Significance of Direct and Indirect Pollination Ecosystem Services to the Apple Industry in the Western Cape of South Africa.

by

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Declaration

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Abstract

Insect pollinators play an important role in producing crops in global agriculture. Pollinatordependent crops contribute to maintaining a healthy variety in the human diet and often have a high market value, beneficial for local or regional economies. Insect crop pollinators can either be from natural areas adjacent to orchards, or they can be brought into orchards by beekeepers that manage them. Pollination by wild pollinators is an ecosystem service, while managed pollinators (mostly honeybees) is a humanly managed service, considered not to be related to the ecosystem. Ecosystem services and their economic value have often been used as an incentive for conservation, although it is sometimes difficult to characterise and quantify them. Wild and managed pollinators have been reported to be threatened in several regions around the world, and there is concern about the effect a pollination deficit may have on crop production. Different crops and cultivars have different levels of dependence on insect pollination due to a combination of biological, physical and management factors. In this study, the pollination dependence of the Granny Smith apple cultivar and the respective contributions of wild and managed pollinators are investigated in the Western Cape province of South Africa. Granny Smith apples show a significant increase in production with insect pollination (wild and managed). Managed honeybees are more abundant in orchards than wild honeybees, and also provide a better pollination service. This difference between the pollination service of wild and managed honeybees are specifically noted in the quality, where managed honeybees pollination result in significantly more seeds per fruit and consequently produce a better shaped apple. The study goes further by quantifying the ecosystem services to the managed honeybee industry through a questionnaire completed by beekeepers. It was found that 49% of the managed hives in the Western Cape rely to some extent on natural vegetation as a forage source. Furthermore 18% of honey produced is also from natural vegetation and the wild honeybee population replenish managed honeybee stocks if they become depleted. Although managed honeybees are not usually considered an ecosystem service, it is clear that they are still linked to the ecosystem via these pathways. It is thus obvious that all pollination sources are linked to the environment, not just wild pollinators. A further economic valuation of the ecosystem service studied, and to the argument for conservation of pollinators and the resources they depend on.

Opsomming

Insek bestuiwing speel 'n belangrike rol in die produksie van gewasse in landbou wêreldwyd. Gewasse wat bestuiwing-afhanklik is, dra by tot 'n gesonde verskeidenheid in die mens se dieët en hul hoë mark waarde is voordelig vir plaaslike en streeks ekonomieë. Insek bestuiwers kan of van natuurlike areas langs boorde afkomstig wees, of bestuurde bestuiwers kan deur byeboere in boorde ingebring word. Bestuiwing deur wilde bestuiwers is 'n ekosisteem diens, maar die byeboere verskaf 'n bestuurde diens, wat nie altyd gereken word om aan die ekosisteem verwant te wees nie. Ekosisteem dienste en hul ekonomiese waarde word gereeld gebruik as insentief vir bewaring, alhoewel dit soms moeilik is om dit te karaktariseer en te kwantifiseer. In sekere streke wêreldwyd is dit bewys dat wilde, asook bestuurde bestuiwers, bedreig is en daar heers bekommernis dat 'n tekort aan bestuiwers gewas produksie negatief sal beïnvloed. Verskillende gewasse en kultivars het verskillende vlakke van bestuiwing-afhanklikheid as gevolg van verskillende biologiese en fisiese faktore en bestuurspraktyke. In hierdie studie is die bestuiwings-afhanklikheid van die Granny Smith appel kultivar ondersoek, asook die bydrae van wilde en bestuurde heuningbye in die Wes-Kaap provinsie van Suid Afrika. Granny Smith appels toon 'n betekenisvolle produksie verbetering met insek bestuiwing (wilde en bestuurde bye). Daar is 'n groter hoeveelheid bestuurde bye in 'n boord as wilde bye, en hulle verskaf ook dus 'n beter bestuiwingsdiens. Die voordeel van bestuurde bye bo wilde bye word veral in vrug kwaliteit opgemerk. As bestuurde bye gebruik word, is daar betekenisvol meer sade per vrug en gevolglik het die appels ook 'n beter vorm. Verder fokus die studie ook op die kwantifisering van ekosisteem dienste wat aan die bestuurde heuningby industrie verskaf word, deur inligting van byeboere te gebruik. Daar is bevind dat 49% van die kolonies bestuurde bye in die Wes-Kaap is tot 'n mate afhanklik van natuurlike plantegroei vir voedsel. Verder is 18% van die geproduseerde heuning ook afkomstig van natuurlike plantegroei se nektar en byeboere vang wilde kolonies om uitgestorwe bestuurde kolonies te vervang. Dit is dus duidelik dat alle bestuiwings bronne gekoppel is aan die omgewing, nie slegs wilde bestuiwers nie. 'n Verdere ekonomiese waardasie van die onderskeie ekosisteem dienste wat bestudeer is, voeg motivering by tot die bewaring van bestuiwers en die hulpbronne waarvan hulle afhanklik is.

