

**POLLINATION IN WILD PLANT COMMUNITIES ALONG ALTITUDINAL AND
LAND USE GRADIENTS ON MOUNT KILIMANJARO, TANZANIA**



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“Every mountain top is within reach if you just keep climbing.”

Barry Finlay



"Life is all about enjoying every sunset and looking forward for the next sunrise."

Sandeep Shergill



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I hereby confirm that my thesis entitled “*Pollination in wild plant communities along altitudinal and land use gradients on Mount Kilimanjaro, Tanzania*” is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis.

Furthermore, I confirm that this thesis has not been submitted as part of another examination process neither in identical nor in similar form.

Würzburg, 14th July, 2014



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SUMMARY

1. Pollination of sexually reproducing plants requires pollen transfer agents, which can be biotic, abiotic or a combination of biotic and abiotic agents. The dominance of one of pollination system in wild plant communities depends on climatic factors and/or degrees of anthropogenic influences, which have effects on pollinator diversity and pollination function. Anthropogenic activities and climate change are also considered as main causes of ongoing invasion of invasive species into wild and managed habitats which can bring up competition for pollinators with possible negative consequences for the reproduction of co-occurring native plant species.
2. The study aimed to determine pollination systems and pollination limitation of invasive and native plants in natural savannah between 870 – 1130 m and semi-natural (managed) grassland between 1300 – 1750 m above sea level; effects of flower density and pollinator abundance on seed production of cross-pollinated and self-pollinated plants; and relationships of bee abundance and the proportion of cross-pollinated plants at the southern slope of Mount Kilimanjaro, Tanzania.
3. Pollinator-exclusion, open pollination and supplemental hand-pollination treatments were applied to 27 plant species in savannah and grassland habitats. Flowers were counted in each clusters based upon their species. Pollinators were sampled by using pan traps. Information-theory-based multi-model averaging and generalized linear mixed effects models were used to identify and analyze the effects of flower density, pollinator abundance, pollination treatments and habitat types on seed production. Regression models were used to determine relationships of altitude with bee abundance, and with proportion of cross-pollinated plants.
4. My results show that mean seed numbers of native plants were significantly lower in pollinator-exclusion treatments than in open-pollination treatments, indicating their reliance on pollinators for reproductive success. In contrast, seed numbers of invasive plants were similar in pollinator-exclusion and open-pollination treatments, demonstrating an ability of reproduction without pollinators. Despite of higher levels of self-pollination in invasive plants, supplemental hand-pollination treatments revealed pollen limitation in grassland and marginally in savannah habitats. There

were no significant differences in seed numbers between supplemental hand pollination and open pollination treatments of native plant communities in savannah and grassland, which indicates no pollination limitation in the studied ecological system for native communities. Besides, grassland plants produced comparatively more seeds than savannah plants, however seeds in grasslands were lighter than those of the savannah which may be due to nutrient limitation in grassland.

5. I found 12 cross-pollinated and 15 self-pollinated plants along the altitudinal gradient after comparing seeds from pollinator-excluded and open-pollinated experiments. I also found that proportions of cross-pollinated plants and bee abundance simultaneously decreased with increasing altitude. All cross-pollinated plants were native and grew in savannah habitats, with an exception of one species.
6. Neither effects of focal flower density nor a significant interaction between focal flower density and bee abundance for self-pollinated plants were observed. However, there were significant effects of focal flower density and interactions of flower density with bee abundance for cross-pollinated plants. Non-focal flower density had no significant effect on seed production of cross-pollinated and self-pollinated plants.
7. The results show that native plants depend more on cross-pollination than invasive plants, despite of most native plants in managed habitat (grassland) rely on self-pollination for reproduction. The tendency of having more cross-pollinated plants in natural savannah which are in low altitude coincides with other finding that the cross-pollinated plants and bee abundance simultaneously decrease with increasing altitude. Therefore, our findings support the hypotheses that self-fertilization of flowering plants increases with increasing altitude, and pollinator limitation is most pronounced in managed or disturbed habitats. Despite of reduction of pollinators in grassland, only invasive plants experience pollen limitation, which may be due to poor integration with available pollinator networks.
8. Climate change and anthropogenic activities in natural habitats are factors that influence pollinator abundance and functioning, which lead to a shift of mating systems in plant communities so as to assure their reproduction.

ZUSAMMENFASSUNG

1. Für die erfolgreiche Bestäubung sich sexuell reproduzierender Pflanzen werden biotische und/oder abiotische Pollenvektoren benötigt. Ob fremd- oder selbstbestäubte Bestäubungssysteme in Pflanzengemeinschaften dominieren, kann vom Klima abhängen, aber auch von anthropogenen Aktivitäten, da diese sich negativ auf die Bestäuberdiversität und damit assoziierte Bestäubungsfunktionen auswirken können. Klimaveränderungen und anthropogene Aktivitäten werden auch als die Hauptursache dafür gesehen, dass sich invasive Pflanzen in natürlichen und genutzten Habitaten ausbreiten und die Reproduktion nativer Pflanzen gefährden, da diese nun mit den invasiven Pflanzen um Bestäuber konkurrieren müssen.
2. In dieser Studie wurden die Bestäubungssysteme nativer und invasiver Pflanzenarten in Pflanzengemeinschaften natürlicher Savannen (870 – 1130m ü. NN) und semi-natürlicher, bewirtschafteter Graslandflächen (1300 – 1750m ü. NN) an den südlichen Hängen des Kilimandscharos (Tansania) untersucht. Es wurde analysiert, in welchem Ausmaß die Pflanzen bestäubungslimitiert sind und welchen Effekt Blütendichten und Bestäuberabundanzen auf die Samenproduktion von fremd- und selbstbestäubten Pflanzen haben. Zudem wurde betrachtet, ob sich das Verhältnis von fremd- und selbstbestäubten Arten mit zunehmender Höhe und mit Bestäuberabundanzen verändert.
3. Um die Abhängigkeit von Pflanzen von Bestäubern und den Grad der Bestäubungslimitierung zu bestimmen, wurden an 27 Pflanzenarten aus Savannen und Grasländern Bestäubungsmanipulationsexperimente durchgeführt (d.h. Bestäuber ausschließen vs. Handbestäubung vs. offene Bestäubung). Blütendichten wurden in Clustern um die entsprechende Pflanzenart aufgenommen. Bestäuberabundanzen wurden mit Farbschalen erfasst. Mit Hilfe von „multi-model averaging“ und „generalized linear mixed effects models“ wurden die Effekte der Bestäubungsmanipulationsexperimente, der Blütendichten, der Bestäuberabundanzen und der Habitate auf die Samenproduktion analysiert. Mit Hilfe von Regressionsmodellen wurde untersucht, ob sich das Verhältnis von fremd- und selbstbestäubten Arten mit der Höhe und mit Bienenabundanzen verändert.

4. An den Blüten nativer Pflanzen, an denen Bestäuber ausgeschlossen worden waren, war die mittlere Anzahl der Samen signifikant niedriger, als an den Blüten, die von Bestäubern besucht werden konnten. Dies zeigt, dass der Reproduktionserfolg dieser nativen Pflanzen von Bestäubern abhängt. Bei invasiven Pflanzen waren dagegen die Samenanzahlen unter Bestäuberausschlussnetzen und an offen bestäubten Pflanzen nicht unterscheidbar, was zeigt, dass ihre Reproduktionskapazität nicht von Bestäubern abhängt. Obwohl invasive Pflanzenarten zur Selbstbestäubung tendierten, waren sie pollenlimitiert: Handbestäubung konnte ihren Reproduktionserfolg in Grasländern und marginal auch in Savannen steigern. Native Pflanzen waren dagegen nicht pollenlimitiert. Insgesamt produzierten die Pflanzen der Grasländer mehr Samen als Savannenpflanzen. Auf Grasländern waren die Samen im Durchschnitt aber leichter als auf Savannen, was auf eine Nährstoffarmut in genutzten Grasländern hinweisen könnte.
5. Insgesamt konnte ich durch die Bestäuberausschlussexperimente 12 fremdbestäubte und 15 selbstbestäubte Pflanzenarten entlang der Höhengradienten identifizieren. Der Anteil von fremdbestäubten Arten nahm zusammen mit der Bienenabundanz mit zunehmender Höhe ab. Bis auf eine, waren alle fremdbestäubten Arten nativ und wuchsen in der Savanne.
6. Für fremdbestäubte Arten hatte die Blütendichte von Artgenossen, nicht aber von anderen Arten, einen Einfluss auf den Reproduktionserfolg der Pflanze. Auch wurde ein Interaktionseffekt zwischen der Blütendichte und der Bestäuberabundanz detektiert. Für selbstbestäubte Arten wurden solche Effekte nicht gefunden.
7. Diese Ergebnisse zeigen, dass native Pflanzen mehr von Fremdbestäubung abhängen als invasive Pflanzen, wobei in bewirtschafteten Grasländern die meisten nativen Arten selbstbestäubend sind. Die Tendenz, dass mehr fremdbestäubte Arten in den Savannen vorkommen deckt sich mit dem Ergebnis, dass der Anteil fremdbestäubter Arten und Bienenabundanzen mit zunehmender Höhe abnehmen. Unsere Ergebnisse bestätigen damit die Hypothesen dass Selbstbestäubung mit zunehmender Höhe zunimmt und Bestäuberlimitierung vor allem in landwirtschaftlich genutzten Flächen auftritt. Trotz abnehmender Bestäuberabundanzen, sind nur invasive Pflanzen

pollenlimitiert, was daran liegen könnte, dass sie nur schlecht in die bestehenden Pflanzen-Bestäuber-Netzwerke integriert sind.

8. Klimawandel und anthropogene Aktivitäten in natürlichen Habitaten sind Faktoren, die Bestäuberabundanzen und Bestäuberfunktionen beeinflussen können. Dies könnte zu einer Veränderung von Bestäubungssystemen in Pflanzengemeinschaften führen, um die Reproduktionserfolge zu sichern.

CHAPTER I: GENERAL INTRODUCTION**POLLINATION IN WILD FLOWERING PLANTS**

Flowering plants have developed processes by which pollen from the anther of a flower is released, transported and deposited on a stigma, thereby enabling fertilization and reproduction. This crucial process is known as pollination. In order for pollination to occur, it requires pollen transfer agents, which can be biotic, abiotic or a combination of biotic and abiotic agents (Stelleman 1984; Gómez & Zamora 1999). When pollen grains from the anther are taken, transported and deposited onto a stigma by assistance of biological organisms, it is known as biotic pollination, and whereas it happens without involvement of other organisms is known as abiotic pollination. The organisms involved in the process are called pollinators. In abiotic pollination beside water, wind is considered to be a dominant and potential alternative pollination agent that provides reproductive assurance when pollinators are limited or scarce (Goodwillie 1999; Fausto Jr et al. 2001). Usually, wind pollination prevails in open sites (Goodwillie 1999) or alpine locations (Gómez & Zamora 1996; Totland & Sottocornola 2001; Kuhn et al. 2006), where pollinators are rare and wind is more dependable. In other circumstances, some plants may undergo a combination of abiotic and biotic pollination (Pojar 1973; Stelleman 1984; Gómez & Zamora 1999) in order to assure their reproduction. It may occur either sequentially or simultaneously within the season (Cox & Grubb 1991), depending on pollinator availability.

Pollination is an ecologically important process for maintenance of plant communities and gene flow through reproductive outputs (Ashman et al. 2004; Aguilar et al. 2006; Klein et al. 2007; Ricketts et al. 2008). It also provides important ecosystem services to other organisms, including humans (Kevan 1999; Klein et al. 2007). Pollinators are considered to be important and dependable for the reproductive processes of about 67% - 96% of tropical flowering plants (Ollerton et al. 2011; Rosas-Guerrero et al. 2014) and 78% of temperate flowering plants (Ollerton et al. 2011). In addition, about one-third of the agricultural production volume and two-thirds of crop plants that produce human food (in terms of fruits and seeds) depend on pollinators (Klein et al. 2007). Bees are a major pollinator group (Klein et al. 2007); however there is a great global concern about bees' declines due to conversion and degradation of natural habitats and land use intensification (Potts et al. 2010).

In turn, they may affect reproductive successes and pollination systems of flowering plants in communities.

