The structure of flower visitation webs: how morphology and abundance affect interaction patterns between flowers and flower visitors

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chapter 5

General summary

Not so long ago the relationships between plants and their pollinators were seen as mainly specialized and co-adapted. The concept of pollination syndromes, *i.e.* a certain combination of flower traits that reflects the morphology, physiology and behaviour of a certain visitor group (*e.g.* bees, butterflies or birds), represents this view. However, the idea that interactions between flowers and flower visitors are mainly specialized seems to be mostly a consequence of studying species with specialized interactions. Screening of whole flower visitation webs has shown instead that specialization in the interactions between flowers and flower visitors is rather the exception than the rule. Overall, the degree of ecological generalization varies, even locally, from one to more than hundred interaction partners. Moreover, not only does the degree of generalization across plant species or across flower visitor species differ substantially, there is also a great variation in the degree of generalization of a plant or a visitor and the degree of generalization of its interaction partners. The dominant pattern found is asymmetrical, that is, generalized plants tend to interact with generalized and specialized visitors and specialized plants tend to interact with generalized visitors, and vice versa for the animals.

The mechanisms leading to this variation in the number of interaction partners and the resulting interaction patterns found in flower visitation webs are still poorly understood. In this thesis I tested the role of two simple rules structuring interaction patterns between flowers and flower visitors. The first rule is based on the observation that rewards provided by plants to attract animals to pollinate their flowers differ greatly in their accessibility. The second rule is based on the observation that flower visitor individuals tend to freely distribute themselves in proportion to the available recourses over patches of flowering plants. I tested the importance of these rules by comparing observed interaction patterns in a Mediterranean flower visitation web with expected patterns based on simulation models incorporating these rules. I restricted the analysis in this study to nectar producing plant species and nectar searching visitor species because of the size constraints we wanted to test.

In CHAPTER 2 I studied three possible morphological constraints: the depth and width of tubular structures hiding the nectar (nectar holder depth and width) and the size of flower parts that visitors can land on (size of the alighting place). In addition I tested the role of flower abundance for the number of visitor species. I hypothesized that the stronger the size constraints and the lower the flower abundance, the fewer visitor species on a plant species will be found. Indeed, nectar holder depth, nectar holder width and number of flowers explained a large part of the variation in the number of visitor species. The size of the alighting place did not restrict the body length of the visitors and was not related to visitor species number. The potential number of visitor species, that is the number of species in the local species pool that met the threshold criterion, was significantly positively correlated with the observed number of species. I also found that the observed visitors were a random selection out of the potential visitors. The means of the observed and expected proboscis length means were highly correlated.

In CHAPTER 3 I argued further that if size constraints and interactions proportional to abundance determine the number of interaction partners, these rules should be able to predict whether a plant species interacts with a generalized or a specialized flower visitor, *i.e.* they should also explain the degree of asymmetry in interaction patterns. The Monte Carlo simulations showed that both morphological constraints (nectar holder depth) and abundance were able to generate asymmetric patterns of specialization. However, only nectar holder depth was able to predict the level of asymmetry for an individual species. Thus, asymmetric specialization seems to be primarily the result of the depth threshold. Only when visitors meet the threshold criterion random sampling proportional to abundance plays a role.

In the second part of Chapter 3 I tested the potential consequences of these rules for the extinction risk of species. The simulation models provided the possibility to test if asymmetry is able to equalize extinction risks of generalized and specialized species as proposed in the literature. I hypothesized that, even if the stability of the whole web is stronger if it is asymmetrically structured, the short term extinction risk for morphologically generalized species will be lower than for morphologically specialized species. The simulations indicated that asymmetry caused by a size threshold should indeed lead to higher extinction risk of specialists. In the study system specialists were less abundant than generalists. Therefore, including abundance in the simulation models enlarges the difference in extinction risk between specialists and generalists.

In the last step (Chapter 4) I tested the influence of size thresholds and size distributions across species and individuals on the degree of morphological matching between proboscis lengths and nectar holder depths. The degree of morphological matching can be an important factor influencing visitation rates and per-visit pollination efficiencies of flower visitors. If it is true that a size threshold determines the degree of generalization, and generalization dominates in flower visitation webs, most plant and visitor species should show a high degree of morphological mismatching. However, the frequency distribution of traits across the potential interaction partners will also influence the average degree of matching. By using a simple analytical modeling approach based on size thresholds and interactions proportional to the frequency of traits I showed that a right-skewed distribution of proboscis lengths and a left-skewed distribution of nectar holder depths theoretically will lead on average to equal degrees of matching for all species, all other combinations will produce stronger differences. The analysis of the Mediterranean flower visitation web revealed that proboscis lengths and nectar holder depths were both right-skewed distributed across species and individuals. As predicted by the model, flower visitors with a long proboscis matched on average the nectar holder depth of the flowers less closely than those with a short proboscis, while plant species with shallow and deeply hidden nectar matched their interaction partners on average equally closely. The observed deviations from model expectations will serve as a starting point to search for additional factors that influence visitation patterns.

CHAPTER 5

General conclusion

In this thesis I have shown that the combination of two simple rules can explain surprisingly well a great deal of the observed interaction patterns between plants and flower visitors in a Mediterranean flower visitation web: firstly, the size threshold that the nectar holder depth puts on the proboscis length of potential flower visitor; and secondly, random interactions proportional to the frequency of nectar holder depths and proboscis lengths in the local species pool. To describe the interaction patterns I used the degree of ecological generalization, the degree of interaction asymmetry and the degree of morphological matching. The size threshold and interactions proportional to abundance can explain the observed variation in the number of interaction partners, *i.e.* the degree of ecological generalization. Both rules can also generate the observed asymmetry patterns in the relationship between plants and flower visitors, *i.e.* morphologically generalized plants interact mainly with morphologically specialized visitors and morphologically specialized plants with morphologically generalized visitors. They are also sufficient to predict quite closely the overall pattern of morphological matching between nectar holder depth and proboscis length of plant and visitor species. The average degree of morphological matching for visitors and plants was strongly influenced by the shape of the frequency distributions, which was right-skewed and resemble a lognormal distribution for both nectar holder depths and proboscis lengths. Given these results, the importance of determining size constraints and measuring size distributions across species and individuals in the local species pool of plants and flower visitors has to be emphasized. Including size constraints and size distributions is essential for constructing realistic simulation models which should be used to yield a better understanding of plant–flower visitor interaction patterns at the level of the community. Knowledge about interaction patterns and the underlying causes of these patterns is essential for understanding the evolution of plants and their pollinators. It also will provide an important tool for biodiversity conservation.