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Table of Contents

DECLARATION							
					SAN	SAMEVATTING	
ACI	KNOWLEDGEMENTS	v					
TABLE OF CONTENTS							
					LIS	T OF APPENDICES	XVi
~~~							
CHAPTER 1: GENERAL INTRODUCTION		1					
1.1	ECOSYSTEM SERVICES: AN UTILITARIAN PERSPECTIVE ON	1					
	ENVIRONMENTAL PROTECTION						
1.2	CROP POLLINATION AND IMPORTANCE OF POLLINATORS	3					
1.3	SOURCES OF POLLINATORS FOR CROP POLLINATION SERVICES	4					
	1.3.1 Wild pollination services: the value, threats to and conservation of wild pollinators	5					
	1.3.2 Managed pollination services: the value, threats to and conservation of commercial pollinators	6					
1.4	DECIDUOUS FRUIT PRODUCTION AND POLLINATION RESEARCH IN	8					
	SOUTH AFRICA						
1.5	OBJECTIVES OF THE THESIS	10					
REF	REFERENCES						

CHAPTER 2: WILD POLLINATION SERVICES ARE COMPARABLE TO		
MAI	NAGED POLLINATION SERVICES IN TERMS OF APPLE QUANTITY,	
BUT	T NOT QUALITY	
2.1	INTRODUCTION	20
2.2	METHODS	22
	2.2.1 Apple industry and study cultivar	22
	2.2.2 Study area and sites	23
	2.2.3 Question 1: Is Granny Smith apple production dependent on insect	28
	pollination?	
	2.2.3.1 Exclusion experiment setup	28
	2.2.3.2 Exclusion experiment measurements	29
	2.2.3.3 Analytical methods	31
	2.2.4 Question 2: What pollination system provides the most effective Granny Smith	32
	pollination?	
	2.2.4.1 Forager survey data collection	32
	2.2.4.2 Exclusion experiment	35
	2.2.4.3 Analytical methods	35
2.3.	RESULTS	37
	2.3.1 Question 1: Is Granny Smith apple production dependent on insect	37
	pollination?	
	2.3.2 Question 2: What pollination system provides the most effective Granny Smith	39
	pollination?	
	2.3.2.1 Foragers & visitation rate	39
	2.3.2.2 Number of apples per branch	41
	2.3.2.3 Fruit-set	42
	2.3.2.4 Seed-set	42
	2.3.2.5 Fruit quality and marketability	43
2.4.	DISCUSSION	46
	2.4.1 Question 1: Is Granny Smith apple production dependent on insect	46
	pollination?	

	2.4.2 Question 2: What pollination system provides the most effective Granny Smith	46
	pollination?	