EFFECTS OF LAND USE ON POLLINATION

Human activities have great impacts on biodiversity. Degradation and conversion of natural habitats and intensive land use due to agricultural expansion and practices, development of infrastructure and human settlements are among human activities affecting pollinator abundance and functioning (Tschardt et al. 2005; Winfree et al. 2009), which may lead to the disruption of plant - pollinator interactions in terrestrial plant communities (Herrera 2000; Klein et al. 2003). In turn, it affects seed production due to pollinator limitation (Herrera 2000).

Humans are also known, through their activities, to cause the spread of invasive species by either deliberate or accidental translocation of species outside their natural geographical distribution (Hellmann et al. 2008). Having comparatively higher ability of self-pollination systems (Eckert et al. 2010) than native plants (Ashman et al. 2004), invasive species manage to invade wild and managed habitats by using open niche space (Vila et al. 2009) and then pose a threat to native biodiversity. As shown by other studies in pollination ecology, the presence of invasive plant species in wild plant communities may cause resource competition for pollinators and nutrients (Chittka & Schürkens 2001; Ridenour & Callaway 2001).

Several studies have addressed the effect of pollination limitation on seeds for individual plant populations in the context of habitat fragmentation and land use intensification in temperate regions (Ashman et al. 2004; Dauber et al. 2010). However, the reproductive success of flowering plants has rarely been studied on a community level and even more rarely in tropical habitats, where on-going climate change, conversion and degradation of natural ecosystems, and the spread of alien species pose potential threats for pollinator diversity and wild plant communities relying on their pollination services (Potts et al. 2010).

In order to bridge this knowledge gap, I decided to investigate pollination limitation and pollination systems of native and invasive plants in disturbed grasslands and natural

savannah habitats at the southern slope of Mount Kilimanjaro, Tanzania. Here, I asked two questions: 1. To what extent does seed production of plant species from managed high-elevation grasslands and savannah in low elevations depend on self-pollination and insect-pollination? 2. Do invasive and native plants differ in seed production, their dependence on insect-pollination and the level of pollination limitation? I applied pollinator-exclusion, open pollination and supplemental hand pollination treatment approaches to 27 focal flowering plant species in order to understand pollination limitation and pollination systems of native and invasive plants in savannah and grassland (Chapter II).

EFFECTS OF CLIMATE CHANGE ON POLLINATION

Altitude has major influences on climate and pollination systems of flowering plants of any particular locality. It has been hypothesized that self-fertilization rates increase with increasing altitude (García-Camacho & Totland 2009; Hoiss, et al. 2012). Pollinator abundance and functioning become limiting factors for successful pollination and seed production at higher altitudes (Bingham & Orthner 1998; Medan et al. 2002; Arroyo et al. 2006). In order to combat reduction of pollinators and functioning, plants tend to shift from cross-pollination to self-pollination system so as to assure their production (Lloyd & Schoen 1992; Kalisz & Vogler 2003; Kalisz et al. 2004).

Mount Kilimanjaro is the highest solitary mountain in Africa. Through its altitudinal gradient from 700 m to 5895 m above sea level, it consists of different vegetation and climatic zones. Nevertheless, studies on relationships between plants and pollinators in tropical plants of East Africa, including along altitudinal gradients, have not been performed in contrast to temperate plants. Hence, I decided to investigate the relationships of proportions of cross-pollinated plants and bee abundance along altitudinal gradients in order to identify trends of pollination systems across different habitats (Chapter III).

EFFECTS OF FLOWER DENSITY ON POLLINATION SYSTEMS

Flower density and pollinator abundance are considered as influential factors in the reproductive success of flowering plants. Nevertheless, little is known about how varying flower densities interact with pollinator abundance within wild communities of tropical

African flowering plants, where few or no such studies have been conducted. Many studies in temperate and non-African tropical regions have addressed the effects of flower density on pollinator attraction, visitation frequency and pollinator behaviour within the patches (Kunin 1997). It has been reported that among aggregations of floral resources in a landscape, pollinators may switch to species with higher floral densities (Goulson 2000; Steffan-Dewenter et al. 2001; Westphal et al. 2003). Thus, higher floral density may improve the constancy of pollinators on flowers of the same species, which eventually reduces interspecific pollen transfer and increases the quality of pollinator visits (Kunin 1993). Conversely, small flower patches may attract fewer pollinators, leading to reduction in quality of pollination service in terms of the deposition of viable, conspecific, outcross pollen on stigmas (Larson & Barrett 2000; Klinkhamer & Lugt 2004). Yet, it is hard to find evidence of different levels of flower density that attract sufficient pollinators, which influences their constancy in foraging behaviour to enhance seed production of wild communities of tropical flowering plants.

Therefore, I decided to investigate how different flower densities and pollinator abundance could affect the seed production of cross-pollinated and self-pollinated plants in wild communities. I hereby asked four questions: 1. How do pollinator abundance and the proportion of cross-pollinated and self-pollinated plants change along the elevational gradient of Mt. Kilimanjaro? 2. Does the density of con- or heterospecific flowers in the neighbourhood affect seed set of wild plants? 3. Does pollinator abundance affect the seed set of wild plants? 4. Is seed production affected by the interaction between pollinator abundance and flower densities? Data on flower density of focal and non-focal species of cross-pollinated and self-pollinated plants and pollinator abundance in savannah and grassland along altitudinal gradients were collected and analyzed using generalized linear effects models (Chapter III).

STUDY AREA AND STUDY DESIGNS

STUDY AREA

Mount Kilimanjaro is the volcanic mountain that is located between (37°14'53"-37°41' 03" East, 3° 10' 49"-3°18'28" South) in the Kilimanjaro region, northern part of Tanzania and near the border of Kenya. It is about 300 km south of the equator and west of the Indian

Ocean; hence it gets influences of equator and Indian monsoon system. At the southern foot of the mountain, it starts from savanna plains at 700 m up to its glaciated summit at 5895 m above sea level. Due to its huge altitudinal gradient, it consists of different climatic zones and vegetation zones (Hemp 2001; Hemp 2006).

The Mount Kilimanjaro region has a bimodal rainfall pattern, with long and short rainy seasons from March to May and in November/December, respectively (Coutts 1969). Annual precipitation is modified by elevation and exposure to prevailing winds blowing inland from the Indian Ocean and varies on the wet southern slope from 500 mm at the mountain foothills to about 3000 mm at 2200 m above sea level. The mean annual temperature decreases from 23.4°C at 813 m above sea level linearly to 7.1°C at the highest summit (Hemp 2001).

The degrees of human intervention in vegetation zones along the altitudinal gradient differ, hence lead to a very interesting study area for tropical pollination ecology. Mt Kilimanjaro has several bioclimatic zones: dry and hot colline savanna zone; submontane zone (banana and coffee plantations); montane forest zone (lower forest and cloud forest); subalpine heathlands (Erica zone); alpine vegetation zone (*Helichrysum* dwarf cushion vegetation); upper alpine and nival zone; and glacial zone(Plate I.1) (Hemp 2006).

STUDY DESIGN AND PLANT SELECTION

A stratified random sampling design was employed for the selection of experimental sites. Ten study sites of 50 times 50 m size were selected, five from managed (disturbed) grassland and five from natural savannah habitats. Distances between adjacent study sites were between 1 - 27 km for savannah and 3 - 43 km for grassland. Within each study site, the five most abundant herbaceous flowering plant species were identified and selected. For each selected species five clusters (nested within sites) of 2 times 2 m size were established on each site (Dafni 1992; Larson & Barrett 2000) (Plate I.2). A total of 27 flowering plant species, belonging to 12 families, were involved in the study.

Three experimental treatments, i.e. pollinator-exclusion, open (control) and supplemental hand pollination, were applied to each selected plant species in each cluster, summing up to a total number of 750 replicates (10 study sites x 5 clusters x 3 treatments x 5 plant species). However, some treatments were destroyed and on one site not all selected

plant species occurred with sufficient flower density for the experiments so that the final total number of replicates was 590. Flowers from different individual plants for different treatments were marked with coloured threads for differentiation. For pollinator-exclusion, selected flower buds were covered with a fine nylon mesh bag (mesh size=2x2 mm) and tied with cotton threads to exclude pollinators. The bags were left until the end of the flowering period and fruits became mature for harvesting (Figure I.2). We assumed that the effect of wind pollination to carry outcross pollen through fine nylon mesh bags in pollinator-exclusion treatments would be marginal, thus produced seeds were considered to be mainly due to self-pollination. For supplemental hand pollination, fine brushes were used to collect pollen from flowers of the same species outside the clusters and to carefully deposit the pollen onto the stigmas of selected flowers. Then all flowers of each plant species were counted in each cluster. The sites were monitored in intervals of two days in order to pollinate flowers/florets that were not previously open and to check for mature fruits. The study sites were monitored in intervals of two days so as to check for mature fruits. After fruits being mature, they were collected and subjected in oven at 40°C for 48 hours. All seeds for each species were counted and weighed by using an analytical balance.

Pollinators were sampled by exposing 8 stands (clusters) of three coloured UV-reflecting pan traps. Six clusters of three pan traps (yellow, white, blue) with 40 cm and 120 cm heights were installed / exposed at alternating regular distances of 15 m apart along two transects in the study sites for 48 hours.



Plate I.1: Study sites showing different vegetations along the altitudinal gradient of Mt. Kilimanjaro. The upper two photos show the study sites savannah 1 and 5. The lower left picture is a photo of the southern side of Mt. Kilimanjaro. The picture in the lower right shows grassland 3.

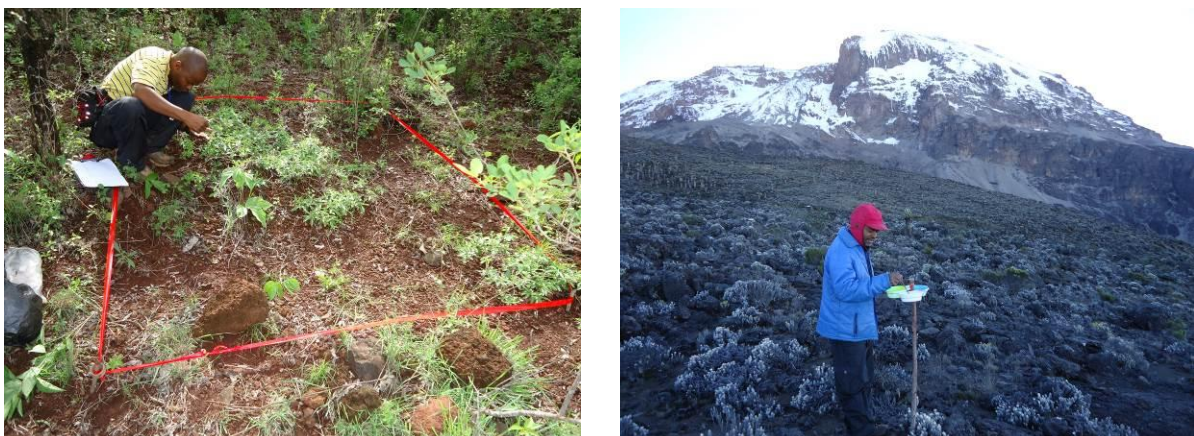


Plate I.2: Pollination experiments in study sites. Left: Cluster of 2 x 2 m size in which pollination treatments were performed. Right: one of pan traps used for capturing bees during experiment.

CHAPTER II: POLLINATION LIMITATION OF NATIVE AND INVASIVE PLANT SPECIES IN SAVANNAH AND GRASSLAND HABITATS AT MOUNT KILIMANJARO, TANZANIA

This chapter has been submitted and is under review as: Kindeketa, W.J., Peters, M.K. & Steffan-Dewenter, I. "Pollination limitation of native and invasive plant species in savannah and grassland habitats at Mount Kilimanjaro, Tanzania". *Journal of Vegetation Science*

KEY WORDS: invasive plants; land use; plant reproduction; pollination limitation; seed set; self-compatibility; tropical ecology

ABSTRACT

QUESTION: The ongoing invasion of invasive species into wild and managed habitats due to land use and climate change can be fostered by self-compatible pollination systems and successful competition for pollinators with possible negative consequences for the reproduction of co-occurring native plant species. We analyzed pollination systems and pollination limitation of invasive and native plants in tropical savannah and grassland communities to test which factors limit reproduction in terms of seed numbers and seed weight.

LOCATION: The study was conducted in natural savannah between 870 – 1130 m above sea level and semi-natural grassland between 1300 – 1750 m above sea level at the southern foothills of Mount Kilimanjaro, Tanzania.

