pollinator density (Appendix 7), and the full model without interaction was selected (Table 7). The conditional R^2 for the final selected model was 0.11, and the marginal R^2 was 0.11. There was little correlation between these two predictors (VIF values=1.000 for quadrat type, and VIF values=1.000 for species type). The final model showed slight under-dispersion (x^2=12.78, dispersion parameter=0.32, rdf=40, *p*=1.000). The quadrat type (-0.22 ± 0.82 [estimate ± SE], *p*=0.794, Table 8, Fig. 9b) and species type (-0.98 ± 0.88 [estimate ± SE], *p*=0.266, Table 8) did not cause statistically significant effect on pollinator density. The variance for the random effect (site) was very small (3.201e-12), suggesting little variation between sites (Appendix 10e).

3.3.3 Conspecific and heterospecific capitulum density effect

We used 45 data points to perform GAMM treating conspecific and heterospecific capitulum density as smooth term together in the same model, specific type as fixed effect, and site as random effect (Appendix 7, Table 9, Appendix 11). There was no significant difference in pollinator density between *E. sonchifolia* and *E. praetermissa* (-0.06 ± 0.06 [estimate ± SE] for native species type, *p*=0.270, Table 9). We found a positive significant non-linear relationship between conspecific capitulum density and pollinator density (edf=2.20, F=9.97, *p*=0.000, Table 9, Fig. 9c), but no significant relationship existed between heterospecific capitulum density and pollinator density (edf=1, F=0.04, *p*=0.841, Table 9, Fig. 9d). The model explained about 35.1% of the variance in pollinator density (adjusted R^2=0.351).

3.4 Piecewise structural equation model

We used 45 data points to perform piecewise SEM (Appendix 12), and model fit

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was good suggested by non-significant Chi-Squared (x^2=0.43, p=0.806, df=2) and Fisher's C tests (Fisher's C=1.49, *p*=0.829, df=4). The effects from impervious surface ratio were not significant in any equation (Table 10, Fig. 10). The presence of heterospecific neighbor had significant positive effects on both female floret ratio (0.10 ± 0.04 [estimate ± SE], *p*=0.012) and pre-dispersal seed predation rate (1.00 ± 0.30 [estimate ± SE], *p*=0.001). The species type had a significant effect on female floret ratio (0.18 ± 0.04 [estimate ± SE], *p*=0.000), indicating that the exotic *E. praetermissa* had higher female floret ratio compared to the native *E. sonchifolia*. But no significant relationships existed between species type and pre-dispersal seed predation rate (0.21 ± 0.19 [estimate ± SE], *p*=0.270) or pollinator density (0.09 ± 0.11 [estimate ± SE], *p*=0.431). The heterospecific capitulum density also had a significant effect on female floret ratio (-0.20 ± 0.06 [estimate ± SE], *p*=0.001), indicating the decrease of female floret ratio with increasing heterospecific capitulum density. Contrarily, we found no significant relationships existed between heterospecific capitulum density and pre-dispersal seed predation rate (-0.57 ± 0.51 [estimate ± SE], *p*=0.267) or pollinator density (-0.53 ± 1.01 [estimate ± SE], *p*=0.602). This model explained a moderate amount of variance in pre-dispersal seed predation rate (25% when including random effect, conditional R^2=0.25), but less for female floret ratio (7% when including random effect, conditional R^2=0.07) and pollinator density (18% without random effect, Nagelkerke R^2=0.18). We found a significant positive correlation between pre-dispersal seed predation rate and pollinator density (coefficient=0.35, *p*=0.009). There was no obvious multicollinearity found in each equation (Appendix 13), but a significant overdispersion existed in the GLMM of female floret ratio (Appendix 13).

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Chapter 4 Discussion

Our study system investigated the influence of large-scale and fine-scale ecological factors on biotic factors that might cause variation in female floret ratio, an important floral reproductive trait for gynomonoecious plant species. Our results show the following: 1) direct significant effects from ecological factors on female floret ratio. We found a significant correlation between pre-dispersal seed predation and female floret ratio, and a marginal effect from pollinator density on female floret ratio based on two-way ANOVA results. But the relationships were not significant at all when considered them in a system according to the result of piecewise SEM. The explanatory power from all variables in our study system is limited for female floret ratio (R^2=0.07, piecewise SEM). We found direct effects from ecological factors on female floret ratio instead of indirect effect through biotic factors in our piecewise SEM, including species type, the presence of heterospecific neighbor, and heterospecific capitulum density. There was a significant difference in female floret ratio between two *Emilia* species. The exotic *E. praetermissa* has a higher female floret ratio compared to native *E. sonchifolia*. The presence of heterospecific neighboring plants increase the female floret ratio, but as the heterospecific capitulum density increases the female floret ratio drops. 2) significant effect from ecological factor on biotic factor was found in pre-dispersal seed predation rate but not for pollinator density considering all variables in our study system together. We found a significant effect from the presence of heterospecific neighboring plants on pre-dispersal seed predation rates from both separate GLMM and piecewise SEM. The pre-dispersal seed predation rate became higher with the presence of heterospecific capitulum density. However, we didn’t find any variable to explain the variation in pollinator density according to our piecewise

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SEM, but the results of separate GLMM and GAMM indicated significant and marginal significant effects from conspecific capitulum density and urbanization. We found a significant positive non-linear relationship between conspecific capitulum density and pollinator density, and a marginal negative effect from urbanization on pollinator density. We discuss a) direct effects from ecological factors on plant reproduction, b) variation in pre-dispersal seed predation rate, c) variation in pollinator density, and d) caveats in our study system.

Our results supported our prediction that there were variations in female floret ratios of gynomonoecious plant species with different ecological factors: species type, the presence of heterospecific neighbor, and heterospecific capitulum density. The exotic *E. praetermissa* had a higher female floret ratio compared to native *E. sonchifolia* (0.17 ± 0.02 vs. 0.27 ± 0.01 [mean ± SE]), suggesting the difference in reproductive strategy between these two *Emilia* species. Higher proportion of female floret ratio reduces the chance of proliferating offspring rapidly, but the fitness of offspring can be promoted by decreasing the probability of inbreeding depression (Porcher & Lande 2016). In addition, *Emilia* species can reproduce offspring asexually with stoloniferous propagation, and hence ensuring the quality instead of quantity of offspring genes becomes very important (Honnay & Jacquemyn, 2010). The nuanced response—increasing female floret ratio with heterospecific presence but decreasing it at high densities—showcases the complex ways plants balance current reproduction, future potential, and resource limitation. If the heterospecific neighbors alter the pollination environment (e.g., by attracting different pollinators), increasing female florets could increase the chances of receiving cross-pollen, potentially leading to offspring with diverse genotypes that might be better suited to variable conditions. The presence of heterospecific neighbors might signal potential future competition (Dorin et al., 2021), and increasing investment in female florets could be a way to maximize current

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reproductive output in case future conditions become less favorable (Broz et al., 2010). However, as capitulum density of heterospecifics increases, competition for resources (light, water, nutrients) intensifies, potentially limiting the ability of plants to invest in producing female florets. In addition, high heterospecific capitulum density might alter pollinator visitation patterns, potentially favoring male function to ensure pollen dispersal. This plastic response in sex allocation could be an adaptive strategy allowing the gynomonoecious species to optimize its reproductive output under varying competitive scenarios.

Our results support our prediction that the presence of heterospecific neighbors provide more attraction for pre-dispersal seed predators and pollinators. The pre-dispersal seed predation rate increases as heterospecific neighboring plants might attract pollinators, which could indirectly increase seed production and subsequently attract more seed predators (Xu et al., 2015). A positive relationship between pre-dispersal seed predation rate and pollinator in piecewise SEM (coefficient=0.35, p=0.009) suggests a potential ecological interaction where higher pollinator activity is associated with higher pre-dispersal seed predation. Both pollinators and pre-dispersal seed predators might be attracted to the same plant traits, and plant-plant interaction with heterospecific neighbors might alter plant traits (e.g., seed size, number, or size of floral display) in ways that make them more attractive or susceptible to predators (Valenta et al., 2017). The effect might be related to broader landscape patterns, where areas with more heterospecific neighbors represent certain habitat types that are preferred by seed predators (Díaz-Guzmán et al., 2022). This relationship highlights the complexity of plant-plant and plant-animal interaction in ecological communities. It emphasizes the importance of considering the broader community context when studying species interaction and ecosystem processes.

We found no significant relationships between ecological factors and pollinator

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density when considered all variables in our system together. However, when examined separately, the variation in pollinator density can be partially explained by the urbanization gradient and conspecific capitulum density. Our results support our prediction that as the urbanization increases, the pollinator density decreases probably due to reduction in floral resources. Urbanization often results in the destruction of natural habitats that pollinators rely on for nesting, foraging, and reproduction (Baldock et al., 2015). Many urban plants are non-native or ornamental species that may not provide adequate nectar or pollen for native pollinators. Pollinators are more attracted to denser patches of capitula, and higher floral densities attract more pollinators, which could enhance potential positive feedback of reproductive success in plants (Duffy & Stout, 2011). This could have significant implications for plant reproductive strategies, particularly for sex allocation in gynomonoecious plant species. However, we did not find significant relationships between pollinator density and female floret ratio, and it might due to issues with the experimental design. The mature capitulum collection and pollinator density surveys were not conduct at the same sampling quadrats at the same time periods, and hence temporal and spatial variation were not to be carefully and thoroughly considered.

Besides the issues of temporal and spatial variation in our study system, there were some limitations should be considered for the future studies. While this study finds supports for the variation in female floret ratio, the explanatory power is low (e.g., R^2=0.07 in piecewise SEM). This suggests that some important variables may not be included in this study. Other potential factors to explain the variation in female floret ratio were not included in our study system, for instance outcrossing rate, microhabitats conditions (nutrients, water, and light). There are other floral reproductive traits we did not examine in our study system, including the size of floral display, the floret number in a capitulum. Including temporal variation such as seasonal changes will help clarify

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the underlying mechanisms for reproductive strategies of gynomonoecious plant species.

In conclusion, this study provides valuable insights into the complex interplay between ecological factors and reproductive strategies in gynomonoecious plant species. We found that fine-scale ecological conditions compared to large-scaled conditions are more important for variation in female floret ratio. Mild competition from heterospecific neighbors might trigger a stress response, leading to increased investment in producing more female florets as a ‘bet-hedging’ strategy referring to an approach where organism sacrifice some fitness in stable conditions to reduce the risk of reproductive failure in variable or unpredictable environments (Gianella et al., 2021).

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FIGURES

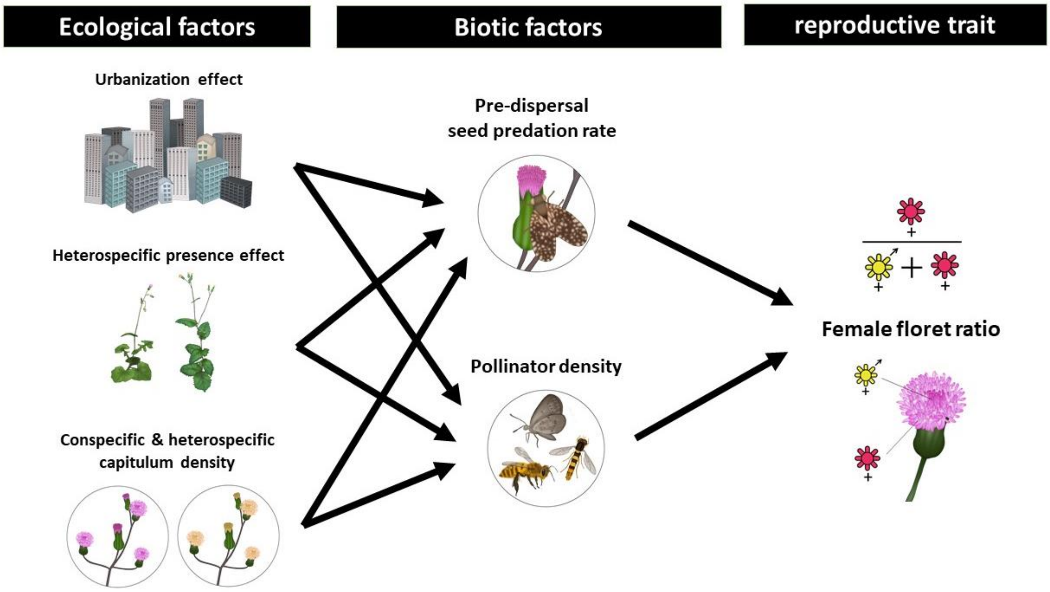

Figure 1. Concept map. This study conducted sampling collection and pollinator surveys at 13 study sites along urbanization gradient and recorded the neighboring plant composition of sampling quadrats to examine the effect of pre-dispersal seed predation rate, and pollinator density on the variation in female floret ratio of two *Emilia* species. This study also examined ecological factors including, the urbanization effect and neighbor effect (heterospecific presence effect, and capitulum density of conspecific and heterospecific) on aforementioned biotic factors.