	2.4.3 Limitations	47
	2.4.4 Conservation recommendations	49
REF	FERENCES	51
CH	APTER 3: ECOSYSTEM SERVICES SUPPORTING THE WESTERN CAPE	57
MA	NAGED HONEYBEE INDUSTRY	
3.1	INTRODUCTION	57
3.2	METHODS	60
	3.2.1 Study area and industry	60
	3.2.2 Questionnaire survey	61
3.3	RESULTS	62
	3.3.1 Natural forage use for colony maintenance and honey production	62
	3.3.2 Colony replenishing	63
3.4	DISCUSSION	64
	3.4.1 Use of natural vegetation	64
	3.4.1.1 Fynbos can sustain populations through periods of otherwise low forage	65
	3.4.1.2 Improved colony condition prior to crop pollination	66
	3.4.1.3 Income for beekeepers from fynbos honey	67
	3.4.2 Colony replenishing	67
3.5	CONCLUSIONS	68
REF	FERENCES	69
СН	APTER 4: GENERAL DISCUSSION AND CONCLUSIONS	73
4.1	OVERVIEW OF THE DIRECT AND INDIRECT POLLINATION ECOSYSTEM	73
	SERVICES TO THE WESTERN CAPE APPLE INDUSTRY	
42	FINANCIAL CONSIDER ATIONS OF POLLINATION SERVICES	74

	4.2.1 Financial valuation of pollination services to Granny Smith apple production	75	
	4.2.2 Valuation of wild pollination services to apple production	77	
	4.2.3 Valuation of ecosystem services supporting the managed honeybee industry	78	
4.3	CONSERVATION AND MANAGEMENT RECOMMENDATIONS	80	
	4.3.1 Farm scale	80	
	4.3.2 Landscape scale	81	
	4.3.3 Industry scale	82	
4.4	FUTURE RESEARCH	82	
REF	REFERENCES		

#### **List of Figures**

Fig. 2.1. A Granny Smith apple blossom, showing the conspicuous reproductive parts.

33

**Fig. 3.1.** Hypothetical flow of ecosystem services from the natural system to the agricultural system via wild and managed pollination. Wild pollinators are directly linked to the natural system (1) as often described, but commercial honey bees are also linked to the ecosystem via an indirect pathway (2).

**Fig. 3.2.** Number of honeybee hives Western Cape beekeepers place on each type of forage source at apiary sites (for the whole year or part of the year). Collectively the percentages add to more than 100%, because some hives are moved around apiary sites and therefore accounted for more than once. The figure indicates the number of colonies that fully or partially use a particular forage source. The proportion of total number of colonies, represented at each forage source is indicated in percentage above each bar. Data was adapted from Allsopp & Cherry (2004).

**Fig. 3.3.** Hypothetical foraging range of a honeybee colony around the apiary site. The bees of a colony stationed at a beekeeper's apiary site can forage optimally up to 1.5km from their hive but have been recorded foraging up to 10km from the hive. Colonies often forage on other vegetation types when the dominant forage source at the apiary site is not flowering. **66** 

**Fig. A1.** Model selection was done by using Akaike's Information Criterion. The model with lowest AIC value is the model where the relationship between the bias and precision of the model has been optimized.

86

#### **List of Tables**

**Table 2.1.** Selection of twelve study sites in three pollination systems, according to two parameters. The three pollination systems (M, MN and N) are defined by whether or not managed bees were present in the system and by the sites' position in the landscape. The landscape parameter (adjacency of natural vegetation) is used as a surrogate for the presence of wild pollinators.

**Table 2.2.** Regression results for the reproductive success of Granny Smith apples in relationship to insect pollination. Positive z- or t-values indicate positive production response to insect pollination (open branches versus mesh enclosed branches). Regression analyses for three of the four production variables were done using GLMMs (M1, M2 and M4) and one were done using a LMM (M3). Fixed variable: branch (open *versus* closed). Random variables: farm (groups = 12 (M1-M4)), row nested in farm (groups = 58 (M1-M4)), tree nested in row (groups = 289 (M1&M2), 217 (M3&M4)). Number observation (M1,M2,M3,M4) = (558,551,553,551).