METHODS: We analyzed the effects of pollination treatments (pollinator-exclusion, open and supplemental hand pollination) and habitat types on seed numbers and average seed weight of native and invasive plant communities by using generalized linear mixed effects models and information-theory-based multi-model averaging.

RESULTS: Mean seed numbers of native plant communities were significantly lower in pollinator-exclusion than in open and supplemental hand pollination treatments, indicating their reliance on pollinators for seed production. In contrast, seed numbers of invasive plants

were similar in pollinator-exclusion and open pollination treatments, demonstrating an ability of producing seeds in the absence of pollinators. Despite higher levels of self-pollination in invasive plants, supplemental hand pollination revealed pollen limitation in grassland and marginally in savannah habitats for invasive but not for native plant communities. Generally, invasive plants produced higher numbers of seeds than native plant species, and plant communities in grasslands showed lighter mean seed weights than those of the savannah which may be due to nutrient limitation in grassland.

CONCLUSION: The results show differences in the pollination systems of invasive versus native plants with the latter more strongly depending on cross-pollination. Invasive plants are advantaged by self-compatible pollination systems but pollination limitation indicates that they are not well integrated into native pollinator networks.

INTRODUCTION

Flowering plants have developed various mechanisms whereby pollen from the male part of a flower is released, transported and deposited to a stigma by biotic and/or abiotic pollination agents. Most flowering plants depend on animal-pollination for successful reproduction and gene flow and the maintenance of plant communities and agricultural productivity (Ashman et al. 2004; Aguilar et al. 2006; Klein et al. 2007; Ricketts et al. 2008). The predictability of pollination syndromes is pronounced in the tropics where the proportion of animal-pollinated plants is particularly high, with approximately 94% of all flowering plants relying on animal-pollination (Ollerton et al 2011; Rosas-Guerrero et al. 2014).

The dependence of plants on cross-pollination by insects may vary among habitats and factors related to the dispersal ecology of plant species. The richness and abundance of ectotherm pollinators is known to decline with decreasing temperatures along elevational gradients (García-Camacho & Totland 2009) which may cause differential levels of pollination limitation among habitats and, over longer temporal scales, changes in the ratio of self-pollinated over cross-pollinated systems. In addition, land use intensification is also considered as a significant driver of the reduction in pollinator diversity and pollinator functioning (Steffan-Dewenter et al. 2005; Aguilar et al. 2006; Goulson et al. 2008; Hegland et al. 2009; Winfree et al. 2009), which may lead to extinctions of both plant and pollinator species (Biesmeijer 2006; Eckert et al. 2010; Grass et al. 2013), and adaptation of favourable mating systems as a potential alternative solution for reproductive assurance. Several studies have addressed the effect of pollination limitation on seed numbers in the context of habitat fragmentation and land use intensification for individual plant populations in temperate regions (Ashman et al. 2004; Dauber et al. 2010). Further, invasive plants and native plants may differ in their reliance on cross-pollination and their integration into pollinator networks (Vilá et al. 2009). Many invasive plants are known to be capable of self-pollination which is assumed to improve their ability to successfully colonize new environments (Rambuda & Johnson 2004; van Kleunen & Johnson 2007; van Kleunen et al. 2008; Eckert et al. 2010; Hao et al. 2011).

However, the reproductive success of flowering plants has rarely been studied on a community level and even less so in tropical habitats, where on-going climate change, conversion and degradation of natural ecosystem, and the spread of alien species, pose potential threats for pollinator diversity and wild plant communities relying on their

pollination services (Potts et al. 2010, Rosas-Guerrero et al. 2014).

To close this knowledge gap, we experimentally investigated pollination limitation and systems of native and invasive plants in managed grasslands and natural savannah habitats on the southern slopes of Mt. Kilimanjaro. We subjected flowers of abundant plants into pollinator-exclusion, open and supplemental hand pollination treatments in order to identify the extent of pollinator-dependence and pollination limitation of individual plant species and within plant communities. In this context, we expected that pollination limitation and the dependence of native and invasive plants on cross-pollination differ between the managed grasslands in high elevations and the natural savannah in lower elevations, thus providing ideal conditions to study changes in the pollination biology of plants along extensive environmental gradients. The study aimed to answer the following questions:

1. To what extent does seed production of plant species from managed high-elevation grasslands and savannah in low elevations depend on self-pollination and insect-pollination?
2. Do invasive and native plants differ in seed production, their dependence on insect-pollination and the level of pollination limitation?

MATERIAL AND METHODS

STUDY AREA

The study was conducted in savannah and grassland habitats at the southern slopes of Mount Kilimanjaro, Tanzania, between 870 and 1750 m above sea level (37°14'53"-37° 41' 03" East, 3° 10' 49"-3°18'28" South, Figure II.1). Mean annual temperature decreases linearly upslope with a lapse rate of 0.56°C per 100 m starting with 23°C at the foothills and decreasing to -7°C at the top of the mountain (Hemp 2006). The area has a bimodal rainfall pattern, with long and short rainy seasons from March to May and in December, respectively (Coutts 1969). Annual rainfall increases to over 2000 mm at 1400 m on the central southern slope and to about 3000 mm at 2100 m in the lower part of the forest belt (Hemp 2001).

The savannah is characterized by a dry and hot climate, and lies between 870 and 1130 m above sea level. It is composed of heterogeneous and scattered trees and shrubs of *Acacia*, *Ozoroa*, *Commiphora*, *Combretum*, *Grewia* and *Lannea* species, while the ground

cover is dominated by tall grasses and a few other herbaceous plants. The savannah is a relatively natural habitat with low levels of human disturbance. Most savannah habitats in the region have now been transformed to agricultural land used for crop production (maize, beans and sunflowers) or pastures. Grassland habitats are situated within the submontane forest belt between 1300 and 1750 m above sea level. Grasslands are semi-natural habitats holding a large diversity of flowering plant species, in which grasses are cut about twice a year for cattle feeding, which subsequently prevent regrowth of bushes and trees. Patches of grasslands are comparatively smaller than savannah patches, and are dominated by grasses and other herbaceous plants with few or no scattered trees. Patches are typically surrounded by mixed cropping and agroforestry systems (Hemp 2006).

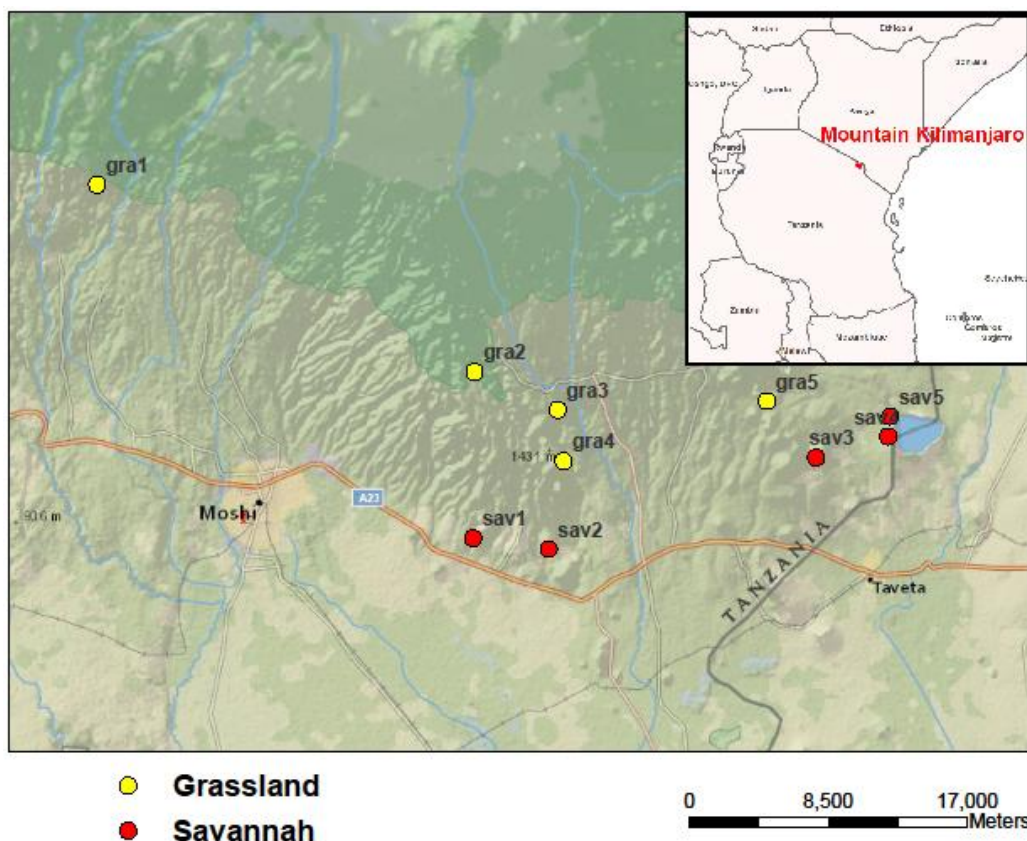


Figure II.1: Map of the study region with ten savannah and grassland sites as drawn from the middle point of sites. Yellow dots indicate study sites in grassland and red dots those in savannah habitats. At the top right corner is a sketch map of East African countries whereby the red dot indicates the study area.

STUDY DESIGN

A stratified random sampling design was employed for the selection of experimental sites. Ten study sites of 50x50 m size were selected, five from grassland and five from savannah habitats (Figure II.1). Distances between adjacent study sites were between 1 - 27 km for savannah and 3 - 43 km for grassland. Within each study site, the five most abundant herbaceous flowering plant species were identified and selected. For each selected species five clusters (nested within sites) of 2x2 m size were established on each site (Dafni 1992; Larson & Barrett 2000). A total of 27 flowering plant species, belonging to 12 families, were investigated (Table II.1).

Three experimental treatments, i.e. pollinator-exclusion, open (control) and supplemental hand pollination, were applied to each selected plant species in each cluster, summing up to a total number of 750 replicates (10 study sites x 5 clusters x 3 treatments x 5 plant species). However, some treatments were destroyed and on one site not all selected plant species occurred with sufficient flower density for the experiments so that the final total number of replicates was 590. Flowers from different individual plants for different treatments were marked with coloured threads for differentiation. For pollinator-exclusion, selected flower buds were covered with a fine nylon mesh bag (mesh size=2x2 mm) and tied with cotton threads to exclude pollinators. The bags were left until the end of the flowering period and fruits became mature for harvesting. We assumed that the effect of wind pollination to carry outcross pollen through fine nylon mesh bags in pollinator-exclusion treatments would be marginal, thus produced seeds were mainly due to self-pollination. For supplemental hand pollination, fine brushes were used to collect pollen from flowers of the same species outside the clusters and carefully deposited the pollen onto the stigmas of selected flowers. The sites were monitored in intervals of two days in order to pollinate flowers/florets that were not previously open and to check for mature fruits. When fruits were mature, they were collected and oven-dried at 40°C for 48 hours. All seeds of each treatment for each species were counted and total seed weight was measured using an analytical balance. Afterwards mean seed weight was calculated by subdividing total seed weight by the number of seeds.

