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The impact of a native dominant plant, *Euphorbia jolkinii*, on plant-flower visitor networks and pollen deposition on stigmas of co-flowering species in sub-alpine meadows of Shangri-La, SW China

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ABSTRACT

1. Anthropogenic activity can modify the distribution of species abundance in a community leading to the appearance of new dominant species. While many studies report that an alien plant species which becomes increasingly dominant can change species composition, plant-pollinator network structure and the reproductive output of native plant species, much less is known about native plant species which become dominant in their communities.

2. *Euphorbia jolkinii* Boissier (*Euphorbia*, hereafter) has become a dominant native plant in the over-grazed meadows of Shangri-La, SW China. During the flowering season of *Euphorbia* and over two years, we quantified the impact of *Euphorbia* on plant richness and flower visitor richness in 12 sub-alpine meadows along a gradient of *Euphorbia* dominance. We also evaluated the floral preferences of flower visitors, interaction evenness of plant-flower visitor networks, and the deposition of pollen on the stigmas of two co-flowering plant species (*Gentiana chungtienensis* and *Anemone rupestris*) in each meadow.

3. The species richness of flower visitors to non-*Euphorbia* plants was negatively correlated with *Euphorbia* dominance. As the proportion of *Euphorbia* increases, flower visitors to *Euphorbia* decreased, while flower visitors to other co-flowering plants increased. Interaction evenness decreased as the proportion of *Euphorbia* increased. Furthermore, the conspecific pollen deposition of one of the two co-flowering plant species studied, *G. chungtienensis*, decreased as the proportion of *Euphorbia* increased.

4. *Synthesis*. There appears to be little substantive difference between the impact of a newly dominant native plant and the impacts reported for many alien plants on native plant-pollinator communities. This suggests that dominance, in addition to plant origin (alien versus native), could play an important role in influencing the structure and functioning of native communities. This finding has considerable implications for restoration ecology.

Thus, communities where natural dominance order has been changed due to anthropogenic activity may not be considered a problem as all the species are native - in

reality though, they may be as damaged as communities invaded by alien species.

Key words: *Euphorbia*, interaction evenness, livestock grazing, mutualistic networks, newly dominant native plants, pollen deposition

INTRODUCTION

Most ecological communities have skewed species distributions, where there are a few dominant species and many rare species (McGill et al., 2007). Anthropogenic activity can modify the distribution of species abundance in a community leading to new dominant species appearing in the community (Goulson, 2003; Albrecht, Padrón, Bartomeus, & Traveset, 2014; Magrath et al., 2018). Changes in the dominant species can affect ecosystem function (Winfree, Fox, Williams, Reilly, & Cariveau, 2015; Lohbeck, Bongers, Martinez-Ramos, & Poorter, 2016), for example new dominant plants can influence soil structure (Weidenhamer & Callaway, 2010), river drainage (van Oorschot et al., 2017) and species interactions (Traveset & Richardson, 2014). There can be indirect interactions too, for example newly dominant, animal-pollinated plants can affect other plants indirectly via shared pollinators, especially if they are super-generalists, i.e. they interact with numerous pollinator species (Albrecht, Padrón, Bartomeus, & Traveset, 2014; Russo, Memmott, Montoya, Shea, & Buckley, 2014). Thus, newly dominant plants in a community can potentially affect ecological and evolutionary dynamics via changes in plant reproduction.

A network of interactions approach provides a community-wide context for understanding how newly dominant plants influence the diversity of species and interactions (Stouffer, Cirtwill, & Bascompte, 2014; Stout & Tiedeken, 2017). Previous studies showed that alien dominant super-generalised plant species can have negative (Moroñ et al., 2009), positive (Lopezaraiza-Mikel, Hayes, Whalley, & Memmott, 2007) or neutral (Bartomeus, Vilà, & Santamaría, 2008) effects on native pollinators. New dominant plants can also result in the rearrangement of interactions among species, with new dominant species appropriating generalised pollinator species from other native plants (Aizen, Morales, & Morales, 2008; Traveset & Richardson, 2014), which could have a large influence on the interaction evenness of pollination networks (Kaiser-Bunbury, Valentin, Mougai, Matatiken, & Ghazoul,

2011; Magrach et al., 2018). These newly dominant plants could affect pollination and reproductive success of other co-flowering species via changes in the quantity and quality of pollen deposition on stigmas as a result of changes in shared pollinator abundance or changes in their behaviour (Moeller, 2004).

While most attention has focused on alien plants and their impact on native communities (e.g. Lopezaraiza-Mikel, Hayes, Whalley, & Memmott, 2007; Bartomeus, Vilà, & Santamaría, 2008; Morales & Traveset, 2009; Holzschuh, Dormann, Tschardtke, & Steffan-Dewenter, 2011; Gibson, Pauw, & Richardson, 2013), human activity can also trigger large increases in some native species (Nackley, West, Skowno, & Bond, 2017). However, considerably less attention has been given to studying these newly dominant native plant species (Pivello, Vieira, Grombone-Guaratini, & Matos, 2018). This is in part due to the assumption that native species are harmless, however, some dominant native species can cause considerable changes to co-occurring native species and ecosystems (Simberloff, Souza, Nuñez, Barrios-Garcia, & Bunn, 2012; Nackley, West, Skowno, & Bond, 2017). It is therefore important to study the causes and consequences of dominant native plants and interesting to compare their impact to that of alien plants.

Livestock grazing is the most widespread human activity and the dominant land use in the world's agricultural lands (Robinson et al., 2014). The selective foraging by livestock can lead to a dramatic increase in the dominance of unpalatable native plants (Grant et al., 1985). Although numerous studies document the effects of dominant unpalatable plants on the abiotic environment (e.g. Kleijn & Müller-Schärer, 2006), plant-plant interactions (e.g. Heckel, Bourg, McShea, & Kalisz, 2010) and diversity of whole plant communities (e.g. Callaway, Kikodze, Chiboshvili, & Khetsuriani, 2005), their effects on plant-pollinator communities have

received much less attention. It is also unclear whether dominant native plants have similar effects to dominant alien plants on plant-pollinator interactions.

Euphorbia jolkinii Boissier (*Euphorbia*, hereafter) is toxic to livestock and has become a dominant native plant in the over-grazed meadows of Shangri-La, SW China. It has highly attractive flowers in high abundance and it is visited by a large number of pollinator species. To understand the effects of *Euphorbia* on the pollination communities, we studied the plant and flower visitor community along a gradient of *Euphorbia* dominance. There were four objectives to our study: 1) To test whether *Euphorbia* dominance is correlated with plant and flower visitor species richness. Due to the overall negative effects of newly dominant plants on species richness at the community level (Morales & Traveset, 2009), we predict that plant and flower visitor richness will decrease as *Euphorbia* increases in dominance. 2) To determine the floral preferences of flower visitors along the *Euphorbia* dominance gradient (i.e. deviations from a null model based on flower relative abundance). Our hypothesis is that *Euphorbia* will be avoided, while non-*Euphorbia* plants will be favoured as the dominance of *Euphorbia* increases. This is because flower visitors need a diverse diet (Goulson, 2000) and one dominated by *Euphorbia* does not provide this. As the dominance of *Euphorbia* increases, that of non-*Euphorbia* plants decreases and consequently any non-*Euphorbia* plants remaining in the plots will be visited more by pollinators. 3) To investigate how interaction evenness changes along the *Euphorbia* dominance gradient. We expect that the increase of *Euphorbia* dominance will be associated with a decrease in interaction evenness. This is based on previous research which reports that an increase in newly dominant plants can lead to a decrease in interaction evenness (Kaiser-Bunbury, Valentin, Mougai, Matatiken, & Ghazoul, 2011). 4) To test whether the conspecific stigma pollen deposition of two co-flowering native plant species is correlated with *Euphorbia* dominance. Given that the impact of dominant alien species on the pollination of natives is frequently reported to be competitive

(e.g. Morales & Traveset, 2009), we predict that conspecific pollen deposition will decrease with increasing *Euphorbia* dominance.

