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Faculty of Science

Pollination ecology of coexisting species

Ph.D. Thesis

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ANNOTATION

Biotic pollination is essential mutualistic relationship that has developed between flowering plants and animals. Long-term co-evolution has given rise to a number of mutual adaptations in both plant and pollinators. However, the topics related to pollination syndromes, specialization of pollination partners or entire communities, pollinator preferences, legitimacy or effectiveness of particular pollinators, and specialized pollinator guilds are little explored in tropical areas.

This thesis is composed of six original studies which are focused on several plant species co-flowering in dry season and on their visitors in mountain tropical areas in Cameroon, one of the important biodiversity hotspot. The synthesis of these studies reveals the processes on pollinator and plant community level.

DECLARATION [IN CZECH]

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LIST OF PAPERS AND AUTHOR'S CONTRIBUTION

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Janeček Š, Hrázský Z, **Bartoš M**, Brom J, Reif J, Hořák D, Bystřická D, Riegert J, Sedláček O and Pešata M (2007): Importance of big pollinators for the reproduction of two *Hypericum* species in Cameroon, West Africa. *African Journal of Ecology* 45: 607–613 (IF=0.631).
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Bartoš M, Tropek R, Spitzer L, Padyšáková E, Janšta P, Straka J, Tkoč M and Janeček Š. Specialization of pollination systems of two co-flowering "generalised" *Hypericum* species in Cameroon (manuscript).
Michael Bartoš participated in experiment preparation and data collection in the field; and was responsible for data assembly, partially for statistical analysis and for writing the manuscript.

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CHAPTER I

General introduction

General introduction

Biotic pollination is key mutualistic relationship that has developed between the two kingdoms of organisms – flowering plants and animals. While this relationship is beneficial for both sides, the main goal for plants is reproduction, for animal pollinators it is primarily a source of food. Given that the vast majority of flowering plants (94% in tropical communities) are pollinated by animals (Ollerton et al., 2011), pollination is one of the most important biotic factors which influence population dynamics, and thus the structure of communities. Long-term co-evolution has given rise to a number of mutual adaptations in both plants and pollinators, and animal pollination is usually associated with rapid diversification of species (Kay et al., 2009). Pollination ecology is a relatively old scientific discipline whose origins can be traced back to the end of the eighteenth century (Sprengel, 1793) and represents a synthesis across many different biological disciplines. Although enjoying considerable popularity among scientists, many fundamental questions in pollination ecology are still discussed and remain unanswered (Mayer et al., 2011). The theme of pollination syndromes, which constitute one of the pillars of pollination ecology, remains current as well as the study of specialization of pollination partners or entire communities. An increasing number of detailed studies, mainly from tropical areas, and new scientific approaches raise a lot of questions around pollinator preferences, legitimacy or effectiveness of particular pollinators and specialized pollinator guilds.

Pollination syndromes

In the 19th century, based on a set of flower traits and observation of flower visitors Federico Delpino (1870) had developed schemes which became the basis for pollination syndromes concept (Vogel, 1954, Faegri and van der Pijl, 1979). This concept pointed to the considerable convergence of flowers across evolutionarily distant plant lineages and assumed that several well distinguishable floral types evolved as an adaptation to fertilization by particular types of pollen vectors, to abiotic pollination by wind or water, as well as to biotic pollination by animal groups such as birds, butterflies or bees.
Fenster et al. (2004) proposed expanded approach to pollination syndromes, according to which can pollinators be clustered into functional groups (e.g., long-tongued flies, small nectar collecting bees, etc.), behaving in similar ways on a flower and exerting similar selection pressures, which generate correlations among floral traits (long and narrow corolla tubes, pollen presented in a certain way, particular nectar quantities and concentrations, etc.). This approach

accepted the original pollination syndromes concept, but placed more emphasis on the functional properties of visitors than their taxonomical affiliation.

In the last two decades the long-standing concept of pollination syndromes was questioned and the breadth of the concept was debated by many authors (Herrera, 1996; Ollerton, 1996; Waser et al., 1996).

Ollerton et al. (2009) conducted global test of the pollination syndrome hypothesis in a multivariate 'phenotype space' defined by the syndromes and showed that almost no plant species fall within the discrete syndrome clusters. Furthermore, in approximately two-thirds of plant species, the most common pollinator could not be successfully predicted. Although this result may seem very poor, Ollerton et al. (2009) points out that: "if one assumes (say) that half of all plant species have generalized flowers, then successful prediction in one-third of all species might evoke the opposite reaction". Ollerton et al. (2009) didn't refuse pollination syndromes as such but challenged the global importance of pollination syndromes in the traditional conception.

Specialization versus generalization

Pollination syndrome concept assumes predominance of co-evolutionary processes leading to specialization in accordance with Stebbin's "most effective pollinator principle"(Stebbins, 1970) which implied that floral characteristics are formed by pollinators which are visiting plant the most frequently and/or are the most efficient pollinators. But the dichotomy between specialization and generalization in pollination systems could be very confusing, because, in fact, pollination systems are rather a continuum between plants pollinated by one pollinator species and plants pollinated by hundreds of pollinator species. Although it was frequently assumed that symmetric specialization occurs in species' interactions (specialists interact with specialists and generalists with generalists), Vázquez and Aizen (2004) drew attention to asymmetric plant–pollinator interaction, which implies that specialized plants are often pollinated by generalist pollinators whereas generalized plants are pollinated by both specialist and generalist pollinators. Ollerton et al. (2007) noted that phenotypic specialization does not necessarily always equate with ecological specialization as phenotypic specialists may be ecological generalists and vice versa. Many studies which dealt with pollination systems of communities in the level of pollination webs suggest plant and pollinator assemblages rather generalized (Herrera, 1996; Ollerton, 1996; Waser et al., 1996).

Pollination webs

Pollination webs (which in general are mapping and documenting the interaction of all plants and visitors in a community) had become a very useful tool for statistical analysis of the relationship but this approach had resulted in suppressing the importance of individual associations (Jordano et al., 2006). Pollination webs give more information about the quantity of interactions than on their quality and are often focused only on pairwise interactions (which animals visit which plant) but they do not deal with frequencies of these visits. In addition, quantification of visitor data is often misleading because the most abundant visitors are frequently not the best pollinators (Ollerton, 1996; Johnson and Steiner, 2000). Pollination networks which include only visitors who contacted any part of the plant reproductive organs are rather an exception (but e.g. Petanidou and Potts, 2006) because such detailed observations are very difficult in the field during transect surveys.

Visitors vs. pollinators

However, web studies where many plant species with specialized plants were frequently visited by broad spectrum of different pollinators often ignore the fact that not all visitors are effective pollinators. Many of them are illegitimate visitors which consume rewards without any benefit for the plant's reproduction and in some cases illegitimate visitors of flower may outnumber the pollinators in diversity or abundance (Inouye, 1980). Inouye (1980) divided these visitors who did not participate in pollination into two groups – robbers, who when attempting to reach the nectar often damage the flower, and thieves, who reach the nectar without any flower damage. Nectar loss or damage of flower or its reproductive parts may result in decreasing flower attractiveness for legitimate pollinators and thus negatively affect the reproductive success of the plant. But as is summarized in a review about nectar robbers by Maloof and Inouye (2000), there may also be indirect benefits to flowers due to changes in pollinator behaviour and they point out that nectar robbing is a common phenomenon that may have evolutionary implications.
Pollination effectiveness is considered the main criterion which determines the degree of mutual adaptation between pollinators and plants. Pollination effectiveness which includes rates of visitation, pollen removal, and pollen deposition had been found to vary between seasons, mainly due to change of visitation rates (Fishbein and Venable,1996). If animal species visiting flowers differ in their effects on the fitness of the plant, then variation in the composition of the assemblage of visitors will most likely result in variation in selective pressures on the plant. Scientists pay great attention especially to birds, as they

are important pollinators in tropical areas and are represented by several evolutionarily quite distant groups with special morphological adaptations allowing them to feed on nectar (Stiles, 1978; Cheke et al., 2001). They studied their degree of specialization (Johnson and Nicolson, 2008), feeding preferences (Nicolson and Fleming, 2003), and their influence on plant evolution (Martinez del Rio et al., 2001). However, while on hummingbirds - the most specialized bird-pollinator - a sufficient number of studies has been done, sunbirds who are nectarivorous specialists in the Old World tropics have been studied on the African continent almost exclusively in South Africa, i.e. at the edge of their area.

Rewards

Most flowering plants whose reproduction is strictly dependent on animal pollination, attract their visitors, who are potential pollinators, with some reward, usually with nectar and/or pollen.

      Floral nectar which represents the most common form of reward is a complex chemical fluid composed of many dissolved substances with multiple different functions. Sugars dominate the total solutes in floral nectar and represent the major energy source for visitors (Wykes, 1952; Hocking, 1968; Gill and Wolf, 1975). Nectar chemical composition permanence within phylogenetically related taxa and positive pollinator adaptation to its components are questions that pollination biologists have posed (Percival, 1961; Percival, 1965; Baker and Baker, 1982, 1990). Most of nectars can be classified as either sucrose or hexose and the association of hexose nectars with ornithophily and sucrose nectars with entomophily was commonly accepted for both basal and derived species (Dupont et al., 2004). However, recently the relation of the nectar sugar composition to the pollinator class has also been repeatedly questioned (e.g. Galetto and Bernardello, 2004; Chalcoff et al., 2006; Wolff, 2006; Schmidt-Lebuhn et al., 2007).

      It is generally accepted that the dynamics of nectar production co-evolved with the requirement of plant pollinators. Detailed morphological characteristics of floral nectaries and nectar secretion were examined in many plant families (Stpiczyńska et al., 2003; Masierowska, 2003; Rosa and Scatena, 2007; Cawoy et al., 2008). Nectar secretion is strongly influenced by floral morph type, plant age and flower position. Nectar is secreted with particular rhythms throughout the lifespan of a flower.

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Objectives and content of the thesis

Although there is large number of detailed studies from the Mediterranean and the temperate zone (e.g. Petanidou and Lamborn, 2005; Pott et al., 2006), relatively little work has been done on pollination biology in Africa, and only a very small portion of pollination relationships has so far been studied. Much of the research which has been done is of evolutionary nature and very little work has been conducted at the community level (Rodger et al., 2004). One of the few well-explored regions is South Africa, which, however, hostes very specific vegetation significantly different from the rest of the continent which lies mostly in the tropical zone. While most of the previous works dealt only with one species and its interacting partners, or were studying the pollination webs that lack a more detailed approach to individual interactions, the main objective of this thesis was to describe in detail pollination systems of coexisting species at the community level. We tried to look at communities of coexisting species from several different points of view, and also from both plants and pollinators perspective to create a comprehensive view on relationship in a community based on detailed studies of its components. In six case studies, we have focused on several plant species richly co-flowering in dry season and on their visitors in poorly explored mountain tropical areas in Cameroon, which is one of important hotspots of biodiversity. The main objectives of this thesis are: (i) to compare and evaluate distinctions in nectar and nectar production of bird-pollinated and other differently specialized plant species, (ii) to assess the influence the density of resources has on the selectivity of visitors, (iii) to interpret the role of particular visitors and evaluate their pollination efficiency on reproductive success of selected plants and (iv) to compare assemblage of visitors and pollinators on morphologically generalized similar flowers differing mainly in the reward and assess their ecological specialization.