DATA ANALYSIS

Calculations on seed numbers and weights, and how they were affected by plant type, habitat type and treatments were performed by using R 3.0.1 (R Development Core Team 2013). We analyzed the effects of pollinator-exclusion, control and supplemental hand pollination treatments on seed numbers and average seed weight using generalized linear mixed effects models ('lmer' and 'glmer' function in the R package 'lme4'). We evaluated all potential two-way interactions of predictor variables (plant type, habitat, treatments) and all models with less complex model structures which can be constructed from this set of predictor variables. Models were calculated assuming a gaussian or poisson distribution of errors with seed weight and seed numbers as response variables, respectively. In case of models with a poisson distribution of errors, over-dispersion of the data was corrected by adding an observational-level random effect (Bates et al. 2013). In all models study site/cluster was added as a nested random effect to meet the hierarchical structure of the study design. Models and explanatory variables were evaluated using information-theory-based on multi-model averaging. Multi model averaging provides a coherent mechanism to account for the uncertainty associated with the choice of models, which is often ignored when it comes to making predictions and computing prediction intervals with the chosen best model (Raftery 1996; Wintle et al. 2003; Ellison 2004). This is particularly relevant (but often neglected) in ecology, in which uncertainty about model structure is usually high (Conroy et al. 1995; Wintle et al. 2003). In the model averaging procedure, first, all models which can be composed of the three explanatory variables and all two-way interactions were evaluated according to model fit (to the data) and complexity, measured by the Akaike information criterion (AIC) and derived Akaike weights. As our sample size was relatively low in comparison to the number of estimated parameters we used the AIC with a second-order bias correction (called AICc) instead of the standard AIC for model evaluation. Second, a new subset of most likely models was compiled. In this subset only models were included which received high to moderate support by the data in comparison to the most supported model ($\Delta AIC_C < 3$). Models which exhibited ΔAIC_C values of > 3 were omitted from all further analyses. Third, for each explanatory variable the effect probability was calculated which can be regarded as a measure of the relative support for an explanatory variable over the whole model space (Johnson & Omland 2004). The effect probability of an explanatory variable is calculated by summing up the Akaike weights (~model probabilities) of each model in which

an explanatory variable is included. Fourth, the average mean and standard error and derived significance level of each coefficient estimate was calculated by weighted averaging of coefficients under each separate model in which an explanatory variable was included, with weights given by the Akaike weights. Using the R package ‘multicomp’ we calculated Tukeys HSD posthoc tests, testing on pairwise differences between mean seed numbers and seed weight of pollinator exclusion, open-pollination and hand pollination treatments. These posthoc tests were conducted for each plant type (invasive/native) in each habitat (savannah, grassland) separately. During analyses we did not include two species since the hand pollination experiments in these species were not successful which lead to significantly decreased seed numbers and weights in the hand pollination compared to control treatments. This might be due to a destruction of flower parts during the treatment.

RESULTS

TREATMENT EFFECTS ON INDIVIDUAL PLANT SPECIES

Among the 27 plant species experimented, 24 plants were native species of which 15 and nine plant species grew in savannah and grassland, respectively (Table II.1). We found 12 plant species set seeds by 50% reduction when pollinators were excluded in which eight species among them showed statistically significant reduction in seed numbers, thus indicating they are cross-pollinated and mainly depend on pollinators for their reproductive success. All 12 cross-pollinated plant species were native of which 11 species grew in savannah and one in grassland. Moreover, two of the 12 plant species completely failed to bear seeds when pollinators were excluded. On the other hand, the 15 remaining plant species showed no statistically significant reduction in seed numbers, indicating at least some capabilities for self-pollination. However, several of these plant species exhibited marginal reductions of seed numbers (Table II.1).

Beside treatment effects on seed numbers, we analysed effects of pollination treatments on mean seed weight. We found six plant species in which seed weight significantly differed between the treatments ($p < 0.02$, Table II.1). All of them were native species with the exception of *Lantana camara* L. Moreover, all species which showed

significant differences were from savannah with the exception of *Emilia discifolia* (Oliv.) C. Jeffrey.

Table II.1: Mean seed number and weight of 27 flowering plant species and results of ANOVA analysis and post-hoc tests. HP (supplemental hand pollination), EP (pollinator exclusion), OP (natural (open) pollination) give mean and SE of seed numbers and seed weights for individual plant species. P gives the significance level of ANOVA analysis and NS (None significant). Additionally, significant levels of post-hoc tests are shown (HP-EP, OP-EP, OP-HP) testing for pairwise differences between treatment levels.

Status	Family	Scientific Name	Mean Seed Numbers			ANOVA for Mean Seed Number				Mean Seed Weight			ANOVA for Mean Seed Weight			
			Exclusion	Open	Hand	P	HP-EP	Op-EP	OP-HP	Exclusion	Open	Hand	P	HP-EP	Op-EP	OP-HP
Invasive	Asteraceae	<i>Ageratum conyzoides</i>	3.17±0.84	3.49±0.84	3.82±0.84	NS	NS	NS	NS	0.11±0.06	0.13±0.06	0.12±0.06	NS	NS	NS	NS
Native	Asteraceae	<i>Aspilia mossambicensis</i>	0.14±0.49	2.53±0.49	2.51±0.49	<0.01	<0.01	<0.01	NS	68.68±11.17	7.53±5.00	8.69±5.00	<0.01	<0.01	<0.01	NS
Native	Asteraceae	<i>Bidens schimperi</i>	3.56±1.55	2.35±1.55	2.95±1.55	NS	NS	NS	NS	0.65±0.18	0.77±0.22	0.80±0.20	NS	NS	NS	NS
Native	Capparaceae	<i>Cleome stenopetala</i>	1.21±0.96	3.36±0.96	3.30±0.96	<0.01	0.01	0.01	NS	4.91±1.50	4.03±0.95	4.23±0.95	NS	NS	NS	NS
Native	Lamiaceae	<i>Clinopodium abyssinicum</i>	1.15±0.25	1.18±0.23	1.22±0.25	NS	NS	NS	NS	0.15±0.06	0.14±0.05	0.09±0.05	NS	NS	NS	NS
Native	Commelinaceae	<i>Commelina Africana</i>	0.82±0.56	1.59±0.56	1.51±0.56	NS	NS	NS	NS	112.75±102.58	10.58±79.45	7.75±79.46	NS	NS	NS	NS
Native	Commelinaceae	<i>Commelina forskoolii</i>	0.69±0.28	0.42±0.28	0.56±0.28	NS	NS	NS	NS	33.734±9.79	33.86±12.64	34.58±10.94	NS	NS	NS	NS
Native	Asteraceae	<i>Conyza pyrrophappa</i>	2.97±0.55	2.25±0.55	2.49±0.55	NS	NS	NS	NS	1.28±1.86	1.32±1.87	1.37±1.87	NS	NS	NS	NS
Native	Campanulaceae	<i>Cyphia glandulifera</i>	0.00	2.79±0.47	2.82±0.47	0.00	0.00	0.00	NS	0.00	0.45±0.35	0.62±0.33	-	0.00	0.00	NS
Native	Acanthaceae	<i>Dyschoriste hildebrandtii</i>	0.62±0.82	0.62±0.82	0.62±0.82	NS	NS	NS	NS	1.15±1.87	0.53±1.87	1.45±1.87	NS	NS	NS	NS
Native	Asteraceae	<i>Emilia discifolia</i>	3.13±0.78	3.84±0.79	3.89±0.80	NS	NS	NS	NS	0.05±0.02	0.10±0.02	0.13±0.02	< 0.01	<0.01	<0.01	NS
Native	Asteraceae	<i>Emilia ukambensis</i>	3.08±1.04	4.09±1.04	4.14±1.04	NS	NS	NS	NS	0.45±0.16	0.37±0.14	0.37±0.14	NS	NS	NS	NS
Native	Asteraceae	<i>Helichrysum forskahlui</i>	1.71±0.61	1.50±0.61	1.64±0.61	NS	NS	NS	NS	0.00±0.59	0.06±0.56	0.62±0.54	NS	NS	NS	NS
Native	Asteraceae	<i>Helichrysum kirkii</i>	2.02±1.30	3.23±1.30	2.48±1.30	NS	NS	NS	NS	0.05±0.01	0.04±0.01	0.03±0.01	NS	NS	NS	NS
Native	Asteraceae	<i>Helichrysum nudifolium</i>	2.39±0.95	3.01±0.95	3.16±0.95	NS	NS	NS	NS	0.03±0.02	0.02±0.01	0.02±0.01	NS	NS	NS	NS
Native	Boraginaceae	<i>Heliotropium steudneri</i>	0.28±0.21	0.69±0.21	0.69±0.21	0.02	0.03	0.03	NS	73.72±2.35	74.00±1.49	73.07±1.49	NS	NS	NS	NS
Native	Asteraceae	<i>Hirpicium diffusum</i>	2.08±0.83	2.73±0.83	2.85±0.83	NS	NS	NS	NS	5.41±3.82	4.37±3.41	3.44±3.41	NS	NS	NS	NS
Native	Acanthaceae	<i>Justicia flava</i>	0.32±0.45	1.57±0.45	1.53±0.45	<0.01	<0.01	<0.01	NS	1.42±1.02	0.84±0.46	0.95±0.51	NS	NS	NS	NS
Invasive	Verbenaceae	<i>Lantana camara</i>	1.30±0.49	1.62±0.49	1.20±0.49	NS	NS	NS	NS	19.69±19.93	28.32±19.77	30.85±19.93	<0.02	<0.01	0.04	NS
Native	Rubiaceae	<i>Oldenlandia herbacea</i>	0.85±1.40	0.98±1.41	2.14±1.41	NS	NS	NS	NS	0.07±0.04	0.05±0.04	0.03±0.03	NS	NS	NS	NS
Native	Rubiaceae	<i>Oldenlandia wiedemannii</i>	0.18±0.71	2.39±0.71	1.13±0.71	<0.01	NS	<0.01	0.03	0.31±0.29	0.14±0.14	0.06±0.18	NS	NS	NS	NS
Native	Asteraceae	<i>Osteospermum vaillantii</i>	0.71±0.59	1.18±0.59	1.66±0.59	NS	NS	NS	NS	13.04±6.54	13.85±4.62	9.76±4.28	NS	NS	NS	NS
Native	Polygonaceae	<i>Oxygonum sinuatum</i>	0.69±0.28	0.69±0.28	0.69±0.28	NS	NS	NS	NS	77.84±5.50	93.84±6.15	76.96±5.50	<0.01	NS	<0.01	<0.01
Native	Turneraceae	<i>Streptopetalum hildebrandtii</i>	0.00	1.77±0.50	2.26±0.50	<0.01	<0.01	<0.01	NS	0.00	2.88±1.26	1.69±1.26	NS	0.00	0.00	NS
Invasive	Asteraceae	<i>Tridax procumbens</i>	3.22±0.73	2.96±0.73	3.66±0.73	NS	NS	NS	NS	0.81±0.32	0.85±0.32	0.72±0.31	NS	NS	NS	NS
Native	Tiliaceae	<i>Triumfetta flavescens</i>	0.28±0.21	0.69±1.17	0.69±0.21	0.02	0.03	0.03	NS	83.13±10.77	82.54±158.27	81.08±6.81	NS	NS	NS	NS
Native	Tiliaceae	<i>Triumfetta rhomboidea</i>	0.69±0.00	0.69±1.39	0.69±0.00	NS	NS	NS	NS	13.74±3.32	15.49±27.67	12.80±3.32	NS	NS	NS	NS

EFFECTS OF TREATMENTS, HABITATS AND PLANT TYPE

Multi-model inference strongly supports an interaction effect between plant type and treatments on seed numbers, while an effect of habitat, or of the interactions between habitat \times treatment and habitat \times plant type were little supported by the data (Table II.2).

Invasive and native plant communities showed different responses in seed production to pollination treatments. Seed numbers of native plants were significantly reduced in the pollinator exclusion treatment compared to seed numbers in the open pollination treatments in both savannah and grassland habitats (Figure II.2, Table II.2). In contrast, for invasive plants, the pollinator-exclusion treatment resulted in no significant reduction of mean seed numbers in both savannah and grassland habitats (Figure II.2, Table II.2). This result indicates that native plant communities depend more on pollinators for reproductive success than invasive plant species.

There were no significant difference in seed numbers between supplemental hand pollination and open pollination treatments of native plant communities in savannah and grassland, indicating no pollination limitation in the studied ecological system for native communities. However, supplemental hand pollination significantly increased seed numbers of invasive plants in grassland, and marginally so in savannah habitats, suggesting that they suffered from pollination limitation (Figure II.2, Table II.2).

Apart from seed numbers, we also tested whether seed weight was affected by treatments, habitat type and plant type to reveal possible trade-offs between pollinators and other resources, including soil nutrient. Pollination treatments, plant type and habitat type were included in the final set of eight highly supported models. However, model uncertainty was very high resulting in low effect probability values for the individual explanatory variables (Table II.3).

While seed weight showed the tendency to increase from the pollinator exclusion to the supplemental hand pollination treatment for invasive communities, it declined in native plants. Despite of having similar seed number between exclusion and open pollination treatments for invasive communities in grassland, mean weight of seeds of the open treatment was significantly higher than the mean weight under pollinator exclusion. Besides, mean seed weight for invasive and native plant communities tended to be lower in grassland than in

savannah habitat (Table II.3), which might be a sign of nutrient limitation in grassland due to frequent vegetation cutting.