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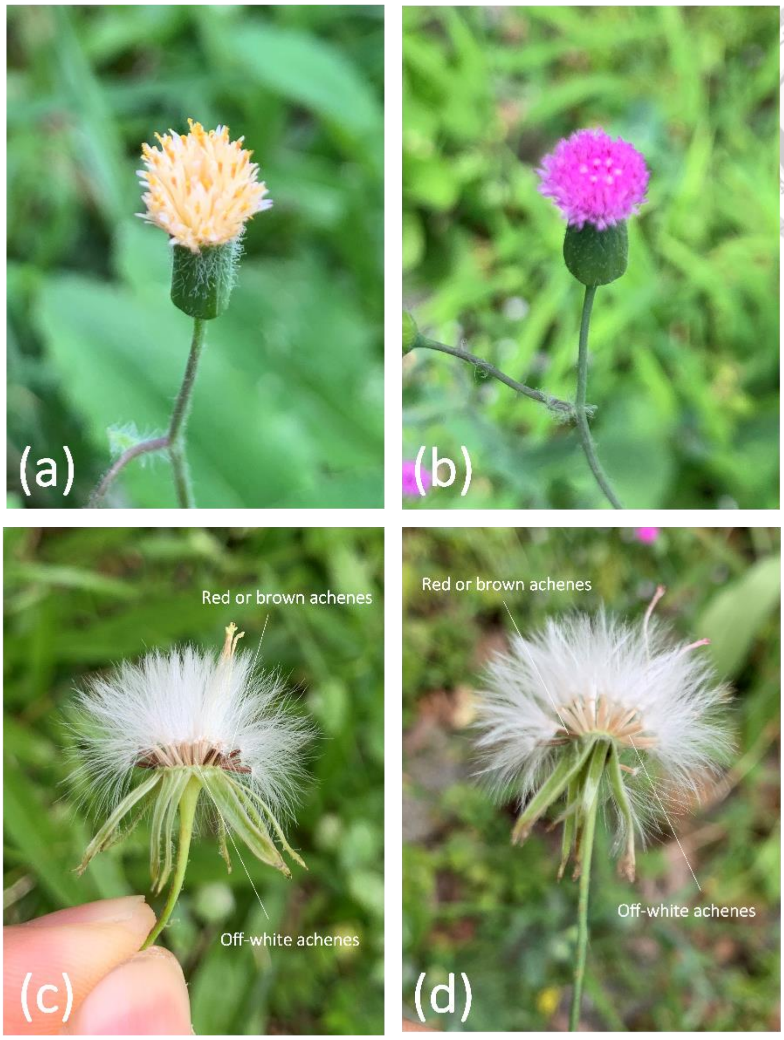

Figure 2. (a) The floret color of *E. praetermissa* is yellowish. (b) The floret color of *E. sonchifolia* is purple or pinkish. (c) The achenes of *E. praetermissa* have two types: red or brown achenes in the inner circle of the capitulum produced from female florets, and off-white achenes in the outer circle of the capitulum produced from bisexual florets. (d) The achenes of *E. sonchifolia* also have two types: red or brown achenes in the inner circle of the capitulum produced from female florets, and off-white achenes in the outer circle of the capitulum produced from bisexual florets.

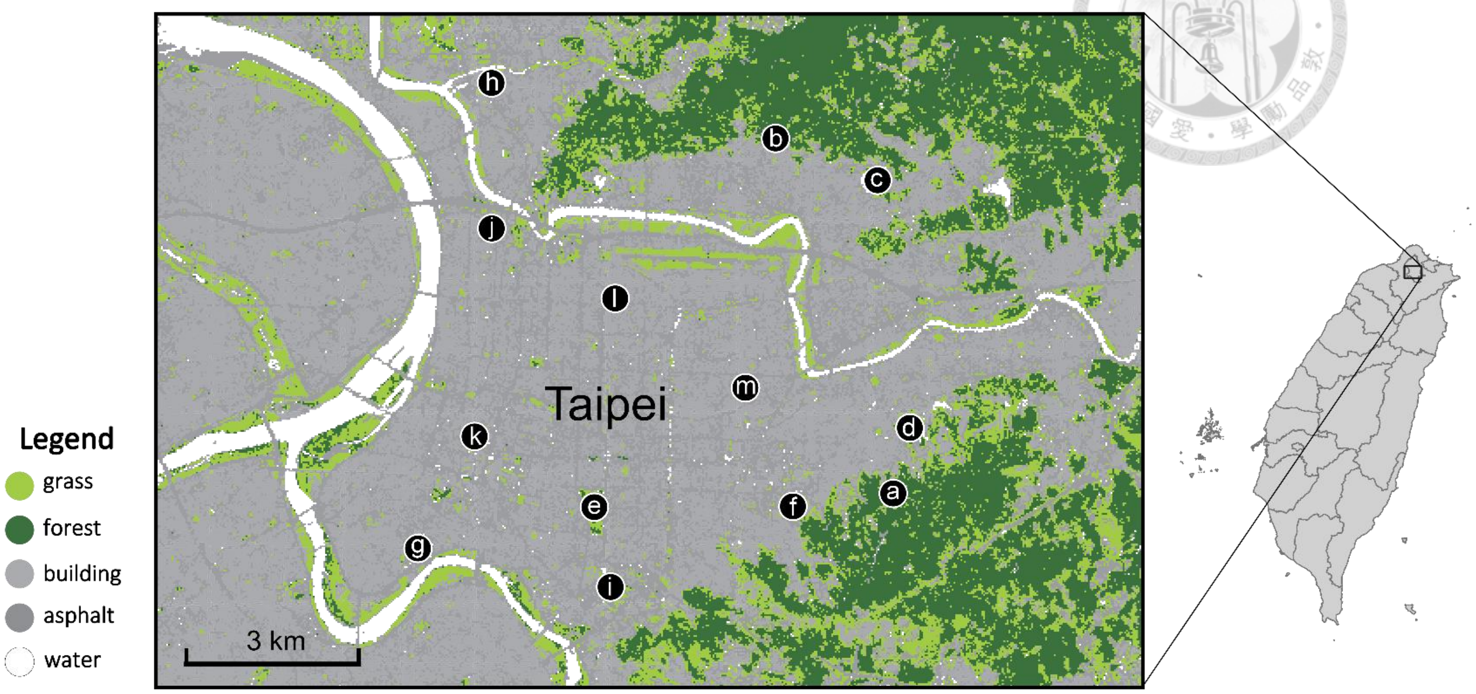

Figure 3. Map of the 13 study sites (a-m) in Taipei City. Light and dark gray areas are asphalt and building, respectively, whereas light and dark green areas indicate grass and forest, respectively, and white areas indicate water.

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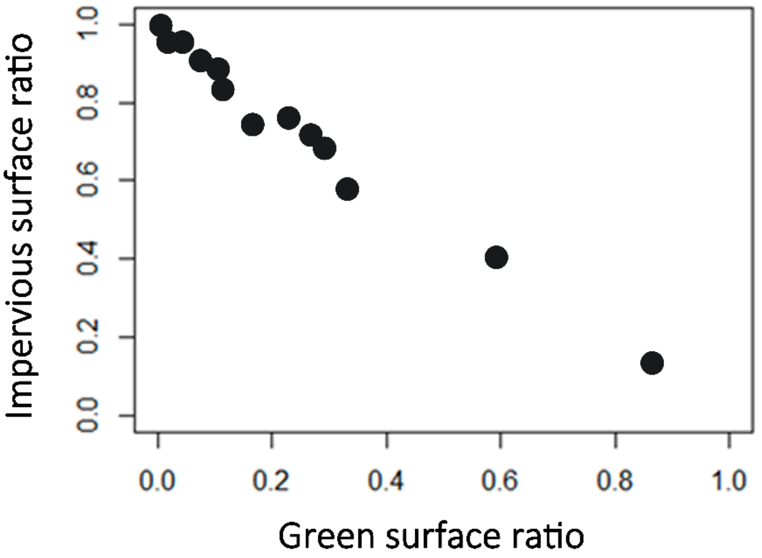

Figure 4. The landscape structure of 13 study sites. Green ratio indicates the proportion of forest and grass areas within 500 m radius range, and impervious surface ratio indicates the proportion of asphalt and building areas within 500 m radius range.

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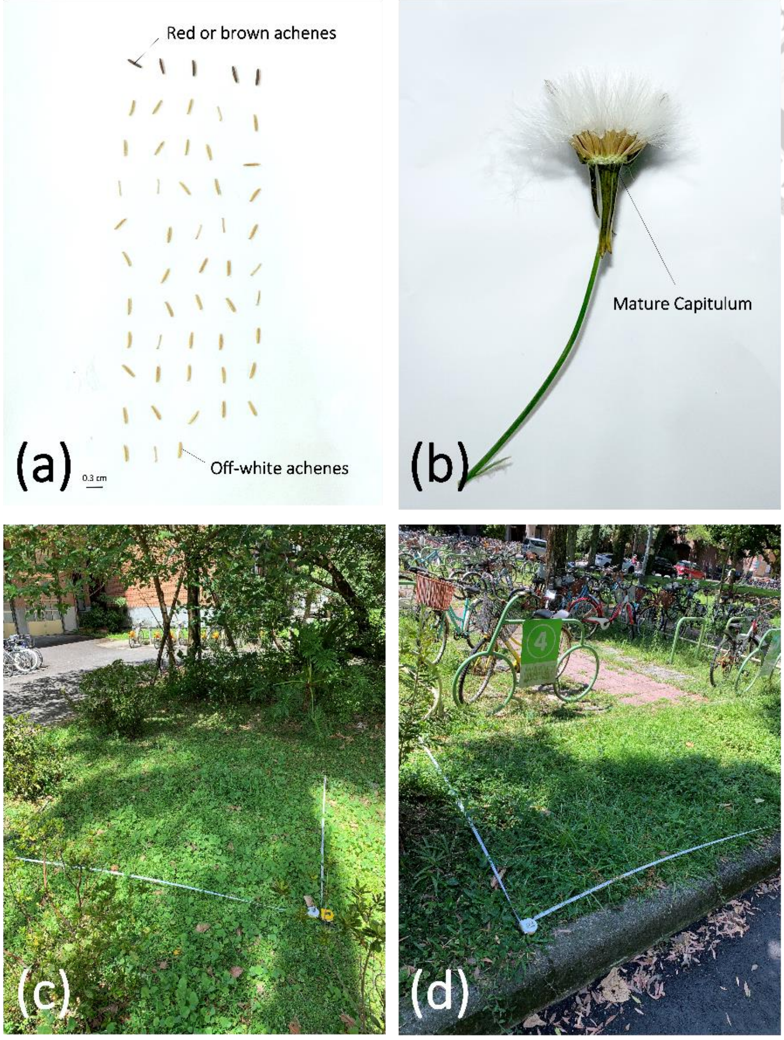

Figure 5. (a) Red or brown achenes and off-white achenes were used to calculate the female floret ratio of both *Emilia* species. (b) Mature capitulum collected from the quadrat at study sites to detect the presence of pre-dispersal seed predators and female floret ratios. (c)(d) The 2m x 2m sampling quadrats at each site to quantify neighbor effect by recording capitulum density of conspecifics and heterospecifics.

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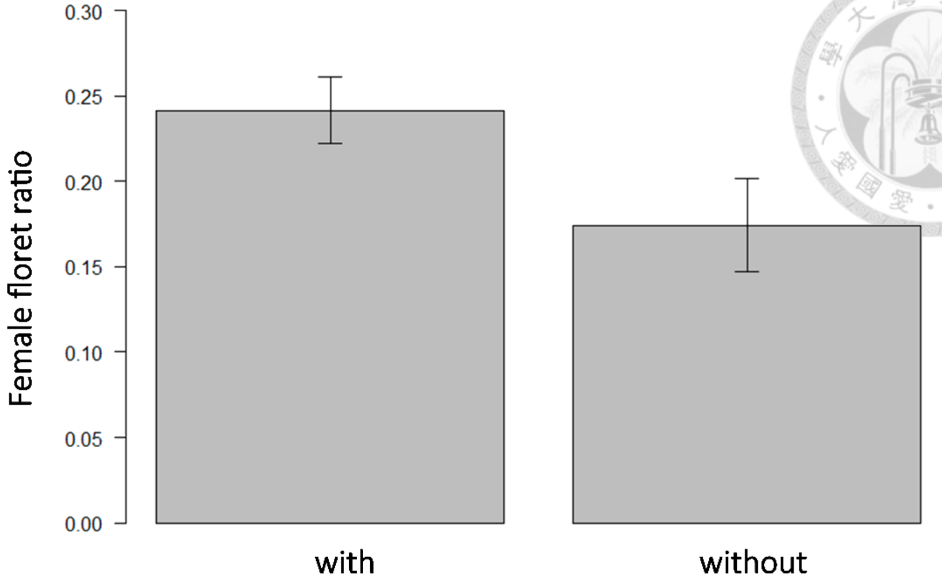

Figure 6. The female floret ratio of both *Emilia* species combined with/without pre-dispersal seed predation. ‘With’ indicates the group with the presence of pre-dispersal seed predation, while ‘Without’ indicates the group without the presence of pre-dispersal seed predation. The error bars indicate the standard error of the female floret ratio for each group.

