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Fungal pseudoflowers can influence the fecundity of insect-pollinated flowers on *Euphorbia cyparissias*

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Abstract

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Euphorbia cyparissias is often infected by a rust fungus from the species complex *Uromyces pisi*. Infected plants do not form flowers but pseudoflowers, rosettes of yellow leaves upon which the fungus presents gametes in a sweet-smelling sugary nectar. Insects feed on the nectar and transfer fungal gametes between mating types. Here we show that pseudoflowers and the flowers of non-infected hosts overlap in "flowering" for more than one month, even though pseudoflowers start "flowering" one month earlier than true flowers. As the fungus and its host also share insect visitors, we hypothesized that they might interact either by facilitating each others' insect visits or by competing for "pollinators". We addressed this question by weekly grid-mapping an *Euphorbia* population near Zermatt in the Swiss Alps and relating the average density and frequency around hosts and pseudoflowers during their "flowering" period to their fitness (success in seed set and spore production). The seed set of uninfected *Euphorbia* plants was significantly higher when they were surrounded by fewer pseudoflowers. The fungus, on the other hand, was not obviously influenced by the presence of host flowers. Instead, the reproductive success of single pseudoflowers decreased with a higher density of pseudoflower-neighbors. Our results suggest that the fungus might be a pollinator-competitor for *Euphorbia* flowers.

Key words: Density dependence, intraspecific competition, phenology, pollination, rost fungi, *Uromyces pisi*.

Introduction

The Cypress spurge, *Euphorbia cyparissias* L., is often infected by rust fungi from the species complex *Uromyces pisi* (Pers.) Wint. The infected *Euphorbia* plant is generally inhibited from flowering, instead, the fungal pathogen induces its host to form a pseudoflower, a rosette of pale yellow leaves that are clustered on top of the stem in a flower-like shape. Not only do fungal pseudoflowers visually resemble true flowers, but just like true flowers, they present a sweet smelling nectar that is produced by the fungus and contains fungal gametes (Gäumann 1959; Roy 1993). The fungus is obligately outcrossing and requires insects to transport gametes and cross-fertilize the fungus while feeding on the nectar (Pfunder and Roy 2000).

Because the *Euphorbia* host and its pathogen often co-"flower" in intermingled populations, we hypothesized that the flowers of uninfected hosts might facilitate insect visits to the fungal pseudoflowers. Theories concerning facilitation of pollination are based on the assumption that a similar looking species can gain from nearby plants that attract pollinators in higher numbers and thus enhance overall visitation (Bobisud and Neuhaus 1975; Feinsinger 1987; Johnson et al. 2003; Feldman et al. 2004). However, for facilitation to occur, the fungus and its uninfected host need to share insect visitors and the visitors need to respond in a positive frequency- and/or density-dependent way to them. Further, if similarity between species is to be favored by selection, then the similarity must increase fitness (Roy and Widmer 1999). Alternatively, the fungal pseudoflowers and the non infected host flowers might compete for pollitators, or they might not influence each others' insect visits at all. In the case of competition, we expect reduced reproductive success for either one or both pseudoflowers and flowers, as a result of fewer visits or improper pollen/gamete transfer (Waser 1978; Rathcke 1983; Feinsinger 1987).

In an earlier study, an artificial array experiment within a natural population of co-flowering hosts and pseudoflowers, we showed that the fungus and its host shared insect visitors, and that the visitors preferred the hosts' true flowers over fungal pseudoflowers in mixtures (Pfunder and Roy 2000). However, we found no evidence that pseudo-flowers and true flowers influenced each others' visitation rates or that insect-visitors behaved in a frequency- or density-dependent way (Pfunder and Roy 2000). While array experiments are useful for separating and controlling density and frequency, their major disadvantage is that only a few combinations of frequency and density can be tested at one time. Observational studies in natural populations have the advantage of including changes in the density and frequency of plants as well as pollinators over the season, but it is difficult to disentangle the effects of density and frequency on plant fitness.

In this paper we outline an observational approach that enables the separation of density and frequency effects on fecundity. We used weekly phenological data from a natural *Euphorbia* population in the Swiss Alps. This information was transformed to spatial grid data using the program Spatial Analyst (ArcView). We then used regression analyses to compare the reproductive success of 49 uninfected flowers and 26 pseudoflowers to the average density and frequency of neighbors that these individuals encountered throughout their flowering periods. Additional information was gained by including other factors such as flowering commencement, flowering time and plant size in the statistical models.