Table II. 2: Results of model averaging analyses evaluating the effects of habitat, plant type, and treatment on the number of seeds produced. For each explanatory variable, the effect probability (i.e. the sum of Akaike weights of models in which the respective explanatory variable was included), the mean and standard error of coefficients, the test statistic z and the corresponding P values are shown. Coefficient estimates were calculated by weighted averaging of parameter estimates over all models for which the difference of the respective AIC_C to the AIC_C value of the most supported model was not higher than 3, i.e. for two component models. Please note that in case of categorical variables the coefficient means of the second level are differences to the first level.

Variable	Effect probability	Mean	SE	z	P
Type: Invasive plants	1.00	2.501	0.763	3.278	0.001
Type: Native plants	1.00	-1.630	0.794	2.053	0.040
Treatment: Open-pollination	1.00	0.067	0.250	0.268	0.789
Treatment: Hand-pollination	1.00	0.338	0.249	1.357	0.175
Type:Native x Treatment:Open-Pollination	1.00	0.765	0.281	2.725	0.006
Type:Native x Treatment:Hand-pollination	1.00	0.516	0.280	1.841	0.066
Habitat: Savannah	0.31	-0.279	0.378	0.738	0.460

Table II. 3: Results of model averaging analyses evaluating the effects of habitat, plant type, and treatment on seed weight. For each explanatory variable, the effect probability (i.e. the sum of Akaike weights of models in which the explanatory variable was included), the mean and standard error of coefficients, the test statistic z and the corresponding P values are shown. Coefficient estimates were calculated by weighted averaging of parameter estimates over all models for which the difference of the respective AIC_C to the AIC_C value of the most supported model was not higher than 3 , i.e. for two component models. Please note that in case of categorical variables the coefficient means of the second level are differences to the first level.

Variable	Effect probability	Mean	SE	z	P
Type: Invasive plants	0.41	1.899	1.084	1.752	0.080
Type: Native plants	0.41	-0.192	1.145	0.168	0.867
Treatment: Open-pollination	0.40	0.163	0.258	0.632	0.528
Treatment: Hand-pollination	0.40	0.145	0.284	0.511	0.609
Type:Native x Treatment:Open-pollination	0.41	-0.508	0.238	2.134	0.033
Type:Native x Treatment:Hand-Pollination	0.41	-0.597	0.238	2.509	0.012
Habitat: Savannah	0.43	1.161	0.926	1.253	0.210

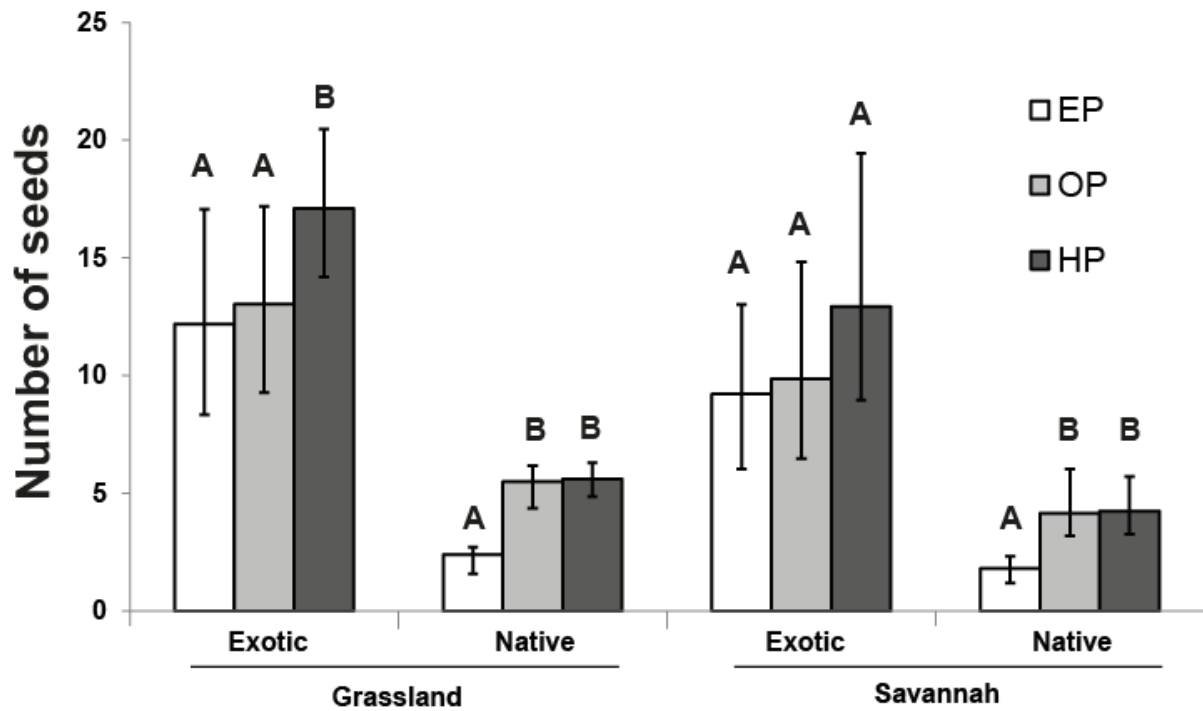


Figure II. 2: Mean (\pm 95% bootstrap confidence intervals) number of seeds produced by invasive and native plant species in grassland and savannah habitats at Mt. Kilimanjaro derived from multi-model averaging analysis. Seeds produced under pollinator exclusion, open-pollination and hand-pollination treatments are indicated by white, light grey and dark grey colours, respectively. Treatments in which seed numbers significantly differed in posthoc tests (Tukey's HSD tests) are indicated by different letters.

DISCUSSION

TREATMENT EFFECTS ON PLANT SPECIES

We assessed the pollination systems of individual focal plant species in grassland and savannah habitats on Mt. Kilimanjaro. Our results indicate that about 27% and 89% of the 24 studied native plant species from natural savannah and managed grasslands are principally capable of self-pollination respectively. The dominance of self-pollinated plants in grassland, as an alternative solution for reproductive assurance (Lloyd & Schoen 1992; Kalisz & Vogler 2003; Kalisz et al. 2004), may be caused by declines in pollinator abundance and pollinator activity due to higher anthropogenic activities and lower temperatures compared to savannah habitats (García-Camacho & Totland 2009). In this study, we did not control for pollinator abundance along the elevational gradient, however, other studies revealed that the abundances of bees, which belong to the most important pollinators, decline along elevation and land use gradients (Hoiss et al. 2012).

The percentage of savannah native plants exhibiting differences between the pollinator exclusion and open control treatments was considerably within the estimated percentage of cross-pollinated plants reported in the literature (67% - 96%) (Ollerton et al. 2011; Rosas-Guerrero et al. 2014), however it was lower in grassland. In our study, all invasive species were self-pollinated and self-compatible (Rambuda & Johnson 2004; van Kleunen & Johnson 2007; van Kleunen et al. 2008; Eckert et al. 2010; Hao et al. 2011). This result supports Baker's hypothesis and coincides (Rambuda & Johnson 2004) that plant species, which are capable of uniparental reproduction, are more likely to be successful colonists than those are self-incompatible or dioecious species. The capacity of self-pollination makes them independent of the present pollinator community, thereby increasing their capacity to invade new habitats.

EFFECTS OF TREATMENTS, HABITATS AND PLANT TYPE

Although some individual native plants were self-pollinated, seed numbers of native plant communities showed a significant reduction when pollinators were excluded in savannah habitats, indicating that among species animal-pollination is of considerable importance for the reproduction of native plant communities of tropical savannah habitats (Ashman et al. 2004). In contrast, invasive plant community showed no significant difference

in seed numbers of open and exclusion pollination treatments, which corresponds to findings of other studies showing that invasive species are often self-compatible (Rambuda & Johnson 2004; van Kleunen & Johnson 2007; van Kleunen et al. 2008; Eckert et al. 2010; Hao et al. 2011). These results add evidence on an accumulated board of knowledge that the majority of invasive plants rely on self-fertilization while native plants' reproductive outputs mainly depend on cross-fertilization (Ashman et al. 2004; Ollerton et al. 2011).

Furthermore, we tested whether there is pollination limitation in native and invasive plant communities in natural savannah and managed grassland habitats by doing supplemental hand pollination. We found that the mean seed number in open pollination treatments of invasive plant species was significantly lower than seed numbers of supplemental hand pollination treatments in grassland, and marginally so in savannah sites. However, such a pattern was not observed for native plant communities in both habitats, although pollination limitation is reported to be a common phenomenon in natural and disturbed habitats (Ashman et al. 2004). We assume that, so far, native plants are well integrated into existing plant-pollinator networks (Vila et al. 2009) while invasive plants suffer from a lack of suitable pollinators and poor pollinator network integration (Richardson et al. 2000; Vila et al. 2009). However, in the course of evolutionary time, invasive species might get more and more integrated into the native plant-pollinator network.

We found a tendency of the mean seed weight of native and invasive plant species to be higher in savannah than in grassland plant communities. This result may indicate that plant communities in the extensively managed grassland habitats, where biomass is regularly removed, suffered more from nutrient deficiency than savannah communities (King et al. 2007; Kettenring et al. 2011). Moreover, mean seed weight of exclusion pollination treatments of invasive plant communities was significantly lower than of open pollination treatment in grassland and savannah, though their seed numbers were similar. This tendency was also observed in *Phragmites* when self-pollinated plants produced significantly smaller viable seeds than cross-pollinated plants which was interpreted as a consequence of low genetic diversity due to selfing (Kettenring et al. 2011).

CONCLUSION

We conclude that native plant communities predominantly relied on cross-pollination but showed no evidence for pollination limitation whereas the reproductive output of invasive plant communities was more pollen-limited despite self-compatible pollination systems. Whether this unexpected constraint on the seed numbers of invasive plants is a mechanism which impedes the spread of invasive species in tropical savannah and grassland plant communities has to be tested in future studies.

CHAPTER III: INTERACTIVE EFFECTS OF FLOWER DENSITY, POLLINATOR ABUNDANCE, AND MATING SYSTEM ON SEED SET IN WILD PLANT COMMUNITIES AT MOUNT KILIMANJARO, TANZANIA

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KEY WORDS: Grassland; Savannah; Pollination; Cross-pollination; Self-pollination; Altitude; Flower density; pollinators; seed set; Kilimanjaro, tropical ecology

ABSTRACT

QUESTIONS: At regional scales, climatic conditions modulate plant mating systems and pollinator diversity whereas at local scales, the distribution of flowers in space is considered an important factor which influences pollinator visitation, and thereby plant reproduction. We investigated the effects of conspecific and heterospecific flower density and pollinator abundance on seed production of cross-pollinated and self-pollinated plants along an elevational gradient at Mt. Kilimanjaro, Tanzania.

METHODS: We measured flower densities and seed production of 27 plant species in ten savannah and grassland sites at 870 to 1750 m above sea level. We used pollinator exclusion and open pollination experiments to differentiate self-pollinated plants from cross-pollinated plants. Further, we assessed pollinator abundances with pan traps and analyzed the data by using generalized linear mixed effects models.

RESULTS: The proportion of cross-pollinated plants and the abundance of bees decreased with increasing elevation in both savannah and grassland study sites. We found a significant effect of conspecific flower density and an interaction with bee abundance on the seed set of cross-pollinated plants, but not on self-pollinated plants. When bee abundance was low, cross-pollinated plants in patches with high local flower density produced less seeds than those with median and low flower density. However, when bee abundance increased, patches

with high flower density produced more seed than patches with median and low flower density.

CONCLUSION: We conclude that regional climatic gradients and local ecological interactions in combination influence plant reproduction. When bee abundance is high, conspecific neighboring flowers facilitate pollination, while when bee abundance is limited, high flower density may experience either intraspecific competition or changes in the composition or in the behavior of foraging bees under different spatial densities of flowers and thereby decreases seed set.

INTRODUCTION

Plant-pollinator interactions are mutualistic relationships that play an important role for gene flow and the maintenance of plant communities (Ashman et al. 2004; Aguilar et al. 2006; Klein et al. 2007; Ricketts et al. 2008), thus assuring their survival. Climate change, flower density of conspecific and heterospecific flowers, and pollinator availability are considered as influential factors for the reproductive success of flowering plants (Hegland et al. 2009; Dauber et al. 2010). Nevertheless, little is known on the interactive effects of flower density and pollinator abundance on reproductive success in wild plant communities (Essenberg 2012).