Chapter II compares the nectar properties of sunbird pollinated plant *Impatiens sakeriana* with the nectar properties of six other co-flowering species and focuses on the specificity of nectar in plants that are pollinated by birds.

Chapter III focuses on feeding behaviour of three sunbird species on the nectar of five plant species with different phenotypic complementarity and observes the impact of resource abundance on bird selectivity.

Chapter IV describes the highly specialised pollination system of *Impatiens sakeriana* which can be pollinated only by two often hovering sunbirds and discusses the role of nectar thieves in the co-evolution of a plant and its pollinators.

Chapter V deals with the effect individual visitors have on the reproductive success of *Hypoestes aristata* and use two statistic models based on single-visit data and frequency data to determine their positive as well as neutral or negative impacts. The degree of specialization in pollination system of *H. aristata* is discussed here.

Chapter VI examines the influence of big pollinators on the reproduction success of *Hypericum roeparianum* and *H. revolutum* and discusses the coexistence of closely related species with similar floral traits in the same plant communities.

Chapter VII compares composition of pollinators assemblage in two closely related *Hypericum spp.* and discusses the importance and effectiveness of pollinator groups. The importance of different methods of collecting insects and detail tracking of visitor behaviour is underlined.

Chapter VIII summarises the main results of this thesis.

References:

Baker, H.G., Baker, I., 1982. Chemical constituents of nectar in relation to pollination mechanisms and phylogeny. In: Nitecki, M.H. (Ed.), Biochemical aspects of evolutionary biology. Proceedings of the 4th Annual Spring Systematics Symposium. University of Chicago Press, Chicago, pp. 131–172.

Baker, H.G., Baker, I., 1990. The predictive value of nectar chemistry to the recognition of pollinator types. Israel Journal of Botany 39,157–166.

Cawoy, V., Kinet, J.-M., Jacquemart, A.-L., 2008. Morphology of nectaries and biology of nectar production in the distylous species *Fagopyrum esculentum*. Annals of Botany 102, 675–684.

Chalcoff, V.R., Aizen, M.A., Galetto, L., 2006. Nectar concentration and composition of 26 species from the temperate forest of South America. Annals of Botany 97, 413–421.

Cheke, R.A., Mann, C.F., Allen, R., 2001. Sunbirds: A guide to the sunbirds, flowerpeckers, spiderhunters and sugarbirds of the world. Christopher Helm, London.

Delpino, F.,1870. Ulteriori osservazioni e considerazioni sulla dicogamia nel regno vegetale. Giuseppe Bernardoni.

Dupont, Y.L., Hansen, D.M., Rasmussen, J.T., Olesen, J.M., 2004. Evolutionary changes in nectar sugar composition associated with switches between bird and insect pollination: the Canarian bird-flower element revisited. Functional Ecology 18, 670–676.

Faegri, K., van der Pijl, L., 1979. The principles of pollination ecology, third revised edition. Pergamon Press, Oxford xii, p. 244.

Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R., Thomson, J.D., 2004. Pollination syndromes and floral specialization. Annual Review of Ecology, Evolution, and Systematics 35, 375–403.

Fishbein, M., Venable, D.L., 1996. Diversity and temporal change in the effective pollinators of *Asclepias tuberosa*. Ecology, 1061–1073.

Galetto, L., Bernardello, G., 2004. Floral nectaries, nectar production dynamics and chemical composition in six *Ipomoea species* (Convolvulaceae) in relation to pollinators. Annals of Botany 94, 269–280.

Gill, F.B., Wolf, L.L., 1975. Economics of feeding territoriality in the golden-winged sunbird. Ecology 56, 333–345.

Hocking, B., 1968. Insect-flower associations in high arctic with special reference to nectar. Oikos 19, 359–388.

Inouye, D.W., 1980. The terminology of floral larceny. Ecology 61, 1251–1253.

Johnson, S.D., Nicolson, S.W., 2008. Evolutionary associations between nectar properties and specificity in bird pollination systems. Biology Letters 4, 49–52.

Johnson, S.D., Steiner, K.E., 2000. Generalization versus specialization in plant pollination systems. Trends in Ecology & Evolution 15, 140–143.

Jordano, P., Bascompte, J., Olesen, J.M., 2006. The ecological consequences of complex topology and nested structure in pollination webs. In: Waser, N.M., Ollerton, J. (Eds.), Plant–pollinator interactions: from specialization to generalization. University of Chicago Press, Chicago, pp. 173–199.

Kay, K.M., Sargent, R.D., 2009. The role of animal pollination in plant speciation: integrating ecology, geography, and genetics. Annual Review of Ecology, Evolution, and Systematics 40, 637–656.

Maloof, J.E., Inouye, D.W., 2000. Are nectar robbers cheaters or mutualists?. Ecology 81, 2651–2661.

Martinez del Rio, C., Schondube, J.E., McWhorter, T.J., Herrera, L.G., 2001. Intake responses in nectar feeding birds: digestive and metabolic causes, osmoregulatory consequences, and coevolutionary effects. American Zoologist 41, 902–915.

Masierowska, M.L., 2003. Floral nectaries and nectar production in brown mustard (*Brassica juncea*) and white mustard (*Sinapis alba*) (Brassicaceae). Plant Systematics and Evolution 238, 97–107.

Mayer, C., Adler, L., Armbruster, W.S., Dafni, A., Eardley, C., Huang, S.-Q., Kevan, P.G., Ollerton, J., Packer, L., Ssymank, A., Stout, J.C., Potts, S.G., 2011. Pollination ecology in the 21st Century: key questions for future research. Journal of Pollination Ecology 3, 8–23.

Nicolson, S.W., Fleming, P.A., 2003. Nectar as food for birds: the physiological consequences of drinking dilute sugar solutions. Plant Systematics and Evolution 238, 139–153.

Ollerton, J., 1996. Reconciling ecological processes with phylogenetic patterns: the apparent paradox of plant-pollinator systems. Journal of Ecology 84, 767–769.

Ollerton, J., Alarcon, R., Waser, N.M., Price, M.V., Watts, S., Cranmer, L., Hingston, A., Peter, C.I., Rotenberry, J., 2009. A global test of the pollination syndrome hypothesis. Annals of Botany 103, 1471–1480.

Ollerton, J., Killick, A., Lamborn, E., Watts, S., Whiston, M., 2007. Multiple meanings and modes: on the many ways to be a generalist flower. Taxon 56, 717-728.

Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? Oikos 120, 321–326.

Percival, M.S., 1961. Types of nectar in angiosperms. New Phytologist 60, 235–281.

Percival, M.S., 1965. Floral Biology. Pergamon Press, Oxford.

Petanidou, T., Lamborn, E., 2005. A land for flowers and bees: studying pollination ecology in Mediterranean communities. Plant Biosystems 139, 279–294.

Petanidou, T., Potts, S.G., 2006. Mutual use of resources in Mediterranean plant–pollinator communities: how specialized are pollination webs? In: Waser, N.M., Ollerton, J. (Eds.), Plant–pollinator interactions: from specialization to generalization. University of Chicago Press, Chicago, pp. 220–244.

Potts, S.G., Petanidou, T., Roberts, S., O'Toole, C., Hulbert, A., Willmer, P., 2006. Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape. Biological conservation 129, 519–529.

Rodger, J.G., Balkwill, K., Gemmill, B., 2004. African pollination studies: where are the gaps? International Journal of Tropical Insect Science 24, 5–28.

Rosa, M.M., Scatena, V.L., 2007. Floral anatomy of Paepalanthoideae (Eriocaulaceae, Poales) and their nectariferous structures. Annals of Botany 99, 131–139.

Schmidt-Lebuhn, A.N., Schwerdtfager, M., Kessler, M., Lohaus, G., 2007. Phylogenetic constraints vs. ecology in the nectar composition of Acanthaceae. Flora 202, 62–69.

Sprengel, C. C., 1793. Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen.-Berlin, Vieweg 1793. Vieweg.

Stebbins, G.L., 1970. Adaptive radiation of reproductive characteristics in angiosperms. I: pollination mechanisms. Annual Review of Ecology, Evolution, and Systematics1, 307–326.

Stiles, F.G., 1978. Ecological and evolutionary implications of bird pollination. American Zoologist 18, 715–727.

Stpiczynska, M., Davies, K.L., Gregg, A., 2003. Nectary structure and nectar secretion in *Maxillaria coccinea* (Jacq.) L.O. Williams ex Hoge (Orchidaceae). Annals of Botany 93, 87–95.

Vázquez, D.P., Aizen, M.A., 2004. Asymmetric specialization: a pervasive feature of plant-pollinator interactions. Ecology 85, 1251–1257.

Waser, N.M., Chittka, L., Price, M.V., Williams, N.M., Ollerton, J., 1996. Generalization in pollination systems, and why it matters. Ecology 77, 1043–1060.

Wolff, D., 2006. Nectar sugar composition and volumes of 47 species of Gentianales from a southern Ecuadorian montane forest. Annals of Botany 97, 767–777.

Wykes, G.R., 1952. The preferences of honeybees for solutions of various sugars which occur in nectar. Journal of Experimental Biology 29, 511–519.

Nectar properties of the sunbird-pollinated plant *Impatiens sakeriana*: A comparison with six other co-flowering species

Nectar properties of the sunbird-pollinated plant *Impatiens sakeriana*: A comparison with six other co-flowering species

Abstract

Adaptations of the nectar traits in bird-pollinated flowers are amongst the most discussed aspects of floral evolution. In the case of sunbird-pollinated plants, data on nectar traits originate almost exclusively from the South African region and are very scarce for tropical Africa, where paradoxically the highest sunbird diversity occurs. Here we present a study on the nectar properties of a sunbird-pollinated plant, *Impatiens sakeriana*, growing in the West African mountains, including the nectar production, diurnal changes in the nectar standing crop, the nectar concentrations, the nectar volumes, total sugar amounts and sugar composition. Moreover we compare the nectar traits of *I. sakeriana* with six other co-flowering insect-visited plant species.

