

Pollen interference between rare and common species

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Abstract

The mechanisms underlying plant species distribution and abundance have been long studied in ecology. However, the role of heterospecific pollen interference in shaping these patterns remains unaddressed. Species distribution and abundance are important factors determining whether a species is endangered or not, thus understanding the impact of heterospecific pollen interference on rare species could help to inform conservation strategies aimed at preserving plant communities. In this study, we conducted a multispecies experiment using eight co-occurring and co-flowering plant species with varying rarity levels in Switzerland. We performed hand-pollination experiments between all species pairs and measured seed set (whether a flower produces seed) and seed number (number of seeds per flower) as outcomes. We looked at the effects of species rarity status, species self-compatibility and recipient-donor relatedness on heterospecific pollen interference. Contrary to expectations, neither seed set nor seed number were affected by heterospecific pollen deposition. Self-compatible species had a higher seed set probability, but this was independent from species rarity. Lastly, rare species showed a decrease in heterospecific pollen interference with more distantly related pollen donors when these were rare as well. In our study setting, heterospecific pollen interference seems to have only minor effects on seed set and seed number, and consequently on recruitment. Thus, heterospecific pollen interference seems to play only a minor role in shaping plant species distribution and abundance. Nevertheless, the higher impact of heterospecific pollen deposition for rare and closely related species might need further investigation for both in-sit and ex-situ conservation strategies.

Pollen interference between rare and common species

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Abstract

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In this study, we conducted a multispecies experiment using eight co-occurring and co-flowering plant species with varying rarity levels in Switzerland. We performed hand-pollination experiments between all species pairs and measured seed set (whether a flower produces seed) and seed number (number of seeds per flower) as outcomes. We looked at the effects of species rarity status, species self-compatibility and recipient-donor relatedness on heterospecific pollen interference.

Contrary to expectations, neither seed set nor seed number were affected by heterospecific pollen deposition. Self-compatible species had a higher seed set probability, but this was independent from species rarity. Lastly, rare species showed a decrease in heterospecific pollen interference with more distantly related pollen donors when these were rare as well. In our study setting, heterospecific pollen interference seems to have only minor effects on seed set and seed number, and consequently on recruitment. Thus, heterospecific pollen interference seems to play only a minor role in shaping plant species distribution and abundance. Nevertheless, the higher impact of heterospecific pollen deposition for rare and closely related species might need further investigation for both in-sit and ex-situ conservation strategies.

Keywords: common species; self-incompatible species; phylogenetic distance; pollen recipient; Caucalidion

Introduction

The drivers of plant species distribution and abundance have been studied under different aspects. Three main drivers are usually suggested to shape plant species distribution and abundance: abiotic factors, dispersal and biotic interactions (Soberon, 2007; Boulangeat, Gravel, & Thuiller, 2012). Abiotic factors, such as soil moisture, temperature, and nutrient availability, influence species distribution and abundance in relation to a species' fundamental niche (Chase & Leibold, 2003). Limited dispersal ability can prevent a species from reaching suitable habitats, even if these are available. Conversely, excellent dispersal ability can enable a species to colonize unsuitable sites through continuous immigration (Pulliam, 2000). Biotic interactions, including both competition and facilitation among plant species, as well as interactions with other trophic levels such as predation, herbivory, and pollination, can also influence species distribution and abundance (Meier et al., 2010).

Pollinators can mediate indirect biotic interactions by acting as vectors, even between non-neighboring individuals, due to their ability to move freely and cover long distances. While pollinators provide the essential function of pollination, they can also have negative effects. Recent studies have shown that among other things, pollinators can transfer viruses between different species (Fetters, 2023). More importantly, through the deposition of pollen mixes from different species on the stigma of a recipient flower, heterospecific pollen interference (HPI hereafter) can occur (T. L. Ashman & Arceo-Gómez, 2013). HPI refers to the reduction in reproductive output in the presence of heterospecific pollen (HP hereafter), despite the presence of conspecific pollen (CP hereafter) that could fertilize the ovules, potentially impacting the fitness of the recipient species (Morales & Traveset, 2008).

Previous studies have explored HPI between native and alien species (e.g. Suárez-Mariño, Arceo-Gómez, Sosenski, & Parra-Tabla, 2019; Malecore, Berthelot, Kleunen, & Razanajatovo, 2021). However, to the best of our knowledge, no study has specifically addressed the role of HPI between co-occurring rare and common species. Given that species distribution and abundance are crucial factors in determining a species' endangerment status, understanding the mechanisms of heterospecific pollen interference for rare species could provide insights for both in-sit and ex-situ conservation strategies aimed at preserving plant communities.