Several studies in temperate and tropical regions have addressed effects of flower density on pollinator attraction and pollinator behaviour within the patches (Kunin 1997). Among aggregations of floral resources in a landscape, pollinators switch to species with higher floral densities (Goulson 2000; Westphal et al. 2003), thus improving constancy and quality of pollinator visits on flowers and hence reduces interspecific pollen transfer (Kunin 1993). However, small flower patches are considered to be less attractive to pollinators, which leads to reduction in quality of pollination service in terms of the deposition of viable, conspecific, outcross pollen on stigmas (Larson & Barrett 2000; Klinkhamer & Lugt 2004). Nevertheless, it is hard to find an evidence at what flower density threshold, pollinators are sufficiently attracted to ensure high seed production of wild plants as previous studies indicate a large regional and species-specific variation in the relationship between seed set and local flower density (Dauber et al. 2010; Essenberg 2012).

We used the elevational gradient of Mt. Kilimanjaro to study the influence of local flower density and climate-related variation in pollinator abundance on the reproductive success of tropical wild plant communities. In natural plant communities, plant species vary in their reliance on pollination systems to assure their reproductive success, with some species depending on self-pollination while others are cross-pollinated or combine both systems. We expected that effects of flower density and pollinator abundance may differ between cross-pollinated and self-pollinated plants in co-existing communities. Due to lack of knowledge on the pollination system of wild tropical plants, we therefore first used pollinator-exclusion and open pollination experiments to determine the dependence of plants on pollinators and determined the distribution of cross-pollinated versus self-pollinated plants along an climatic

elevational gradient. We expected an increase of self-pollinated plants at higher altitudes due to reduced pollinator abundances and lower foraging activities under low temperatures (Hoiss, Gaviria, et al. 2012). In order to understand the interactive effects of flower density, pollinator abundance and plant mating systems, we specifically asked the following questions:

1. How do pollinator abundance and the proportion of cross-pollinated and self-pollinated plants change along the elevational gradient of Mt. Kilimanjaro?
2. Does the density of con- or heterospecific flowers in the neighbourhood affect seed set of wild plants?
3. Does pollinator abundance affect the seed set of wild plants?
4. Is seed production affected by the interaction between pollinator abundance and flower densities?

MATERIALS AND METHODS

STUDY AREA

The study was conducted at the southern slopes of Mount Kilimanjaro, Tanzania, between November 2011 to June 2012. We selected five savannah and five grassland study sites at elevations between 870 and 1750 m above sea level (37°14'53"-37° 41' 03" East, 3° 10' 49"-3°18'28" South). Mean annual temperature decreases linearly upslope with a lapse rate of 0.56°C per 100 m starting with 23°C at the foothills and decreasing to -7°C at the top of the mountain (Hemp 2006). The study region is characterised by a bimodal rainfall pattern, with long and short rainy seasons from March to May and in December respectively (Coutts 1969). Annual rainfall increases to over 2000 mm at 1400 m on the central southern slope and to about 3000 mm at 2100 m in the lower part of the forest belt (Hemp 2001).

The savannah habitat is characterized by a dry and hot climate, and lies between 870 and 1130 m above sea level. It is composed of heterogeneous and scattered trees and shrubs of *Acacia*, *Ozoroa*, *Commiphora*, *Combretum*, *Grewia* and *Lannea* species, while the ground cover is dominated by tall grasses and a few other herbaceous plants. The savannah is a natural habitat with low levels of human disturbance. Most savannah habitats in the region have now been transformed to agricultural uses for crop production (maize, beans and

sunflowers) or pastures. Grassland habitats are situated within the submontane forest belt between 1300 and 1750 m above sea level. Grasslands are semi-natural habitats holding a large diversity of flowering plant species, in which grasses are cut about twice a year for cattle feeding, which subsequently prevent regrowth of bushes and trees. Patches of grasslands are comparatively smaller than savannah patches, and are dominated by grasses and other herbaceous plants with few or no scattered trees. Patches are typically surrounded by mixed cropping and agroforestry systems (Hemp 2006).

STUDY DESIGN AND PLANT SELECTION

The experimental sites were selected by following a stratified random sampling design. A total of ten study sites of 50 m x 50 m size were selected, comprising five grassland and five savannah study sites. Distances between adjacent study sites were between 1 - 27 km for savannah and 3 - 43 km for grassland. Within each study site, the five most abundant herbaceous flowering plant species were identified and selected. For each selected species five clusters (nested within sites) of 2 m x 2 m size were established on each site which differed in the density of focal flowering plants (Dafni 1992; Larson & Barrett 2000). A total of 27 flowering plant species, belonging to 12 families, were studied (Table III.1).

Pollinator-exclusion and open pollination treatments were applied to each selected plant species in each cluster. Flowers for open pollination treatments were marked with coloured threads and left unmanipulated until maturation, while for pollinator-exclusion, selected flower buds were covered with a fine nylon mesh bag (mesh size=2x2 mm) and tied with cotton threads to exclude pollinators. The bags were left until the end of the flowering period and fruits became mature for harvesting. We assumed that the effect of wind pollination to carry outcross pollen through fine nylon mesh bags in pollinator-exclusion treatments would be marginal, thus produced seeds were mainly due to self-pollination.

The flowers or flower units (e.g. inflorescences of Asteraceae) of each plant species were counted in each cluster. In order to harvest mature fruits the study sites were monitored in intervals of two days after cessation of flowering. All seeds per flower or flower unit for each species were counted and recorded. For our experiment, it was supposed to be 250 replicates (10 study sites x 5 clusters x 1 treatment x 5 plant species) but some treatments were destroyed, some species grew in the same cluster, and in one grassland site we did not

find sufficient flowers for the experiment, leading to a total number of 198 replicates from 27 flowering plant species, belonging to 12 families.

Cross-pollinated and self-pollinated plants were obtained by comparing seed numbers from pollinator-exclusion and open pollination treatments. We assumed that those plants, after flowers being pollinator-excluded, which produced less than 50% of actual seed numbers from open pollination treatments relied on pollinators to reach full seed reproduction, while those which produced seeds similar to open pollination treatments were considered as self-pollinated plants.

Pollinators were sampled by exposing eight stands (clusters) of three coloured UV-reflecting pan traps. Six clusters of three pan traps (yellow, white, blue) with 40 cm and 120 cm heights were installed at regular distances of 15 m apart along two transects in the study sites for 48 hours. Bee data was collected once per each annual season, thus abundance data are based on four sampling rounds per site. All bee samples were stored in ethanol and later sorted and identified to genera and species levels if possible (Classen et al., submitted).

DATA ANALYSIS

All statistical analyses were performed by using R 3.0.1 (R Development Core Team 2013). Simple linear regression analysis was used to test on changes in bee abundance and the proportion of self-pollinated and cross-pollinated plants along the elevational gradient. Generalized linear mixed effects models with a poisson distribution of errors were used to test for the effects of flower density and bee abundance on seed production. We tested for density effects of conspecific flowers (from which the seed production was measured) and of heterospecific flowers as explanatory variables in models. We constructed a global model with two-way interaction of both flower density measures and bee abundance and successively deleted least significant explanatory variables from models which exhibited significance levels of $p > 0.10$. Study site/cluster and family/species were added as crossed random terms in models to meet the hierarchical structure of the study design (Bates et al. 2013). Additionally we corrected for overdispersion in poisson models by adding an observational-level random effect (Bates et al. 2013).

RESULTS

POLLINATION AND BEE ABUNDANCE ALONG ELEVATIONAL GRADIENT

First we assessed regional shifts in pollinator abundance and predominant pollination systems along the elevational gradient of Mt Kilimanjaro by analysing the relationships between elevation, bee abundance and proportion of cross-pollinated plants. After comparing seeds from pollinator-excluded and open-pollinated experiments, we found 12 and 15 plant species with cross-pollination or self-pollination systems, respectively (Table III.1). The proportion of cross-pollinated plants, which depend on pollinators for reproductive success, decreased with increasing altitude (Figure III.1). Bee abundance similarly decreased with increasing altitude (Figure III.3). Therefore, we found a trend of declining bee abundance and proportion of cross-pollinated plants with increasing elevation (Figure III. 2, 3).

Table III.1: Seed set of open-pollinated and bagged flowers and derived pollination system for 27 grassland and savannah species. The abbreviations stand for: EP (pollinator exclusion); OP (natural (open) pollination); SP (Self-pollination); and CP (Cross-pollination). Mean seed numbers per flower unit and standard errors are given.

Status	Family	Scientific Name	EP	OP	Pollination system
Invasive	Asteraceae	<i>Ageratum conyzoides</i>	3.17±0.84	3.49±0.84	SP
Native	Asteraceae	<i>Aspilia mossambicensis</i>	0.14±0.49	2.53±0.49	CP
Native	Asteraceae	<i>Bidens schimperi</i>	3.56±1.55	2.35±1.55	SP
Native	Capparaceae	<i>Cleome stenopetala</i>	1.21±0.96	3.36±0.96	CP
Native	Lamiaceae	<i>Clinopodium abyssinicum</i>	1.15±0.25	1.18±0.23	SP
Native	Commelinaceae	<i>Commelina africana</i>	0.82±0.56	1.59±0.56	CP
Native	Commelinaceae	<i>Commelina forskaolii</i>	0.69±0.28	0.42±0.28	SP
Native	Asteraceae	<i>Conyza pyrropapp</i>	2.97±0.55	2.25±0.55	SP
Native	Campanulaceae	<i>Cyphia glandulifera</i>	0.00	2.79±0.47	CP
Native	Acanthaceae	<i>Dyschoriste hildebrandtii</i>	0.62±0.82	0.62±0.82	SP
Native	Asteraceae	<i>Emilia discifolia</i>	3.13±0.78	3.84±0.79	SP
Native	Asteraceae	<i>Emilia ukambensis</i>	3.08±1.04	4.09±1.04	SP
Native	Asteraceae	<i>Helichrysum forskahlii</i>	1.71±0.61	1.50±0.61	SP
Native	Asteraceae	<i>Helichrysum kirkii</i>	2.02±1.30	3.23±1.30	CP
Native	Asteraceae	<i>Helichrysum nudifolium</i>	2.39±0.95	3.01±0.95	SP
Native	Boraginaceae	<i>Heliotropium steudneri</i>	0.28±0.21	0.69±0.21	CP
Native	Asteraceae	<i>Hirpicium diffusum</i>	2.08±0.83	2.73±0.83	SP
Native	Acanthaceae	<i>Justicia flava</i>	0.32±0.45	1.57±0.45	CP
Invasive	Verbenaceae	<i>Lantana camara</i>	1.30±0.49	1.62±0.49	SP
Native	Rubiaceae	<i>Oldenlandia herbacea</i>	0.85±1.40	0.98±1.41	CP
Native	Rubiaceae	<i>Oldenlandia wiedemannii</i>	0.18±0.71	2.39±0.71	CP
Native	Asteraceae	<i>Osteospermum vaillantii</i>	0.71±0.59	1.18±0.59	CP
Native	Polygonaceae	<i>Oxygonum sinuatum</i>	0.69±0.28	0.69±0.28	SP
Native	Turneraceae	<i>Streptopetalum hildebrandtii</i>	0.00	1.77±0.50	CP
Invasive	Asteraceae	<i>Tridax procumbens</i>	3.22±0.73	2.96±0.73	SP
Native	Tiliaceae	<i>Triumfetta flavescens</i>	0.28±0.21	0.69±1.17	CP
Native	Tiliaceae	<i>Triumfetta rhomboidea</i>	0.69±-0.00	0.69±1.39	SP

Table III.2: Results of mixed effects models testing the impact of conspecific flower density and bee abundance on seed set of cross-pollinated and self-pollinated plants. Shown are parameter estimates, standard errors and test statistics for each explanatory variable of minimum adequate models.