Our results showed that many nectar properties, including high volume (approx. 38 μL in flowers unvisited by sunbirds), low sugar concentration (approx. 30% w/w) and high sucrose content (95%), are specific to *I. sakeriana*, compared to the insect-visited plants. These are in accordance with the most recent theory that nectar properties of the sunbird-pollinated plants are similar to those pollinated by hummingbirds.

Abstrakt

Adaptace nektaru na ptačí opylovače patří při studiu evoluce květů k velmi diskutovaným tématům. V případě rostlin opylovaných strdimily pochází převážné množství informací o vlastnostech nektarů především z oblasti jižní Afriky a tropické oblasti Afriky, kde je největší biodiverzita strdimilů, bývají opomíjeny. Zde jsou prezentovány vlastnosti nektaru u strdimily opylovaného druhu *Impatiens sakeriana*, který se vyskytuje v horách západní Afriky. Byla sledována produkce nektaru, změny v denní nabídce nektaru, koncentrace nektaru, objem nektaru, celkové množství cukrů a jejich zastoupení v nektaru. Tyto vlastnosti byli porovnávány s vlastnostmi nektaru u šesti hmyzem navštěvovaných rostlin kvetoucích společně s druhem *I. sakeriana*.

Naše výsledky ukázaly, že mnoho vlastností nektaru u druhu *I. sakeriana*, mezi které patří velký objem nektaru, nízká koncentrace cukrů a vysoké zastoupení sacharózy, jsou v porovnání s druhy opylovanými hmyzem specifické. Tyto výsledky jsou v souladu s názorem, že nektar u rostlin

opylovaných strdimily má obdobné vlastnosti jako nektar u rostlin opylovaných kolibříky.

Následující pasáž o rozsahu 21 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.
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Food selection by avian floral visitors: an important aspect of plant–flower visitor interactions in West Africa

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Food selection by avian floral visitors: an important aspect of plant–flower visitor interactions in West Africa

Abstract

Community-level studies have shown that plant–pollinator interactions are much more generalized than previously expected. Consequently, many authors have questioned the significance of phenotypic complementarity between plants and pollinators and abundance effects in pollination interactions. Here, we compare the behaviour of three sunbird species feeding on the nectar of five plant species in afromontane vegetation. We studied the feeding behaviour with and without consideration of plant abundance (i.e. diet selectivity and diet composition, respectively). The aims of the study were to estimate: (1) how relative resource abundance influences flower selectivity; (2) the degree of phenotypic matching; and (3) whether different plant resource assessment methods give different answers to this question. The results showed that, although sunbirds frequently feed on both morphologically adapted and nonadapted plants, food selectivity data are consistent with the hypothesis of phenotypic complementarity. Moreover, we found that the type of plant abundance measurement can change conclusions in some cases, as individual plants differ in their growth habits and nectar production. This effect was most obvious for the assessment of selectivity of the northern double-collared sunbird (*Cinnyris reichenowi*) and for *Hypoestes aristata*, a plant producing inflorescences composed of a large number of small flowers possessing small amounts of nectar per flower (a high abundance of flowers, but a low abundance of nectar relative to the remaining plant community).

Abstrakt

Studie na úrovni společenstev odhalily, že vztahy mezi rostlinami a opylovači jsou daleko více generalizované než se očekávalo. V důsledku toho mnozí autoři zpochybňují jak význam fenotypové komplementarity mezi rostlinami a opylovači, tak i vliv abundance na polinační interakce. V této studii jsme porovnávali chování tří druhů strdimilů živících se nektarem na pěti afromontánních rostlinách. Studovali jsme jejich potravní chování s ohledem na abundanci rostlin (tj. potravní selektivitu) i bez efektu abundance rostlin (tj. potravní složení). Cílem studie bylo odhadnout: (1) jak relativní abundance zdrojů ovlivňuje výběr květů; (2) stupeň fenotypové komplementarity mezi

rostlinou a opylovačem; a (3) zda různé metody vyhodnocování rostlinných zdrojů dají různé odpovědi na tyto otázky. Výsledky ukázaly, že ačkoliv se strdimilové často živí na všech rostlinách bez ohledu na to, zda jsou na ně adaptováni, při zaměření na selektivitu jsou data v souladu s hypotézou fenotypové komplementarity. Navíc jsme zjistili, že způsob měření abundance rostlin může v některých případech ovlivnit závěry, neboť jednotlivé rostliny se liší v růstové formě i produkci nektaru. Tento efekt byl nejzřetelnější v případě strdimila *Cinnyris reichenowi* a rostliny *Hypoestes aristata*, která má květenství složená z velkého počtu drobných květů produkujících malé množství nektaru na květ (vysoká abundance květů, ale nízká abundance nektaru vzhledem ke zbývajícím rostlinám ve společenstvu).

Následující pasáž o rozsahu 19 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.
Podíl studenta na publikaci: 20%

Hovering sunbirds in the Old World: occasional behaviour or evolutionary trend?

Hovering sunbirds in the Old World: occasional behaviour or evolutionary trend?

Abstract

The nectarivory of sunbirds in the Old World and hummingbirds in the New World evolved independently. While both groups are specialised in their feeding apparatuses, hummingbirds are moreover famous for their adaptations to sustained hovering flight. Recently, an example of a pollination system of the invasive plant *Nicotiana glauca* has been used to show that less adapted sunbirds also are frequently able to hover. Nevertheless, the question has remained why plants adapted to bird hovering pollination do not occur outside the New World. In this paper we show that the long-peduncle Cameroonian *Impatiens sakeriana* is not capable of autonomous selfing and can be pollinated only by two often hovering sunbirds, the Cameroon sunbird *Cyanomitra oritis* and the northern double-collared sunbird *Cinnyris reichenowi*. Our study revealed that this plant is highly specialised for pollination by *C. oritis*. *Cinnyris reichenowi* hovers less frequently and often thieves nectar by piercing the flower spur when perching. This study shows that pollination systems occurring in the Old World follow similar evolutionary trends as systems including hovering hummingbirds in the New World.

Absrtakt

Nektarivorie se u strdimilů ve Starém světě a u kolibříků v Novém světě vyvinula nezávisle. Ačkoliv obě skupiny mají specializované zobáky k sání nektaru, kolibříci jsou navíc známí pro své adaptace k vířivému letu. Nedávno bylo na příkladu polinačního systému invazní rostliny *Nicotiana glauca* ukázáno, že hůře adaptovaní strdimilové jsou také často schopni třepotání u květů. Nicméně otázkou zůstává, proč se rostliny přizpůsobené k opylování třepotajícími ptáky nevyskytují mimo Nový svět. V tomto článku představujeme dlouze stopkatou kamerunskou netýkavku *Impatiens sakeriana*, která není schopna samoopylení a je opylována pouze dvěma často třepotajícími strdimily, druhy *Cyanomitra oritis* a *Cinnyris reichenowi*. Naše studie ukázala, že *I. sakeriana* je úzce specializovaná na opylení druhem *C. oritis*. *Cinnyris reichenowi* třepotá méně často a nezřídka i krade nektar tak, že při přisednutí ke květu probodává květní ostruhu. Tato studie ukazuje, že polinační systémy vyskytující se ve Starém

světě vykazují podobné evoluční trendy jako systémy zahrnující vířivý let novosvětských kolibříků.

Následující pasáž o rozsahu 11 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.
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Generalization versus specialization in pollination systems: visitors, thieves, and pollinators of *Hypoestes aristata* (Acanthaceae)

Generalization versus specialization in pollination systems: visitors, thieves, and pollinators of *Hypoestes aristata* (Acanthaceae)

Abstract

Many recent studies have suggested that the majority of animal-pollinated plants have a higher diversity of pollinators than that expected according to their pollination syndrome. This broad generalization, often based on pollination web data, has been challenged by the fact that some floral visitors recorded in pollination webs are ineffective pollinators. To contribute to this debate, and to obtain a contrast between visitors and pollinators, we studied insect and bird visitors to virgin flowers of *Hypoestes aristata* in the Bamenda Highlands, Cameroon. We observed the flowers and their visitors for 2-h periods and measured the seed production as a metric of reproductive success. We determined the effects of individual visitors using 2 statistical models, single-visit data that were gathered for more frequent visitor species, and frequency data. This approach enabled us to determine the positive as well as neutral or negative impact of visitors on *H. aristata*'s reproductive success. We found that (i) this plant is not generalized but rather specialized; although we recorded 15 morphotaxa of visitors, only 3 large bee species seemed to be important pollinators; (ii) the carpenter bee *Xylocopa* cf. *inconstans* was both the most frequent and the most effective pollinator; (iii) the honey bee *Apis mellifera* acted as a nectar thief with apparent negative effects on the plant reproduction; and (iv) the close relationship between *H. aristata* and carpenter bees was in agreement with the large-bee pollination syndrome of this plant. Our results highlight the need for studies detecting the roles of individual visitors. We showed that such an approach is necessary to evaluate the pollination syndrome hypothesis and create relevant evolutionary and ecological hypotheses.

Abstrakt

Nedávné studie naznačují, že většina rostlin opylovaných živočichy vykazuje mnohem větší rozmanitost opylovačů, než je očekávalo vzhledem k jejich polinačnímu syndromu. Tato generalizace, založená především na datech z polinačních sítí, je zpochybňována s tím, že mnozí návštěvníci zahrnutí do polinačních sítí nejsou efektivními opylovači. Abychom ozřejmili rozdíl mezi návštěvníky a opylovači, studovali jsme hmyzí a ptačí návštěvníky doposud

nenavštívených květů druhu *Hypoestes aristata* v kamerunské oblasti Bamenda Highlands. Sledovali jsme květy a jejich návštěvníky ve dvouhodinových periodách a zaznamenávali produkci semen, která byla měřítkem reprodukční úspěšnosti. Efekt jednotlivých návštěvníků byl stanoven pomocí dvou statistických modelů využívajících jedno-příletových dat získaných u nejčastějších návštěvníků a frekvenčních dat. Tento přístup nám umožnil určit pozitivní, stejně jako neutrální nebo negativní vliv návštěvníků na reprodukční úspěšnost druhu *H. aristata*. Zjistili jsme, že (i) tato rostlina není generalizovaná ale spíše specializovaná; přestože jsme zaznamenali 15 morfologických skupin návštěvníků, pouze 3 druhy velkých včel se zdaly být důležitými opylovači; (ii) drvodělka *Xylocopa* cf. *inconstans* byla nejčastějším a nejefektivnějším opylovačem; (iii) včela *Apis mellifera*, která se chovala jako zlodějka nektaru, měla zjevný negativní dopad na rozmnožování rostlin; a (iv) úzký vztah mezi druhem *H. aristata* a drvodělkami byl v souladu s polinačním syndromem této rostliny. Naše výsledky zdůrazňují potřebu prací zaměřených na detailní studium rolí jednotlivých návštěvníků. Ukázali jsme, že tento přístup je nezbytný pro správné vyhodnocení polinačních syndromů a navrhování dalších ekologických a evolučních hypotéz.

