Passionflowers and their Birds, Bees and Butterflies

The ecology and evolution of pollination and herbivory in Passiflora

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This thesis includes a general introduction to the genus *Passiflora*, four manuscripts and a Danish summary. The manuscripts describe aspects of the ecology and evolution of a selected set of *Passiflora* species. The first manuscript concerns the vulnerability to habitat fragmentation of the specialised pollinator-plant interaction between *P. mixta* and the Sword-billed hummingbird *Ensifera ensifera* in the Andean highlands. The second describes the factors influencing fruit set in the hermit-pollinated Amazonian species *P. vitifolia.* The third compares flower morphology and scent chemistry in twelve *Passiflora* species, and the fourth elucidates the importance of factors influencing the level of herbivory in five sympatric rainforest species.

The genus *Passiflora* comprises some 450 species, mainly occurring in tropical and subtropical America, where they grow in habitats ranging from desert to rain forest and from sea level to 4,500 metres in the Andes. The genus is not only known for its showy passion flowers and its tasty passion fruits, but also for its sophisticated interactions with both pollinators and herbivores. The very variable flowers are specialised to pollinators such as bees, wasps, hummingbirds and bats. The main herbivores of *Passiflora* is the larvae for the Heliconiine butterflies. The interactions between *Passiflora* and Heliconiine have been suggested as an example of coevolution.

The fragility of extreme specialisation: Passiflora mixta *and its pollinating hummingbird* Ensifera ensifera

Extreme specialisation between plants and their pollinators is expected to be very sensitive to habitat fragmentation, since the loss of one interactant inevitably will affect the other. In the present study, the effect of habitat fragmentation on the specialised interactions between the long-tubed flowers of *Passiflora mixta* and its extremely long-billed pollinator, the Sword-billed hummingbird *Ensifera ensifera*,

was studied in natural forest and in open land. Pollen collection from skinned specimens of *E. ensifera* contained high levels of *Passiflora* pollen and indicated that this hummingbird is a frequent and important visitor of *Passiflora*. Low fruit set was observed in open land, where *E. ensifera* was lacking in both 1994 and 1995. Higher fruit set was found in the forest, where *E. ensifera* was a frequent visitor of *P. mixta*. Only the lack of *E. ensifera* in the open land could explain the reduced fruit set. This study may therefore represent an example of a vital breakdown of a specialised plant-pollinator interaction due to habitat fragmentation. We suggest that many endemic *Passiflora* species in the Andean highlands are threatened due to the disappearance of their pollinator. The study of pollination and seed set of these species would therefore be good indicators of 'health of the community'.

Trap-line pollination and fruit fate in Passiflora vitifolia *(Passifloraceae) in the Peruvian Amazonas*

Tropical plants at low densities are often pollinated by trap-lining animals. The lowland rainforest species *Passiflora vitifolia* (Passifloraceae) is pollinated by trap-lining hermits. In Peruvian Amazonas we studied its pollinator activity, the influence of flowering pattern on pollinator visitation, and the effect of visitation on fruit set. The White-bearded Hermit was the primary pollinator. The number of visits per hour increased with numbers of open flowers on the vine, whereas the arrival time of the first hermit after flower opening was not influenced by numbers of open flowers. The visitation rate did not influence fruit set. Flight routes of hermits were mapped by the daily addition of fluorescent dye powder to anthers on one vine. The rediscovery of fluorescent dye and timing of visits to individual vines showed that hermit flight routes were entangled with each other. The fate of all developing fruits was followed. Factors influencing flowering, fruiting and abortion on levels of population and individual vines were studied. About 24% of the flowers set fruits. Most new fruits were aborted during the first five days, indicating genetic incompatibility. Later abortion was mainly due to fruit parasitism. Flowering, fruiting and abortion of individual vines were to some extent synchronised on population level responding to overall conditions in the region, whereas correlations within individual vines indicated energy trade-offs.

The independence of floral morphology and scent chemistry as trait groups in a set of Passiflora *species*

A presence of broad pollination flower syndromes suggests that floral traits

such as form, colour and scent are correlated. We examined whether flower morphology and the scent chemistry of a set of *Passiflora* (Passifloraceae) species could be regarded as one or two floral traits, and examined the relative importance of phylogeny and present-day ecology to this pattern. Floral morphology divided the species into three major groups varying in flower colour, nectar accessibility and spatial arrangement of reproductive organs. Four species were scentless, with scentless species occurring in all three morphological groups. The scent profile for each of the eight remaining species was unique. Twenty-six mostly parsimonious trees were constructed from 19 vegetative characters, one being chosen for further analysis by incorporating two additional flower morphological characters. Comparison between species was more conservative when analyses were corrected for phylogeny. Only two positive correlations were found between morphological and scent chemistry, indicating that floral morphology and scent are independent. Therefore, we expect them to serve different ecological functions during pollination of the flowers.

Variation in leaf herbivory among coexisting Amazonian Passiflora *species*
Two interacting Amazonian rain forest communities of five *Passiflora* species and a set of herbivores were analysed. Among the latter were two Heliconiine species. *Passifloras* always grew in relatively light parts of the forest, whereas Heliconiines foraged independently of light. The *Passiflora* species had a linear rank-abundance relationship and larger species were rarer than smaller ones. Their general morphology was described by 16 shoot variables and was in accordance with the literature. Leaf herbivory was extensive and the most damaging herbivores were Heliconiines. The area consumed per leaf was constant irrespective of *Passiflora* species. Species with more extrafloral nectaries had a higher density of ants. The level of herbivory measured, as a percentage of leaf area per herbivory, differed between shoots within species, but not between species. The *Passiflora* species varied in leaf abortion risk and the number of attacked leaves. *Passiflora quadrangularis* suffered the least, and *P. micropetala* was the most severely attacked.