MATERIALS AND METHODS

Study sites

Our field sites were in sub-alpine meadows around Shangri-La county (27°50' N, 99°42' E, 3280-3400 m above sea level), Yunnan province, SW China (Figure 1), meadows which have been exposed to grazing by yaks (*Bos grunniens* Linnaeus) and pigs (*Sus scrofa domestica* Erxleben) for many years prior to this study. In meadows with a long history of heavy grazing, unpalatable plants have become common, in particular, *Euphorbia jolkinii* Boissier which is the focus of this study as it is the dominant unpalatable plant at our field sites. *Euphorbia* is a long-lived, perennial, native herb in this area with a mean height 56.56 ± 16.28 cm (mean + SD), with multiple branches (20 ± 12) and several yellow actinomorphic flowers (17 ± 3) at the terminal inflorescence of each branch. Our study sites consisted of 12 meadows along a gradient of *Euphorbia* dominance (here measured as the proportion of *Euphorbia* flowers to the total number of flowers) which ranged from 0% to 94% *Euphorbia* (Table S1 in supplementary material). The meadows were similar in terms of abiotic conditions (e.g. temperature, rainfall, and soil nutrients). The linear distance between pairs of meadows ranged from 1.0 km to 22.3 km.

Sampling flower visitors and their interactions with flowers

We selected a 50 m x 50 m plot within each of the 12 meadows for sampling flower visitors. *Euphorbia* flowered early May to early July, and flower visitor sampling took place during this time approximately every two weeks in 2017 and 2018. This resulted in four sampling rounds per meadow per year. Flower-visiting insects were sampled from 10:00 - 16:00 h on sunny days or during sunny periods on cloudy days. We collected flower visitors by walking along

three randomly placed transects 50 m in length and 2 m in width in each plot. For each sampling round, each transect was sampled at least twice in the morning (10:00 - 12:00), twice in the early afternoon (12:00 - 14:00), and twice in the late afternoon (14:00 - 16:00). The total sampling time was approximately 12 hours per site, per year. We collected all flower visitors individually using hand-nets and stored them in separate tubes filled with 95% ethanol. Only flower visitors that contacted plant reproductive organs or were foraging for nectar and/or pollen were classified as legitimate visitors and collected; the identity of the plant species visited was recorded for each floral visitor.

There are no field guides or taxonomic keys for the insects in Shangri-La, rather we identified the flower visitor specimens according to a combination of morphological and molecular techniques. The following groups were identified using morphology: bumblebees (7 species), hoverflies (65 species), beetles (51 species), and butterflies (14 species) (see Acknowledgements for taxonomic expertise). For the other groups (non-syrphid Diptera, non-bumblebee Hymenoptera, moths and Hemiptera), the mitochondrial cytochrome c oxidase 1 (CO1) gene was used to barcode each specimen. A single leg was removed from each specimen for DNA extraction and in total we sequenced CO1 gene for 1172 specimens. The molecular identification was conducted with the Barcode of Life Data Systems (BOLD; Ratnasingham & Hebert, 2007) and we used a match of 98-100% to assign a sequence record to a species. When the match between our specimen and the identified record in BOLD was between 95-98%, we recognized it as belonging to the same genus. When the match between our specimen and the identified record in BOLD was lower than 95%, we accepted a family classification. All specimens are preserved at the Kunming Institute of Botany, Chinese Academy of Sciences.

Floral abundance

Flower abundance of *Euphorbia* was estimated by using three 20 m x 2 m transects randomly placed at each plot in the flowering peak of *Euphorbia* (Figure 1). The number of branches with open flowers was recorded for each individual plant. We randomly selected inflorescences from 20 individual plants (i.e. 20 branches total from 20 individual plants) to count the number of open flowering units in each meadow. Flower abundance of the other plants was estimated by using nine 2 m x 1 m quadrats, which were placed at both ends and in the middle of each of the three transects (Figure 1). Different methods were used for *Euphorbia* and non-*Euphorbia* species as their distribution patterns were very different, specifically, the *Euphorbia* was clumped and could have been missed using a quadrat approach. The number of open flowering units produced by each species, excluding wind-pollinated grasses, inside the quadrats were recorded. Flowering units were defined as either individual flowers or whole inflorescences depending on species. For species with densely compact inflorescences (e.g. Asteraceae and Apiaceae) each inflorescence was counted as a single flowering unit (e.g. Lázaro, Nielsen, & Totland, 2010). The flower abundance of each species was defined as the number of open flowering units per square meter. The proportion of *Euphorbia* flowers in each site and year was calculated as the number of *Euphorbia* flowers per square meter divided by the total number of *Euphorbia* and non-*Euphorbia* flowers per square meter.

Plant-flower visitor networks

For each meadow and year, we built a matrix of interactions based on the total number of observed interaction events (i.e. the number of visits) between plant and flower visitor species. To detect changes in the network structure along the *Euphorbia* gradient, we calculated plant species richness, flower visitor species richness and interaction evenness, the latter using a quantitative measure of evenness of network interactions to measure the uniformity of the frequency of interactions in a network (Bersier, Banašek-Richter, & Cattin,

2002; Tylianakis, Tschardt, & Lewis, 2007).

We also performed these analyses after controlling for the varying number of individuals (for plant and flower visitor species richness analysis) or species (for the interaction evenness analysis) sampled across different meadows and years (Pellissier et al., 2018). We used the smallest network to derive a standardized value for plant species richness, flower visitor species richness and interaction evenness in each plot. Thus, for the larger networks, we randomly removed flower visitor individuals or species without replacement and recalculated each network metric. We repeated this procedure 1000 times and the mean of these values was used as a standardized value for each metric (Vanbergen et al., 2014; Lázaro et al., 2016).

We calculated all network-related metrics using the bipartite v 2.15 package (Dormann, Gruber, & Fründ, 2008) in R 4.0.2 (R Core Team, 2020).

Pollen deposition analysis

We evaluated the effects of *Euphorbia* on the conspecific pollen deposition of two co-flowering plant species (*Gentiana chungtienensis* and *Anemone rupestris*) which were present in all 12 meadows, by quantifying the number and proportion of conspecific pollen grains deposited on flower stigmas. *Gentiana chungtienensis* had tubular flowers, while *A. rupestris* had open flowers. Both plant species shared flower visitors with *Euphorbia* and may face strong competition from *Euphorbia*. Self-pollination of individual flowers for both species can likely be avoided through temporal or spatial separation of male and female reproductive structures (personal observations). In addition, geitonogamy may also be largely avoided by the low flower display of the two species (mean \pm sd: *G. chungtienensis*, 1.13 ± 0.44 flowers per plant; *A. rupestris*, 1.35 ± 0.63 flowers per plant). We selected 20-40 individuals of *G.*

chungtienensis (mean \pm SD = 30.1 \pm 8.8) and 10-22 individuals for *A. rupestris* (13.9 \pm 4.16) per meadow, per year, and then selected a senescent flower (i.e. a wilting flower with enlarged ovaries) from each individual plant each year, which was stored in 70% ethanol until processing (Tur, Saez, Traveset, & Aizen, 2016).