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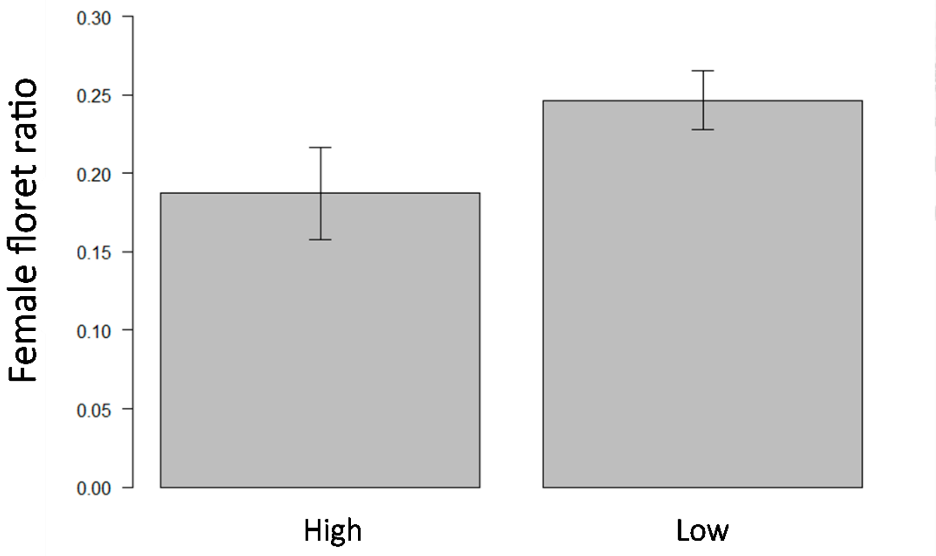

Figure 7. The female floret ratio of both *Emilia* species combined for high/low pollinator density level. ‘High’ indicates the group with pollinator density level higher than the mean pollinator density, while ‘Low’ indicates the with pollinator density level lower than the mean pollinator density. The error bars indicate the standard error of the female floret ratio for each group.

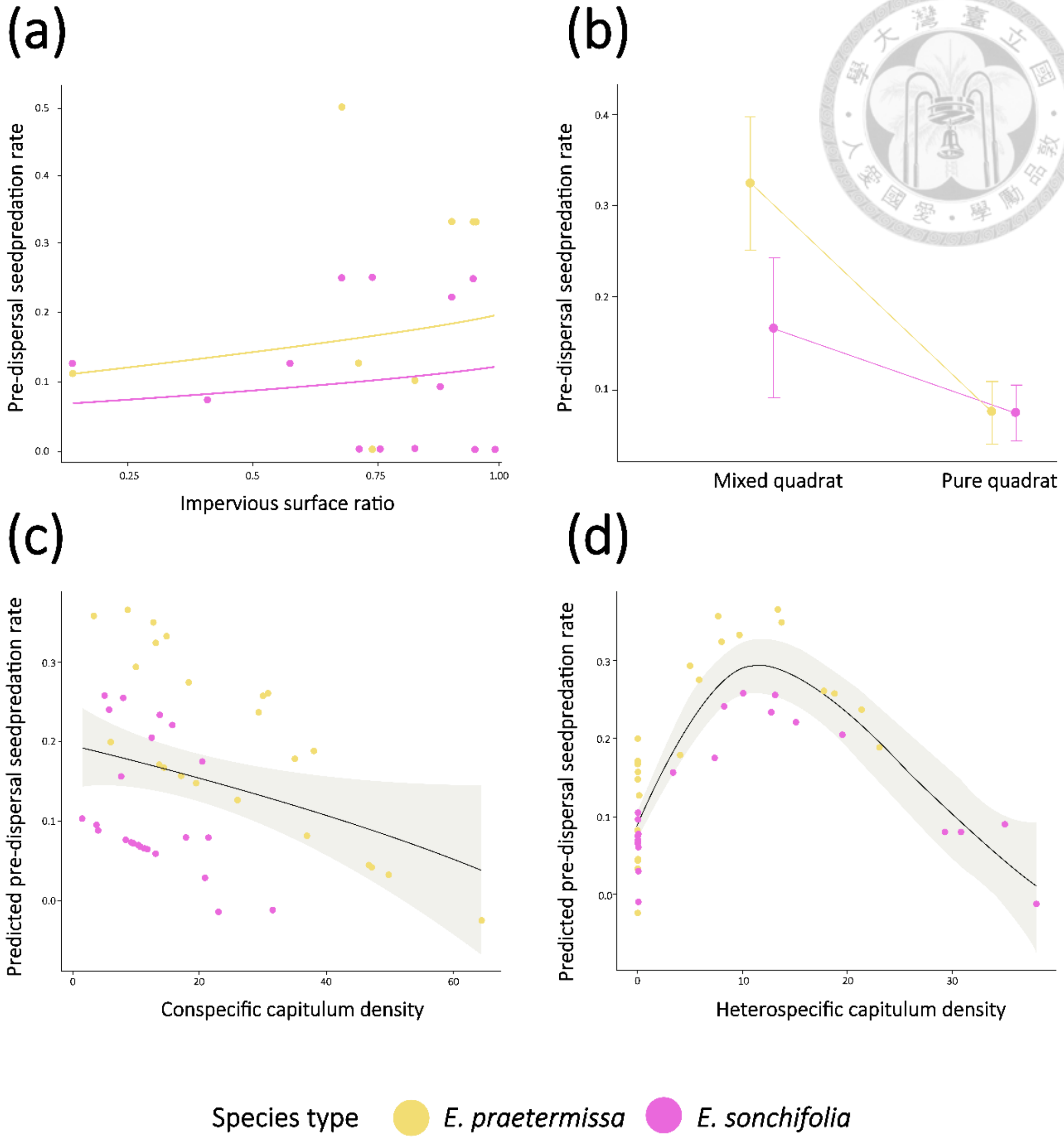

Figure 8. The relationships between pre-dispersal seed predation rate and ecological factors. (a) The regression model of GLMM predicted by the observed impervious surface ratio, and the points are observation data. (b) The pre-dispersal seed predation rates of both *Emilia* species from two quadrat types. The points indicate the mean value, and the error bars indicate the standard error. (c) The regression model of GAMM predicted by the observed conspecific capitulum density. The light grey area indicates the 95% confidence interval. (d) The regression model of GAMM predicted by the observed heterospecific capitulum density. The light grey area indicates the 95% confidence interval.

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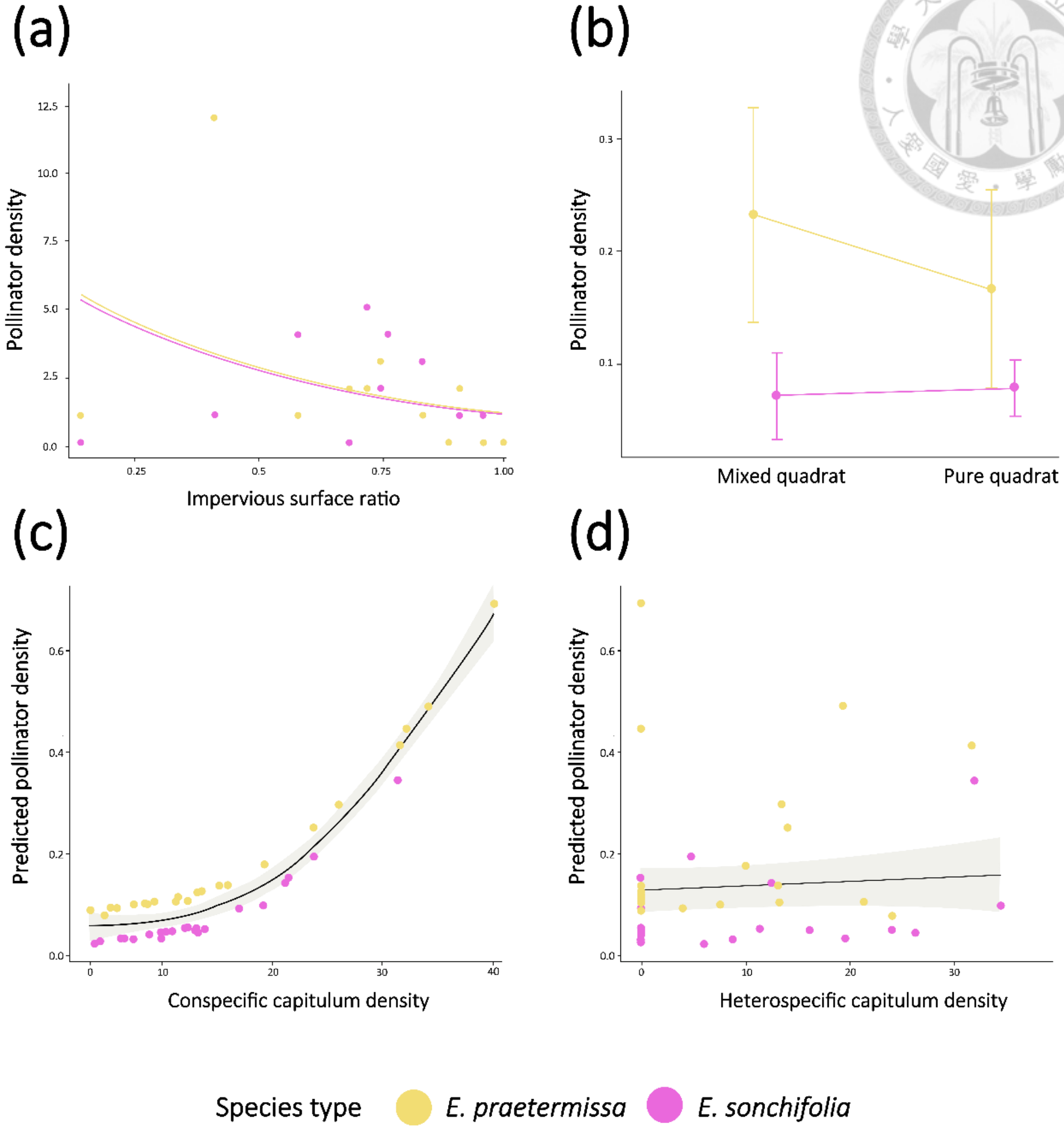

Figure 9. The relationships between pollinator density and ecological factors. (a) The regression model of GLMM predicted by the observed impervious surface ratio, and the points are observation data. (b) The pollinator density of both *Emilia* species from two quadrat types. The points indicate the mean value, and the error bars indicate the standard error. (c) The regression model of GAMM predicted by the observed conspecific capitulum density. The light grey area indicates the 95% confidence interval. (d) The regression model of GAMM predicted by the observed heterospecific capitulum density. The light grey area indicates the 95% confidence interval.

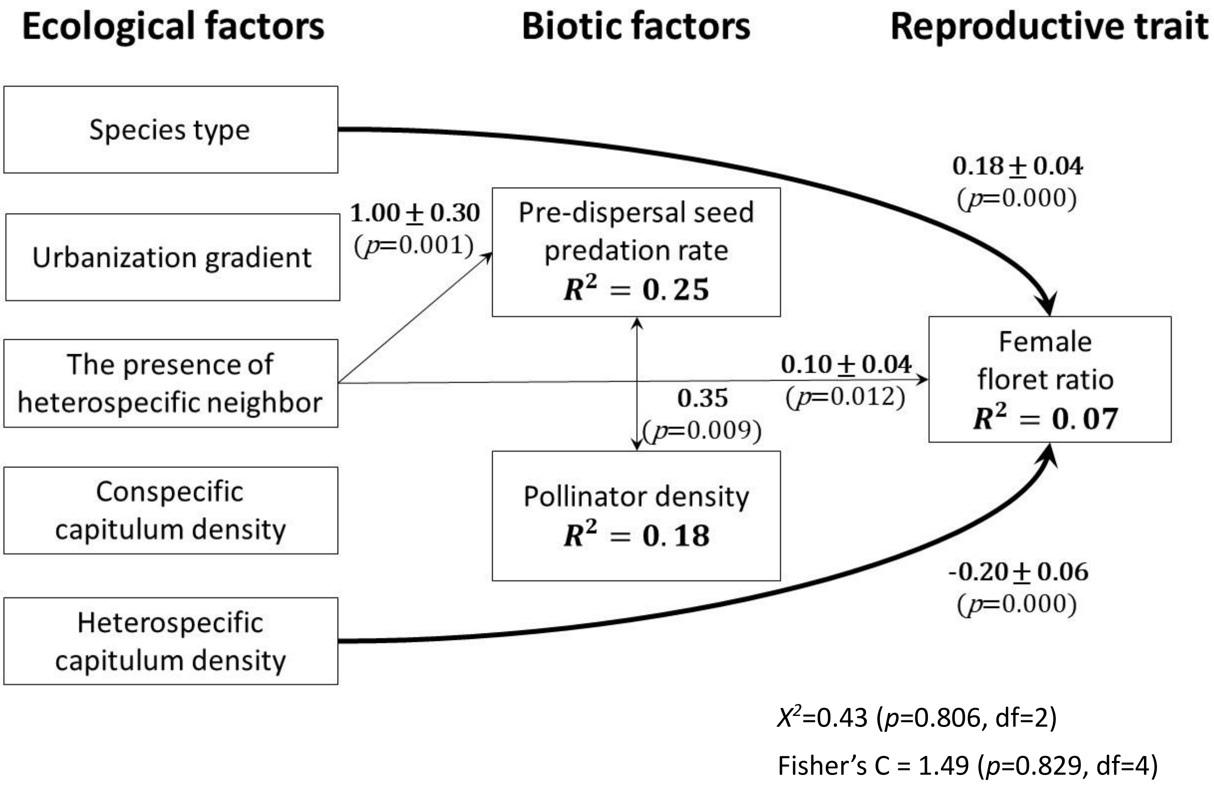

Figure 10. The result of the piecewise structural equation model (piecewise SEM). The thickness of the arrows in piecewise SEM represents the strength of the relationship between variables, and significant coefficients are labeled (estimate ± SE, *p*-value). Model fits are shown as Chi-Squared and Fisher's C tests in the lower-right corner, and the model fitted the data well ($p > 0.05$). We treated categorical data, including species type (native=0/exotic=1), and quadrat type (pure=0/mixed=1) as numerical data to perform piecewise SEM.