Následující pasáž o rozsahu 17 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.
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CHAPTER VI

Importance of big pollinators for the reproduction of two *Hypericum* species in Cameroon, West Africa

Importance of big pollinators for the reproduction of two *Hypericum* species in Cameroon, West Africa

Abstract

Two woody *Hypericum* species (*H. roeparianum* and *H. revolutum*) often coexist in forest edge and stream mantle communities in the Bamenda-Banoso Highlands, Cameroon. Morphologically nonspecialized flowers of both species are visited by specific eye-catching visitors. Nectarless flowers of *H. roeparianum* are visited by a large carpenter bee *Xylocopa* sp. (Hymenoptera) and nectar-producing flowers of *H. revolutum* are the main source of nectar for sunbirds (*Cyanomitra oritis*, *Cinnyris reichenowi* and *C. bouvieri*). Using a manipulative experiment, we showed that the carpenter bee plays an important role in the reproduction success of *H. roeparianum*, whereas sunbirds affect seed production of *H. revolutum* only little. We suggest that a clear differentiation of pollination niches enables the coexistence of both *Hypericum* species. The study showed that the pollination system of *H. roeparianum* with morphologically nonspecialized flowers can be ecologically specialized. Sunbirds are not decisive for the reproductive success of *H. revolutum* and thus have only little selection pressure on its floral traits. The results indicate the importance of reproduction success assessment in pollination studies.

Abstrakt

Dva druhy třezalek (*H. roeparianum* a *H. revolutum*) často koexistují v lesním okraji a lemové potoční vegetaci v Bamenda-Banoso Highlands, Kamerun. Morfologicky nespecializované květy obou druhů jsou navštěvovány specifickými nápadnými návštěvníky. Květy druhu *H. roeparianum*, které neprodukují žádný nektar, jsou navštěvovány velkými drvodělkami rodu *Xylocopa* (Hymenoptera) a nektar produkující květy druhu *H. revolutum* jsou hlavním zdrojem nektaru pro strdimily (*Cyanomitra oritis*, *Cinnyris reichenowi* a *C. bouvieri*). Pomocí manipulativního experimentu jsme ukázali, že drvodělka hraje důležitou roli v reprodukční úspěšnosti druhu *H. roeparianum*, zatímco strdimilové ovlivňují produkce semen druhu H. revolutum jen velice málo. Zdá se, že jasná diferenciace polinačních nik umožňuje koexistenci obou druhů rodu *Hypericum*. Studie ukázala, že polinační systém druhu *H. roeparianum* s morfologicky nespecializovanými květy může být ekologicky specializovaný. Strdimilové nejsou rozhodující pro reprodukční úspěch druhu *H. revolutum*, a tak mají jen

malý selekční tlak na své květní znaky. Výsledky ukazují, že reprodukční úspěšnost a její posouzení hraje důležitou roli v polinačních studiích.

Následující pasáž o rozsahu 11 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.
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Specialization of pollination systems of two co-flowering "generalised" *Hypericum* species in Cameroon

Bartoš M, Tropek R, Spitzer L, Padyšáková E, Janšta P, Straka J, Tkoč M, Janeček Š (manuscript)

Specialization of pollination systems of two co-flowering "generalised" *Hypericum* species in Cameroon

Abstract

It is a general assumption that plants with phenotypicaly generalized flowers are pollinated by width spectrum of floral visitors. Here we compare pollination systems of two closely related co-flowering *Hypericum* species (*H. roeperianum* and *H. revolutum*) with phenotypically generalized flowers. We found that both phenotypically generalized *Hypericum spp.* are highly functionally specialized. Although they are visited by many different groups of visitors, reproductive organs of both *Hypericum spp.* were primarily contacted by visitors belonging to Hymenopterans. *H.roeperianum* seems to be much more specialized than *H. revolutum*, because almost all pollination service is mediated only by narrow groupe of *Xylocopa spp.* Our study demonstrated that also phenotipically generalized flowers can be functionally highly specialized and that not only knowledge on presence of visitors but also their behaviour is crucial for understanding to pollination systems of individual plant species.

Abstrakt

Je obecným předpokladem, že fenotypově generalizované květy jsou opylovány širším spektrem návštěvníků. Zde porovnáváme polinační systémy dvou úzce příbuzných společně kvetoucích druhů rodu *Hypericum* (*H. roeperianum* a *H. revolutum*) s fenotypově generalizovanými květy. Zjistili jsme, že oba fenotypově generalizované druhy rodu *Hypericum* jsou značně funkčně specializované. Přestože jsou navštěvovány mnoha různými skupinami návštěvníků, reprodukčních orgánů u obou druhů se dotýkali především návštěvníci patřící k řádu Hymenoptera. Druh *H. roeperianum* se zdá být specializovanější než druh *H. revolutum*, neboť téměř veškeré kontakty s bliznou mají na svědomí zástupci rodu *Xylocopa*. Naše studie prokázala, že také fenotypově generalizované květy mohou být funkčně vysoce specializované, a že nejen znalosti o přítomnosti návštěvníků, ale i jejich chování jsou klíčové pro pochopení polinačních systémů jednotlivých rostlinných druhů.

Podíl studenta na publikaci: 70%

Introduction

Last few decades, debates in pollination biology are often focused on specialisation and generalisation in plant pollination systems (e.g., Waser et al., 1996; Johnson and Steiner, 2000; Waser and Ollerton, 2006; Ollerton et al., 2009). It has been repeatedly shown that not nearly all floral visitors are real pollinators, as many of them consume floral rewards without any benefits for plant reproduction (e.g. Padyšáková et al., 2013**)**. In some cases, the number of the reward thieves visiting a flower may even outnumber the pollinators in both diversity and abundance (Inouye 1980). Nevertheless, these relationships were studied presumably in pollination systems of plant with more or less specialized flowers, where any visitor-plant relationship could be expected, whilst generalised flowers are rather neglected.

One of the simplest and very common floral shape is an open disk (Willmer, 2011). The radial flowers with a centrally situated cluster of anthers have usually shallow exposed nectaries (when present) and both pollen and nectar are thus easily available to visitors (Willmer, 2011). Besides real pollinators (Simpson and Neff, 1981) these flowers are known to be often visited for different reasons, such as stealing the flower rewards or waiting for mates, hosts or prey without any contribution to plant's reproduction (Simpson and Neff, 1981). Having no obvious specialised morphology, plants with these floral characteristics, which are ordinarily considered to be generalists. This floral shape occurred in the earlier linages of angiosperms since the angiosperm-pollinator coevolution started (Friis et al., 2011). Nevertheless, a presence of such generalized flowers in many evolutionarily advanced lineages suggests that they are not necessarily primitive traits (Weberling, 2007).

Ollerton et al. (2007) distinguished between three main ways how to define generalization of flowers: 1/ *phenotypic* – i.e. open access flowers (as above-mentioned), where the rewards are available for width spectrum of floral visitors; 2/ *ecological* – flowers pollinated by relatively high number of species; and 3/ *functional* – flowers are pollinated by relatively high number of functional groups (e.g. by bees, flies and birds; see also Fenster et al., 2004). Ollerton et al. (2007) also noted that phenotypic specialization does not necessarily always equate with ecological and/or functional specialization as phenotypic specialists may be ecological and/or functional generalists, a vice versa.

Pollination-web based studies indicated that majority of plants are more generalized than it was expected from the pollination syndromes hypothesis (Waser et al., 1996). Similarly Olesen and Jordano (2002) notes that extensive generalization in plant–pollinator interactions is the rule rather than the exception, and demonstrates that very few plant or pollinator taxa are indeed specialized. But much of the studies of pollination webs, however, do not

distinguish between visitors and pollinators (Dicks, 2002; Forup and Memmott, 2005), although only little proportion of visitors recorded in pollination webs are effective pollinators (Sabatino et al., 2010; Aizen et al., 2008). The data for these studies are moreover collected by different ways. In these studies the all insect visiting flowers (Dicks et al., 2002; Forup and Memmott, 2005), insect on any part of reproductive organs (i.e stamens or styles; Sabatino et al., 2010; Aizen et al., 2008) or insect which contacted the receptive parts of the flower only (i.e. anthers or stigma; Neuschulz et al., 2012) is collected.

In this paper, we focused on testing the mentioned theoretical discrepancies between phenotypic and other specialization of flowers. The objects of our study were two co-flowering, phylogenetically closely related (Meseguer et al., 2013) *Hypericum spp.* with flat flowers visited by numerous insect functional groups (Fig. 1, Bartoš et al., 2012). These two species differ in offered floral rewards: whereas *H. roeperianum* offer pollen only, *H. revolutum* produce also relatively high amount of nectar (Janeček et al., 2007; Bartoš et al., 2012), which allows us to study generalized flower with different strategies of their pollinators rewarding. Both studied plants are relatively common (both locally and across Africa) and their rich rewards should make them important in African ecological networks (Janeček et al., 2012). More specifically, we focused on five main questions: 1) How broad are spectra of visitors in both studied *Hypericum* species? 2) Which visitors are potentially effective pollinators in distinct *Hypericum* species? 3) Is diversity and abundance of both visitors and pollinators of nectar-offering *H. revolutum* higher? 4) What is the overlap between visitors and potential pollinators between target *Hypericum* species? 5) Are distinct methods of the sampling of visitors (e.g. collection from whole flowers vs. from their reproductive organs) comparable?

Materials and methods

Study species

We targeted two *Hypericum spp.* with flowers of similar morphology and similar size of stamen cluster and gyneceum. In the study area, they often occur in mixed populations.

Hypericum roeperianum Schimp. ex A. Rich. (Syn. *H. riparium* A. Chev.) is a shrub or small tree up to 5 m tall, with yellow radially symmetrical large flowers 5–7 cm in diameter placed in terminal cymes (Fig 1A). Flower longevity is about three days and flowers do not produce any nectar. Its reproduction seems to depend on large pollinators, probably carpenter bees (Janeček et al., 2007), but the pollination system has never been studied in detail. *H. roeperianum* grows in West Africa, Angola, Congo, eastern tropical Africa, Ethiopia, Sudan, located in evergreen forests and bushlands, moist bamboo

thickets and grasslands in upland and submontane regions, often along rivers and streams (Robson, 1961).