In the lab, we removed and attached each stigma to a scanning electron microscope stub with the receptive surface upward. After drying at room temperature for 48 h the stigma samples were viewed under a scanning electron microscope and the number of conspecific and heterospecific pollen grains on each stigma were counted. Conspecific pollen grains were identified by comparison to a reference library of pollen from the field site, heterospecific pollen grains were not identified due to time constraints. There were other Ranunculaceae (4 species) and Gentianaceae (1 species) in flower at our study sites. While misidentification of pollen grains is a possibility because the pollen of related species cannot not be distinguished by morphology, the risk of this is low because the related species are all rare.

Statistical analysis

Objective 1: To test whether Euphorbia dominance is correlated with plant and flower visitor species richness in the networks.

We used generalised linear mixed-effects models (GLMMs) to test the effects of *Euphorbia* dominance on the observed and rarefied non-*Euphorbia* plant richness, flower visitor richness of *Euphorbia*, flower visitor richness of non-*Euphorbia* plants, the proportion of flower visitor species unique to *Euphorbia*, and the proportion of flower visitor species unique to non-*Euphorbia* plants. The GLMMs included the linear and quadratic terms of the proportion of *Euphorbia* flowers, a two-level factor for year (2017 or 2018), and distance to forest (i.e. the distance between each site and its nearest forest) as fixed effects, and site as a random factor to account for non-independence of the repeated surveys carried out across two years.

We used a quadratic term in each model to explore whether there is a hump-shaped relationship between *Euphorbia* dominance and each of the response variable based on the intermediate disturbance hypothesis (Grime, 1973). We included year in the model as a fixed rather than a random effect as two levels are insufficient to estimate the variance of random effects reliably (around five levels is recommended as a minimum; Gelman & Hill, 2007). We used distance to forest as a factor because research has previously shown forest proximity can affect pollination networks (Sritongchuay, Hughes, Memmott, & Bumrungsri, 2019). Species richness was analysed with a Poisson error distribution. The proportion data was analysed with a binomial error distribution, with the exception of rarefied proportion of flower visitor species unique to *Euphorbia*, which was fitted with a negative binomial error to control for data overdispersion (Zuur, Leno, Walker, Saveliev, & Smith, 2009).

Objective 2: To determine the floral preferences of flower visitors along the Euphorbia dominance gradient.

We used the resource selection null model in the R package *econullnet* v 0.2.0 (Vaughan et al., 2018) to identify whether the flowers of each plant species were visited more or less frequently than expected based on their abundance. We ran the null model twice, first treating all pollinators as a single taxon to calculate the overall attractiveness of each plant species to all flower visitors combined, and secondly considering pollinator species separately to examine their individual preferences. The null model assumes that the probability of a plant species being visited by flower visitors is in proportion to its abundance. The non-*Euphorbia* species in 675 of the plant-visitor interactions (4.3% of the total interactions) had no flower abundance data, due to being rare and not found in the quadrats sampled. For these species, we assumed a minimal abundance of 0.001 flowers per square meter (i.e. less than 1 flower in the 18 square meters sampled in each plot), in order to include their interactions in the analyses.

To assess whether *Euphorbia* dominance influenced the links between species which were more or less frequent than expected based on flower abundance (binary response variables: 1 to represent yes and 0 to represent no), GLMMs were fitted with binomial error distribution and logit link function, doing this for *Euphorbia* and non-*Euphorbia* species separately. All models included the linear and quadratic terms of the proportion of *Euphorbia* flowers, year, and distance to forest as fixed effects, and site and the identity of plant-flower visitor links as crossed random effects. To control for potential external confounding factors, we also included flower visitor richness and flower visitor abundance of the community as fixed effects. None of the GLMMs were overdispersed.

Objective 3: To investigate how interaction evenness changes along the Euphorbia dominance gradient.

We used LMMs to analyse the effects of *Euphorbia* on the observed and rarefied interaction evenness of plant-flower visitor networks. All models included the linear and quadratic terms of proportion of *Euphorbia* flowers, year, and distance to forest as fixed effects, and site as a random factor.

Objective 4: To test whether the conspecific stigma pollen deposition of two co-flowering native plant species is correlated with Euphorbia dominance.

To estimate the effects of *Euphorbia* dominance on pollen deposition on stigmas, we first fitted negative binomial GLMMs separately for each study species with the number of conspecific pollen grains (i.e. the quantity of pollinator service) as response variable; this error distribution being used to control data overdispersion (Zuur, Leno, Walker, Saveliev, & Smith, 2009). In both models the linear and quadratic terms of the proportion of *Euphorbia* flowers, year and distance to forest were included as fixed effects. To control for potential confounding

factors, we also included flower abundance, flower visitor richness and flower visitor abundance of each plant species as fixed effects. Site was included as a random factor for *G. chungtienensis*, while flower identity nested within site was included as a random factor for *A. rupestris*. For *G. chungtienensis* we then fitted a binomial GLMM with the proportion of conspecific pollen (i.e. the quality of pollinator service) as response variable. This model included the linear and quadratic terms of the proportion of *Euphorbia* flowers, year, and distance to forest as fixed effects, and site as a random factor. This analysis was not used on *A. rupestris* as its stigmas had very few heterospecific pollen grains (mean percentage of conspecific pollen \pm SD = 99.6% \pm 0.5%).

To avoid collinearity between linear and quadratic terms of the proportion of *Euphorbia* flowers, we first scaled the proportion of *Euphorbia* flowers and then calculated its quadratic term (Lázaro et al., 2016). Prior to each analysis, we used variance inflation factors (VIF) to check for collinearity among our explanatory variables. A VIF for each fixed factor (< 5) indicates no severe multicollinearity (Quinn & Keough, 2002). We simplified maximal models by removing non-significant fixed terms ($P > 0.05$) to obtain a minimum adequate model (Crawley, 2012). We investigated the spatial dependency of the residuals of our minimum adequate models using Moran's I statistic since spatially autocorrelated data violates the assumption of independence of statistical models (Dormann et al., 2007). We found that none model residuals had a significant spatial autocorrelation ($P > 0.05$). The significance of fixed effects for each GLMM and LMM was tested by comparing the full model with models that excluded only the specific predictor by means of likelihood ratio tests (Zuur, Leno, Walker, Saveliev, & Smith, 2009). All analyses were carried out in R (R Core Team, 2020), using the *lmer*, *glmer*, and *glmer.nb* function of lme4 v 1.1-23 package for mixed effects model analyses (Bates, Mächler, Bolker, & Walker, 2015), the *moran.test* function of spdep v 1.1-5 package for spatial autocorrelation analyses (Bivand et al., 2020), and the *visreg* function of visreg v

2.7.0 package for visualization of predictor effects (Breheny & Burchett, 2017).

RESULTS

In total we sampled 15,768 interactions among 52 plant species and 464 flower visitor species in the 12 meadows over the two years of sampling; the number of interactions, flower visitor species, and plant species, per meadow, per year are shown in Table S1. Most flower visitors were Diptera (40.8%), followed by Hymenoptera (32.6%), Coleoptera (16.0%), and Lepidoptera (5.5%) (Figure S1).

Objective 1: To test whether *Euphorbia* dominance is correlated with plant and flower visitor species richness in the networks.