Materials and Methods

Field work was done in an *Euphorbia cyparissias* population near Zermatt in the Swiss Alps (Swiss co-ordinates 624 662/095 537) located at 1960 m above sea level, growing on dry grassland, oriented south-south-east at a roughly 30° angle. We chose a plot of 8×10 m^2, which enclosed almost the entire population, and marked the position of each m^2 within the plot with stakes. We then laid a 1-m^2 aluminum frame divided into 100 cm^2 over each m^2 to monitor the number and estimate the height of all *E. cyparissias* stems within each 100-cm^2 square. Height estimation was done by eye, controlling the estimation from time to time by actual measurements. We assessed whether stems were infected or not; if uninfected, we recorded their flowering status, if infected, we recorded the stage of the infection. We also counted and recorded all other species that were flowering in the field. Weekly surveys were performed from April 2 to June 24, 1998, except April 15 and April 29, when snow covered the site.

The flowers of *E. cyparissias* are organized in pseudo-cymes on each stem. Each pseudo-cyme consists of many cyathia, and each cyathia consists of an involvucre with one female and several male flowers (Stahevitch et al. 1988). For simplicity, we refer to both the pseudoflowers on one stem, as well as the pseudo-cymes on one stem, as inflorescences. Pseudoflowers were defined as "flowering" as long as the fungus produced nectar; uninfected plants were defined as flowering as long as we found flowers in the pseudo-cymes of one inflorescence. *E. cyparissias* is partially self-compatible: Schürch et al. (2000) observed low seed set in 10 percent of a total of 20 plants from which insects were excluded. The fungus, on the other hand, is nearly obligately outcrossed; insect exclusion led to very reduced aecia production in only one out of 20 tested pseudoflowers (Pfunder and Roy 2000).

We evaluated the flowering periods (phenology) for all flowering plant species as well as for nectar producing pseudoflowers throughout the season. Plant species represented by fewer than 10 flowers over the whole observation period are not presented here.

To relate the effect of the density and frequency of flowering neighbors on the reproductive success of pseudoflowers and true host flowers, we collected all aecia bearing and seed carrying stems after the end of their flowering period. Fungal fecundity was measured as the proportion of infected leaves that bore aecia. Aecia are fungal organs in which aeciospores, the spores responsible for dispersal to other hosts, are produced. Aecia are only formed when the fungus is successfully cross-fertilized by insects (Pfunder and Roy 2000). Aecia were counted on dried samples under a dissecting microscope (Wild, M5A, Heerbrugg, CH) at $60-120\times$ magnification. Fecundity of *E. cyparissias* flowers was measured by absolute seed set.

E. cyparissias is a perennial plant that can spread through seeds but also through lateral root buds. *Uromyces pisi* is a systemic rust fungus that overwinters in the roots of a plant and may also spread over lateral shoots. We therefore have no possibility to unambiguously define single genotypes without digging up the plants. In this study we considered the stems that were found within the same 100-cm^2 grids as one plant individual or one fungal individual, based on the following assumptions: a) during monitoring, different stems grown from one root bud were always assigned to one single grid, b) typically, only stems from a single root bud physically fitted into one grid (10×10 cm^2), and c) all stems from one root bud showed the same infection status. By pooling the stems of one grid to one individual we tried to average variability within genotypes, but in particular we wanted to avoid overestimation through pseudorepli-

cation among inflorescences with the same density and frequency of neighbors. Pooling of nearby stems led to an overall total of 49 flowering host individuals comprising 66 single inflorescences, and 26 fungal individuals comprising 38 single inflorescences.

While fecundity was pooled among single inflorescences within a grid, frequency and density around the individuals were calculated from single inflorescences, including the inflorescences of the individuals themselves. This is reasonable, because insect visitors respond to density and frequency of single inflorescences rather than to genotypes. However, by adding individual's stems to the frequency and density, these values were enhanced proportionally more within the smaller circular area than in the larger area. This fact is responsible for most of the differences observed between the two areas.