To mitigate HPI, plant species can either avoid or reduce heterospecific pollen deposition or evolve tolerance to it (Arceo-Gómez, Raguso, & Geber, 2016; Streher, Bergamo, Ashman, Wolowski, & Sazima, 2020; Hao, Fang, & Huang, 2023). Avoidance or reduction mechanisms can occur at the pre-pollination stage through

alterations in flower phenology, development of flower restrictiveness, reliance on specialized pollinators, or the use of different deposition sites on the pollinator’s body (Montgomery & Rathcke, 2012). Tolerance mechanisms occur at the post-pollination stage through pollen-stigma or pollen-pollen interactions. Tolerance is expected to evolve after exposure to heterospecific pollen. Therefore, in a plant community, if no avoidance or reduction mechanism prevents heterospecific pollen deposition, we can expect co-flowering species sharing common pollinators to evolve mechanisms to tolerate HPI.

In a co-flowering plant community, it is expected that common species receive more frequent visits from pollinators, while rare species receive fewer visits. Thus, according to the tolerance hypothesis (Hao et al., 2023), both rare and common species should be adapted to receive heterospecific pollen from other common species. On the other hand, both common and rare species should receive heterospecific pollen less frequently from other rare species. A reduced exposure means a lower need and chance to adapt to potential negative effects from heterospecific pollen. We predict that both common and rare species will experience HPI from rare donors but not from common donors.

The breeding system or self-compatibility of donor and recipient species could be another factor determining the strength of HPI for co-occurring species. Self-incompatible species present either mechanical or chemical mechanism to avoid self-pollination (Tom J. de Jong, Nickolas M. Waser, 1993) , and these mechanisms might similarly help in avoiding HPI. Thus, self-incompatible species could be better equipped against HPI. In a conservation context, self-compatibility could represent in some cases the only way for small populations to persist.

Another factor that has received attention in relation to HPI is the recipient-donor species relatedness. For example, due to similar recognition mechanism, it could be that only pollen from closely related species germinate on the stigma of the recipient species. Therefore, HPI might be reduced among distantly related species. While in a previous study we showed that the phylogenetic distance between recipient and donor species did not affect the overall strength of HPI (Malecore, Berthelot, Kleunen, & Razanajatovo, 2021), this pattern could change depending on the commonness or rarity of recipient and donor species.

In this study, we conducted hand-pollination experiments on a total of eight co-occurring and co-flowering species, collected from wild population. Five of these species are rare, and three are common in Switzerland. We will refer to species rarity or commonness with species status. We performed pairwise heterospecific pollen crosses as well as conspecific control treatments and measured seed set and seed number as our outcome variables. Seed set and seed number serve as proxies for reproductive success and thus of population viability. We asked following questions: 1) Does heterospecific pollen reduce seed set and seed number for common and rare recipient species and does this reduction depend on recipient and donor status? 2) Does heterospecific pollen reduce seed set for self-compatible and self-incompatible species and does this reduction depend on recipient and donor self-compatibility? 3) Does heterospecific pollen interference depend on recipient and donor relatedness? By addressing these questions, we aimed to shed new light on the complex interplay of factors that determine the distribution and abundance of plant species within co-flowering communities. Ultimately, gaining a deeper understanding of the mechanisms underlying heterospecific pollen interference could help inform conservation efforts aimed at preserving endangered species.

Material and Methods

Study species

We used a total of eight species (see Table S 1) with different distribution and IUCN red list status within Switzerland. All species are co-occurring in the lime-rich crop fields habitat (“Caucalidion” according to the classification by Delarze, Gonseth, Eggenberg, & Vust, 2015), insect-pollinated and have overlapping flowering times in nature (Landolt et al., 2010; Lauber, Wagner, & Gygax, 2018). We classified species as “common” if their IUCN status in Switzerland was “least concern”, and as rare otherwise. IUCN status in

Switzerland correlated strongly with number of observation within Switzerland pooled between the years 2000 and 2020 (cor: 0.86, p-value < 2.2×10^{-16}). Breeding system (self-compatible vs self-incompatible) was extracted from the BioFlor database (Kuehn, Durka, & Klotz, 2004). To test the relationship between recipient-donor relatedness and heterospecific pollen interference, we constructed a phylogenetic tree for our species (see Figure S 1) by pruning a modified version (Malecore, Dawson, Kempel, Müller, & van Kleunen, 2018) of the dated DaPhnE supertree of Central European plant species (Durka & Michalski, 2012) and then calculated the phylogenetic distance using the cophenetic function of the “ape” package (Paradis, E. Claude & Strimmer, 2004) in R.