Non-*Euphorbia* plant species richness did not show any systematic change along the *Euphorbia* gradient (Table 1; Table S1). *Euphorbia* flower visitor richness tended to be highest at intermediate *Euphorbia* dominance sites, but the effect was non-significant (Figure 2a; Table 1), while non-*Euphorbia* flower visitor richness decreased significantly with increasing *Euphorbia* dominance (Figure 2b; Table 1). Non-*Euphorbia* flower visitor richness decreased significantly as the distance between the study sites and their nearest forest increased (Table 1). The proportion of visitor species unique to *Euphorbia* increased significantly as *Euphorbia* dominance increased (Figure 2c; Table 1), while the proportion of visitor species unique to non-*Euphorbia* plant species decreased significantly with increasing *Euphorbia* dominance (Figure 2d; Table 1). These patterns were maintained in analyses based on the rarefied data to account for differences in sample size, with the exception of the relationship between the rarefied proportion of visitor species unique to *Euphorbia* and *Euphorbia* dominance which was no longer significant (Table S2).

Objective 2: To determine the floral preferences of flower visitors along the *Euphorbia* dominance gradient.

Euphorbia was visited more than expected according to its abundance when at low abundance and it was visited less than expected where its abundance was high (Figure S2). Forty-seven percent ($n = 24$) of the non-*Euphorbia* plant species were visited more frequently than expected in all the sites in which they occurred (Figure S2). However, visitation depended upon the proportion of *Euphorbia*, in particular, *Gentiana chungtienensis*, *Potentilla centigra*, *P. lineata*, and *Ranunculus tanguticus* were favoured when the proportion of *Euphorbia* was high (Figure S2).

For *Euphorbia*'s links with visitors, $8.5\% \pm 7.3\%$ were more frequent than expected based on flower abundance, while $8.6\% \pm 5.0\%$ were less frequent than expected based on flower abundance. For non-*Euphorbia* plant links with visitors, $61.5\% \pm 12.6\%$ were stronger than expected, while only $0.7\% \pm 1.0\%$ were weaker than expected. The proportion of stronger links between flower visitor and *Euphorbia* decreased (Figure 3a; Table 2), while the proportion of weaker links of *Euphorbia* increased along the *Euphorbia* dominance gradient (Figure 3b; Table 2). At the same time, the proportion of stronger links of non-*Euphorbia* plants was lowest at intermediate *Euphorbia* dominance sites (Figure 3c; Table 2), while the proportion of weaker links of non-*Euphorbia* plants decreased with the increase of *Euphorbia* dominance (Figure 3d; Table 2). Thus, as *Euphorbia* becomes less visited as it becomes more abundant, the visits to other plant species increase.

Objective 3: To investigate how interaction evenness changes along the *Euphorbia* dominance gradient.

The interaction evenness of plant-flower visitor networks decreased significantly as the proportion of *Euphorbia* increased (Figure 4a; Table 3). A similar pattern was observed in

analyses based on the rarefied data (Figure 4b; Table 3).

Objective 4: To test whether the conspecific stigma pollen deposition of two co-flowering native plant species is correlated with *Euphorbia* dominance.

For *G. chungtienensis*, we counted a total of 81,052 pollen grains on 722 stigmas (from 722 flowers) from the 12 meadows, 89.4% of which were conspecific and 10.6% of which were heterospecific. The number of conspecific pollen grains on stigmas was highest at sites with intermediate *Euphorbia* dominance (Figure 5a; Table 4). The proportion of conspecific pollen grains on stigmas decreased significantly as *Euphorbia* dominance increased (Figure 5b; Table 4). In addition, the proportion of conspecific pollen of *G. chungtienensis* was correlated positively with its flower visitor abundance (Table 4).

For *A. rupestris*, we counted a total of 82,807 pollen grains on 5436 stigmas (from 333 flowers) from the 12 meadows, 99.4% of which were conspecific and 0.6% of which were heterospecific. The number of conspecific pollen grains on the stigmas did not change significantly along the *Euphorbia* dominance gradient and did not relate to its flower abundance or its flower visitor abundance (Table 4).

DISCUSSION

Our study shows that the structure of our plant-flower visitor networks changes as a native species of plant becomes increasingly dominant. Thus, pollinator preferences changed, interaction evenness decreased with increasing *Euphorbia* dominance and the number of conspecific pollen grains on stigmas decreased in one of our two focal species. These changes provide some insights into how dominant plants influence plant-flower visitor interactions. In what follows we first consider the limitations of our approach and then consider our results in the context of the wider literature and habitat management.

Limitations

There are three main limitations to our approach. First, our focus on the *Euphorbia* flowering period means that we did not investigate the post-flowering effects of *Euphorbia* on plant-flower visitor interactions. The influence of a dominant plant on pollination networks can continue after its flowering period as seen. For example, abundant and generalist pollinator species may transfer from a mass-flowering plant after flowering finishes, leading to an increase in the interaction evenness of the overall pollination network (e.g. Magrath et al., 2018). Second, while we studied the effects of *Euphorbia* on the deposition of pollen on the stigmas of two co-flowering native species, we do not have data on seed set or recruitment. While stigma pollen deposition can affect seed production (e.g. Larson, Royer, & Royer, 2006; Briggs et al., 2015), it doesn't always (e.g. Ferrero et al., 2013), and to truly understand the impact of *Euphorbia* on the population dynamics of co-occurring plants, it would be ideal to estimate reproductive success using more direct measures, such as seed set (e.g. Kaiser-Bunbury, Valentin, Mougai, Matatiken, & Ghazoul, 2011) and plant recruitment (e.g. Fontaine, Dajoz, Meriguet, & Loreau, 2006). Finally, it was not always possible to confidently differentiate the pollen of *A. rupestris* from other Ranunculaceae at the field site; that said no change in the proportion of conspecific pollen was seen in this species along the *Euphorbia* dominance gradient. In contrast, the Gentian pollen was straightforward to differentiate from other pollens and it was this species which showed changes in the proportion of conspecific pollen as *Euphorbia* dominance increased.

The impact of *Euphorbia* on other native plant species

Contrary to expectation, non-*Euphorbia* plant richness did not show any systematic change as *Euphorbia* dominance increased, suggesting that the decrease in the flower abundance of non-*Euphorbia* plants has not caused a local extinction of these species. The insect visitor

richness of non-*Euphorbia* plants decreased with increasing *Euphorbia* dominance though. This probably due, at least in part, to *Euphorbia* appropriating some specialised flower visitors from non-*Euphorbia* plants. We did find that the proportion of unique flower visitors of non-*Euphorbia* plants decreased as the proportion of *Euphorbia* increased. The effects of *Euphorbia* dominance on flower visitor richness of co-flowering plants are in line with the results found for alien plants, which have been reported to appropriate pollinator species, but mainly generalised ones, from other native plants (Aizen, Morales, & Morales, 2008; Traveset & Richardson, 2014).

Euphorbia tended to be preferred by flower visitors when at low abundance but tended to be avoided when at high abundance. The explanation to this likely lies in the insects need for a diverse diet and the fact that the different plant species provide different nutritional needs (Goulson, 2000). Thus, once *Euphorbia* has provided these needs it is no longer visited, and this leads to the observed decrease in visitation as its dominance increases.