**Table 2.3.** Difference in fruit production when insect pollination is either excluded or allowed.

**38** 

**Table 2.4.** Difference in fruit-set: number of apples per hundred flowers when insect pollination is either excluded or allowed.

**Table 2.5.** Differences in seed-set (number of seeds per fruit), fruit size (weight (g) and diameter (mm)) and fruit shape, when insect pollination is either excluded or allowed.

**Table 2.6.** Regression results for the number of honeybee foragers present in three pollination systems using a GLMM model with a Poisson distribution. The fixed variables are wind and pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 330 forager observations. The random variables are farm (groups = 11, intercept standard deviation = 0.73) and row (nested in farm, groups = 33, intercept standard deviation = 0.26). **40** 

**Table 2.7.** Regression results for the visitation rate (number of flowers visited per minute) of honeybee foragers in three pollination systems using a LMM with a Gaussian distribution. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 66 observations (visitors per minute). Random variable (farm): groups = 10, intercept standard deviation = 0.00. Standardized within-group residuals: Q1 = -0.573, Median = -0.167, Q3 = 0.644.

**Table 2.8.** Regression results for the improvement* in number of apples per branch in three pollination systems using a LMM. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 57 observations (branches). Random variable (farm): groups = 12, intercept standard deviation = 0.25. Standardized within-group residuals: Q1 = -0.477, Median = 0.040, Q3 = 0.617.

**Table 2.9.** Regression results for the improvement* in fruit-set in three pollination systems using a LMM. Fruit-set is defined as the number of apples produced per 100 flowers. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 57 observations (branches). Random variable (farm): groups = 12, intercept standard deviation = 3.41. Standardized within-group residuals: Q1 = -0.496, Median = -0.118, Q3 = 0.306.

**Table 2.10.** Regression results for the number of seeds per fruit in three pollination systems using a LMM. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 553 observations (number of fruit analysed for seed-set). The random variables are farm (groups = 12, intercept standard deviation = 0.00) and branch (nested in farm, groups = 24, intercept standard deviation = 1.62). Standardized within-group residuals: Q1 = -0.675, Median = -0.044, Q3 = 0.712.

**Table 2.11.** Regression results for the marketability* the apple fruit produced in three pollination systems using a GLMM with a Binomial distribution. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 551 observations (number of fruit analysed for marketability). Random variable (branch): groups = 2, intercept standard deviation = 0.13.

**Table 2.12.** Regression results for the diameter of the apple fruit produced in three pollination systems using a LMM with a Gaussian distribution. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 551 observations (number of fruit measured). The four random variables are farm (groups = 12, intercept standard deviation = 3.08), row (nested in farm, groups = 58, intercept standard deviation = 1.84), tree (nested in row, groups = 217, intercept standard deviation = 2.70) and branch (nested in tree, groups = 294, intercept standard deviation = 2.44). Standardized within-group residuals: Q1 = -0.546, Median = -0.020, Q3 = 0.596.

**Table 2.13.** Regression results for the weight of the apple fruit produced in three pollination systems using a LMM with a Gaussian distribution. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 551 observations (number of fruit weighed). The four random variables are farm (groups = 12, intercept standard deviation = 13.75), row (nested in farm, groups = 58, intercept standard deviation = 8.07), tree (nested in row, groups = 217, intercept standard deviation = 12.59) and branch (nested in tree, groups = 294, intercept standard deviation = 11.57). Standardized within-group residuals: Q1 = -0.593, Median = -0.040, Q3 = 0.531.

**Table 2.14.** Regression results for the shape of the apple fruit produced in three pollination systems using a GLMM with a Binomial distribution. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 551 observations (number of fruit analysed for marketability). Random variable (branch): groups = 2, intercept standard deviation = 0.13.

**Table 3.1.** Annual honey production (kg) in the Western Cape from different sources of honeybee forage, as reported by Western Cape beekeepers in 2004 (Allsopp & Cherry, 2004). **62** 

**Table 3.2**: The number of wild honeybee colonies collected annually by Western Cape beekeepers to replenish their managed colony stock. Colonies are collected either by removal from urban areas or by placing empty trap boxes in specific areas with forage sources that are attractive to honeybees.