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TABLES

Table 1. The area of five land-use type within 500 m radius range of 13 study sites. Impervious surface ration is the proportion of building and asphalt area within 500 m radius range, and green surface ratio is the proportion of grass and forest within 500 m radius range.

Site name	**Site ID**	**Land-use type areas (m^2)**					**Impervious surface ratio**	**Green surface ratio**
		water	**forest**	**grass**	**building**	**asphalt**		
HST	a	2700.8	538940.9	127872.6	40393.2	62865.5	0.13	0.86
JMST	b	0	327614.3	130276.4	192984.0	121887.2	0.41	0.59
BHP	c	71121.0	133428.2	123346.3	214707.8	230168.2	0.58	0.33
NGP	d	20706.2	67503.0	157913.3	310187.5	216464.6	0.68	0.29
DA	e	10617.1	54914.3	153482.0	204393.5	349337.2	0.72	0.27
XSP	f	7202.1	74485.6	104316.6	253188.5	333570.7	0.76	0.23
YP	g	68254.1	24302.1	105419.8	242648.7	332102.0	0.74	0.17
NTSEC	h	42993.3	867.5	87024.1	299393.2	342456.0	0.83	0.11
NTU	i	10805.2	1800.5	78324.9	267834.9	413980.3	0.88	0.10
MLSH	j	13077.5	9582.2	50177.0	360269.8	339627.6	0.91	0.08
228PP	k	1800.5	8102.1	26495.2	458156.0	278192.5	0.95	0.05
RXG	l	22700.8	2700.7	13503.3	331328.8	402498.8	0.95	0.02
CLSH	m	0	0	4501.3	523832.5	244425.1	0.99	0.01

Table 2. Two-way ANOVA table for the presence of pre-dispersal seed predation and species type on female floret ratio considering variation between sites. ‘*’ indicates the 0.05 significant level.

Source of variation	**Female floret ratio**			
	df	**Mean Squared**	**F**	***p***
The presence of pre-dispersal seed predation	1	0.026	6.30	**0.033***
Species type	1	0.008	1.95	0.196
The presence of pre-dispersal seed predation x Species type	1	0.010	2.32	0.162
Residuals	9	0.037		

Table 3. Two-way ANOVA table for the effect of pollinator density and species type on female floret ratio considering variation between sites. ‘·’ indicates the 0.1 significant level.

Source of variation	**Female floret ratio**			
	df	**Mean Squared**	**F**	***p***
Pollinator density level	1	0.020	4.56	**0.061·**
Species type	1	0.012	2.67	0.137
Pollinator density level x Species type	1	0.009	1.99	0.192
Residuals	9	0.040		

Table 4. Model selection ANOVA table for GLMM featuring urbanization and species type as explanatory variables, sites as random effect for pre-dispersal seed predation rate.

Response variable	**GLMM Model**	x^2	**df**	***p***
Pre-dispersal seed predation rate	(Presence of egg, Absence of egg) = Impervious surface ratio + Species type (Presence of egg, Absence of egg) = Impervious surface ratio x Species type	0.336	1	0.562
	(Presence of egg, Absence of egg) = Impervious surface ratio + Species type (Presence of egg, Absence of egg) = Impervious surface ratio	1.922	1	0.166
	(Presence of egg, Absence of egg) = Impervious surface ratio + Species type (Presence of egg, Absence of egg) = Species type	0.46	1	0.498

Table 5. Model selection ANOVA table for GLMM featuring presence of heterospecific neighbor and species type as explanatory variables, sites as random effect for pre-dispersal seed predation rate.

Response variable	**GLMM Model**	x^2	**df**	***p***
Pre-dispersal seed predation rate	(Presence of egg, Absence of egg) = Quadrat type + Species type (Presence of egg, Absence of egg) = Quadrat type x Species type	0.937	1	0.333
	(Presence of egg, Absence of egg) = Quadrat type + Species type (Presence of egg, Absence of egg) = Quadrat type	1.879	1	0.171
	(Presence of egg, Absence of egg) = Quadrat type+ Species type (Presence of egg, Absence of egg) = Species type	13.474	1	**<0.001***

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Table 6. Model selection ANOVA table for GLMM featuring urbanization and species type as explanatory variables, sites as random effect for pollinator density.

Response variable	**GLMM Model**	x^2	**df**	***p***
Pollinator density	(Pollinator density) = Impervious surface ratio + Species type (Pollinator density) = Impervious surface ratio x Species type	0.381	1	0.537
	(Pollinator density) = Impervious surface ratio + Species type (Pollinator density) = Impervious surface ratio	0.006	1	0.941
	(Pollinator density) = Impervious surface ratio + Species type (Pollinator density) = Species type	2.227	1	0.136

Table 7. Model selection ANOVA table for GLMM featuring the presence of heterospecific neighbor and species type as explanatory variables, sites as random effect for pollinator density.

Response variable	**GLMM Model**	x^2	**df**	***p***
Pollinator density	(Pollinator density) = Quadrat type + Species type (Pollinator density) = Quadrat type x Species type	0.937	1	0.333
	(Pollinator density) = Quadrat type + Species type (Pollinator density) = Quadrat type	1.879	1	0.171
	(Pollinator density) = Quadrat type+ Species type (Pollinator density) = Species type	13.474	1	**<0.001***

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Table 8. Fixed effects table for the GLMMs fitted to the pre-dispersal seed predation rate and pollinator density as response variables, site as random effect. ‘*’ indicates the 0.05 significant level, and ‘·’ indicates the 0.1 significant level.

	Estimate	**SE**	***z***	***p***
Pre-dispersal seed predation rate				
Intercept	-2.195	0.870	-2.523	**0.012***
Impervious surface ratio	0.781	1.135	0.688	0.491
Species type (Native)	-0.566	0.413	-1.373	0.170
Pre-dispersal seed predation rate				
Intercept	-0.859	0.390	-2.200	**0.028***
Quadrat type (Pure)	-1.550	0.439	-3.528	**<0.001***
Species type (Native)	-0.583	0.429	-1.357	0.175
Pollinator density				
Intercept	1.953	0.798	2.448	**0.014***
Impervious surface ratio	-1.889	1.112	-1.698	**0.090·**
Species type (Native)	-0.034	0.462	-0.075	0.941
Pollinator density				
Intercept	-1.514	0.600	-5.524	**0.012***
Quadrat type (Pure)	-0.215	0.820	-0.262	0.794
Species type (Native)	-0.984	0.883	-1.113	0.266

Table 9. Parametric coefficients and approximate significance of smooth terms for the GAMMs fitted to the pre-dispersal seed predation rate, and the pollinator density. ‘Con’ and ‘Het’ indicate the conspecific capitulum density and heterospecific capitulum density respectively. ‘*’ indicates the 0.05 significant level, ‘edf’ indicates the effective degree of freedom for smooth terms, and ‘Ref.df’ indicates the reference degree of freedom for smooth terms.

	Estimate	**SE**	***z***	***p***
Pre-dispersal seed predation rate				
Intercept	0.214	0.053	4.062	**<0.001***
Species type (Native)	-0.113	0.079	-1.439	0.158
Pollinator density				
Intercept	0.168	0.040	4.174	**<0.001***
Species type (Native)	-0.064	0.057	-1.119	0.270

	edf	**Ref. df**	**F**	***p***
Pre-dispersal seed predation rate				
s(con)	1.000	1.000	2.577	0.116
s(het)	2.416	2.416	2.975	0.100
Pollinator density				
s(con)	2.196	2.196	8.970	**<0.001***
s(het)	1.000	1.000	0.041	0.841

Table 10. Fixed effects table for the GLMM fitted to the female floret ratio, pre-dispersal seed predation rate, and the GLM fitted to the pollinator density in piecewise SEM. We treated categorical data, including species type (native=0/exotic=1), and quadrat type (pure=0/mixed=1) as numerical data to perform piecewise SEM. '*' indicates the 0.05 significant level.

	Estimate	**SE**	***z***	***p***
Female floret ratio				
Pre-dispersal seed predation rate	0.214	0.194	1.104	0.270
Pollinator density	0.087	0.111	0.788	0.431
Species type	0.181	0.036	5.026	**<0.001***
Quadrat type	0.103	0.041	2.515	**0.012***
Heterospecific capitulum density	-0.196	0.058	-3.361	**0.001***
Pre-dispersal seed predation rate				
Impervious surface ratio	0.167	0.290	0.575	0.565
Species type	-0.013	0.398	-0.033	0.974
Quadrat type	0.998	0.304	3.278	**0.001***
Conspecific capitulum density	-0.209	0.306	-0.682	0.495
Heterospecific capitulum density	-0.567	0.511	-1.110	0.267
Pollinator density				
Impervious surface ratio	0.148	0.472	0.314	0.754
Species type	-0.153	0.812	-0.188	0.851
Quadrat type	0.350	0.504	0.695	0.487
Conspecific capitulum density	0.586	0.430	1.365	0.172
Heterospecific capitulum density	-0.528	1.012	-0.521	0.602

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APPENDIX

Appendix 1. The sampling mature capitula collected from two *Emilia* species: native *E. sonchifolia*, and exotic *E. praetermissa* from 13 study sites. The capitulum of *E. praetermissa* was unavailable in the site ‘XSP’. The ‘egg’ refers to the egg of fruit fly which is the major pre-dispersal seed predator of *Emilia* species.