The impact of *Euphorbia* dominance on network structure

In line with our prediction, interaction evenness decreased as the proportion of *Euphorbia* increased. This suggests that interaction frequency of plant-flower visitor networks became more heterogeneous with the increase in dominance of *Euphorbia*. The interaction evenness of pollination networks has been shown to decline with the dominance of alien plants (Aizen, Morales, & Morales, 2008; Kaiser-Bunbury, Valentin, Mougai, Matatiken, & Ghazoul, 2011; Magrath et al., 2018), suggesting that native and alien dominant plants can have similar effects on mutualistic networks. Natural habitats tend to have many moderate-strength interactions (Tylianakis, Tschardtke, & Lewis, 2007) and the rearrangement of interactions caused by new dominant super-generalised plants can erode this balance (Aizen, Morales, & Morales, 2008).

The impact of *Euphorbia* on pollen deposition in co-flowering native species

A change in pollinator richness, visitation rate and/or foraging behaviour due to the disturbances is likely to have an effect either on the number or quality of pollen deposition on stigma and thus may have consequences for overall plant success (Vázquez & Simberloff, 2004). A recent meta-analysis demonstrated that invasive plants could have both negative and positive effects on reproductive success of co-flowering native species (Charlebois & Sargent, 2017). We found that both the number and proportion of conspecific pollen on stigmas of *G. chungtienensis* decreased with the increasing *Euphorbia*, indicating that *Euphorbia* might have negative effects on the quality and quantity of pollination services for this species if it is pollen limited or vulnerable to heterospecific pollen deposition. This effect is likely to be due to the reduced visitation rates due to the strong competition with *Euphorbia*. Moreover, our results showed that lower flower visitor abundance was related to lower deposition of conspecific pollen grains. *Gentiana chungtienensis* was visited by a higher proportion of bees compared to flies in low *Euphorbia* dominance communities (Figure S1). Bees carry more pollen grains than flies (Orford, Vaughan, & Memmott, 2015) and show high flower constancy (Waser, 1986), which may help explain why there were more conspecific pollen grains on stigmas in communities with a low proportion of *Euphorbia*.

It is striking that although *A. rupestris* has open flowers, more than 99% of the pollen deposited on its stigmas was conspecific in both the high and low *Euphorbia* dominance communities. Our previous study found that open flowers reduce the overlap in visitation in plant species with which they share pollinators in sub-alpine meadows of Yulong Mountain, SW China (Zhao et al., 2016). Thus, plant species with open flowers may have adaptations to avoid pollen interference by interacting with specific pollinators. Unlike *G. chungtienensis*, there was no evidence of a change in the number of pollen grains deposited on *A. rupestris* flowers along the *Euphorbia* dominance gradient. This suggests that although total visitation

of this species might be reduced in high *Euphorbia* dominant communities, pollen deposition is maintained by specialist pollinators which show higher flower constancy (Stavert et al., 2019).

CONCLUSIONS

In terms of impacts on co-flowering, native species and plant-flower visitor networks, there is potentially less functional difference between dominant native and alien plants than previously thought. Thus, our dominant native species, *Euphorbia jolkinii*, showed many of the impacts that are associated with a dominant alien plant species. This suggests that it might be dominance, rather than plant origin (alien versus native), can play an important role in influencing the structure and functioning of native communities. Therefore, the restoration approaches used for alien-dominant communities, such as species translocations (Bullock, 1998) and the eradication of invasive species (Kaiser-Bunbury et al., 2017), could also be very relevant for habitat restoration schemes for communities which have become dominated by a native plant species. Moreover, focusing on alien plants in restoration schemes, while understandable, could be misguided in some cases as it is possible that native plants could have at least as large an effect on the community.

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AUTHORS' CONTRIBUTIONS

HW, DZL and YHZ conceived the ideas and designed methodology; YHZ, XX and WJW collected the data; YHZ, JM, IPV and HDL analysed the data; YHZ and JM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data archived in Dryad.

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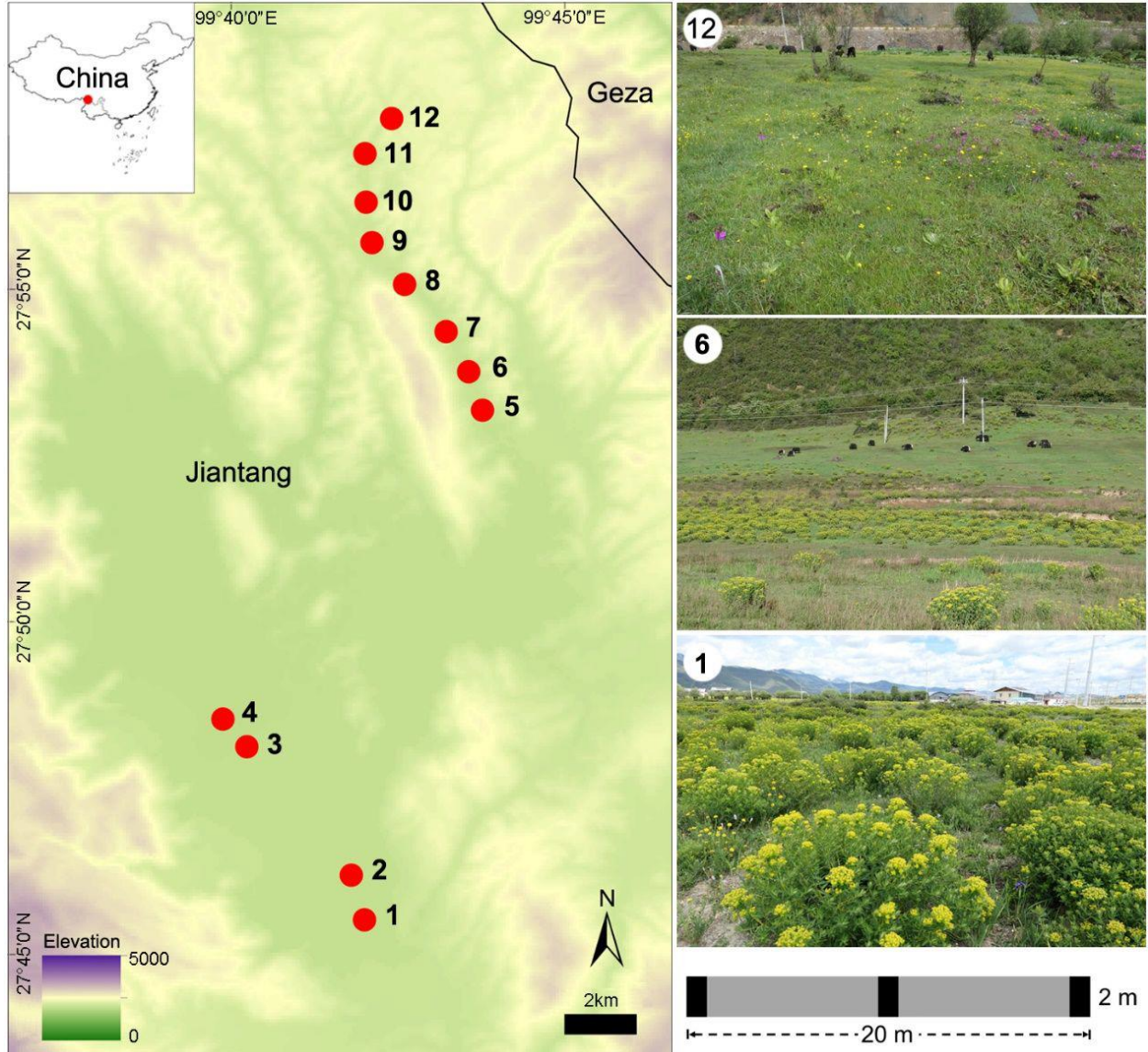


Figure 1. Location of the study plots (left) and photographs of three of the meadows (right) in Shangri-La, SW China. The tallest and most dominant herbaceous plant species in meadows 1 and 6 is *Euphorbia jolkinii*. The lower right figure shows a 20 m x 2 m transect used to estimate *Euphorbia* flower abundance and the three 2 m x 1 m quadrats placed within it, which were used to estimate the flower abundance of other co-flowering plants.