   Hypericum revolutum Vahl. (Syn. *H. lanceolatum* Lam.) is a shrub or tree up to 12 m high, with smaller flowers 4–6 cm in diameter growing solitarily on shoot apices (Fig 1B). Yellow radially symmetric flower has nectaries at the base of each of five petals. Flower longevity is about two days with cumulative nectar production higher than 19 µl per flower (Bartoš et al., 2012). *H. revolutum* is known to be frequently visited by sunbirds, which, however, contribute only little to its pollination (Janeček et al., 2007; Janeček et al., 2012). *H. revolutum* is widespread throughout Africa and Arabian Peninsula, in submontane evergreen forest and bushlands, and in stream-sides of upland and submontane grasslands (Robson, 1961).
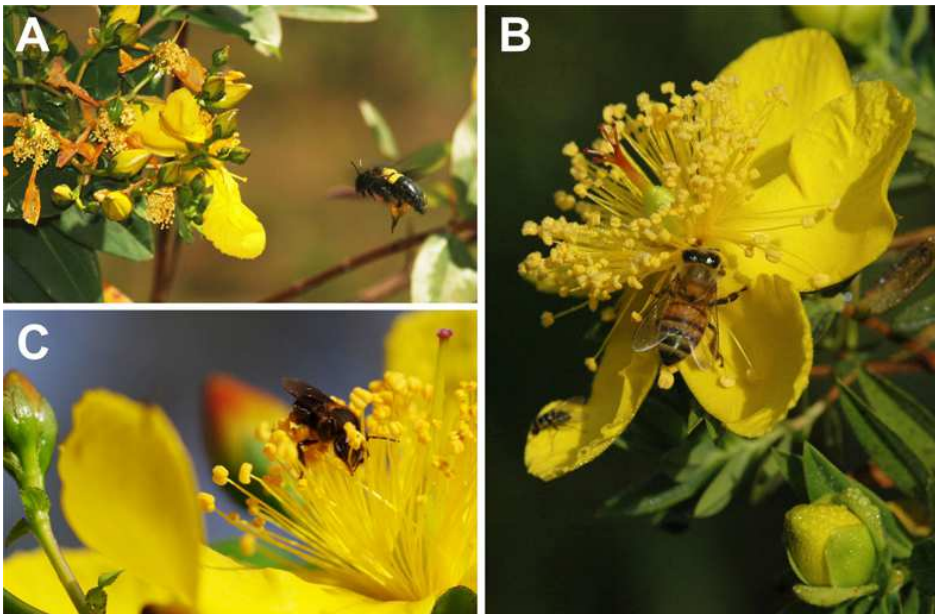
Figure 1. Visitors of *Hypericum roeperianum* and *H. revolutum*. **A/** *Xylicopa cafra* visiting *H. roeperianum*. **B/** *Apis mellifera* searching for nectar on a flower of *H. revolutum* and resting fly. **C/** *Meliplebeia ogouensis* collecting pollen on *H. roeperianum*.

Study area and sites

All fieldworks were carried out in the Mendong Buo area, near the Big Babanki village, the Bamenda Highlands, North-West Province, Cameroon (06°05′26″ N, 10°18′09″E; 2200 m a.s.l.) from November 2009 to January 2010. The study area experiences a single wet season from March/April to mid-November, with the precipitation ranging from 1780 to 2290 mm/year (Cheek et al., 2000). The

area includes a mosaic of remnants of species-rich submontane tropical forests dominated mainly by *Schefflera abysinica* , *S. manii* , *Bersama abyssinica* , *Syzigium staudtii* , *Carapa grandiflora* and *Ixora foliosa* , intensive pastures dominated by *Sporobolus africanus* and *Pennisetum clandestianum*, extensive species-rich grasslands and shrubs with *Geniosporum rotundifolium*, *Saturea robusta*, *Pycnostachys eminii*, *Hypoestes aristata, Hypericum revolutum, H. roeperianum* and *Gnidia glauca*, gallery vegetation along streams with *Brillantaisia lamium*, *Pentas schimperiana*, *Virectaria major* , and vegetation dominated by bracken on abandoned pastures and forest clearings.*.*

Visitors and their behaviour

To identify a local diversity of insect visitors of the two *Hypericum spp.* we collected insect visitors on flowers of 106 individuals of each plant species. Insects were sampled by two distinct methods: (i) all insects present on whole flowers, and (ii) insects touching the plant reproductive organs (stigma or anther) only. Each method was applied separately on 53 different individuals of each studied *Hypericum spp.* Insect visitors were caught with entomological nets, forceps and exhaustors for 15 min. per shrub. Specimens from the most abundant taxonomical groups (Hymenoptera: Parasitica, Hymenoptera: Apoidea, Diptera and Coleoptera; together, they cover more than 90% of all collected visitors) were later classified to morphospecies.

We also focused on behaviour of the distinct visitors on flowers to reveal their potential role in the studied plants pollination systems more precisely. After the insect sampling, each shrub was observed for 20 min and behaviour of all visitors categorised to 19 morphotaxonomical (functional) groups according to their possible role in the pollination system, relative abundance and possibility to recognise them without catching (modified after Williams and Adam, 2001 and Fenster et al., 2004: small and large beetles (Coleoptera); hoverflies (Diptera: Syrphidae); small and large unspecialised flies (Diptera); highly specialised bees with long tongues (Hymenoptera: Xylocopini); two species of bees with large societies: *Apis mellifera* and *Meliplebeia ogouensis* (Hymenoptera: Apinae); bees with small societies together with solitary species (Hymenoptera: Apinae); small and large parasitoid hymenopterans (Hymenoptera: Parasitica); ants (Hymenoptera: Formicoidea); sawflies (Symphyta); leafhoppers (Hemiptera: Auchenorrhyncha); true bugs (Hemiptera: Heteroptera); whiteflies (Hemiptera: Aleyrodidae); aphids (Hemiptera: Apidoidea); thrisps (Thysanoptera); moths (Lepidoptera)) was recorded. Interactions of individual visitors of distinct flowers were considered as independent records. We distinguished three types of the behaviour: (i) *nectar consumption* and/or collecting, (ii) *pollen consumption* and/or collecting, and (iii) any *other behaviour* not related to these two plants'

food rewards. We also recorded any contacts with the plant reproductive organs, i.e. stigma and anther.

Data analyses

Differences in univariate response variables (numbers of individuals, species and functional groups) between plant species and method of insect collection were tested by two-factorial ANOVA in STATISTICA 10 (StatSoft, Inc. 2011). Differences in composition of communities visiting both *Hypericum spp.* and caught by the two sampling methods were tested by Permutational MANOVA´s using Euclidean distances between individual plants in PERMANOVA+ for PRIMER (Anderson et al., 2008). Data were log transformed to improve normality and homoscedasticity.

Results

A relatively high diversities of insect visitors were recorded on both studied *Hypericum spp.* We identified 77 morphospecies visiting *H. revolutum* and 70 morphospecies visiting *H. roeperianum* (Appendix 1), but only 17 and 14 of them were regular visitors who were recorded more then 5-times (Table 1).
Numbers of insect individuals, morphospecies and functional groups did not significantly differ between the plant species. Differences were found in comparing the two methods of insects sampling (Table 2), because only a few morphospecies from the total visiting assemblages were caught on the flower reproductive organs.

Table 1. Number of insect morphospecies according to major taxonomical groups.

	H. revolutum	*H. roeperianum*	both *Hypericum sp.*
Parasitica	8	5	4
Apoidea	4	5	3
Diptera	2	0	0
Coleoptera	3	4	3

The two plant species significantly differed in composition of the visiting assemblages (Table 3, Fig. 2). On the other hand, the most abundant visiting morphospecies were presumably shared by the two *Hypericum spp.* (Fig. 3). Similarly, with sorting of insects into the functional groups, the significant differences between the two studied plants disappeared (Table 3).

Table 2. Comparison of the number of individuals, species and functional groups on *Hypericum* species (Factorial ANOVA).

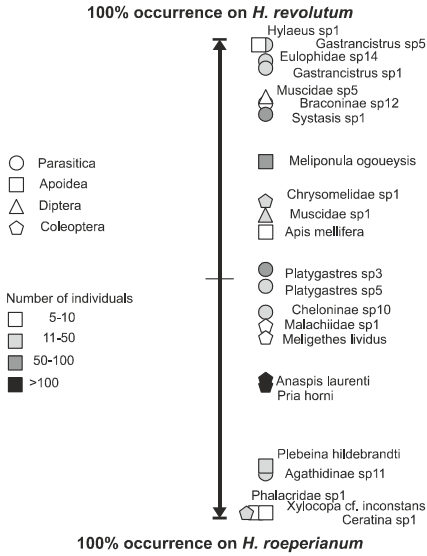|	No. of individuals (logN)		No. of species (logS)		No. of functional groups	
	F	p	F	p	F	p
Hypericum spp. (H)	0.01	0.922	2.08	0.151	0.09	0.769
Metod (M)	24.63	0.000	26.39	0.000	31.93	0.000
H x M	0.01	0.923	0.15	0.698	0.05	0.826

Among visitors sampled from the plant reproductive organs the proportion of bees in the most abundant visitor species is twice higher in comparison with insects the whole flowers (i.e., 4 vs. 2 in *H. roeparianum*, and 2 vs. 1 in *H. revolutum*). Besides this, the species composition of the most abundant visitors collected by both methods is very similar within the two plant species.

Table 3. Comparison of the visitor assemblages composition on Hypericum species (PERMANOVA).