Experimental set-up

We sowed all species into 12 cm x 17 cm trays filled with Seedling substrate (Klasmann-Deilmann GmbH, 49741 Geeste, Germany) and put them into the dark coolroom at -4°C for stratification between 5 and 8 weeks. Once seeds would start to germinate, we moved the trays to a greenhouse compartment. We transplanted seedlings into 11 cm x 11 cm x 12 cm pots filled with Selmaterra (fertilized heavy soil with 30% volume peat, see Table S 2). We randomized pots on tables of a single greenhouse compartment and watered as well as fertilized regularly. We treated aphids and fungi whenever necessary.

All species flowered between May 2021 and October 2021. To assure continuing of flowering, we regularly cut untreated flowers. To assess the effect size of heterospecific pollen interference, we performed hand pollinations among all species and measured seed set (yes/no) and seed number (counts). For the heterospecific pollen treatment, we prepared a saturated mix of conspecific pollen and heterospecific pollen and applied it to the stigma of the recipient flower. For each flower treated with heterospecific pollen mixture, we treated a second flower on the same plant individual on the same day with conspecific pollen only as a control, using the same conspecific pollen donor that we used for the heterospecific pollen mix. The two flowers with heterospecific and conspecific treatment would constitute a pair with the same “pair ID” (see Figure 1). Pollen grain number per anther differed greatly depending on individual and on anther ripeness, thus we standardized treatment by always applying a pollen amount above saturation level. We extracted the pollen for the treatments from the anthers by tapping them on a glass slide and with the help of tweezers, and then mixed it for the heterospecific treatment using tweezers. We then applied the pollen mixture (HP) or the conspecific pollen (CP) to the open stigma of the recipient flower. To avoid selfing, we emasculated recipient flowers by removing the anthers some days before treatment. For some species (*Bupleurum rotundifolium*, *Fallopia convolvulus*, *Myosotis arvensis*), anther removal would cause too much flower damage due to the small size, thus anthers were not removed. For these species, selfing could not be completely excluded.

For each donor-recipient combination, we treated between 2 and 16 flower pairs (HP and CP; median: 12 flower pairs per donor-recipient combination). We collected seeds after ripening, and counted them either by hand or by using an imaging method with imageJ (Abramoff, Magalhaes, & Ram, 2004) (for *Papaver rhoeas*, see “Protocol seed counting in ImageJ” in Supporting Information).

Statistical analysis

Do pollen type and recipient status affect seed set and seed number?

To test whether seed set and seed number are affected by pollen type (conspecific=0, heterospecific=1) and whether the effect size depends on recipient status (common=0, rare=1), and to account for the high proportion of zeroes (~24%), we run a hurdle model using the function *glmmTMB* of the homonymous package (Brooks et al., 2017). In a hurdle model, zero counts and non-zero counts are treated as two separate categories, meaning that a binomial model is fitted for zeroes vs non-zeroes (the “zero-inflated” model), and a separate model for the non-zero counts only (“conditional model”). For the conditional model, we used a truncated negative binomial error distribution (“truncated nbinom2” in *glmmTMB*). We implemented the same formula for both the zero-inflated and the conditional model, with pollen type (conspecific vs

heterospecific), recipient status (rare vs common) and their interaction as fixed effects. To account for non-independence, we included pair ID, treatment date, recipient species, recipient individual ID and donor individual ID as random factors.

After running the models, we used the functions *emmeans* and *pairs* of the *emmeans* package (Lenth, 2023) to calculate the 95% confidence intervals of the estimated marginal mean for each group (conspecific and heterospecific treatments for common and rare recipients) and to test for significance of the comparisons of interest (conspecific vs heterospecific treatment for common recipients, conspecific vs heterospecific treatment for rare recipients).

Does donor status affect seed set and seed number ?

To explore in more detail the effects of donor and recipient status on seed set and seed number, we separately analyses a subset including only the HP treatment. We run a hurdle model using the function *glmmTMB* of the homonymous package with recipient status (common=0, rare=1), a dummy factor indicating whether the heterospecific pollen donor was of the same or the opposite status (same=0, opposite=1), as well as their interaction, as fixed effects. We included the same random factors as in the previous model (pair ID, treatment date, recipient species, recipient individual ID and donor individual ID).