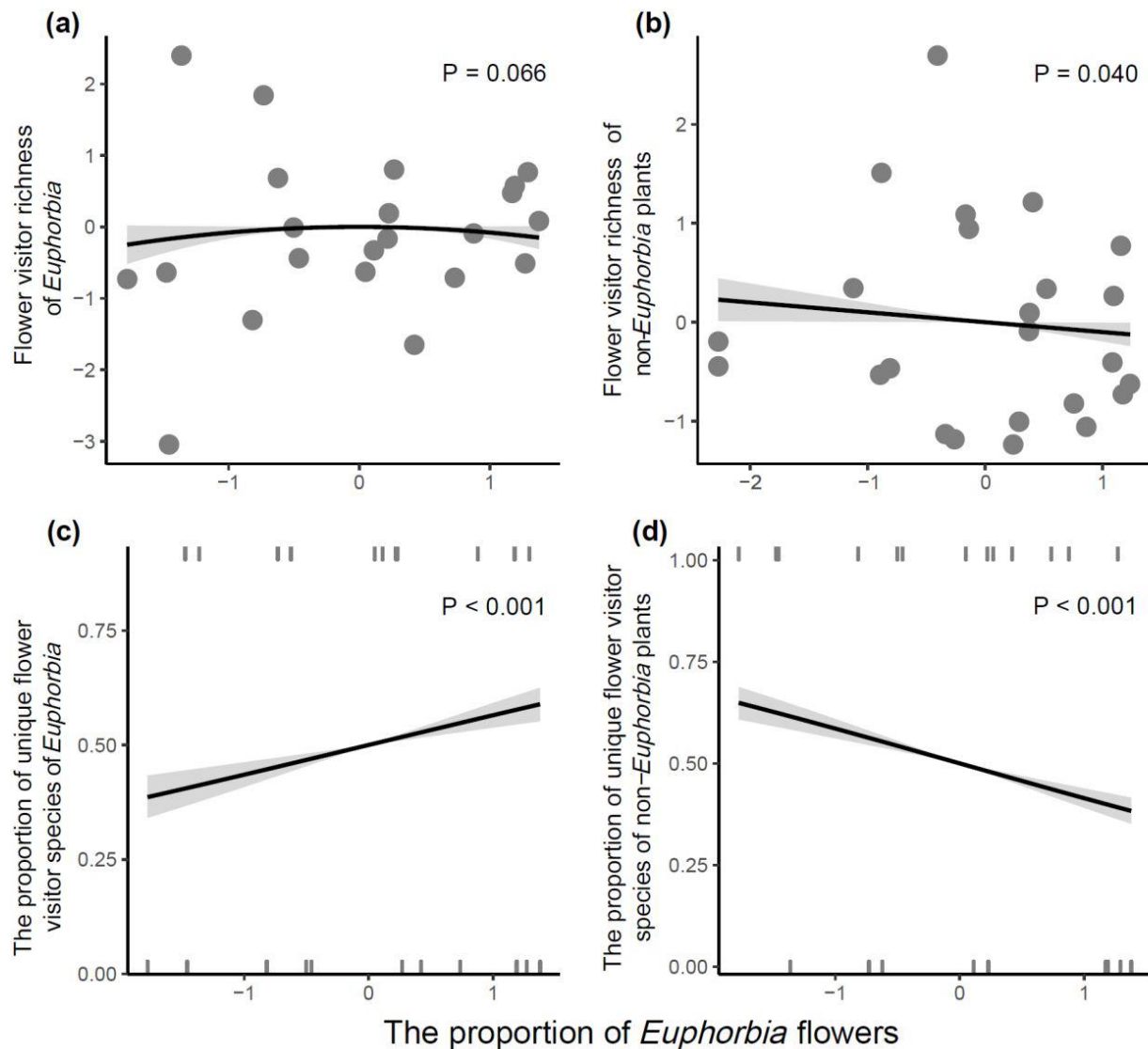


Figure 2. Relationships between the proportion of *Euphorbia* flowers in the community and (a) flower visitor richness of *Euphorbia*; (b) flower visitor richness of non-*Euphorbia* plants; (c) the proportion of unique flower visitor species of *Euphorbia*; and (d) the proportion of unique flower visitor species of non-*Euphorbia* plants. The proportion of *Euphorbia* flowers was scaled to a mean of 0 and a standard deviation of 1. The black lines represent predictions based on the minimum adequate GLMMs, and the grey bands represent the 95% confidence intervals. The partial residuals of the models are shown as grey circles in (a) and (b).