Each pseudoflower and true flower was assigned to its locality on a digital map using the program Spatial Analyst, an extension program of ArcView (ESRI 1996). For each individual with known fecundity we calculated the average density and frequency of neighbors during its flowering period, using the same grids (100 cm^2) as during mapping in the field. We used two different scales, circular areas with 35 cm and 85 cm radii, respectively (Fig. 1). To make data from the two different area measures directly comparable, the calculated densities were standardized to areas of 1 m^2 by multiplying densities of the smaller area (Fig. 1a: r = 35 cm; 0.29 m^2) by the factor 3.45, and densities of the larger area (Fig. 1b: r = 85 cm; 1.97 m^2) by 0.51. Frequency was calculated by the ratio of pseudoflowers to the sum of pseudoflowers and host inflorescences. We ignored interdependencies for this comparison. No edge effects influence this analysis: Only two individuals, one pseudoflower and one *E. cyparissias* individual, were positioned closer than 1 m from the periphery of the study plot, and they were only included in the analysis because we knew that on that side no flowers existed outside the plot. For each individual of known fecundity, we further recorded the following variables that may also influence visitation: commencement of flowering (in days, maximum over stems), flowering duration (in days, maximum over stems), and the mean height during flowering (average over stems).

Stepwise (backward removal) logistic regression analyses were used, one for the seed set of host plant individuals, and one for the aecia set of pseudoflower individuals. We present results from models including both frequency and density in the same model (Tab. 1) as well as from models separating the two factors. We included the following effects in the models: (a) mean height during flowering (cm), (b) flowering period (days), (c) flowering commencement (days), (d) density of pseudoflowers at the small scale, (e) density of pseudoflowers at the large scale, (f) density of host inflorescences at the small scale, (g) density of host inflorescences at the large scale, (h) frequency of pseudoflowers (number of pseudoflowers per total number or pseudoflowers and host inflorescences) at the small scale, and (i) frequency of pseudoflowers at the large scale.

Results

We observed the phenology of flowering plants as well as of the fungal pseudoflowers over the entire flowering season. Pseudoflowers were among the first presenting nectar reward, and they remained "flowering" for 83 days. *E. cyparissias* host plants started flowering one month after the first pseudoflowers, and ended flowering together with them. Four other species were present with more than 10 flowers or inflorescences during the observation period (Fig. 2), all of them overlapping only

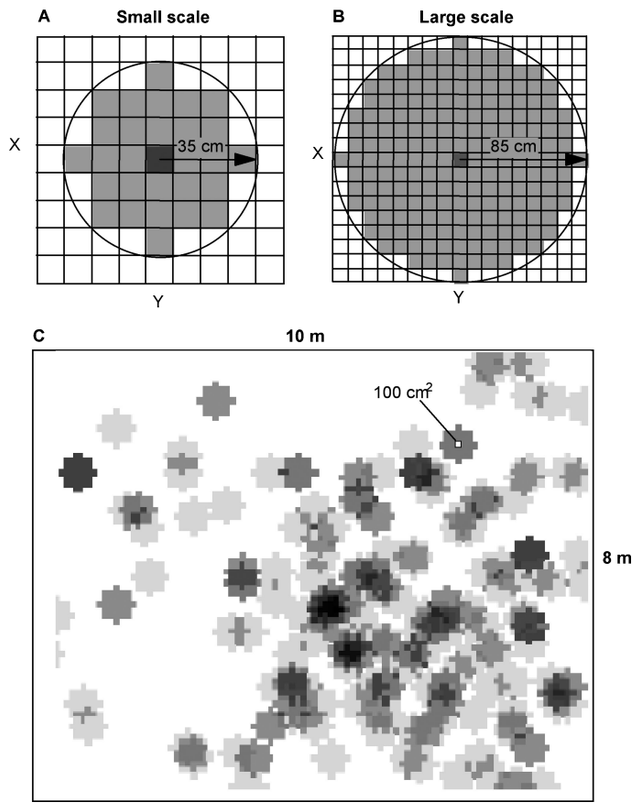

Fig. 1. Grid system used to calculate density and frequency for two different sized areas. The dark cell in the center of the circle represents the location of the individual for which density and frequency were estimated. The density and frequency surrounding this individual was averaged over (a) 29 cells (r = 35 cm) and (b) 197 cells (r = 85 cm). (c) An example of how density and frequency was evaluated for single inflorescences in a given week for the whole field site. Each cell is 100 cm^2, giving a total of 8000 cells, and shows the number of host inflorescences at the area r = 35 cm by which an individual in the given cell was surrounded. The darker the colors, the more neighbors there are.