Variable	Cross-pollinated plants				Self-pollinated plants			
	Estimate	SE	Z	P	Estimate	SE	Z	P
Intercept	1.58837	0.87799	1.809	0.07043	0.92665	0.65204	1.421	0.1553
Focal flower density	-0.09182	0.03055	-3.006	0.00265	-0.00959	0.00494	-1.942	0.0521
Bee abundance	0.00060	0.00892	0.068	0.94615	-0.00424	0.00495	-0.857	0.3916
Focal flower density \times bee abundance	0.00121	0.00037	3.255	0.00113	0.00021	0.00012	1.832	0.0669

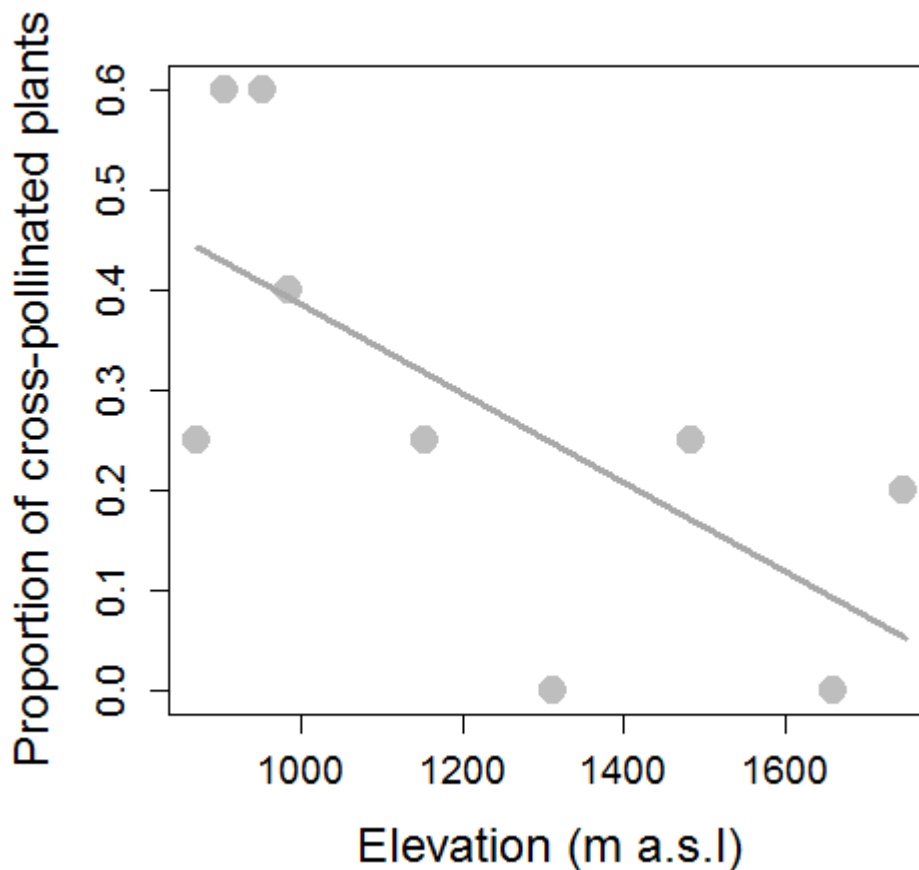


Figure III.1: Proportion of cross-pollinated plants declines with increasing altitude (ordinary linear regression, $r^2 = 0.46$; $n = 9$, $p < 0.05$).

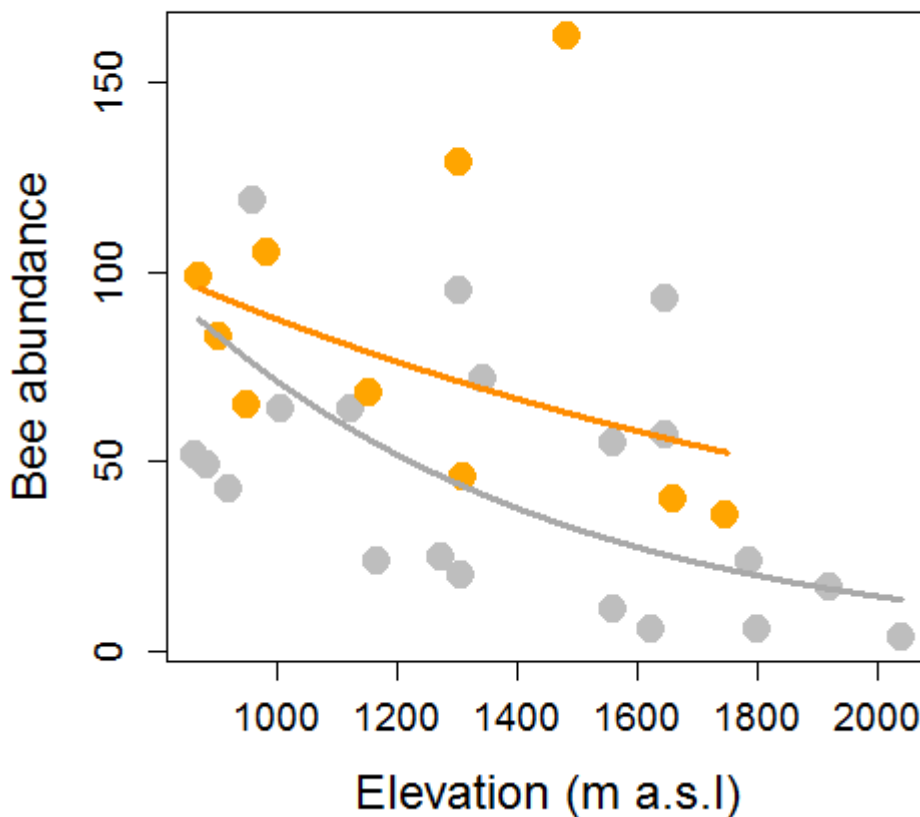


Figure III.2: Bee abundance decreases with increasing altitude. Dots show original measurements of bee abundance on study plots and lines show predictions based on simple linear regression analyses for plots where experiments were conducted (orange) and for a number of additional study plots where bee abundances were also measured during the study time (grey). A general trend of decreasing bee abundance (ln-transformed) with increasing altitude observed at 30 study plots between 870 and 2050 m a.s.l. (grey + orange dots, $n = 30$, $r^2 = 0.35$, $p < 0.01$) was also observed by tendency along the shorter altitudinal gradient of grassland and savannah ecosystems with reduced number of replicates (orange, $n = 10$, $r^2 = 0.17$, $p = 0.21$).

EFFECTS OF FLOWER DENSITY AND BEE ABUNDANCE

In the next step, we assessed the role of local focal (conspecific) and non-focal (heterospecific) flower density on seed production and possible interactive effects with bee abundance. The final minimum adequate model included the effects of focal and non-focal flower density, and their interactions with bee abundance. For cross-pollinated plants, we

found that seed production was significantly affected by an interaction between focal flower density and bee abundance ($z = 3.255$, $P = 0.003$, Figure III.3). When bee abundance was low, focal flowers produced more seeds in patches with low density than those flowers standing in patches with median or high flower densities. However, the situation changed when bee abundance increased. Plants in patches with low densities of focal flowers produced lesser amount of seeds than those in patches with median and high flower density (Figure III.3, Table III.2). Moreover, seed production was neither significantly affected by none focal flower density nor its interaction with bee abundance.

For self-pollinated plants, we did not find significant effects of focal flower densities ($z = 1.942$, $P = 0.052$) (Table III. 2). Moreover, there was no difference in seed production among patches of low, median and high flower density when bee abundance was low (Fig. III.3). Nevertheless, when bee abundance increased, plants in patches with high focal flower densities tended to produce more seeds than plants in patches with median and low flower densities (Figure III.3, Table III.2). Yet, neither the density of none-focal flowers nor the interaction with bee abundance had significant effects.

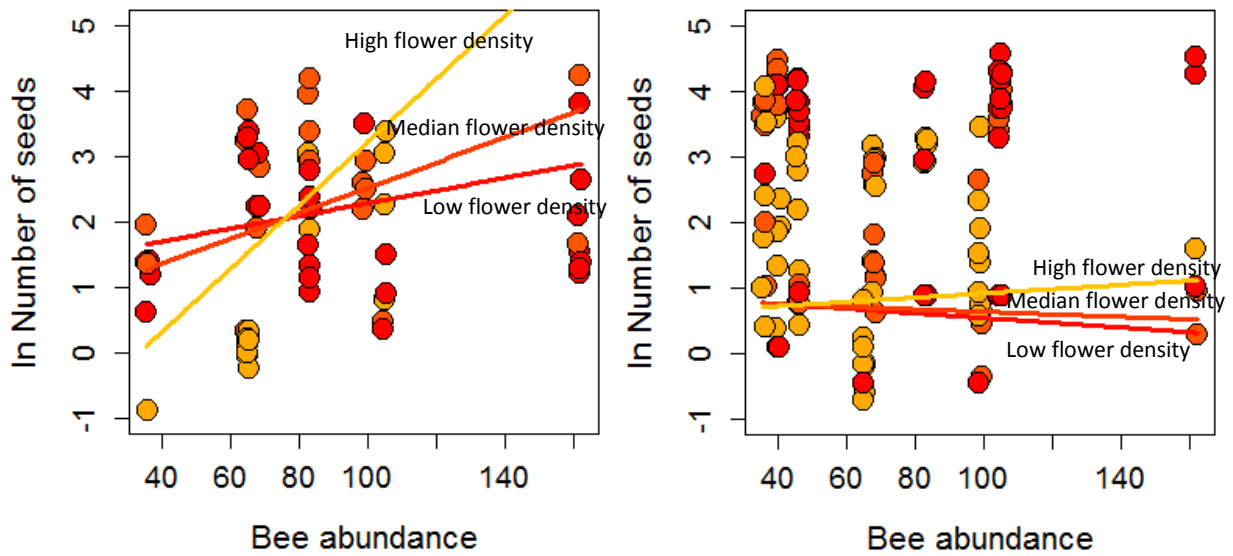


Figure III.3: Effects of flower density and pollinator abundance on seed production of cross-pollinated (left panel) and self-pollinated plants (right panel). Dots represent fitted values of mixed effect models with different colors indicating the flower densities on study sites (orange to red = high to low flower density). Regression lines shown predictions of mixed effect models conditional on the flower density observed on study sites (dark orange = 25%, red = 50%, orange = 75% quintile of flower density)

DISCUSSION

In our study we found that the proportion of cross-pollinated plants tended to decline along the altitudinal gradient. We also found that bee abundance decreased with increasing altitude. The decline of proportion of cross-pollinated plants and pollinator abundance could be due to changes in climatic conditions along the altitudinal gradient or alternatively due to more regular anthropogenic management activities on grassland compared to savannah habitats (Steffan-Dewenter et al. 2005; Aguilar et al. 2006; Goulson et al. 2008; Hegland et al. 2009; Winfree et al. 2009). Therefore, it indicates that in plant communities at higher altitudes, self-pollination as an alternative solution of reproductive assurance has been selected to combat the limited abundance and activity of pollinators (Arroyo et al. 1985; Bingham & Orthner 1998; Hoiss, Gaviria, et al. 2012). The tendency of increasing proportion of self-pollinated plants with increasing altitude supports the hypothesis that selfing rates increase with increasing altitude due to reduced availability of pollinators (García-Camacho & Totland 2009; Hoiss, Gaviria, et al. 2012).

The pollination requirements among members in wild plant communities are very complex and variable, especially when some flowering plants shift mating systems in order to assure their reproductive success (Gulias & Traveset 2012). In our study, flowering plants within tropical savannah and grassland wild plant communities were found to rely more on either biotic, abiotic or combination of biotic and abiotic pollination agents (Stelleman 1984; Gómez & Zamora 1999) to fulfil their reproductive obligation. Pollinator availability is one of the factors which determine pollination systems. However, when pollinators are limited or scarce, self-pollination is considered to be a potential alternative pollination agent which provides reproductive assurance of flowering plants (Fausto Jr et al. 2001; Hoiss, et al. 2012). Despite of other factors at local scales, pollinator availability and behavior are influenced by focal flower density (Kunin 1997; Dauber et al. 2010), consequently posing an impact on reproduction of flowering plants.

In our study we categorized co-existing plants regarding cross-pollination and self-pollination systems. For cross-pollinated plants, focal flower density and its interactive effects with bee abundance have significant effects on the seed production. At lower bee abundance, flower patches with low density produced more seeds than flower patches with median and high densities, but when bee abundance increased, seed production was higher in patches of median and higher densities of focal flowers. The tendency of increasing seed

production with increasing density of conspecific flowers coincides with findings of other studies (Kunin 1997; Dauber et al. 2010) that larger flower density of focal plant species attract more pollinators, thus enhance constancy of foraging behavior through flower density dependence and increase the chance of conspecific pollen transfer (Kunin 1997). Our study indicates that the facilitative effect of higher flower densities on reproductive success may switch to seed reduction when bee abundance is limited due to intraspecific competition for pollinators.