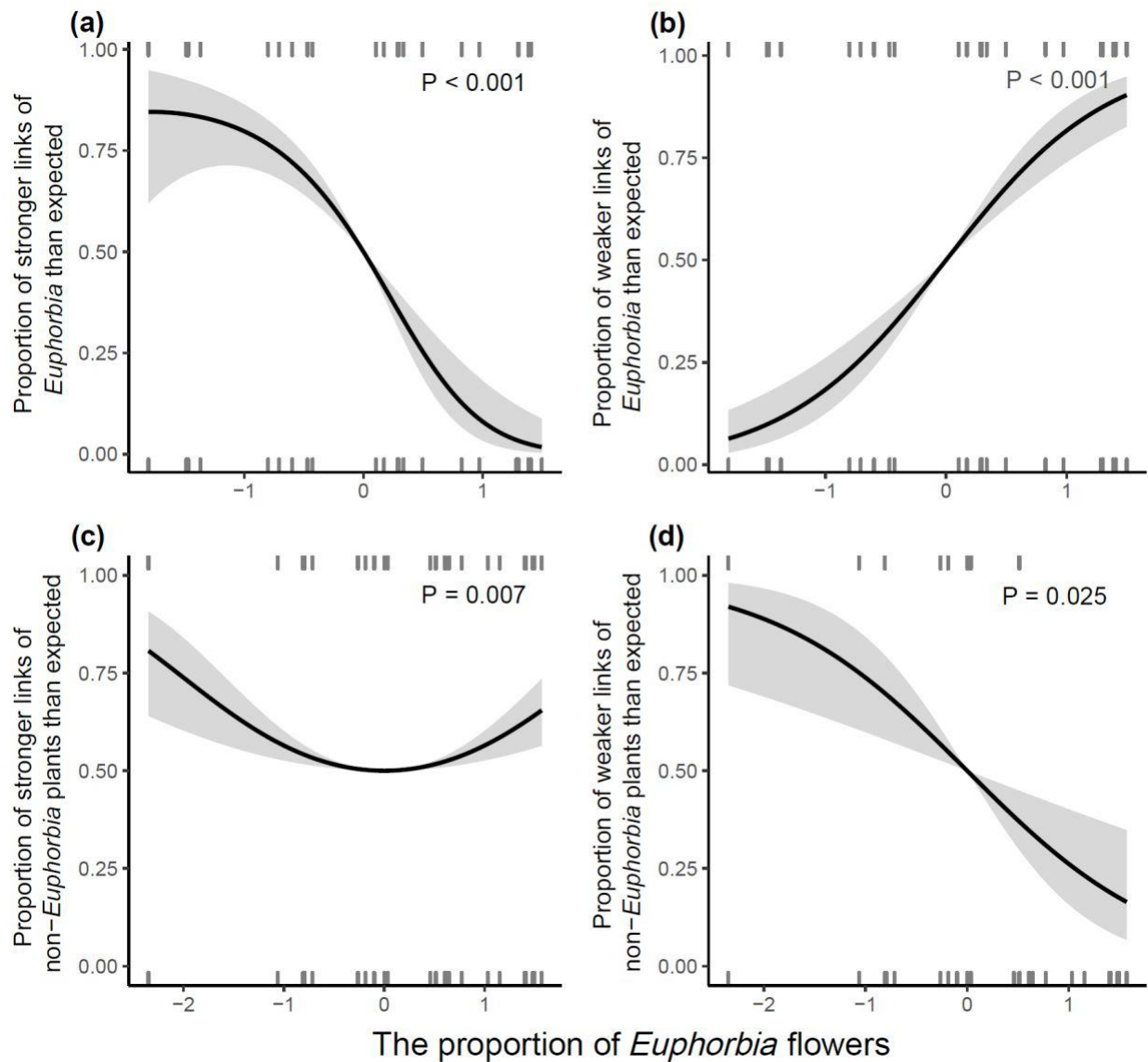


Figure 3. Relationships between the proportion of *Euphorbia* flowers in the community and (a) the proportion of stronger links of *Euphorbia* than expected by flower abundance; (b) the proportion of weaker links of *Euphorbia* than expected by flower abundance; (c) the proportion of stronger links of non-*Euphorbia* plants than expected by flower abundance; and (d) the proportion of weaker links of non-*Euphorbia* plants than expected by flower abundance. The proportion of *Euphorbia* flowers was scaled to a mean of 0 and a standard deviation of 1. The black lines represent predictions based on the minimum adequate GLMMs and the grey bands represent the 95% confidence intervals.

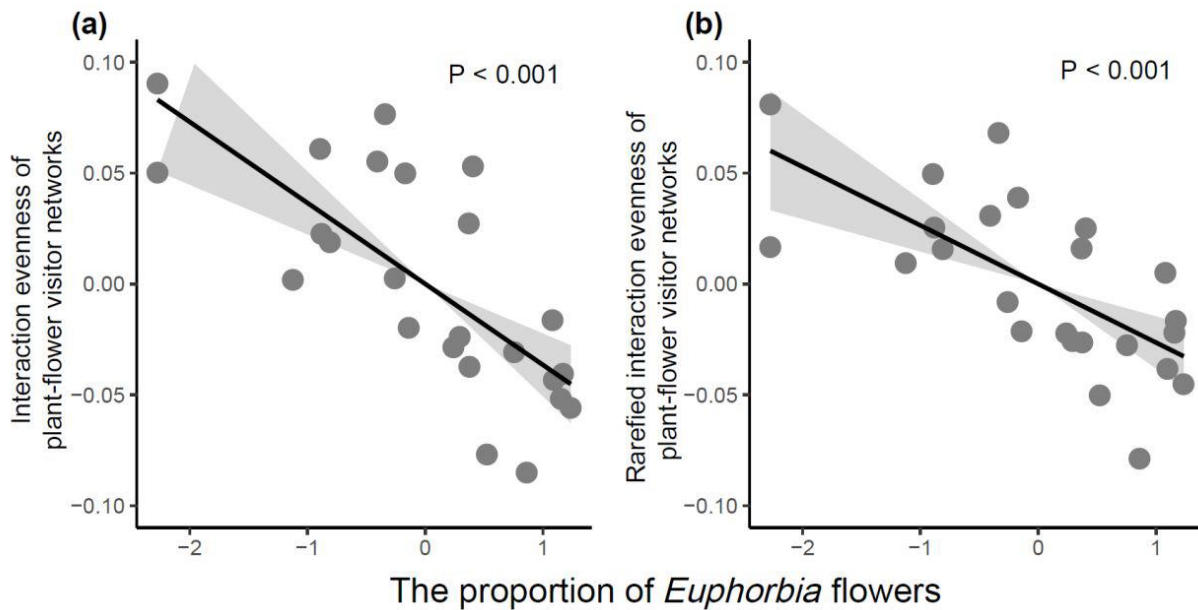


Figure 4. Relationships between the proportion of *Euphorbia* flowers in the community and (a) interaction evenness of the plant-flower visitor networks; and (b) rarefied interaction evenness of the plant-flower visitor networks. The proportion of *Euphorbia* flowers was scaled to a mean of 0 and a standard deviation of 1. The black lines represent predictions based on the minimum adequate LMMs and the grey bands represent the 95% confidence intervals; the partial residuals of the models are shown as grey circles.

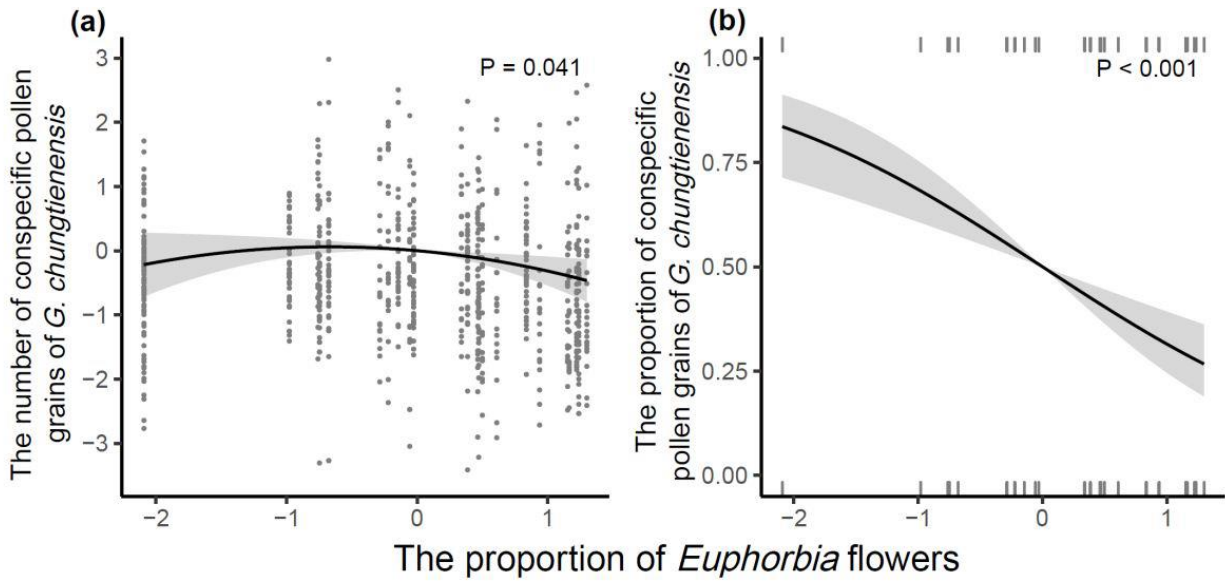


Figure 5. Relationships between the proportion of *Euphorbia* flowers and pollen deposition in *Gentiana chungtienensis* (i.e. the number and proportion of conspecific pollen grains deposited on its stigmas). The proportion of *Euphorbia* flowers was scaled to a mean of 0 and a standard deviation of 1. The black lines represent predictions based on the minimum adequate GLMMs, and the grey bands represent the 95% confidence intervals; the partial residuals of the model are shown as grey circles

Table 1. Results of the generalised linear mixed models used to test the effects of *Euphorbia* on species richness of non-*Euphorbia* plants, flower visitor richness of *Euphorbia*, flower visitor richness of non-*Euphorbia* plant species, the proportion of unique visitors of *Euphorbia* and the proportion of unique visitors of non-*Euphorbia* plant species. The values highlighted in bold are statistically significant based on likelihood ratio tests ($P < 0.05$).