After running the models, we used the functions *emmeans* and *pairs* of the *emmeans* package to calculate the 95% confidence intervals of the estimated marginal mean for each group (heterospecific treatment for common and rare recipients with common and rare donors) and to test for significance of the comparisons of interest (heterospecific treatment: common donors vs rare donors on common recipients, common donors vs rare donors on rare recipients).

Do recipient and donor self-compatibility affect seed set and seed number?

To test whether seed set and seed number are affected by the self-compatibility of recipient and donor species in interaction with heterospecific pollen deposition, we repeated the same analyses as above, replacing recipient and donor status with recipient and donor self-compatibility.

Does recipient-donor relatedness affects seed number?

To test whether the phylogenetic distance between recipients and donors affects seed set and seed number, we calculated for all non-zero counts the log-response ratio of seed-number with HP treatment on seed number with CP treatment, within each pair (same pair ID). We then fitted a Gaussian *glmmTMB* model including recipient-donor phylogenetic distance, recipient status (common=0, rare=1), a dummy factor indicating whether the heterospecific pollen donor was of the same or the opposite status (same=0, common=1), as well as all their interactions, as fixed effects. To account for non-independence, we included treatment date, recipient species, donor species, recipient individual ID and donor individual ID as random factors.

After running the model, we used the functions *emmtrends* of the *emmeans* package to calculate the estimated trends with their 95% confidence intervals for the relationship between log-response ratio and recipient-donor relatedness for each group (common recipient with common donor, common recipient with rare donor, rare recipient with rare donor, rare recipient with common donor).

For all models, we inspected Pearson residuals for homogeneity of variance against all grouping variables.

Results

At the end of the experiment, we successfully treated 1320 flowers (660 flower pairs). Zero counts made up 24% of the total data, and seed number ranged from 1 to 1282 seeds per flower (depending on species), with a median of 4 seeds per flower.

The effect of pollen type, recipient and donor status on seed set and seed number

Heterospecific pollen did not reduce seed set, and neither seed number (see Figure S 2-3, Table S 3-4. Overall, rare species tended to have higher seed number compared to common species, but this trend was not significant. Similarly, recipient status and donor status did not affect seed set nor seed number (see Figure S 4-5, Table S 5-6).

The effect of recipient and donor self-compatibility on seed set and seed number

Self-incompatible recipient species showed a lower seed set probability compared to self-compatible species (SI/SC odds ratio = 0.0206, SE = 0.0416, p-Value = 0.05). This effect was independent of pollen type treatment (see Figure 2 and Table 1-2). Seed number was not affected by self-compatibility of recipient and donor species). (see Figure S 6-8; Table S 7-8).

The effect of recipient-donor relatedness on seed number

Overall, phylogenetic relatedness between recipient and donor species did not affect the strength of HPI. For rare recipients with rare donors, HPI tended to decrease with relatedness ($\Delta_{\text{irr}}/\Delta_{\text{PD}} = -0.0017$, SE = 0.0010, p-Value = 0.08), with more distantly related recipient-donor species pairs less affected by HP. (see Figure 3 and Table 3-4).

Discussion

Surprisingly, in our study heterospecific pollen interference did not affect seed set nor seed number, i.e. it did not affect whether a flower would produce or not at least one seed nor the amount of seeds produced. Rare species had a tendency to produce more seeds, but this trend was not significant. Breeding system did affect seed set, but not in relationship with conspecific or heterospecific pollen treatments, with self-incompatible species less likely to set seed compared to self-compatible species. Lastly, we could show that for rare recipients treated with pollen from rare donors, more distantly related recipient-donor species pairs had a lower reduction in seed number compared to closely related recipient-donor species pairs. Hereafter we discuss these results as well as potential ecological and evolutionary implication.

In a co-flowering community, we can expect common species to receive pollen from a rare species unfrequently, thus an adaptation to that type of pollen is unlikely. On the other hand, a rare species is likely to receive frequently pollen from common species, thus making an adaptation to heterospecific pollen receipt more likely, like predicted by the tolerance-hypothesis (Hao et al., 2023). Indeed, in a study by Arceo-Gomez and colleagues (Arceo-Gómez et al., 2016) the authors showed how HP tolerance for a *Clarkia* species did depend on previous exposure of the population to HP, but rather than acting on the recipient individual, would act on the donor individual, by improving CP performance. On the other hand, such adaptation was not observed for a congeneric *Clarkia* species, suggesting that adaptation is context- and species-specific. Adaptation could explain the low effect of HP overall in our study species. On the other hand, despite our study species do co-occur and co-flower in nature, the seed-material did not consistently originate from populations co-occurring at local scale, but co-occurring only at regional scale, thus missing potential adaptations at the population level. Further, the (co-occurrence) history of the populations from which the seed material was collected is unknown.