	Species		Morphotaxonomical funcional groups		Taxonomical groups	
	Pseudo-F	p (perm)	Pseudo-F	p (perm)	Pseudo-F	p (perm)
Hypericum spp. (H)	4.741	0.001	7.142	0.001	5.605	0.002
Metod (M)	4.486	0.001	11.087	0.001	13.696	0.001
H x M	2.088	0.014	2.483	0.026	1.619	0.163

Patterns in behaviour of the individual functional groups visiting the studied *Hypericum spp.* are shown in Fig.4. Behaviour not related to nectar and pollen prevails in all abundant visitors of *H. roeparianum*, except *M. ogouensis*, *Xylocopini*¸and *other bees*, which visit the flowers almost exclusively for collecting of pollen. In *H. revolutum*, proportion of pollen consumption was generally similar. Nevertheless, majority of the abundant visitors concentrated on nectar rewards to the detriment of other behaviour. H*. revolutum* was visited by insects mainly for nectar while pollen collecting was rather marginal and "other Apidae" were its only important collectors. Contacts with the plant reproductive organs (Fig. 5) are generally congruent to the behaviour patterns, as visitors looking for pollen or nectar rewards contacted both anthers and

Insect taking on all parts of a flower

100% occurrence on _H. revolutum_

Hylaeus sp1
Gastrancistrus sp5
Eulophidae sp14
Gastrancistrus sp1
Muscidae sp5
Braconinae sp12
Systasis sp1

Meliponula ogoueysis

Chrysomelidae sp1
Muscidae sp1
Apis mellifera

Platygastres sp3
Platygastres sp5
Cheloninae sp10
Malachiidae sp1
Meligethes lividus

Anaspis laurenti
Pria horni

Plebeina hildebrandti
Agathidinae sp11
Phalacridae sp1
Xylocopa cf. inconstans
Ceratina sp1

100% occurrence on _H. roeperianum_

Insect taking on reproduction organs of a flower

100% occurrence on _H. revolutum_

Platygastres sp3
Systasis sp1

Gastrancistrus sp1
Meliponula ogoueysis

Anaspis laurenti

Chrysomelidae sp1
Cheloninae sp10
Pria horni
Apis mellifera
Plebeina heldebrandti

Xylocopa cf inconstans

100% occurrence on _H. roeperianum_

Parasitica
Apoidea
Diptera
Coleoptera

Number of individuals
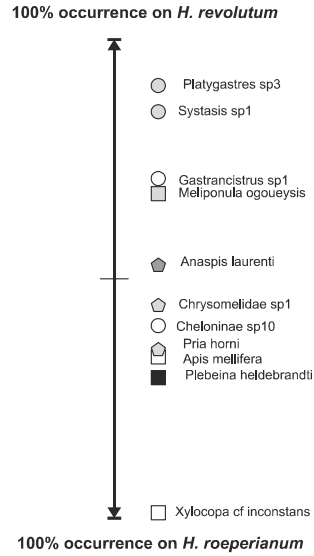5-10
11-50
50-100
>100

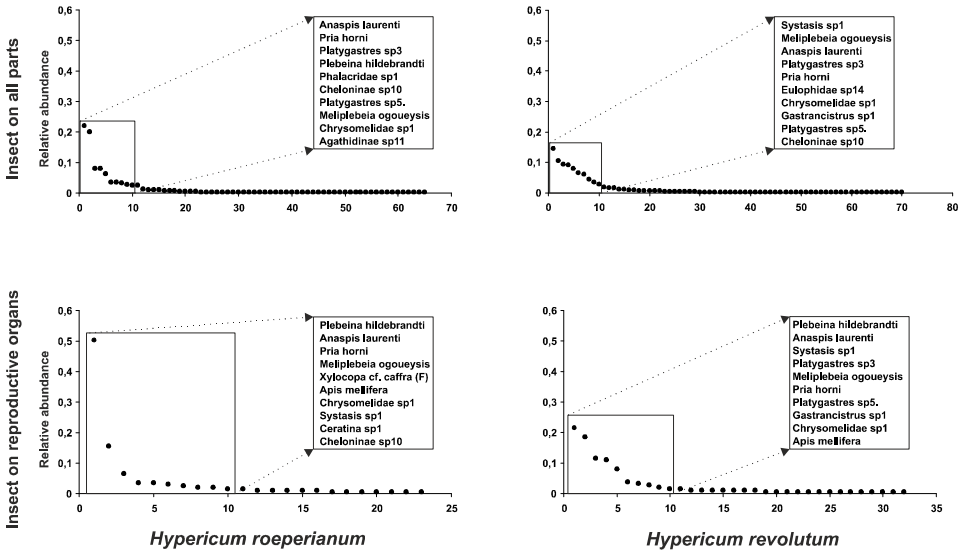Figure 2. Insect morphospecies present on _Hypericum_ species

Figure 3. Relative abundance of insect species on _Hypericum spp._

stigma more often . Especially anthers were touched relatively often in both *Hypericum spp.* and were observed in most of the abundant functional groups. On the other hand, contacts with stigma were relatively less frequent and were presumably realised by only a few functional groups. In *H. roeparianum*, the overwhelming majority of the stigma contacts were done by carpenter bees which usually contact both reproductive organs when collecting pollen by buzzing (sensu Proenca, 1992). Other visitors relatively often touching both anthers and stigma of this plant were *other bees*, *M. ogouensis*, *small beetles*, *big flies*, *small parasitoids* and *lepidopterans*, but their impact seems too be considerably smaller as they touch stigma rather accidentally. In *H. revolutum* flowers the majority of contacts with the both plant reproductive organs were done by *A. mellifera*, *M. ogouensis* and *other bees*. Especially *A. mellifera* and *M. ogouensis* very often used flower pistils with stigma on the top for landing and leaving flowers for either pollen or nectar, *A. mellifera* also often touch both anthers and stigma by their hind legs during nectar collecting.

Discussion

Total species richness of visitors can be seen as a consequence of morphological generalisation both *Hypericum spp.* flowers and easy availability of rewards which attracts many random visitors. However, majority of species on both *Hypericum spp.* (78% in *H. revolutum* and 80% in *H. roeparianum*) were rather accidental visitors as they were collected less than 5 times on target plants. These patterns are even clearer when focusing on contacts with the plants' reproductive organs. Because overwhelming majority of the contacts with stigmas of both plants were carried out by bees (*A. mellifera*, *M. ogouensis*, and *other bees* in *H. revolutum* and *carpenter bees* in *H. roeparianum*), both plants are ecologically and/or functionally specialized to the bee pollination syndrom (sensu Ollerton et al., 2007). On *H.revolutum* bees *A. mellifera* and *M. ogouensis* are visitors which have same middle-sized bodies and very often used at the end divided style with five stigmas on the top for landing and leaving from flower, where they are foraging for nectar or pollen. Nectarless flowers of *H. roeparianum* are visited by *Xylocopa spp.* females which due to body size and position on the flowers when collecting pollen are in contact with reproductive organs of *H. roeperianum* during each visit. Our findings confirm previous observations which indicating that *Xylocopa spp.* and its visitation is important for reproductive success of *H. roeperianum* (Janeček et al., 2007) and carpenter bees appear to be important pollinators of many others tropical plants (Padyšáková et al., 2013; Raju and Rao, 2006).
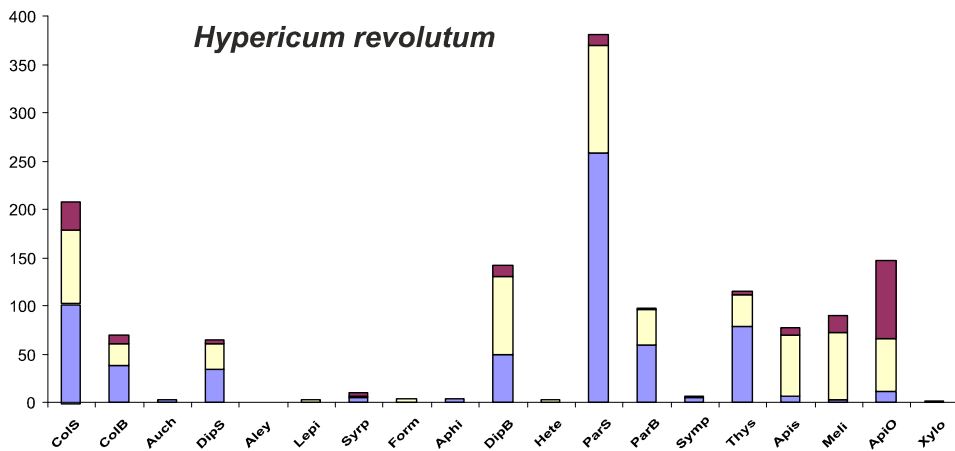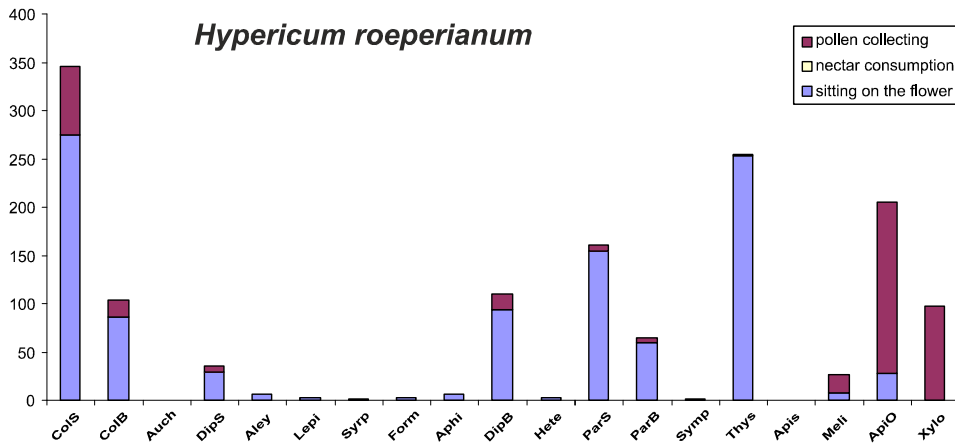
Figure 4. Behaviour of individual morphotaxonomical functional groups on flowers of both Hypericum species. (Morphotaxonomical funcional groups: *ColS, small Coleoptera; ColB, big Coleoptera; Auch, Auchenorrhyncha; DipS, small Diptera; Aley, Aleyrodidae; Lepi, Lepidoptera; Syrp, Syrphidae; Form, Formicidae; Aphi, Aphidoidea; DipB, big Diptera; Hete, Heteroptera; ParS, small parasitic wasps; ParB, big parasitic wasps; Symp, Symphyta; Thys, Thysanoptera; Apis, Apis mellifera; Meli, Meliplebeia ogouensis; ApiO, other Apidae; Xylo, Xylocopini*)

Although *H.revolutum* produces unlike *H. roeperianum* nectar, which may increase its attractiveness for visitors, the diversity of species and quantity of individuals was not significantly affected.