**Table 4.1.** The economic valuation of pollination using the comparison of two scenarios: Scenario 1 depicts Granny Smith apple production with insect pollination and scenario 2 depicts Granny Smith apple production without insect pollination. Both the quantity (yield) and quality (marketable *versus* processed) is taken into account for the monetary valuation. The proportion of the production value (R / ha) attributed to insect pollination is obtained.

**Table 4.2.** A summary of the annual flow value of the ecosystem services (ES) for the managed honeybee industry. At ES 1 the cost of replacement was used for valuation, and at ES 2 and ES 3 the direct market values were used.

78

**Table A1.** Model selection for the number of foragers (honeybees) data. A GLMM was used to analyse the data. The following factors were modelled against the number of foragers: pollination system, wind, temperature, relative humidity, percentage cloud cover and average number of open flowers per orchard. The factors farm and row were set as random variables, with row nested in farm. Model 5 was selected as the best model. All the variables that were removed from the model 5 did not have a significant influence on the dependent variable.

87

**Table A2.** Model selection for the honeybee visitation rate data. A LMM was used to analyse the data. The following factors were modelled against the visitation rate: pollination system, wind, temperature, relative humidity, percentage cloud cover and average number of open flowers per orchard. The factors farm was set as a random variable. Model 6 was selected as the best model. All the variables that were removed from the model 6, except for relative humidity, did not have a significant influence on the dependent variable.

**Table A3.** Model selection for seed-set data. A LMM was used to analyse the data. Pollination system is the only variable modelled against seed-set. The random variables were selected by using the AIC method. Model 8 was selected as the best model.

88

**Table A4.** Model selection for the fruit-quality (marketability factor) data. A GLMM was used to analyse the data. Pollination system is the only variable modelled against the marketability of the fruit. The random variables were selected by using the AIC method. Model 7 was selected as the best model.

**Table A5.** Model selection for the fruit-quality (diameter) data. A LMM was used to analyse the data. Pollination system is the only variable modelled against the fruit diameter. The random variables were selected by using the AIC method. Model 1 was selected as the best model. **89** 

**Table A6.** Model selection for the fruit-quality (weight) data. A LMM was used to analyse the data. Pollination system is the only variable modelled against the fruit weight. The random variables were selected by using the AIC method. Model 1 was selected as the best model. **89** 

**Table A7.** Model selection for the fruit-quality (shape) data. A GLMM was used to analyse the data. Pollination system is the only variable modelled against the fruit shape. The random variables were selected by using the AIC method. Model 15 was selected as the best model. **90** 

# **List of Appendices**

Appendix A	
Model Selection for Question 2 of Chapter 2	86
Appendix B:	
Questionnaire on Colony Replacement	91

#### Chapter 1

#### **General Introduction**

#### 1.1 Ecosystem services: an utilitarian perspective on environmental protection

The services and benefits humanity receive from ecological systems, and the species that make them up, have obtained considerable attention in the last two decades (Daily 1997; De Groot *et al.* 2002; MEA 2005). To emphasize the importance of environmental protection ecosystem services have been extensively valued in monetary terms, although this approach has been both praised and critiqued as a tool used for conservation.

Those against economic valuation argue on an ethical basis that the environment has intrinsic value and its priceless qualities should not be viewed as a utility (Mc Cauley 2006) On a practical basis, some argue that the economic benefits of ecosystem services are over inflated (Mc Cauley 2006), and difficult to prove if all trade-offs and opportunity costs are considered (Ghazoul 2007). The ecosystem service concept combined with market driven forces, could lead to environmental decision-makers considering economic factors only and non-conservation options could very well find preference, rather than the other way round (Redford & Adams 2009). Furthermore, ecosystem services are essentially difficult to assign value to, as most are not traded and have public properties (Jarvis *et al.* 2007).