minimally with pseudoflowers or true flowers of *E. cyparissias*. Uninfected hosts showed a peak number of 247 inflorescences, infected pseudoflowers reached a maximum of about 70% of these (178 pseudoflowers). As a result of the staggered flowering of pseudoflowers and host flowers, the overall frequency of pseudoflowers decreased over the season as *E. cyparissias* flowers increased. The density of inflorescences was highly variable and depended on the size of the areas used for calculation. The smaller area showed an overall higher density and frequency, which reflects the inclusion of inflorescences of the individuals in question in the total counts of inflorescences. The density of hosts around pseudoflowers and vice versa shows no such effect, densities and fre-

Tab. 1. Significant results from two step-wise multiple logistic regressions testing the following effects on the seed set of host plants and the aecia set of pseudoflowers: density of host inflorescences vs. pseudoflowers at two scales (radius = 35 and 85 cm), frequency of host inflorescences vs. pseudoflowers at two scales (r = 35 and 85 cm), flowering commencement, flowering period, and mean plant height during the flowering period. Effects that have been removed are not shown (i.e. all effects from scale r = 85 cm).

Dependent variable	Predictor variable	slope	df	MS	F	P
seed set of host plants ($n = 49$)	Mean height during flowering	1.46	1	1397	33.06	< 0.0001
	Density pseudoflowers (r = 35 cm)	−0.84	1	361	8.56	0.0054
	Frequency* (r = 35 cm)	5.09	1	231	5.47	0.0239
aecia set of pseudoflowers ($n = 26$)	Starting time of flowering	−0.01	1	0.28	9.75	0.0048
	Density pseudoflowers (r = 35 cm)	−0.02	1	0.14	4.85	0.0379

* Number of pseudoflowers divided by the sum of pseudoflowers and host flowers.

quencies being similar at both scales. Density as well as frequency effects of neighbor inflorescences on the fecundity of the individual flowers and pseudoflowers were only detectable at the smaller radius of 35 cm when combined in the stepwise regression model (Tab. 1).

Flowers with more seeds were surrounded by a lower density and frequency of pseudoflowers. Both frequency and density of surrounding pseudoflowers were highly correlated (Pearson's $r = 0.936$). We therefore also tested these two factors in two separate stepwise multiple logistic regressions, but surprisingly, neither frequency nor density alone showed a significant effect on seed set of the uninfected *E. cyparissias* flowers, instead, in both models the starting time of flowering (slope = 0.48, df = 1, $F = 4.0$, $P = 0.05$), flowering period (slope = 0.55, df = 1, $F = 6.9$, $P = 0.01$), and stem height (slope = 1.19, df = 1, $F = 22.1$, $P < 0.0001$) explained most of the variation among individual success. Not surprising, the seed set of host individuals significantly increased with the mean height of the plant during its flowering period. Neither the starting time of flowering nor the length of the flowering period had a measurable effect on *Euphorbia* seed set in the combined model including frequency and density.

Pseudoflowers produced more aecia when the density of pseudoflowers in their neighborhood was low (Tab. 1). But an even stronger influence was the starting time of pseudoflower "flowering". The earlier they started presenting nectar, the higher was their fecundity by the end of their flowering period. This result is strongly correlated with the flowering period (Pearson's $r = 0.907$): The earlier they started "flowering", the longer they "flowered". Neighboring *Euphorbia* inflorescences did not seem to influence the fecundity of the rust fungus in the combined model of frequency and density. In a regression model including frequency only, the one factor explaining variation in aecia set was the flowering period (slope = 0.006, df = 1, $F = 7.1$, $P = 0.01$). However, a model including only density was consistent with the combined model, showing a significant effect of the starting time of flowering as well as the density of surrounding pseudoflowers in the small area (Tab. 1).