Site name	Species type	Collected capitula	Presence of egg	Absence of egg	pre-dispersal seed predation rate	pre-dispersal seed predation	female floret ratio
228PP	Exotic	9	3	6	0.33	with	0.31
BHP	Exotic	8	1	7	0.13	with	0.34
CLSH	Exotic	2	0	2	0.00	without	0.28
DA	Exotic	8	1	7	0.13	with	0.25
HST	Exotic	9	1	8	0.11	with	0.29
JMST	Exotic	14	1	13	0.07	with	0.26
MLSH	Exotic	9	3	6	0.33	with	0.29
NGP	Exotic	10	5	5	0.50	with	0.34
NSEC	Exotic	10	1	9	0.10	with	0.26
NTU	Exotic	11	1	10	0.09	with	0.27
RXG	Exotic	3	1	2	0.33	with	0.27
YP	Exotic	8	0	8	0.00	without	0.17
228PP	Native	12	3	9	0.25	with	0.18
BHP	Native	8	1	7	0.13	with	0.09
CLSH	Native	2	0	2	0.00	without	0.12
DA	Native	12	0	12	0.00	without	0.15
HST	Native	8	1	7	0.13	with	0.32
JMST	Native	14	1	13	0.07	with	0.21
MLSH	Native	9	2	7	0.22	with	0.26
NGP	Native	8	2	6	0.25	with	0.26
NSEC	Native	10	0	10	0.00	without	0.17
NTU	Native	11	1	10	0.09	with	0.08
RXG	Native	7	0	7	0.00	without	0.25
XSP	Native	2	0	2	0.00	without	0.08
YP	Native	4	1	3	0.25	with	0.08

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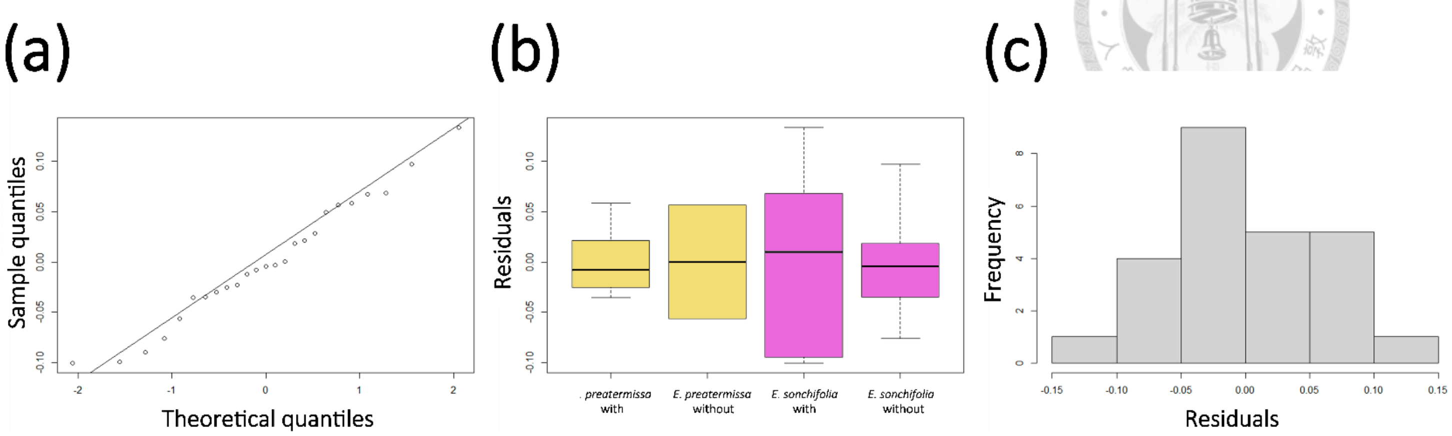

Appendix 2. (a) The normal Q-Q plot: residuals of 25 data points fitted in two-way ANOVA for pre-dispersal seed predation and species type. (b) The boxplot: residuals of 25 data points fitted in two-way ANOVA. The yellow indicates *E. praetermissa* and the pink indicates *E. sonchifolia*. ‘With’ indicates the data points from the sites with pre-dispersal seed predation, while ‘Without’ indicates the data points from the sites without pre-dispersal seed predation. (c) The histogram: residuals of 25 data points fitted in two-way ANOVA for pre-dispersal seed predation and species type.

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Appendix 3. The 25 data points for pollinator density of both *Emilia* species from each site. Female floret ratio was obtained from the mature capitulum collection experiment. The capitulum of *E. praetermissa* was unavailable in the site 'XSP'.

Site name	**Impervious surface ratio**	**Species type**	**Pollinator density**	**Pollinator density level**	**Female floret ratio**
228PP	0.95	Native	1	low	0.18
228PP	0.95	Exotic	1	low	0.31
BHP	0.58	Native	4	high	0.09
BHP	0.58	Exotic	1	low	0.34
CLSH	0.99	Native	0	low	0.12
CLSH	0.99	Exotic	0	low	0.28
DA	0.72	Native	5	high	0.15
DA	0.72	Exotic	2	high	0.25
HST	0.13	Native	0	low	0.32
HST	0.13	Exotic	1	low	0.29
JMST	0.41	Native	1	low	0.21
JMST	0.41	Exotic	12	high	0.26
MLSH	0.91	Native	1	low	0.26
MLSH	0.91	Exotic	2	high	0.29
NGP	0.68	Native	0	low	0.26
NGP	0.68	Exotic	2	high	0.34
NSEC	0.83	Native	3	high	0.17
NSEC	0.83	Exotic	1	low	0.26
NTU	0.88	Native	0	low	0.08
NTU	0.88	Exotic	0	low	0.27
RXG	0.95	Native	1	low	0.25
RXG	0.95	Exotic	0	low	0.27
XSP	0.76	Native	4	high	0.08
YP	0.74	Native	2	high	0.08
YP	0.74	Exotic	3	high	0.17

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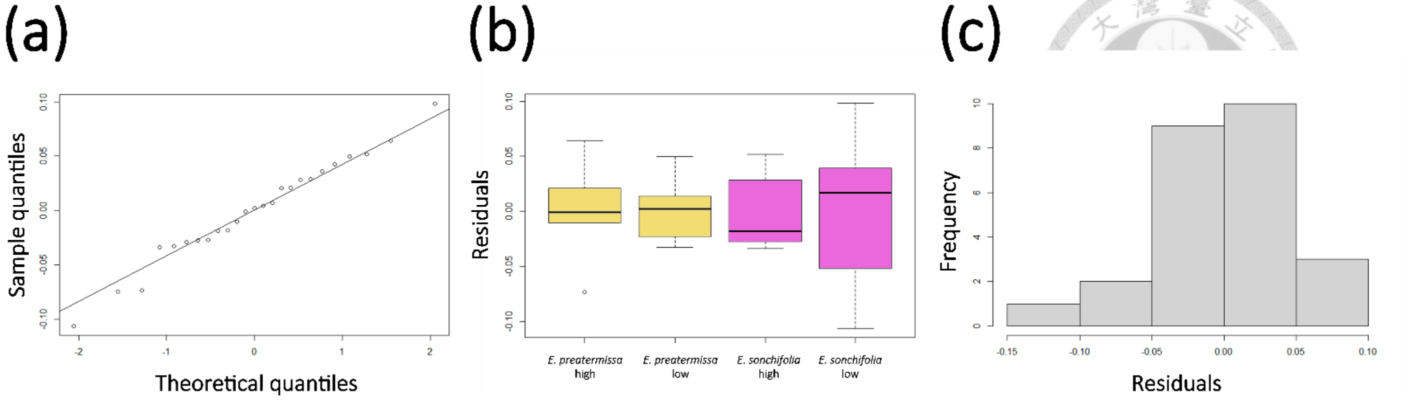

Appendix 4. (a) The normal Q-Q plot: residual of 25 data points used in two-way ANOVA for pollinator density and species type. (b) The boxplot: residuals of 25 data points used in two-way ANOVA for pollinator density and species type. ‘High’ indicates the data points from the sites with pollinator density level higher than the overall mean value, while ‘low’ indicates the data points from the sites with pollinator density level lower than the overall mean value. (c) The histogram: residuals of 25 data points used in two-way ANOVA for pollinator density and species type.

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Appendix 5. The 25 data points for GLMM regression featuring the urbanization gradient and species type as explanatory variables for pre-dispersal seed predation rate. The urbanization effect was quantified with impervious surface ratio. The capitulum of *E. praetermissa* was unavailable in the site 'XSP'.

Site name	**Impervious surface ratio**	**Species type**	**Collected capitula**	**Presence of egg**	**Absence of egg**	**Pre-dispersal seed predation rate**	**Red or brown achenes**	**Off-white achenes**	**Total achenes**	**Female floret ratio**
228PP	0.95	Exotic	9	3	6	0.33	123	276	399	0.31
BHP	0.58	Exotic	8	1	7	0.13	184	351	535	0.34
CLSH	0.99	Exotic	2	0	2	0.00	47	119	166	0.28
DA	0.72	Exotic	8	1	7	0.13	120	360	480	0.25
HST	0.13	Exotic	9	1	8	0.11	150	373	523	0.29
JMST	0.41	Exotic	14	1	13	0.07	216	626	842	0.26
MLSH	0.91	Exotic	9	3	6	0.33	139	342	481	0.29
NGP	0.68	Exotic	10	5	5	0.50	145	282	427	0.34
NSEC	0.83	Exotic	10	1	9	0.10	165	468	633	0.26
NTU	0.88	Exotic	11	1	10	0.09	170	457	627	0.27
RXG	0.95	Exotic	3	1	2	0.33	42	116	158	0.27
YP	0.74	Exotic	8	0	8	0.00	84	424	508	0.17
228PP	0.95	Native	12	3	9	0.25	92	428	520	0.18
BHP	0.58	Native	8	1	7	0.13	40	387	427	0.09
CLSH	0.99	Native	2	0	2	0.00	17	125	142	0.12
DA	0.72	Native	12	0	12	0.00	109	623	732	0.15
HST	0.13	Native	8	1	7	0.13	154	324	478	0.32
JMST	0.41	Native	14	1	13	0.07	175	646	821	0.21
MLSH	0.91	Native	9	2	7	0.22	129	376	505	0.26
NGP	0.68	Native	8	2	6	0.25	105	306	411	0.26
NSEC	0.83	Native	10	0	10	0.00	99	475	574	0.17
NTU	0.88	Native	11	1	10	0.09	60	683	743	0.08
RXG	0.95	Native	7	0	7	0.00	104	306	410	0.25
XSP	0.76	Native	2	0	2	0.00	8	97	105	0.08
YP	0.74	Native	4	1	3	0.25	22	250	272	0.08

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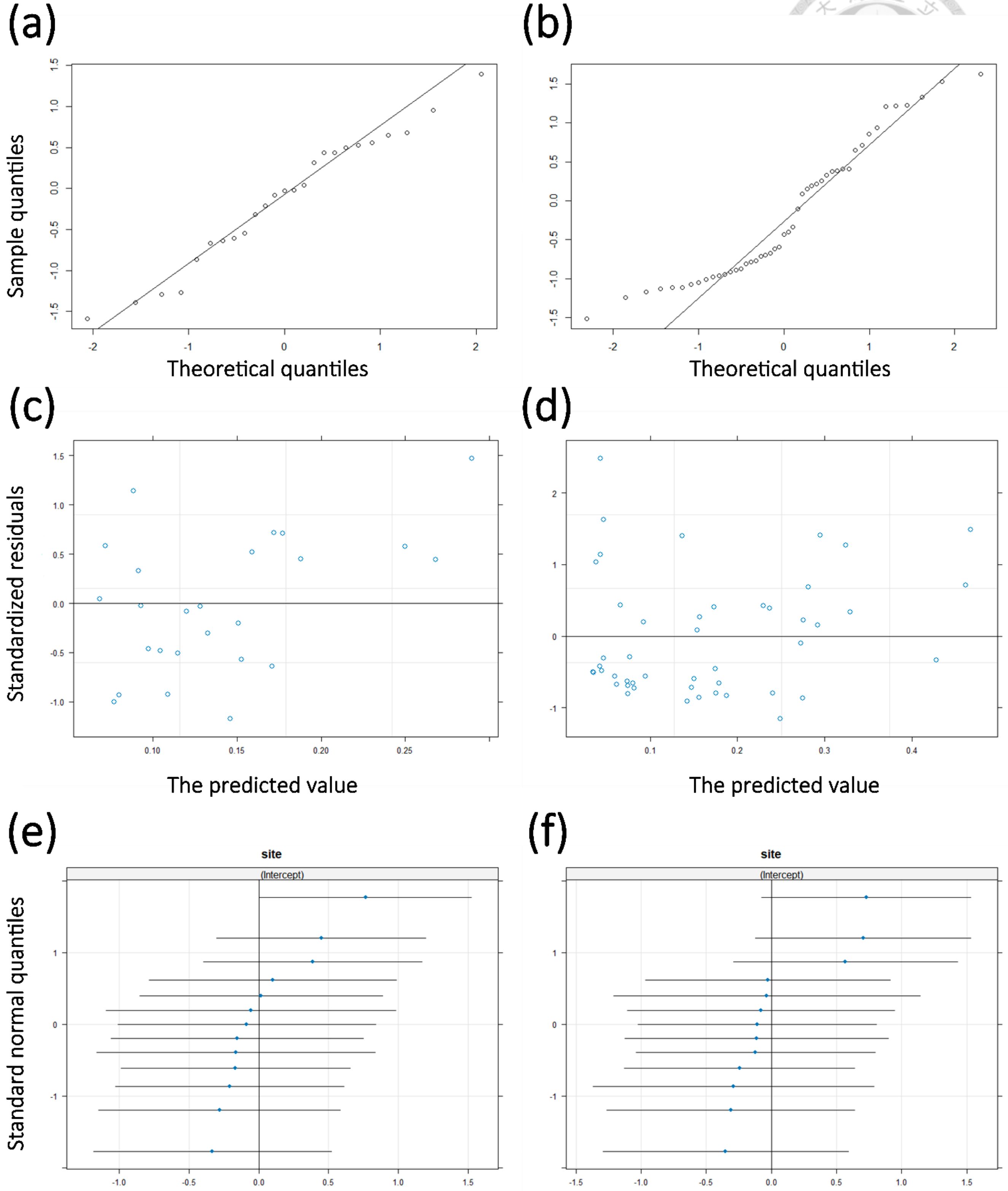
Appendix 6. The 47 data points to perform GLMM regression featuring the presence of heterospecific neighbor (‘Quadrat type’) and species type as fixed effect; and GAMM regression featuring conspecific (‘Con’) and heterospecific (‘Het’) capitulum density as smooth term, species type as fixed effect for pre-dispersal seed predation rate (‘Pre’).