Response	Explanatory variable	Estimate	SE	X^2	d.f.	P
Species richness of non- <i>Euphorbia</i> plants	Distance to forest	-0.016	0.072	0.05	1	0.825
	Year (2018)	-0.142	0.109	1.71	1	0.192
	<i>Euphorbia</i> ²	-0.026	0.051	0.26	1	0.607
Flower visitor richness of <i>Euphorbia</i>	<i>Euphorbia</i>	-0.058	0.055	1.09	1	0.296
	Distance to forest	-0.165	0.043	9.54	1	0.002
	Year (2018)	0.128	0.049	6.77	1	0.009
Flower visitor richness of non- <i>Euphorbia</i> plant species	<i>Euphorbia</i>	-0.079	0.044	3.37	1	0.066
	Distance to forest	0.058	0.05	1.19	1	0.276
	Year (2018)	-0.244	0.055	11.79	1	<0.001
Proportion of unique visitors of <i>Euphorbia</i>	<i>Euphorbia</i> ²	-0.034	0.058	0.34	1	0.56
	Distance to forest	-0.071	0.035	3.69	1	0.055
	Year (2018)	-0.1	0.049	4.21	1	0.04
Proportion of unique visitors of non- <i>Euphorbia</i> plant species	<i>Euphorbia</i>	-0.012	0.085	0.02	1	0.892
	Distance to forest	0.295	0.086	11.91	1	<0.001
	Year (2018)	-0.059	0.066	0.82	1	0.365
Proportion of unique visitors of non- <i>Euphorbia</i> plant species	<i>Euphorbia</i> ²	0.261	0.056	13.36	1	<0.001
	Distance to forest	-0.002	0.085	<0.001	1	0.984
	Year (2018)	-0.18	0.097	3.44	1	0.064
	<i>Euphorbia</i>	0.034	0.06	0.32	1	0.571
	<i>Euphorbia</i>	-0.346	0.051	23.08	1	<0.001

Table 2. Results of the generalised linear mixed models used to test the effects of *Euphorbia* on floral preferences of flower visitors for *Euphorbia* and non-*Euphorbia* plants separately. The values highlighted in bold are statistically significant based on likelihood ratio tests ($P < 0.05$).

Response	Explanatory variable	Estimate	SE	χ^2	d.f.	<i>P</i>
The percentage of stronger links of <i>Euphorbia</i> than expected	Distance to forest	0.214	0.264	0	1	1
	Year (2018)	1.144	0.312	14.6	1	<0.001
	<i>Euphorbia</i> ²	-0.534	0.236	5.72	1	0.017
	<i>Euphorbia</i>	-1.906	0.295	42.85	1	<0.001
	Flower visitor richness	-0.344	0.258	1.82	1	0.177
The percentage of weaker links of <i>Euphorbia</i> than expected	Distance to forest	-0.379	0.178	4.47	1	0.034
	Year (2018)	-0.187	0.452	0.17	1	0.68
	<i>Euphorbia</i> ²	0.31	0.177	3.03	1	0.082
	<i>Euphorbia</i>	1.494	0.232	25.74	1	<0.001
	Flower visitor abundance	0.186	0.187	0.99	1	0.319
The percentage of stronger links of non- <i>Euphorbia</i> plants than expected	Distance to forest	0.141	0.001	2.12	1	0.145
	Year (2018)	-0.475	0.132	10.96	1	<0.001
	<i>Euphorbia</i> ²	0.259	0.079	7.16	1	0.007
	<i>Euphorbia</i>	0.01	0.001	0	1	1
	Flower visitor richness	-0.42	0.109	11.95	1	<0.001
	Flower visitor abundance	0.608	0.116	17.37	1	<0.001
The percentage of weaker links of non- <i>Euphorbia</i> plants than expected	Distance to forest	-1.416	3.12	0.63	1	0.429
	Year (2018)	-0.661	0.65	2.35	1	0.125
	<i>Euphorbia</i> ²	0.12	0.439	0.07	1	0.789
	<i>Euphorbia</i>	-1.038	0.326	5.03	1	0.025

Table 3. Results of the generalised linear mixed models used to test the effects of *Euphorbia* on observed and rarefied interaction evenness of the plant-flower visitor networks. The values highlighted in bold are statistically significant based on likelihood ratio tests ($P < 0.05$).

Response	Explanatory variable	Estimate	SE	X^2	d.f.	p
Interaction evenness	Distance to forest	-0.016	0.009	3.81	1	0.051
	Year (2018)	-0.023	0.013	3.57	1	0.059
	<i>Euphorbia</i> ²	-0.001	0.007	0.03	1	0.862
	<i>Euphorbia</i>	-0.037	0.007	14.73	1	<0.001
Rarefied interaction evenness	Distance to forest	-0.006	0.008	0.67	1	0.412
	Year (2018)	-0.012	0.012	1.24	1	0.266
	<i>Euphorbia</i> ²	-0.002	0.006	0.17	1	0.683
	<i>Euphorbia</i>	-0.026	0.006	12.97	1	<0.001

Table 4. Results of the generalised linear mixed models used to test the effects of *Euphorbia* on pollen deposition on stigmas of co-flowering species (i.e. the number and proportion of conspecific pollen deposition on stigma) of *Gentiana chungtienensis* and *Anemone rupestris* separately. The values highlighted in bold are statistically significant based on likelihood ratio tests ($P < 0.05$).

Response	Explanatory variable	Estimate	SE	X^2	d.f.	P
The number of conspecific pollen of <i>G. chungtienensis</i>	Distance to forest	-0.099	0.091	1.21	1	0.271
	Year (2018)	-0.462	0.07	43.73	1	<0.001
	<i>Euphorbia</i> ²	-0.136	0.061	4.19	1	0.041
	<i>Euphorbia</i>	-0.181	0.076	4.04	1	0.045
	Flower abundance	0.046	0.052	0.79	1	0.373
	Flower visitor richness	0.044	0.07	0.39	1	0.531
	Flower visitor abundance	-0.098	0.073	1.77	1	0.183
The proportion of conspecific pollen of <i>G. chungtienensis</i>	Distance to forest	-0.067	0.193	0.11	1	0.746
	Year (2018)	-1.391	0.483	9.93	1	0.002
	<i>Euphorbia</i> ²	-0.247	0.138	3.13	1	0.077
	<i>Euphorbia</i>	-0.777	0.174	23.57	1	<0.001
	Flower abundance	0.414	0.347	2.11	1	0.146
	Flower visitor richness	0.732	0.357	3.33	1	0.068
	Flower visitor abundance	3.116	0.952	29.72	1	<0.001
The number of conspecific pollen of <i>A. rupestris</i>	Distance to forest	0.204	0.095	3.83	1	0.05
	Year (2018)	0.013	0.113	0.01	1	0.911
	<i>Euphorbia</i> ²	0.046	0.059	0.63	1	0.428
	<i>Euphorbia</i>	-0.043	0.11	0.14	1	0.707
	Flower abundance	-0.071	0.081	0.67	1	0.413
	Flower visitor abundance	-0.114	0.074	2.26	1	0.133