However, pollen which is the main offer for visitors on *H. roeperianum* attracts large amount of beetles. As demonstrated by numerous studies around

the world, beetles can be effective pollinators (Dafni et al., 1990; Goldblatt et al.,
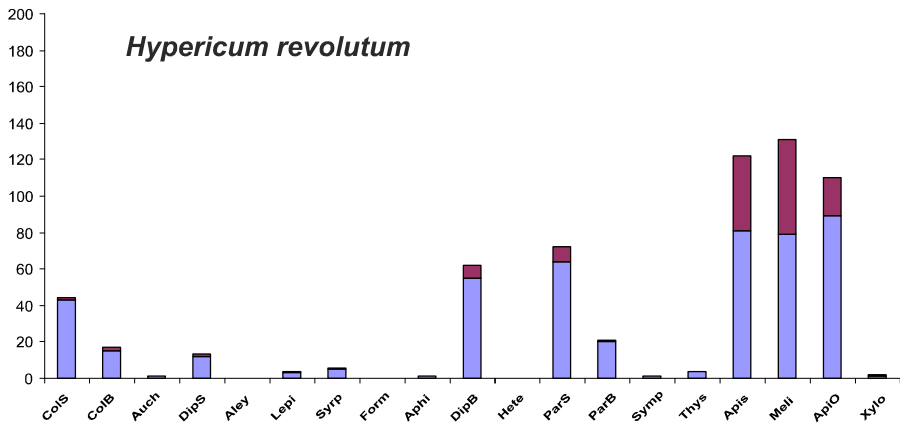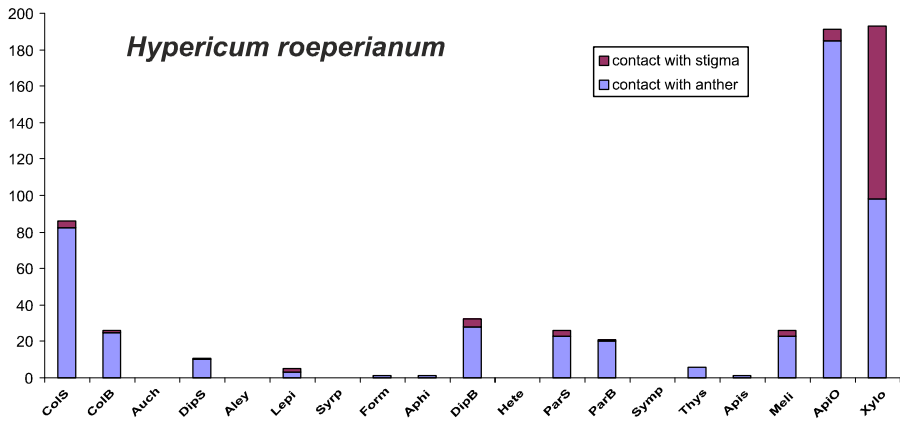

Figure 5. Contacts of individual morphotaxonomical functional groups with plant reproductive organs on flowers of both Hypericum species

1998; Gottsberger, 1989), though beetles species collected on *Hypericum spp.* belong rather to the pollen eaters group (Willmer, 2011), who due their little size and behavior on flowers (sitting on the base of anthers and non contact with stigma) do not affect reproductive success of target plants.

The same applies to and thrips, who at appropriate flower can be effective pollinators (Gottsberger, 1999; Jürgens et al., 2000). Similar conclusions were made by de Oliveira and Sazima (1990) in pollination system of two *Kielmeyera spp.* (Guttiferae) with generalized flat flowers, where probability of contact with stamens and style, and consequently of successful pollination seems to increase with the body size of the visitors.

Although stingless bee *P. hildebrandti* was the most numerous visitor species collected on reproductive organs of both *Hypericum spp.*, with tendency to collect a full charge of pollen from each flower, detailed behaviour observation revealed only occasional contact with stigma. Stingless bees are small-generalized flower visitors often considered as rather robbers or thieves than pollinators (Inouye, 1980; Ramalho, 2004). This fact stems from the morphological discrepancy between the size of the body of stingless bees and visited blossoms.

It seems that many visitors both *Hypericum spp.* have no importance for pollen transfer and taxonomical composition of visitor assemblage could be largely random and undoubtedly vary in different years. A very similar conclusion reached Niemirski and Zych (2011) when they study specialization in *Angelica sylvestris* which is considered by some authors as a supergeneralist. Although its flowers were visited by over 70 species of insects grouped in 10 morphospecies, only a relatively narrow assemblage of muscoid and syrphid flies contributed to pollination.

Although *Hypericum spp.* has easily accessible open flowers, it turned out that important part of pollination is not only the quantity of pollinators, but also their morphological suitability and behaviour on the flower. Transfer of pollen to the stigma seems to be a limiting factor for pollination, and therefore is necessary focusing on the detail behaviour of individual visitors in the study of pollination relationships.

Acknowledgements

References

Aizen, M.A., Morales, C.L., Morales, J.M., 2008. Invasive mutualists erode native pollination webs. PLoS biology 6, e31.

Anderson, D. R., 2008. Model based inference in the life sciences: a primer on evidence. Springer.

Bartoš, M., Janeček, Š., Padyšáková, E., Patáčová, E., Altman, J., Pešata, M., Kantorová, J., Tropek, R., 2012. Nectar properties of the sunbird-pollinated plant *Impatiens sakeriana*: a comparison with six other co-flowering species. South African Journal of Botany 78, 63–74.

Cheek, M., Onana, J.M., Pollard, B.J., 2000. The Plants of Mount Oku and the Ijlm Ridge, Cameroon, a Conservation Checklist. Kew, Royal Botanic Gardens.

De Oliveira, P.E.A.M., Sazima, M., 1990. Pollination biology of two species of *Kielmeyera* (Guttiferae) from Brazilian cerrado vegetation. Plant Systematics and Evolution 172, 35–49.

Dafni, A., Bernhardt, P., Shmida, A., Ivri, B.Y., Greenbaum, S., O'Toole, C., Losito, L., 1990. Red bowl-shaped flowers: convergence for beetle pollination in the Mediterranean region. Israel Journal of Botany 39, 81–92.

Dicks, L.V., Corbet, S..A., Pywell, R.F., 2002. Compartmentalization in plant–insect flower visitor webs. Journal of Animal Ecology 71, 32–43.

Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R., Thomson, J.D., 2004. Pollination syndromes and floral specialization. Annual Review of Ecology, Evolution, and Systematics 35, 375–403.

Forup, M.L., Memmott, J., 2005. The restoration of plant–pollinator interactions in hay meadows. Restoration Ecology 13, 265–274.

Friis, E.M., Crane, P.R., Pedersen, K.R., 2011. Early flowers and angiosperm evolution. Cambridge University Press, Cambridge.

Goldblatt, P., Bernhardt, P., Manning, J.C., 1998. Pollination of petaloid geophytes by monkey beetles (Scarabaeidae: Rutelinae: Hopliini) in southern Africa. Annals of the Missouri Botanical Garden 85, 215–230.

Gottsberger, G., 1989. Beetle pollination and flowering rhythm of *Annona spp.* (Annonaceae) in Brazil. Plant Systematics and Evolution 167, 165–187.

Gottsberger, G., 1999. Pollination and evolution in neotropical Annonaceae. Plant Species Biology 14, 143–152.

Inouye, D.W., 1980. The terminology of floral lacerny. Ecology 61, 1251–1253.

Janeček, Š., Hrázský, Z., Bartoš, M., Brom, J., Reif, J., Hořák, D., Bystřická, D., Riegert, J., Sedláček, O. Pešata. M., 2007. Importance of big pollinators for the reproduction of two *Hypericum* species in Cameroon, West Africa. African Journal of Ecology 45, 607–613.

Janeček, Š., Riegert, J., Sedláček, O., Bartoš, M., Hořák, D., Reif, J., Padyšáková, E., Fainová, D., Antczak, M., Pešata, M., Mikeš, V., Patáčová, E., Altman, J., Kantorová, J., Hrázský, Z., Brom, J., Doležal, J., 2012. Food selection by avian floral visitors: an important aspect of plant–flower visitor interactions in West Africa. Biological Journal of the Linnean Society 107, 355–367.

Johnson, S.D., Steiner, K.E., 2000. Generalization versus specialization in plant pollination systems. Trends in Ecology & Evolution 15, 140–143.

Jürgens, A., Webber, A.C., Gottsberger, G., 2000. Floral scent compounds of Amazonian Annonaceae species pollinated by small beetles and thrips. Phytochemistry 55, 551–558.

Meseguer, A.S., Aldasoro, J.J., Sanmartín, I., 2013. Bayesian inference of phylogeny, morphology and range evolution reveals a complex evolutionary history in St John's wort (*Hypericum*). Molecular Phylogenetics and Evolution 67, 379–403.

Neuschulz, E.L., Grass, I., Botzat, A., Johnson, S.D., Farwig, N., 2013. Persistence of flower visitors and pollination services of a generalist tree in modified forests. Austral Ecology 38, 374–382.

Niemirski, R., Zych, M., 2011. Fly pollination of dichogamous *Angelica sylvestris* (Apiaceae): how (functionally) specialized can a (morphologically) generalized plant be? Plant Systematics and Evolution 294, 147–158.

Olesen, J.M., Jordano, P., 2002. Geographic patterns in plant-pollinator mutualistic networks. Ecology 83, 2416–2424.

Ollerton, J., Killick, A., Lamborn, E., Watts, S., Whiston, M., 2007. Multiple meanings and modes: on the many ways to be a generalist flower. Taxon 56, 717–728.

Ollerton, J., Alarcón, R., Waser, N.M., Price, M.V., Watts, S., Cranmer, L., Hingston, A., Peter, C.I., Rotenberry, J., 2009. A global test of the pollination syndrome hypothesis. Annals of Botany 103, 1471–1480.

Padyšáková, E., Bartoš, M., Tropek R., Janeček Š., 2013. Generalization versus specialization in pollination systems: visitors, thieves, and pollinators of *Hypoestes aristata* (Acanthaceae). PLos ONE 8(4), e59299.

Proenca, C.E.M., 1992. Buzz pollination – older and more widespread than we think? Journal of Tropical Ecology 8, 115–120.

Raju, A.J.S., Rao, S.P., 2006. Nesting habits, floral resources and foraging ecology of large carpenter bees (*Xylocopa latipes* and *Xylocopa pubescens*) in India. Current Science 90, 1210–1217.

Ramalho, M., 2004. Stingless bees and mass flowering trees in the canopy of Atlantic Forest: a tight relationship. Acta Botanica Brasilica 18, 37–47.

Robson, N.K.B., 1961. Guttiferae. In: Exell, A.W., Wild, H. (Eds.), Flora Zambesiaca. Kew Publishing and Flora Zambesiaca Managing Committee, London.

Sabatino, M., Maceira, N., Aizen, M.A., 2010. Direct effects of habitat area on interaction diversity in pollination webs. Ecological Applications 20, 1491–1497.

Simpson, B.B., Neff, J.L., 1981. Floral rewards: alternatives to pollen and nectar. Annals of the Missouri Botanical Garden 9, 301-322.

StatSoft, I. (2011). STATISTICA, ver. 10., http://www.statsoft.com/

Waser, N.M., Chittka, L., Price, M.V., Williams, N.M., Ollerton, J., 1996. Generalization in pollination systems, and why it matters. Ecology 77, 1043–1060.