Site name	Species type	Quadrat type	Con	Het	Collected capitula	Presence of egg	Absence of egg	Pre	Red or brown achenes	Off-white achenes	Total achenes	Female floret ratio
228PP	Exotic	pure	20	0	6	1	5	0.17	94	204	298	0.32
BHP	Exotic	pure	14	0	5	0	5	0.00	126	226	352	0.36
DA	Exotic	pure	47	0	5	0	5	0.00	81	245	326	0.25
HST	Exotic	pure	37	0	5	0	5	0.00	95	236	331	0.29
JMST	Exotic	pure	50	0	10	1	9	0.10	153	441	594	0.26
MLSH	Exotic	pure	17	0	6	2	4	0.33	83	266	349	0.24
NGP	Exotic	pure	14	0	5	1	4	0.20	70	238	308	0.23
NSEC	Exotic	pure	26	0	7	0	7	0.00	127	304	431	0.29
NTU	Exotic	pure	47	0	8	0	8	0.00	117	359	476	0.25
RXG	Exotic	pure	6	0	1	0	1	0.00	13	37	50	0.26
YP	Exotic	pure	65	0	6	0	6	0.00	72	318	390	0.18
228PP	Exotic	mixed	13	14	3	2	1	0.67	29	72	101	0.29
BHP	Exotic	mixed	29	21	3	1	2	0.33	58	125	183	0.32
CLSH	Exotic	mixed	10	5	2	0	2	0.00	47	119	166	0.28
DA	Exotic	mixed	9	13	3	1	2	0.33	39	115	154	0.25
HST	Exotic	mixed	31	18	4	1	3	0.25	55	137	192	0.29
JMST	Exotic	mixed	38	23	4	0	4	0.00	63	185	248	0.25
MLSH	Exotic	mixed	3	8	3	1	2	0.33	56	76	132	0.42
NGP	Exotic	mixed	18	6	5	4	1	0.80	75	44	119	0.63
NSEC	Exotic	mixed	30	19	3	1	2	0.33	38	164	202	0.19
NTU	Exotic	mixed	15	10	3	1	2	0.33	53	98	151	0.35
RXG	Exotic	mixed	13	8	2	1	1	0.50	29	79	108	0.27
YP	Exotic	mixed	35	4	2	0	2	0.00	12	106	118	0.10
228PP	Native	pure	10	0	9	1	8	0.11	80	324	404	0.20
BHP	Native	pure	21	0	5	1	4	0.20	29	244	273	0.11
DA	Native	pure	11	0	7	0	7	0.00	56	374	430	0.13
HST	Native	pure	10	0	4	0	4	0.00	73	164	237	0.31
JMST	Native	pure	9	0	10	1	9	0.10	141	460	601	0.23
MLSH	Native	pure	32	0	6	0	6	0.00	95	275	370	0.26
NGP	Native	pure	13	0	3	0	3	0.00	49	187	236	0.21
NSEC	Native	pure	12	0	7	0	7	0.00	67	356	423	0.16
NTU	Native	pure	8	0	8	1	7	0.13	43	460	503	0.09
RXG	Native	pure	4	0	5	0	5	0.00	91	214	305	0.30
XSP	Native	pure	2	0	2	0	2	0.00	8	97	105	0.08
YP	Native	pure	11	0	3	1	2	0.33	18	174	192	0.09
228PP	Native	mixed	14	13	3	2	1	0.67	12	104	116	0.10
BHP	Native	mixed	21	29	3	0	3	0.00	11	143	154	0.07
CLSH	Native	mixed	5	10	2	0	2	0.00	17	125	142	0.12
DA	Native	mixed	12	19	5	0	5	0.00	53	249	302	0.18
HST	Native	mixed	18	31	4	1	3	0.25	81	160	241	0.34
JMST	Native	mixed	23	38	4	0	4	0.00	34	186	220	0.15
MLSH	Native	mixed	8	3	3	2	1	0.67	34	101	135	0.25
NGP	Native	mixed	6	8	5	2	3	0.40	56	119	175	0.32
NSEC	Native	mixed	20	7	3	0	3	0.00	32	119	151	0.21
NTU	Native	mixed	16	15	3	0	3	0.00	17	223	240	0.07
RXG	Native	mixed	8	13	2	0	2	0.00	13	92	105	0.12
YP	Native	mixed	4	35	1	0	1	0.00	4	76	80	0.05

Appendix 7. The 45 data points to perform GLMM regression featuring the presence of heterospecific neighbor (‘Quadrat type’) and species type as fixed effect; and GAMM regression featuring conspecific (‘Con’) and heterospecific (‘Het’) capitulum density as smooth term, species type as fixed effect for pollinator density.

Site name	Impervious surface ratio	Species type	Quadrat type	Quadrat number	Female floret ratio	Pollinator count	Pollinator density	Con	Het
228PP	0.95	Exotic	mixed	5	0.26	1	0.20	5	24
228PP	0.95	Exotic	pure	6	0.42	0	0.00	8	0
228PP	0.95	Native	mixed	5	0.08	1	0.20	24	5
228PP	0.95	Native	pure	19	0.29	0	0.00	21	0
BHP	0.58	Exotic	mixed	8	0.40	0	0.00	24	14
BHP	0.58	Exotic	pure	6	0.36	1	0.17	32	0
BHP	0.58	Native	mixed	8	0.06	3	0.38	14	24
BHP	0.58	Native	pure	16	0.09	1	0.06	12	0
CLSH	0.99	Exotic	mixed	1	0.28	0	0.00	6	4
CLSH	0.99	Native	mixed	1	0.12	0	0.00	4	6
DA	0.72	Exotic	mixed	3	0.24	1	0.33	19	10
DA	0.72	Exotic	pure	5	0.25	1	0.20	5	0
DA	0.72	Native	mixed	3	0.18	0	0.00	10	19
DA	0.72	Native	pure	22	0.13	5	0.23	10	0
HST	0.13	Exotic	mixed	1	0.22	0	0.00	16	13
HST	0.13	Exotic	pure	17	0.29	1	0.06	15	0
HST	0.13	Native	mixed	1	0.33	0	0.00	13	16
HST	0.13	Native	pure	12	0.31	0	0.00	6	0
JMST	0.41	Exotic	mixed	5	0.25	0	0.00	12	21
JMST	0.41	Exotic	pure	13	0.26	13	1.00	40	0
JMST	0.41	Native	mixed	5	0.16	0	0.00	21	12
JMST	0.41	Native	pure	12	0.26	1	0.08	10	0
MLSH	0.91	Exotic	mixed	5	0.28	3	0.60	32	31
MLSH	0.91	Exotic	pure	5	0.20	0	0.00	14	0
MLSH	0.91	Native	mixed	5	0.29	1	0.20	31	32
MLSH	0.91	Native	pure	20	0.25	0	0.00	12	0
NGP	0.68	Exotic	mixed	3	0.62	3	1.00	26	13
NGP	0.68	Exotic	pure	9	0.23	1	0.11	8	0
NGP	0.68	Native	mixed	3	0.34	0	0.00	13	26
NGP	0.68	Native	pure	18	0.21	0	0.00	11	0
NSEC	0.83	Exotic	mixed	4	0.19	1	0.25	9	8
NSEC	0.83	Exotic	pure	10	0.30	0	0.00	13	0
NSEC	0.83	Native	mixed	4	0.19	0	0.00	8	9
NSEC	0.83	Native	pure	16	0.15	3	0.19	9	0
NTU	0.88	Exotic	mixed	7	0.36	0	0.00	11	13
NTU	0.88	Exotic	pure	11	0.25	0	0.00	9	0
NTU	0.88	Native	mixed	7	0.07	0	0.00	13	11
NTU	0.88	Native	pure	12	0.08	0	0.00	7	0
RXG	0.95	Exotic	pure	2	0.26	0	0.00	4	0
RXG	0.95	Native	pure	28	0.30	1	0.04	6	0
XSP	0.76	Native	pure	16	0.08	3	0.19	17	0
YP	0.74	Exotic	mixed	6	0.11	1	0.17	34	19
YP	0.74	Exotic	pure	7	0.18	2	0.29	12	0
YP	0.74	Native	mixed	6	0.05	0	0.00	19	34
YP	0.74	Native	pure	14	0.11	2	0.14	4	0


(a)
(b)
Sample quantiles
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2
-1
0
1
2
Theoretical quantiles
Theoretical quantiles
(c)
(d)
Standardized residuals
1.5
1.0
0.5
0.0
-0.5
-1.0
0.10
0.15
0.20
0.25
2
1
0
-1
0.1
0.2
0.3
0.4
The predicted value
The predicted value
(e)
(f)
Standard normal quantiles
site
(Intercept)
1
0
-1
-1.0
-0.5
0.0
0.5
1.0
1.5
site
(Intercept)
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5

Appendix 8. (a) The normal Q-Q plot: residuals of 25 data points for GLMM featuring urbanization gradient and species type as explanatory variables for pre-dispersal seed predation rate. (b) The normal Q-Q plot: residuals of 47 data points for GLMM featuring presence of heterospecific neighbor and species type as explanatory variables for pre-dispersal seed predation rate. (c) The relationship between fitted values and Pearson residuals from GLMM featuring urbanization gradient and species type as explanatory variables for pre-dispersal seed predation rate. (d) The relationship between fitted values and Pearson residuals from GLMM featuring presence of heterospecific neighbor and species type as explanatory variables for pre-dispersal seed predation rate. (e) The Q-Q plot for the random effect of GLMM featuring urbanization gradient and species type as explanatory variables for pre-dispersal seed predation rate. (f) The Q-Q plot for the random effect of GLMM featuring presence of heterospecific neighbor and species type as explanatory variables for pre-dispersal seed predation rate.