For self-pollinated plants, we did not find any differences in seed production at low, median and high focal flower densities when bee abundance was low since they highly rely on self-pollination (Gómez & Zamora 1999; Gulias & Traveset 2012). However when bee abundance increased, patches with median and high flower densities produced slightly more seeds than patches with low flower density, thus indicating that they still benefit from pollinators and require cross-pollination to reach their full reproductive output.

We conclude that the dominance of cross-pollination systems in tropical plant communities and the effect of focal flower density on the reproductive success of plants depend on the regional variation in pollinator abundances. The influence of flower density on pollinator attraction and behavior is a potential factor for cross-pollinated plants rather than self-pollinated plants. Altitude and anthropogenic activities such as habitat conversion and degradation are factors that may limit pollinator abundance and pollinator activities, thus leading plants to rely more on self-pollination than cross-pollination. However further studies are needed to determine the relative importance of pollinator limitation, plant reproductive systems and conspecific flower densities along climatic and land use gradients at a plant community level.

CHAPTER IV: GENERAL DISCUSSION**EFFECTS OF LAND USE ON POLLINATION**

The dominance of biotic, abiotic or a combination of biotic and abiotic pollination agents during reproduction in wild plant communities (Stelleman 1984; Gómez & Zamora 1999; Gulias & Traveset 2012) are being influenced by climate change and anthropogenic activities in a particular habitat. In my study, I chose lowland natural savannah and highland disturbed grassland as study sites. Due to having different degrees of human activities, I expected that self-pollination system and pollination limitation would be more pronounced in disturbed habitat than natural habitat for individual plant species and communities.

My results for individual species, I found that 27% and 89% of native savannah and grassland plant species, respectively, are principally capable of self-pollination but with varying degrees of reliance. The dominance of self-pollinated plants in disturbed habitats can be due to ongoing anthropogenic activities (Tscharntke et al. 2005; Winfree et al. 2009; García-Camacho & Totland 2009), which lead to reduction of pollinator abundance and activities (Steffan-Dewenter et al. 2005; Aguilar et al. 2006; Hendrickx et al. 2007; Goulson et al. 2008; Winfree et al. 2009). Therefore, self-pollination system becomes an alternative solution for reproductive assurance (Fausto Jr et al. 2001; Gulias & Traveset 2012)). In other hand, approximately 73% of tropical savannah plants depend on pollinators for reproduction which coincides with a previous estimation of 67% - 96% (Ollerton et al. 2011; Rosas-Guerrero et al. 2014) of tropical plant species. However, only 11% of native grassland species depend on pollinators for reproduction, which is much lower than the estimated amount. All invasive species in savannah and grassland were self-pollinated and self-compatible (Rambuda & Johnson 2004; van Kleunen & Johnson 2007; van Kleunen et al. 2008; Eckert et al. 2010; Hao et al. 2011).

My results for community level, native plants indicate that cross-pollination is the favourable pollination system for successful reproduction (Ashman et al. 2004) in savannah and marginally in grassland habitats. Whilst invasive plants in savannah and grassland showed reliance on self-pollination (Rambuda & Johnson 2004; van Kleunen & Johnson 2007; van Kleunen et al. 2008; Eckert et al. 2010; Hao et al. 2011) by producing a similar amount of seeds in pollinator-exclusion and open pollination treatments. However, seeds in open pollination treatments of invasive plants were significantly lower than seeds of supplemental hand-pollination treatments in grassland, and marginally so in savannah sites,

indicating sign of pollinator limitation. Nevertheless, such a pattern was not observed for native plant communities in both habitats, may be due to longer integration with existing pollinator networks (Vila et al. 2009) than invasive plants (Richardson et al. 2000; Vila et al. 2009).

Seed weight of plants in disturbed grassland habitat, where biomass is regularly removed, were lighter than in natural savannah habitats, which indicate plants in grassland may experience nutrient deficiency (King et al. 2007; Kettenring et al. 2011).

EFFECTS OF FLOWER DENSITIES ON POLLINATION SYSTEMS

Focal flower density is one of the factors that influence pollinator availability (Kunin 1997; Westphal et al. 2003) and behaviour (Kunin 1997), and consequently impact on reproduction of flowering plants. Pollinators are attracted to a species with higher floral densities in a landscape (Goulson 2000; Steffan-Dewenter et al. 2001; Westphal et al. 2003) than in small densities, and hence improve pollination services and quality by reducing interspecific pollen deposition on stigmas (Kunin 1993). Despite of small flower patches attracting fewer pollinators, it reduces pollinator constancy and quality in terms of the deposition of viable, conspecific, outcross pollen on stigmas (Larson & Barrett 2000; Klinkhamer & Lugt 2004). Nevertheless, it is hard to find evidence from literature concerning amount focal and non-focal flower density that will attract sufficient pollinators to enhance seed production of wild communities of tropical flowering plants and also to understand if all plants in community are being affected by flower density in their reproduction.

I assessed the effects of focal and non-focal flower density and possible interactive effects with bee abundance on seed production of plant communities, cross-pollinated and self-pollinated plants. For whole plant community, I did not find significant effects of focal and non-focal flower densities or its interactive effects with bee abundance. For cross-pollinated plants, I found a significant effect of focal flower density and interactive effect with bee abundance. When bee abundance was low, focal flowers produced more seeds in patches with low density than those flowers standing in patches with median or high flower densities. However, when bee abundance increased, plants in patches with low densities of focal flowers produced lesser amount of seeds than those in patches with median and high

flower density. Moreover, seed production was neither significantly affected by non-focal flower density nor its interaction with bee abundance for both self-pollinated and cross-pollinated plants. On the side of self-pollinated plants, I neither found significant effects of focal flower densities nor its interactive effects with bee abundance. Furthermore, there was no difference in seed production among patches of low, median and high flower density when bee abundance was low. Yet, when bee abundance increased, plants in patches with high focal flower densities tend to produce more seeds than plants in patches with median and low flower densities. According to results obtained, it seems that focal flower density and its interaction with bee abundance have only significant effects on seed production of cross-pollinated plants and not of self-pollinated plants. Therefore, assessing effects of flower density and bee abundance to cross-pollinated and self-pollinated plants together as whole community will not reflect the reality. For instance, some species within a community that undergo self-pollination do not need pollinators and flower density as much as those which fully or partially depend on pollinators for seed production. Hence, combining different mating systems within a study, it can lead to different conclusion as we observed.

EFFECTS OF ELEVATION ON POLLINATION SYSTEMS

Altitude has major influences on the climate of any particular locality and the pollination systems of its plant communities. I tested the hypothesis that self-fertilization rates increase with increasing altitude (García-Camacho & Totland 2009) because of reduction of pollinator abundance and functioning with increasing altitude, and hence become limiting factors for successful pollination and seed production (Bingham & Orthner 1998; Medan et al. 2002; Arroyo et al. 2006). I found that the proportion of cross-pollinated plants decreased with increasing altitude and also bee abundance decreased with increasing altitude, and therefore plants tend to adapt self-pollination system so as to assure seed production (Arroyo et al. 1985; Lloyd & Schoen 1992; Bingham & Orthner 1998; Kalisz & Vogler 2003; Kalisz et al. 2004; Trøjelsgaard & Olesen 2013). My results support the hypothesis that self-fertilization rates increase with increasing altitude (García-Camacho & Totland 2009) along southern slope of Mt. Kilimanjaro.

CONCLUSION

I conclude that native plant communities predominantly relied on cross-pollination but showed no evidence for pollinator limitation whereas the reproductive output of invasive plant communities was more pollen-limited despite of ability of undertaking self-compatible pollination system. Whether this unexpected findings may be a constraint on invasive plants which impedes their spread in natural savannah and semi-natural grassland, however, has to be tested in future studies.

In wild plant communities, there are different mating systems which differ in pollination requirement factors during the reproductive processes. Flower density dependence is a potential determinant for cross-pollinated plants rather than for self-pollinated plants to reach full reproductive outputs. Elevation and degrees of humans' influence into habitats are factors that may limit pollinator abundance and functioning, and thus lead plants to adapt self-pollination to assure their reproduction.

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LIST OF PUBLICATIONS ASSOCIATED WITH THE DOCTORAL STUDY

1. **Kindeketa, W.J.**, Peters, M.K. & Steffan-Dewenter, I. (submitted): “Pollination limitation of native and invasive plant species in savannah and grassland habitats at Mount Kilimanjaro, Tanzania”. *Journal of Vegetation Science*
2. **Kindeketa, W.J.**, Classen, A., Peters, M.K. & Steffan-Dewenter, I. (in preparation for submission): “Interactive effects of flower density, pollinator abundance, and mating system on seed set in wild plant communities at Mount Kilimanjaro, Tanzania”
3. Classen, A. Peters, M.K., **Kindeketa, W.J.**, Appelhans, T., Eardley, C.D., Gikungu, M.W., Hemp, A., Nauss, T. & Steffan-Dewenter, I. (submitted): Temperature versus resource constraints: which factors determine bee diversity on Mt. Kilimanjaro, Tanzania? *Global Ecology and Biogeography*
4. Classen, A., Steffan-Dewenter, I., **Kindeketa, W. J.**, Peters, M.K. (ready for submission): Small and cold or large and hungry: trade-offs in bee body size along climatic gradients.

DECLARATION OF AUTHORSHIP

This chapter 2 has been submitted to Journal of Vegetation Science as: Kindeketa, W.J^{1,2}, Peters, M.K². & Steffan-Dewenter, I². “Pollination limitation of native and invasive plant species in savannah and grassland habitats at Mount Kilimanjaro, Tanzania”.

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- 2003 - 2007: Master of Science in “Biodiversity Conservation and Management” at University of London, Imperial College, London. MSc thesis: “Conservation status of Verbenaceae in the Eastern Arc Mountains and Coastal Forests of Tanzania and Kenya”.
- 1993 - 1997: Bachelor of Science in “Forestry” at Sokoine University of Agriculture, Tanzania. Special project: “Evaluation of the socio-economic importance of establishing teak plantations in Ulunga District”.

OTHER PUBLICATIONS

1. Marshall, A.R., P. J. Platts, R. E. Gereau, W. Kindeketa, S. Kang’ethe & R. Marchant (2012). The genus *Acacia* (Fabaceae) in East Africa: distribution, diversity and the protected area network *Plant Ecology and Evolution* 145 (3): 289–301.
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3. Kindeketa, W.J. (2010). Conservation priority areas for threatened Verbenaceae in the Eastern Arc Mountains and Coastal Forests of Tanzania and Kenya. In: X. van der Burgt, J. van der Maesen & J.-M. Onana (eds), *Systematics and conservation of African plants*, pp. 477–480. Royal Botanic Gardens, Kew
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INTERNATIONAL WORKSHOPS

1. 2014: XXth Association for the Taxonomic Study of the Flora of Tropical Africa (**AETFAT**) Congress at Stellenbosch Cape Town, South Africa
13 – 17th January 2014
2. 2014: The International Union for the Conservation of Nature (**IUCN**) Eastern Africa Plant Red Listing Authority Workshop in Nairobi, Kenya
3. 2013: The International Union for the Conservation of Nature (**IUCN**) Eastern Africa Plant Red Listing Authority Workshop in Nairobi, Kenya

4. 2010: XIXth Association for the Taxonomic Study of the Flora of Tropical Africa (**AETFAT**) Congress at Antananarivo, Madagascar.
25th – 30th April 2010
5. 2010: The International Union for the Conservation of Nature (**IUCN**) Eastern Africa Plant Red Listing Authority Workshop in Nairobi, Kenya
6. 2007: XIXth Association for the Taxonomic Study of the Flora of Tropical Africa (**AETFAT**) Congress at Yaoundé, Cameroon. *26th – 2nd March 2007*
7. 2007: The International Union for the Conservation of Nature (**IUCN**) Eastern Africa Plant Red Listing Authority Workshop in Dar es Salaam, Tanzania
8. 2006: The International Union for the Conservation of Nature (**IUCN**) Eastern Africa Plant Red Listing Authority Workshop in Nairobi, Kenya
9. 2001: Workshop on Sustainable Production of African Blackwood in Tanzania by **Fauna & Flora International**
10. 2001: Curatorial workshop on Herbarium Management and Botanical Research in United States of America, the Missouri Botanical Garden.



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