Waser, N.M., Ollerton, J., 2006. Plant-pollinator interactions: from specialization to generalization. University of Chicago Press, Chicago.

Weberling, F., 2007. The problem of generalized flowers: morphological aspects. Taxon 56, 707–716.

Williams, G., Adam, P., 2001. The insect assemblage visiting the flowers of the subtropical rainforest pioneer tree *Alphitonia excelsa* (Fenzl) Reiss. ex Benth.(Rhamnaceae). In *Proceedings of the Linnean Society of New South Wales* 123, 235-259.

Willmer, P., 2011. Pollination and floral ecology. Princeton University Press, Oxford.

Appendix

Insect visitors on Hypericum revolutum (part 1)

Group	Functional group	Species	All parts	Contact with rep. organs
Parasitica	ParB	*Agathidinae sp11*	1	2
		Braconinae sp12	7	2
		Braconidae sp16	1	
		Braconidae sp17	1	
		Ichneumonidae sp1	3	1
		Ichneumonidae sp4		1
		Rogadinae sp14	2	
	ParS	*Cheloninae sp10*	12	2
		Eucoilinae sp4	1	
		Eucharitidae sp1	1	
		Eulophidae sp14	28	2
		Eulophidae sp15	1	
		Eulophidae sp16	1	
		Eulophidae sp17		1
		Gastrancistrus sp1	19	5
		Gastrancistrus sp2	2	1
		Gastrancistrus sp3	3	
		Gastrancistrus sp5	5	
		Mymaridae sp3		1
		Platygastres sp3	39	21
		Platygastres sp5.	15	6
		Platygastridae sp7	4	1
		Pteromalidae sp6	2	
		Pteromalidae sp7	1	
		Systasis sp1	63	22
Apoidea	Apis	*Apis mellifera*	3	3
	Meli	*Meliplebeia ogouensis*	45	15
	ApiO	*Hylaeus sp1*	5	
		Lasioglossum sp1	1	
		Lasioglossum sp2	1	
		Patellopsis sp2	1	1
		Plebeina hildebrandti	4	41
Diptera	DipB	*Anthomyiidae sp1*	3	
		Anthomyiidae sp2	1	

Insect visitors on Hypericum revolutum (part 2)

Group	Functional group	Species	All parts	Contact with rep. organs
		Anthomyiidae sp4	1	
		Empididae sp1		1
		Muscidae sp1	7	3
		Muscidae sp3	2	
		Muscidae sp4	1	
		Muscidae sp5	8	2
		Tephritidae sp2		2
		Tephritidae sp3	2	
		Tephritidae sp5	1	
	DipS	*Brachycera sp1*	1	
		Brachycera sp2	1	
		Brachycera sp4	1	
		Brachycera sp5	1	
		Brachycera sp6	1	
		Brachycera sp7	1	
		Brachycera sp8	1	
		Brachycera sp9	1	
		Brachycera sp10		1
		Nematocera sp1	1	
		Nematocera sp3	1	
		Nematocera sp4	1	
		Nematocera sp5		1
		Nematocera sp6	1	
		Nematocera sp8	1	
		Nematocera sp9	1	
		Nematocera sp10	1	
		Nematocera sp12	1	
		Phoridae sp1	1	
		Simuliidae sp1	1	
	Syrp	*Syrphidae sp1*	2	1
		Syrphidae sp2	1	
Coleoptera	ColB	*Alleculidae sp1*	1	
		Bruchidae sp1	1	
		Chrysomelidae sp1	26	4
		Curculionidae sp1	1	
		Malachiidae sp1	2	2
	ColS	*Anaspis laureáti*	40	35
		Helodidae sp1	1	
		Meligethes pivodus	3	1
		Meligethes sp2	1	1
		Meligethes sp4	1	
		Pria horni	34	7
		Pria sp1	1	1

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Insect visitors on Hypericum roeperianum (part 1)

Group	Functional group	Species	All parts	Contact with rep. organs
Parasitica	ParB	*Agathidinae sp11*	11	1
		Braconidae sp9	1	
		Braconinae sp12	1	
		Braconidae sp18	1	
		Braconidae sp19	1	
		Rogadinae sp14	1	
	ParS	*Ceraphronidae sp2*	1	
		Ceraphronidae sp3	1	
		Cheloninae sp10	16	3
		Diapriidae sp1	1	
		Eucoilinae sp4	1	
		Encyrtidae sp3		1
		Encyrtidae sp8	1	
		Encyrtidae sp9	1	
		Eulophidae sp13	1	
		Eulophidae sp14	1	
		Eulophidae sp17	1	
		Eupelmus sp1	1	
		Gastrancistrus sp1	1	2
		Platygastres sp3	36	2
		Platygastres sp5.	16	1
		Platygastridae sp8	1	
		Pteromalidae sp6	2	
		Scelionidae sp1	1	
		Scelionidae sp2	1	
		Systasis sp1	11	4
Apoidea	Apis	*Apis mellifera*	2	6
	Meli	*Meliplebeia ogouensis*	15	7
	Xylo	*Xylocopa cf. caffra (F)*	5	7
		Xylocopa lugubris (F)	1	
	ApiO	*Bethylidae sp1*	1	
		Ceratina sp1	6	4
		Ceratina sp4	1	
		Lasioglossum sp1	1	
		Patellopsis sp2		3
		Patellopsis sp3	2	
		Plebeina hildebrandti	36	101
Diptera	DipB	*Anthomyiidae sp2*	1	
		Anthomyiidae sp3	1	
		Empididae sp2	1	
		Lauxaniidae sp1	1	

I

Group	Functional group	Species	All parts	Contact with rep. organs
		Muscidae sp1	4	
		Muscidae sp2	2	2
		Muscidae sp3	1	
		Muscidae sp5	1	
		Tephritidae sp1		1
		Tephritidae sp2	1	2
		Tephritidae sp4	1	
		Tephritidae sp5	1	
	DipS	*Brachycera sp3*	1	
		Nematocera sp2	1	
		Nematocera sp7	1	
		Nematocera sp11	1	
		Phoridae sp2	1	
		Sepsidae sp1	1	
	Syrp	*Syrphidae sp3*	1	
Coleoptera	ColB	*Bruchidae sp1*		2
		Coccinelidae sp1		1
		Chrysomelidae sp1	13	5
		Curculionidae sp1	3	
		Malachiidae sp1	3	1
	ColS	*Anaspis laurenti*	100	31
		Cryptophagidae sp1	1	
		Latridiidae sp1	1	
		Meligethes lividus	5	
		Meligethes sp2	1	
		Mordellistena stribistrigosa	1	
		Phalacridae sp1	28	
		Pria horni	91	13
		Pria sp1	3	1

CHAPTER VIII

Summary of results

Summary of results

The main objective of this thesis was to describe in detail the pollination systems of coexisting species at the community level based on detailed studies of its components. In six case studies we have focused on several plant species richly co-flowering in dry season and on their visitors.

The nectar properties of target plant species showed considerable variability in volume, concentration and composition of nectar and in the dynamics of its production. Just in the case of *I. sakeriana* that was proven to be the only target plant species phenotypically and ecologically specialized exclusively to bird pollination (Chapter IV) we found specific nectar properties (high volume, low sugar concentration, and high sucrose content) in comparison with the insect-visited plants (Chapter II). The specific characteristics of the nectar of *I. sakeriana* can be seen as a co-adaptation between *I. sakeriana* and a specialized nectarivorous *Cyanomitra oritis* (Chapter IV). It is therefore very probable that nectar properties in plants exclusively specialized on the sunbird pollination are similar to those pollinated by hummingbirds. Nevertheless, sunbirds are often feeding on plants without traits related to the bird-pollination syndrome which confirms the hypothesis of common occurrence of asymmetric specialisation in plant-pollinator relationships (Chapter III). Because sunbirds readily feed on unspecialized flowers they could be considered to be ecologically generalized despite the fact that they have phenotypically specialized bills. However, by inclusion of abundance as a possible factor for the analysis of individual plant species visitation we detected a clear pattern of bird selectivity for specialized long tubular flowers, as well as separating of trophic niche, among the sunbirds studied. Moreover, we did not notice any effect on reproductive success in phenotypically generalized plants with easily accessible nectar (*Hypericum revolutum*; Chapter VI) or in plants with bee pollination syndrom (*Hypoestes aristata*; Chapter V). It is obvious that complementary phenotypes are important determinants in plant–flower visitor interactions.

The best example of this close relationship is *I. sakeriana* which is reproductively dependent on pollination mainly by the sunbird *C. oritis,* although it is also frequently visited by the sunbird *Cinnyris reichenowi*, which is in most cases a nectar robber. However, long peduncles of I sakeriana forcing birds to hover could be evolved rather as a defence against *C. reichenowi* than as adaptations increasing the effectiveness of *C. oritis* (Chapter IV).

Effects of nectar robbers or thieves on plant fitness were found also in the pollination system of *H.aristata*, where *Apis mellifera* acted as a nectar thief with apparent negative effects on the plant reproduction (Chapter V). In the pollination system of *H.aristata,* the carpenter bees *Xylocopa sp.* were both the most frequent and the most effective pollinator. Carpenter bees *Xylocopa sp.* also played a crucial role in the pollination system of *Hypericum roeperianum* (Chapter VI), where despite relatively low attendance they were the most frequent visitor who touches both stamens and stigmas and can therefore be considered the most effective pollinators (Chapter VII). When we compared *H. roeperianum* with the closely related *H. revolutum*, which have similar floral traits and coexist in the same plant communities, we found that pollination systems of both plants are probably much more specialised than could be expected from their morphology. Although in both plant species the bee pollinators represented reproductively the most effective visitors (in terms of contact with reproductive organs) the bee pollinators should be divided further into large-bee and small-bee guild according to their preferences (Chapter VII).

General conclusion and future perspectives

This work reveals a mosaic of several interconnected pollination systems and provides insight into the relations in a community. We demonstrate that pollination systems, which are often considered as very generalized, are in fact relatively closely ecologically specialized and specialized pollinators are able to feed on many plant which belongs to different pollination syndromes. We also show that the 'trait-matching' between flowers and their visitors plays an important role in pollination interactions. Some visitors, even though they are not frequent, represent the crucial pollinators of a plant due to their effectivity. In contrast, many frequent visitors of flowers have no or even negative effects on plant reproduction.
Nevertheless, we are just at the start of understanding the functioning and evolution of pollination systems in tropical Africa. Given that tropical regions are the richest habitats, we can assume a wide range of unique pollination systems that are still waiting to be discovered. However, before we create any large scale comparisons and big hypotheses, detailed studies of the different pollination systems are needed as many surprises in already known relationships could be revealed.