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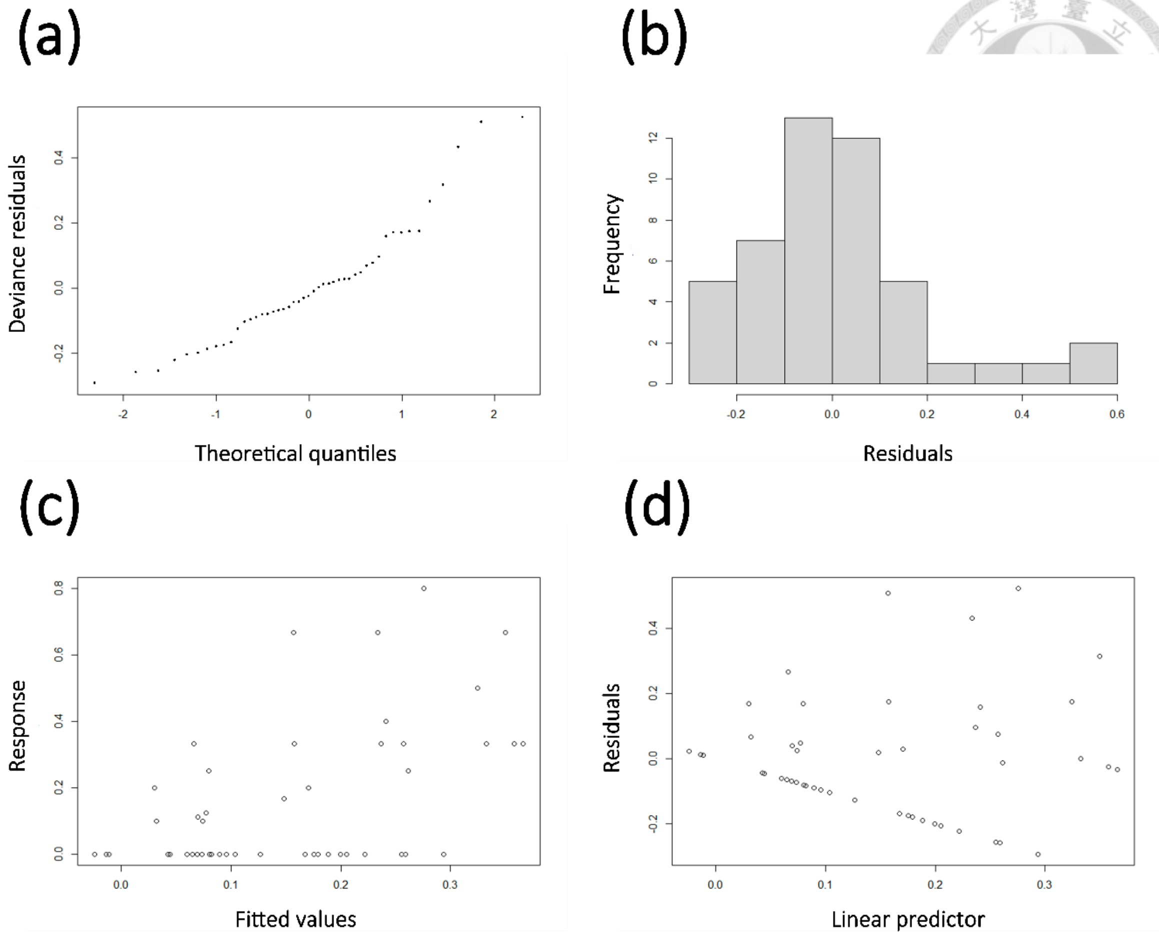
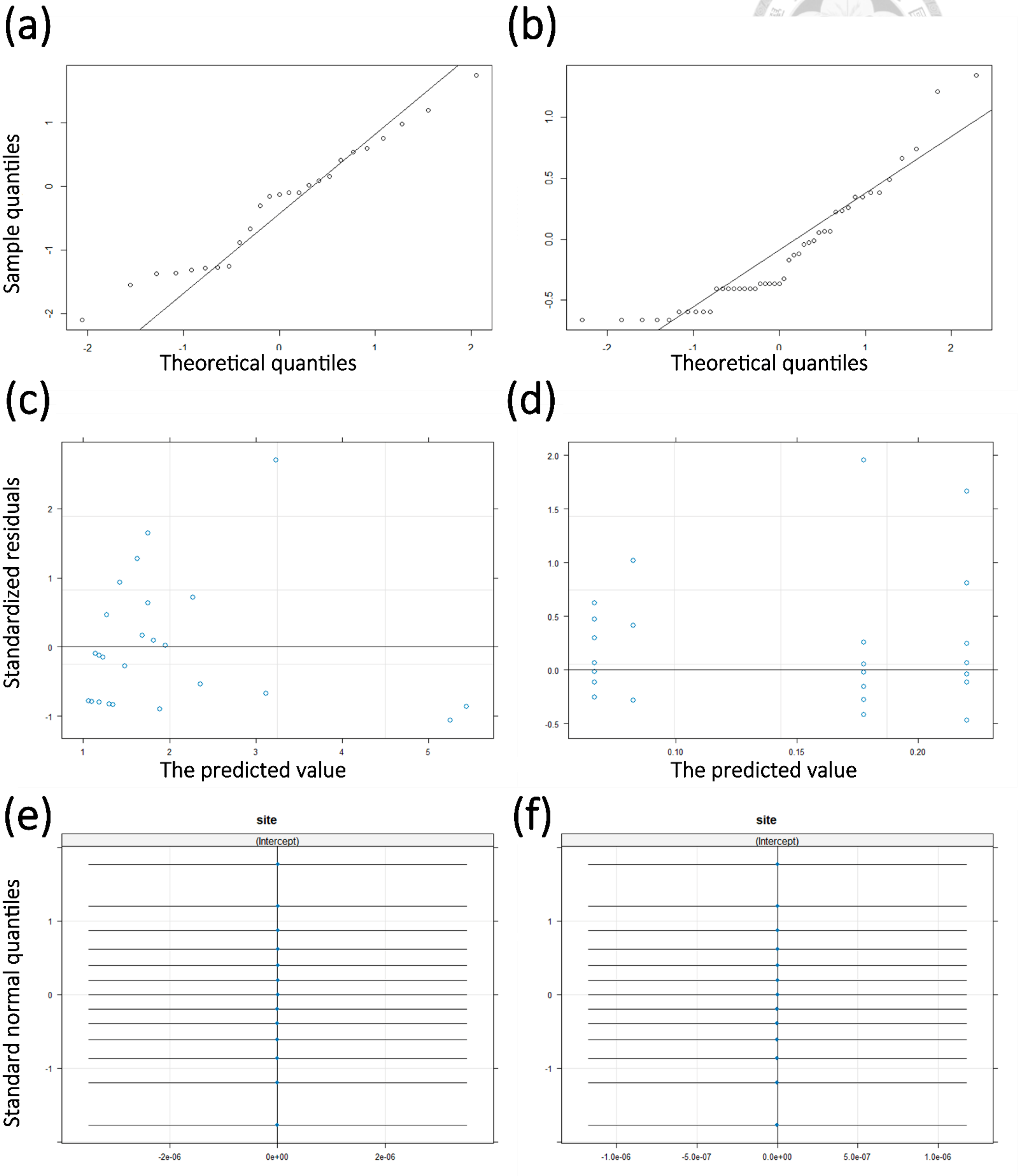
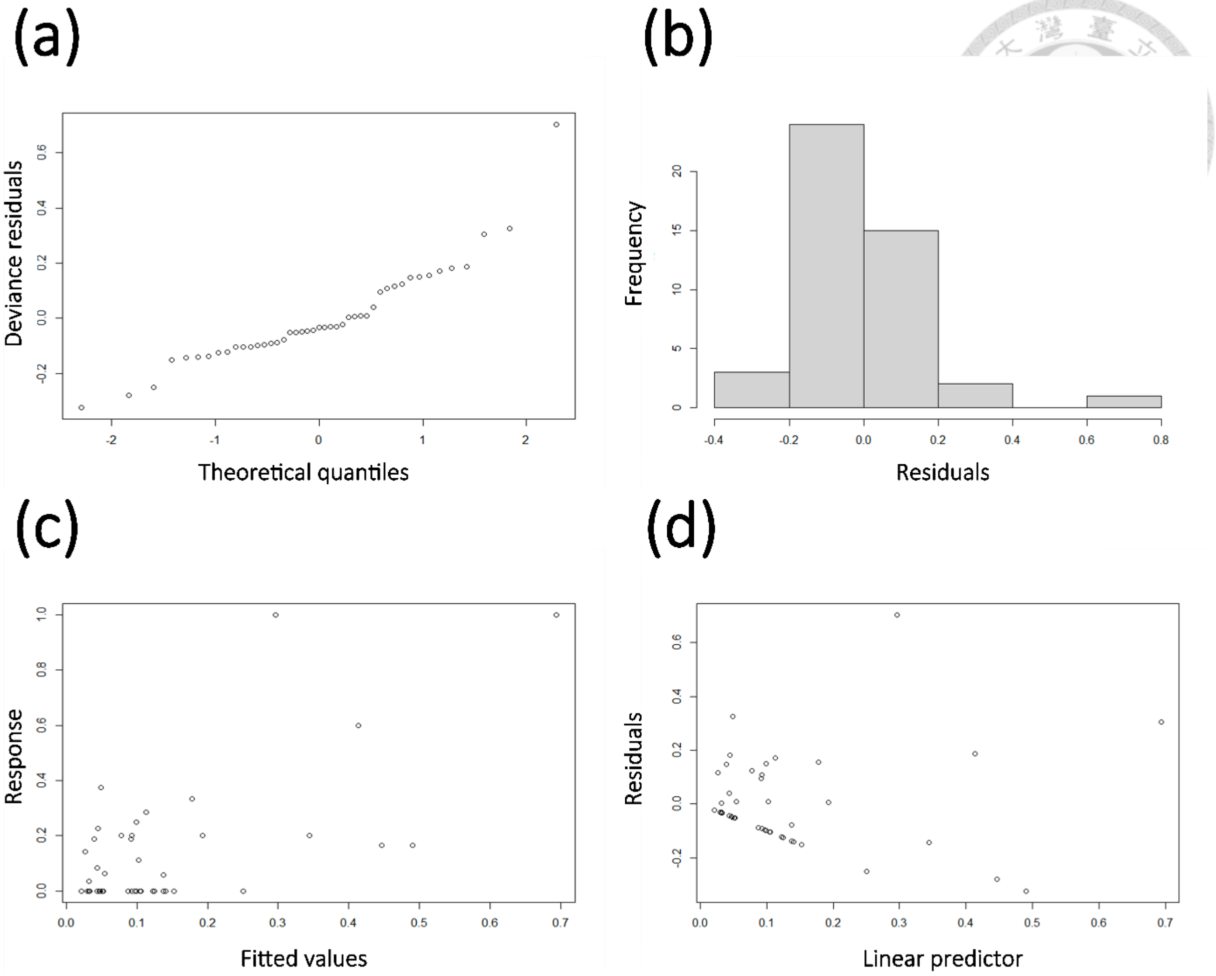


Appendix 9. Diagnostic plots for GAMM treating conspecific and heterospecific capitulum density as smooth term, species type as fixed effect, ad sites as random effect for pre-dispersal seed predation rate. (a) Normal Q-Q plot: the points generally follow the diagonal line, indicating that the residuals are approximately normally distributed. (b) Histogram of residuals: the histogram is roughly bell-shaped but slightly right-skewed, indicating a minor deviation from normality. (c) Response vs. fitted values: this plot shows a clear pattern, with many points clustered at 0 on the y-axis and others spread out above. (d) Residuals vs. linear predictor: this plot shows some pattern, with residuals seeming to decrease as the linear predictor increases, suggesting there might be some non-linarity in the relationship that the model hasn’t fully captured.



doi:10.6342/NTU202403023

Appendix 10. (a) The normal Q-Q plot: residuals of 25 data points for GLMM featuring urbanization gradient and species type as explanatory variables for pollinator density. (b) The normal Q-Q plot: residuals of 45 data points for GLMM featuring presence of heterospecific neighbor and species type as explanatory variables for pollinator density. (c) The relationship between fitted values and Pearson residuals from GLMM featuring urbanization gradient and species type as explanatory variables for pollinator density. (d) The relationship between fitted values and Pearson residuals from GLMM featuring presence of heterospecific neighbor and species type as explanatory variables for pollinator density. (e) The Q-Q plot for the random effect of GLMM featuring urbanization gradient and species type as explanatory variables for pollinator density. (f) The Q-Q plot for the random effect of GLMM featuring presence of heterospecific neighbor and species type as explanatory variables for pollinator density.



Appendix 11. Diagnostic plots for GAMM treating conspecific and heterospecific capitulum density as smooth term, species type as fixed effect, and sites as random effect for pollinator density. (a) Normal Q-Q plot: the points deviate from the theoretical straight line, suggesting the residuals are not perfectly normally distributed. (b) Histogram of residuals: the histogram is somewhat right-skewed. (c) Response vs. fitted values: this plot shows a positive relationship between fitted values and response, and a cluster of points at the lower end of fitted values suggest the model might be struggling to differentiate among lower responses. (d) Residuals vs. linear predictor: this plot shows some pattern. The spread of residuals in not entirely consistent across the range of the linear predictor, suggesting some heteroscedasticity.

Appendix 12. The 45 data points for SEM. ‘Con’ and ‘Het’ indicate the mean values of conspecific and heterospecific capitulum density per quadrat from mature capitula collection and pollinator survey. ‘Pre’ indicates pre-dispersal seed predation rate per quadrat. We treated categorical data, including species type (native=0/exotic=1), and quadrat type (pure=0/mixed=1) as numerical data to perform piecewise SEM.

Site name	impervious surface ratio	Species type	Quadrat type	Pollinator density	Con	Het	Pre	Female floret ratio
228PP	0.95	1	0	0.00	14.0	7.9	0.17	0.32
BHP	0.58	1	0	0.17	23.0	8.1	0.00	0.36
DA	0.72	1	0	0.20	26.0	8.3	0.00	0.25
HST	0.13	1	0	0.06	26.0	8.5	0.00	0.29
JMST	0.41	1	0	1.00	45.0	8.7	0.10	0.26
MLSH	0.91	1	0	0.00	15.5	8.9	0.33	0.24
NGP	0.68	1	0	0.11	11.0	9.1	0.20	0.23
NSEC	0.83	1	0	0.00	19.5	9.4	0.00	0.29
NTU	0.88	1	0	0.00	28.0	9.6	0.00	0.25
RXG	0.95	1	0	0.00	5.0	9.9	0.00	0.26
YP	0.74	1	0	0.29	38.5	10.2	0.00	0.18
228PP	0.95	1	1	0.20	9.0	10.5	0.67	0.29
BHP	0.58	1	1	0.00	26.5	10.2	0.33	0.32
CLSH	0.99	1	1	0.00	8.0	10.0	0.00	0.28
DA	0.72	1	1	0.33	14.0	10.2	0.33	0.25
HST	0.13	1	1	0.00	23.5	10.1	0.25	0.29
JMST	0.41	1	1	0.00	25.0	9.9	0.00	0.25
MLSH	0.91	1	1	0.60	17.5	9.5	0.33	0.42
NGP	0.68	1	1	1.00	22.0	9.1	0.80	0.63
NSEC	0.83	1	1	0.25	19.5	9.1	0.33	0.19
NTU	0.88	1	1	0.00	13.0	9.0	0.33	0.35
YP	0.74	1	1	0.17	34.5	8.9	0.00	0.10
228PP	0.95	0	0	0.00	15.5	8.7	0.11	0.20
BHP	0.58	0	0	0.06	16.5	9.1	0.20	0.11
DA	0.72	0	0	0.23	10.5	9.6	0.00	0.13
HST	0.13	0	0	0.00	8.0	10.1	0.00	0.31
JMST	0.41	0	0	0.08	9.5	10.6	0.10	0.23
MLSH	0.91	0	0	0.00	22.0	11.2	0.00	0.26
NGP	0.68	0	0	0.00	12.0	11.8	0.00	0.21
NSEC	0.83	0	0	0.19	10.5	12.6	0.00	0.16
NTU	0.88	0	0	0.00	7.5	13.4	0.13	0.09
RXG	0.95	0	0	0.04	5.0	14.4	0.00	0.30
XSP	0.76	0	0	0.19	9.5	15.5	0.00	0.08
YP	0.74	0	0	0.14	7.5	16.8	0.33	0.09
228PP	0.95	0	1	0.20	19.0	18.3	0.67	0.10
BHP	0.58	0	1	0.38	17.5	19.2	0.00	0.07
CLSH	0.99	0	1	0.00	4.5	18.4	0.00	0.12
DA	0.72	0	1	0.00	11.0	19.7	0.00	0.18
HST	0.13	0	1	0.00	15.5	19.8	0.25	0.34
JMST	0.41	0	1	0.00	22.0	19.2	0.00	0.15
MLSH	0.91	0	1	0.20	19.5	18.0	0.67	0.25
NGP	0.68	0	1	0.00	9.5	18.1	0.40	0.32
NSEC	0.83	0	1	0.00	14.0	18.5	0.00	0.21
NTU	0.88	0	1	0.00	14.5	23.8	0.00	0.07
YP	0.74	0	1	0.00	11.5	34.5	0.00	0.05