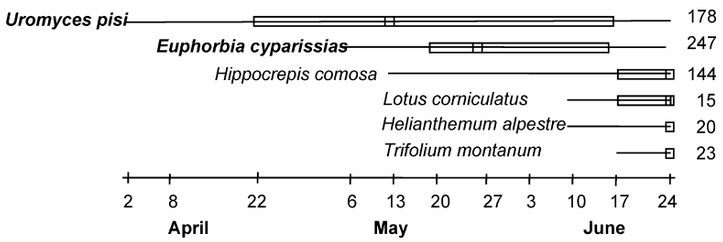

Fig. 2. Flowering phenology in Zermatt 1998. Thickened bars represent the time during which $\geq$50% of the peak number of flowers/pseudoflowers were present on the field. The black boxes represent the peak of flowering, the peak number of flowers/pseudoflowers are given behind each line.

Discussion

Differential response of pollinators to density and frequency of co-flowering plants is thought to be responsible for the evolution of much of the morphological and phenological variation in plant species. The two target species observed in this study were the rust fungus *Uromyces pisi* and its host plant *Euphorbia cyparissias*. Both species present nectar, depend on the same insects for fertilization, and their co-occurrence is given because the pathogen is host-specific. The phenological study at Zermatt showed that pseudoflowers started to flower exactly one month before the first host flowers (Fig. 2). Exactly the same shift of one month from pseudoflowers to flowering *E. cyparissias* plants was also observed in the same year at a different site, at Vicques in the Swiss Jura Mountains, 550 m a.s.l. (Pfunder 1999). *Uromyces pisi* infected plants are known to have an enhanced concentration of growth-regulating hormones (auxines) and to keep this high concentration over a longer time than uninfected *E. cyparissias* host plants (Pilet 1952). However, it is not known whether the fungus produces these hormones or whether the high concentration is a reaction of the infected plant. Our results show that the fungus clearly benefited from early "flowering"; earlier "flowering" fungal inflorescnces had greater reproductive success. Early growth might enhance the overall duration of "flowering", or it might be adaptive and initiated by the fungus to avoid competition for pollinators with flowers of *E. cyparissias* through temporal displacement. Support for this hypothesis comes from an earlier array study in which we showed that insects preferred host flowers over pseudoflowers in mixtures (Pfunder and Roy 2000). However, it is very difficult to establish whether temporal displacement is actually the result of interspecific competition (Connell 1980), and the fact that we found no negative influence of co-flowering true *E. cyparissias* plants on the fungal pseudoflowers in the current study rather contradicts the competition theory.

At the same time, the absence of positive frequency- or density-dependent effects of *Euphorbia* on the pseudoflowers' reproductive success in Zermatt also rejects the theory of facilitation. Roy (1994) showed in array experiments that rust pseudoflowers of a *Puccinia* rust profited from co-flowering with buttercups by attracting more insects. Our array study (Pfunder and Roy 2000) as well as the present study suggest that the *Euphorbia – Uromyces* system is different, at least in the studied population.

Surprisingly, we found that higher density of conspecific neighbors decreased the reproductive success of pseudoflowers (intraspecific negative density-dependence). This was true for the model including both frequency and density as well as in the model including only density, while frequency had no effect in either of the models. A possible explanation for these observations might be the mating system of the fungus. Each infected plant usually has only one fungal mating type on it as the fungus is systemic, and the fungus is 80 to 95% self-incompatible (Pfunder and Roy 2000; Schürch et al. 2000). Our density and frequency measures include the number of stems from the individual tested, we thus suspect that the effect seen might be the result of ineffective gamete transfer, resulting from the transfer of the same mating type from one stem to the other. Improper pollen transfer has also been shown to affect plant reproduction in a negative way (Waser 1978). The earlier experimental array study showed that higher frequency as well as higher density of pseudoflowers led to longer pollinator visits (Pfunder and Roy 2000), but no effect was found on the visitation rates. Therefore, if higher density decreases pseudoflower fecundity, we could interpret the results in the way that longer visits negatively influence the fungus through decreased outcrossing rates.

Inflorescences of *E. cyparissias* had lower seed set when surrounded by a higher density and frequency of infected plants (Tab. 1). Pseudoflowers might therefore be serious competitors for their uninfected hosts. The fact that both frequency and density remain in the stepwise removal regression model suggests that although correlated, the two factors might have influenced pollinator visitation in concert. When we run separate models including either density or frequency alone, neither of the two factors significantly explains seed set variation. In all models, the most significant effect on seed set of true flowers was plant height. Plant height was included in the analysis to correct for at least some of the morphological variation based on genetic and environmental factors on absolute seed set. Thus, the inclusion of height in the model improves the chances of finding a model with good fit for other variables.