Another factor we analyzed is the evolutionary relatedness, measured as phylogenetic distance, between recipient and donor species in interaction with recipient and donor status. While overall no pattern emerged, we could show a decrease of HPI for more distantly related recipient-donor pairs when both were rare. The likely reason for the absence of these patterns for common recipients and rare recipients with common donors could be the lack of close relatives for these groups in our study species set. Indeed, the range for these groups included only phylogenetic distances larger than 189×10^6 years. For closely related recipient-donor pairs, a stronger HPI could be caused by similar recognition systems between recipient stigma and donor pollen

grains. For a better understanding of these patterns, a study species set with a broader range should be used.

In this study we looked only at pairwise HP interactions, while in a plant community it is likely to have multi-species mixes of HP that are transferred between flowers. Arceo-Gomez (T. Ashman & Arceo-Gómez, 2011) performed HP hand-pollinations with mixes up to three species and showed that HPI increased with the number of heterospecific pollen donors. Further, the strength depended on specific species composition. Indeed, in our study, HPI varied considerably among different species-pairs. Some species are known to produce strongly allelopathic pollen (Kanchan & Chandra, 1980), but in our study it did not look like a specific species had a consistent negative effect on all other species in terms of HPI (see Figure S 9).

For our species, self-incompatible species showed an overall lower seed set, while breeding system did not affect seed number or HPI in any way. Self-compatibility might play a role especially in a natural community, where HP can act through the mentor effect (de Nettancourt, 1997), and allowing for self-fertilization even in self-incompatible flowers, with consequent ovule abortion (Lynn, Sullivan, & Galen, 2022). In our study we showed how self-incompatible species are less likely to produce seeds even when enough pollen is present. We emasculated our recipient species whenever possible prior to treatment, but due to the small flower size, three out of eight species were left with their anthers to avoid complete flower abortion. These three species (*Bupleurum rotundifolium*, *Fallopia convolvulus* and *Myosotis arvensis*) are all self-compatible. Thus, one explanation could be that seed set induced by selfing is more secure compared to seed set from outcrossed pollen, despite the genetic advantages of outbreeding.

Specific flower morphology and in particular a smaller stigma size in restrictive flowers (i.e. flowers with a reduced access to the flower interior) have been shown to reduce HP deposition, while at the same time increasing CP deposition (Montgomery & Rathcke, 2012). In our study, we did not analyze the effect of flower morphology or flower traits, since due to our small sample size in species number (eight species in total), species and trait would be confounded. In a natural community, flower morphology would also play an important role in terms of pollinator sharing and flower constancy (the tendency of pollinators to forage on the same flower type (Waser, 1986)) since some flowers are adapted to specific groups of pollinators and thus sharing among these species is more likely. For example, both *Ajuga chamaepitys* and *Fallopia convolvulus*, being lip flowers, rely on bumblebees as their most common pollinators (Kuehn et al., 2004).

While in our study we did not find any strong effect of HP on seed set and seed number, HPI remains an important aspect of co-flowering communities (T. L. Ashman & Arceo-Gómez, 2013), since it allows species to affect other species without direct competition and at a distance above the direct interactions. In a co-flowering community; we can expect a variable and complex pollination landscape that could promote evolution of flower morphology and avoidance mechanism also due to HPI. It seems that while mechanisms as HPI and adaptations to it do play a role in shaping plant communities, this patterns are highly variable depending on the context and on the species observed. We conclude that heterospecific pollen interference plays a minor role for rare plant species. Rather, other factors, like pollen limitation mediated by low pollinator visitation rates, are likely to affect rare plant species at the level of interactions. Adaptation and species-specific interactions may explain the low overall effect of HPI in our study. The complexity of multi-species interactions and the specific composition of heterospecific pollen mixes may further influence the strength of HPI. Additional research is needed to explore these factors and their implications for both in-sit and ex-situ conservation strategies.

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Authors' contributions

E.M. developed the idea for the study, collected the data, analysed the data, and prepared a first draft of the manuscript. M.F. revised the manuscript and provided useful insight during the writing process.

Data accessibility

The data that supports the findings of this study is available on Dryad <https://doi.org/10.5061/dryad.x69p8czs3>.

Competing interests

The authors declare no competing financial interests.

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