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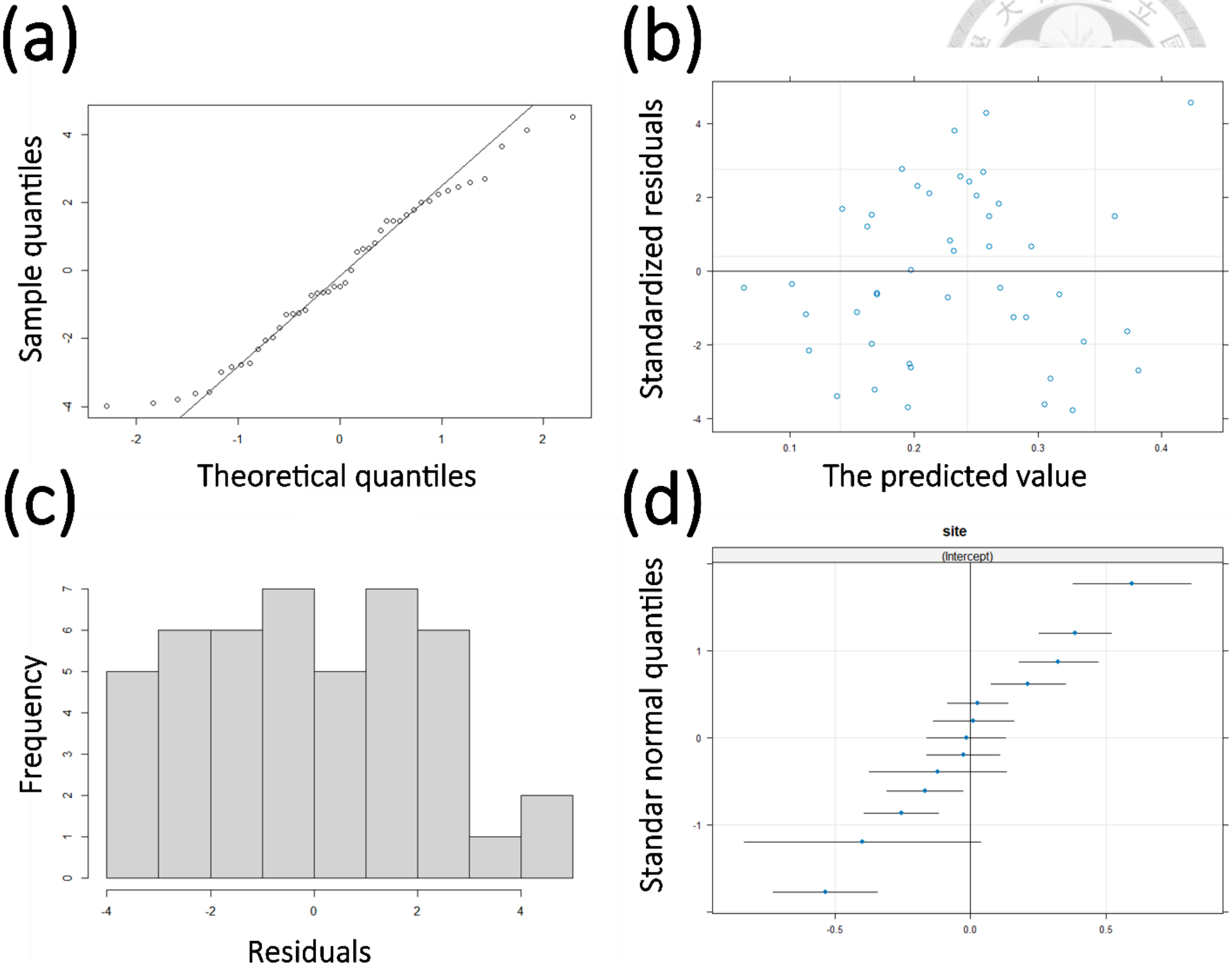
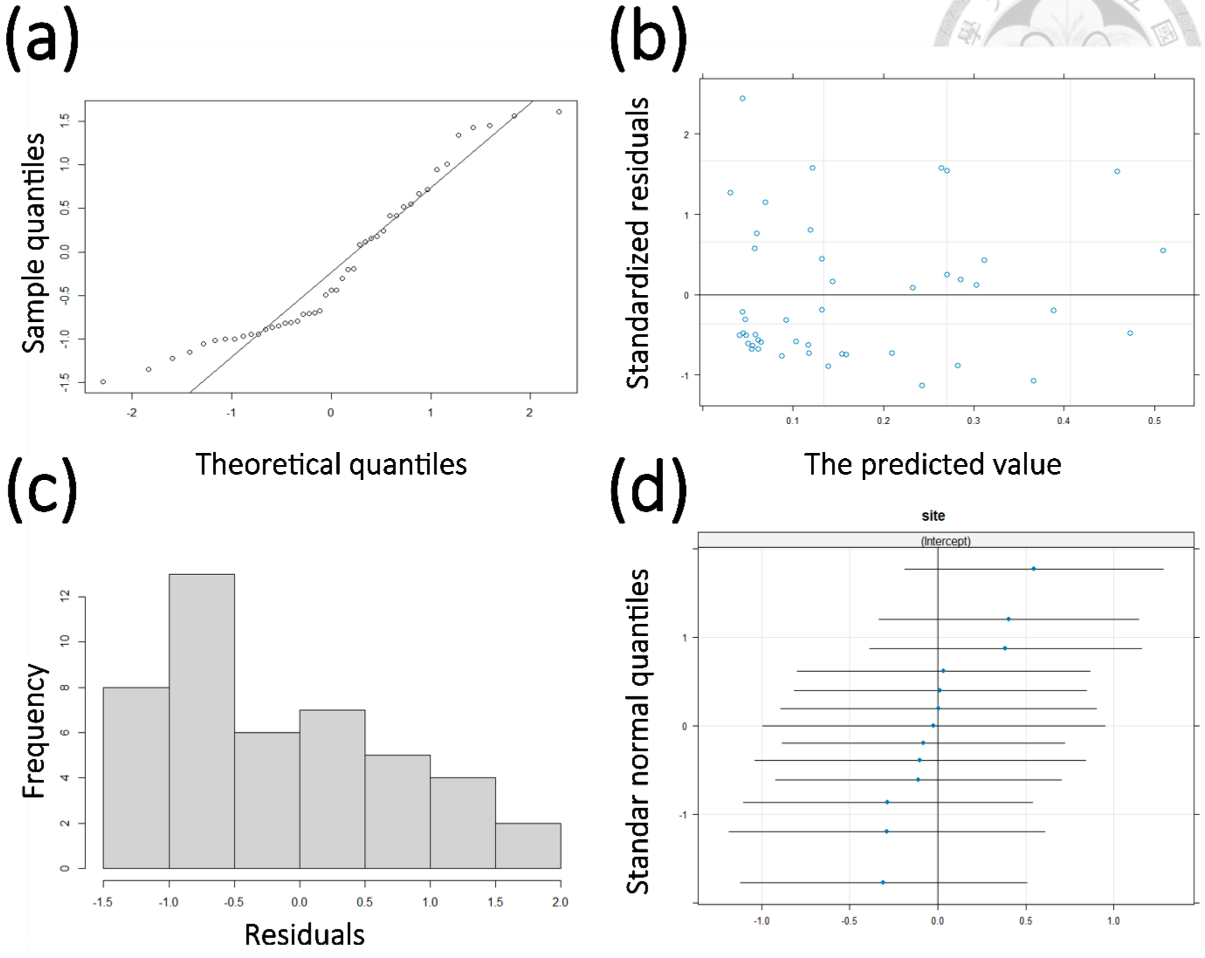
Appendix 13. Multicollinearity and overdispersion examination results of models fitted in SEM. There is no obvious multicollinearity found in each model, and there is a significant overdispersion in the GLMM of female floret ratio.

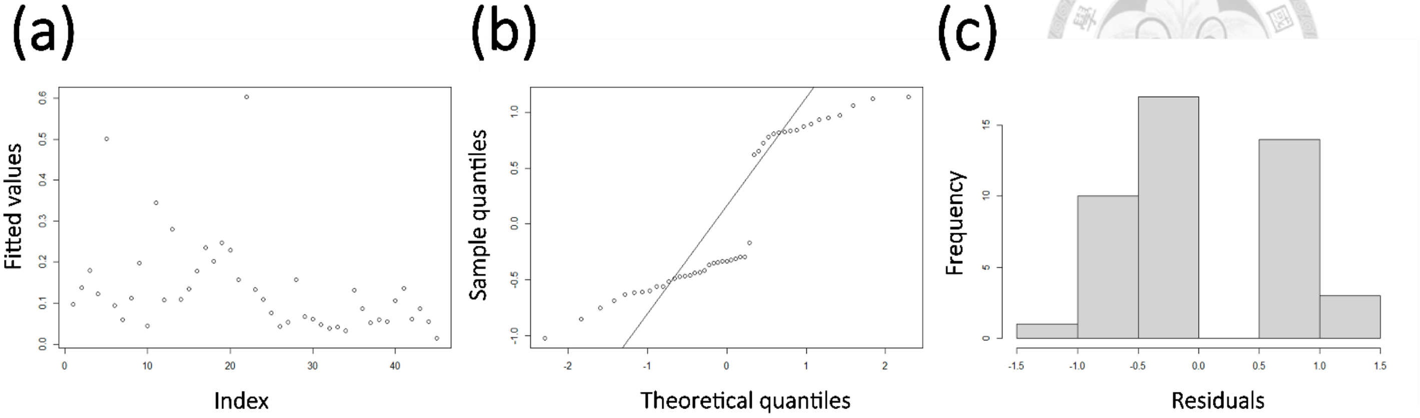
Model	**VIF values**	x^2	**ratio**	**rdf**	***p***
Female floret ratio					
Pre-dispersal seed predation rate	1.805	225.8	5.943	38	**<0.001***
Pollinator density	1.306				
Species type	2.411				
Quadrat type	2.641				
Heterospecific capitulum density	3.199				
Pre-dispersal seed predation rate					
Species type	3.325	32.4	0.853	38	0.725
Quadrat type	1.851				
Impervious surface ratio	1.114				
Conspecific capitulum density	1.381				
Heterospecific capitulum density	3.535				
Pollinator density					
Species type	3.162	9.328	0.239	39	1.000
Quadrat type	1.496				
Impervious surface ratio	1.170				
Conspecific capitulum density	1.636				
Heterospecific capitulum density	2.880				



Appendix 14. Diagnostic plot for GLMM for female floret ratio fitted in SEM. (a) The normal Q-Q plot: points fall close to the diagonal line, indicating the residuals are approximately normally distributed. (b) standardized residuals vs. the predicted values: the residuals are scattered fairly evenly around zero line. (c) histogram of residuals: overall it approximates a normal distribution (W=0.970, *p*=0.280, Shapiro-Wilk normality test). (d) random effects plot: the variation in random effects suggests that accounting for site-specific differences was important.



Appendix 15. Diagnostic plot for GLMM for pre-dispersal seed predation fitted in SEM. (a) the normal Q-Q plot: points deviate from the diagonal line, especially at the tails. (b) standardized residuals vs. the predicted value: there's no clear pattern or trend in the residuals across fitted values. (c) histogram of residuals: the residuals are somewhat left-skewed (W=0.916, *p*=0.003, Shapiro-Wilk normality test). (d) random effects plot: most sites have confidence intervals crossing zero, indicating their effects may not be significantly different from the overall mean.



Appendix 16. Diagnostic plot for GLM for pollinator density fitted in SEM. (a) fitted values plot: there's a cluster of lower fitted values (below 0.2) and some scattered higher values. (b) the normal Q-Q plot: there's a clear S-shaped pattern, which confirms the non-normality of residuals. (c) histogram of residuals: the distribution of residuals is bimodal, with two distinct peaks.