In the regression models, density or frequency effects on the fecundity of pseudoflowers and their hosts were significant only within the closer area around a plant ($r = 35$ cm). The correlation coefficient (pairwise Pearsons product-moment correlations) among the density of the two scales after normalization to 1 m^2 lay between 0.2 and 0.5. The correlation coefficient for the frequency of pseudoflowers in the two areas was 0.3 around non-infected and 0.37 around infected individuals. The smaller scale showed an overall higher density which, as we already described, reflects the inclusion of inflorescences of the individual in question in the total counts of surrounding inflorescences, leading to a stronger influence at the smaller scale. As the densities and frequencies at the two scales were not highly correlated, the inclusion of the two factors into one model seemed appropriate. The fact that we only found significant effects within the 35 cm radius suggests that, if the differences in seed and aecia set are pollinator mediated, insect behavior may be influenced more within relatively small areas than within larger plots.

We observed at Zermatt that density and frequency around single individuals during their flowering periods varied strongly. In addition, the importance of frequency and density to pollinators will vary between species (Roy 1996) and even between individual insects (Motten 1986; Herrera 1989; Jones 1997), and will also vary temporally and spatially (Thompson 1994; Molofsky et al. 2001). Therefore, we have to assume that the outcome of pollination activity -seed set and aecia production of flowers and pseudoflowers, respectively – also varies strongly among years and populations. The results from our phenology study in Zermatt suggest that the density of pseudoflowers

was the most important factor determining the fecundity of pseudoflowers and true flowers in the population studied. Our mapping technique allowed us to come to this conclusion despite the fact that the density of pseudoflowers was highly variable over the season and even within flowering periods of single individuals. A short-term study of insect behavior in arrays can give a false impression of the importance of density and frequency, as averaged over the season, but can yield important information on insect preferences and constancy. We submit that a combination of arrays and our mapping/ fitness regression approach at different sites and different times would be best for understanding the consequences of the behavior of flower visiting insects and their impact on plant and fungal fitness.

Zusammenfassung

Die Zypressen-Wolfsmilch *Euphorbia cyparissias* ist häufig mit einem Rostpilz aus dem Formenkreis *Uromyces pisi* befallen. Die Blütenbildung wird bei infizierten Pflanzen verhindert. Stattdessen bilden sie durch den Einfluss des Pathogens so genannte Pseudoblüten aus, Rosetten von Sprossblättern, auf deren Oberfläche der Pilz seine Gameten in einer süss duftenden Zuckerlösung präsentiert. Insekten ernähren sich von diesem Nektar und transportieren Gameten unterschiedlichen Geschlechts zwischen verschiedenen befallenen Pflanzen. Unsere Feldstudien in den Schweizer Alpen zeigten, dass die "Blühzeit" von Pseudoblüten und nicht infizierten Wirtspflanzen während mehr als einem Monat überlappt, obwohl die Pseudoblüten einen Monat früher mit der Nektarproduktion anfangen. Weil der Pilz und die Wirtspflanzen auch ihre "Bestäuber" teilen, stellten wir die Hypothese auf, dass sie durch gemeinsames "Blühen" positiv interagieren und die Gesamtzahl der Insektenbesuche gegenseitig fördern könnten.Wir nahmen uns dieser Frage an, indem wir an einer *Euphorbia*-Population in der Nähe von Zermatt wöchentliche Grid-Kartierungen vornahmen und die mittlere Dichte und Häufigkeit der umgebenden Wirtsblüten und Pseudoblüten während ihrer "Blühzeit" mit dem Fortpflanzungserfolg, gemessen in Sporen- und Samenproduktion, in Zusammenhang setzten. Die Samenproduktion von nicht-infizierten *Euphorbia*-Pflanzen war signifikant höher, wenn sie von weniger Pseudoblüten umgeben waren, während der Pilz nicht offensichtlich von der Gegenwart der Wirtsblüten beeinflusst wurde. Die Daten deuten im Gegensatz eher darauf hin, dass der Reproduktionserfolg einzelner Pseudoblüten mit zunehmender Dichte an umgebenden Pseudoblüten abnahm. Unsere Ergebnisse lassen vermuten, dass der Pilz ein ernst zu nehmender Konkurrent für Bestäuber von nicht-infizierten *Euphorbia*-Blüten sein könnte.

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