On the other hand, Costanza *et al.* (1997) argue that the issue of valuation is inseparable from the choices and decisions we have to make about ecological systems. They go on to value global ecosystem services between US\$16-54 trillion (10¹²) per year, making a compelling case for the maintenance of the world's ecosystems (Costanza *et al.* 1997). Furthermore, the value assigned to ecosystem services are increasingly used by the public and private sectors of society. Examples of this are the Costa Rican government's landmark 'payment for ecosystem services'

(PES) scheme, and the commercial trading of environmental credits by a public Australian company (Chichilnisky & Heal 1998; Daily *et al.* 2000).

The ecosystem service concept has received further scrutiny as a tool for conservation planning. The provision of ecosystem services are usually reliant on a whole process involving several physical and biological attributes, making it more likely that a whole system is conserved rather than just one species (Mc Cauley 2006). Consequently, ecosystem service incentives for conservation are generally more inclusive than single species conservation, providing further credence for the use of ecosystem services. But, research has shown that areas important for sustaining ecosystem service flows is often incongruent with priority areas for biodiversity conservation and focusing on ecosystem services alone would not suffice to protect biodiversity (Chan *et al.* 2006; Anderson *et al.* 2009; Egoh *et al.* 2009; O'Farell *et al.* 2010). Anderson *et al.* 's results showed large variation between areas showing that the extent of congruence between biodiversity and ecosystem service hotspot are very location specific. Moreover, there is often weak congruence among important areas for different ecosystem services on a global scale (Naidoo *et al.* 2008), but also particularly in South Africa, because of the highly heterogeneous landscape (Egoh *et al.* 2008).

Where funding is concerned, ecosystem service projects could secure more than four times the funding than biodiversity focused projects could, mainly from corporate sources, while also able to create protected areas no less than biodiversity aimed projects (Goldman *et al.* 2008). By deriving funding from more diverse and novel sources, ecosystem service projects does not draw from the already limited finances available for conservation, but rather creates new opportunities by engaging with different stakeholders and encompassing working landscapes (Goldman *et al.* 2008).

In conclusion, conservation planning should never lose sight of the goal of biodiversity protection in the wake of ecosystem services and decision making should happen at multiple levels, reflecting both local conditions and broader priorities of all stakeholders (Anderson *et al.* 2009; O'Farell *et al.* 2010). The valuation of ecosystem service and the use of the concept in

conservation projects are useful to reach a much wider audience and secure necessary additional resources for conservation (Skroch & López-Hoffman 2009).

#### 1.2 Crop pollination and importance of pollinators

Cultivated systems, such as the agricultural landscape, contain planned biodiversity (crops and livestock), as well as associated natural biodiversity (biophysical environment) (Jarvis *et al.* 2007). This natural biodiversity sustains and supports production which provides food for the human population (Daily 1997). Not surprisingly, ecosystem services and its connection to food security have been well studied in the agricultural context. Fifteen years ago, agricultural ecosystem services in the United States, were already valued at \$4.1 billion a year (Buchman & Nabhan 1996). Examples of these ecosystem services are: genetic resources, directly harvested products and essential regulating services such as pest control, nutrient cycling and pollination (MEA 2005; Jarvis *et al.* 2007). As agricultural practises generally degrade the natural environment, the high value of ecosystem services linked to food security could be a conservation incentive for both producers and consumers alike.

Animal (mostly insect) pollination is an essential and valuable service to agriculture (Jarvis *et al.* 2007). Seventy percent of tropical crops have at least one variety that is improved by animal pollination (Roubik 1995); while 84% of 264 studied European crops depend to some extent upon animal pollination (Williams 1994). About 130 crop types in the USA (McGregor 1976) and 39 in the UK (Carreck & Williams 1998) are insect pollinated, with estimated values of over US\$ 9 billion and £ 202 million respectively. In both cases between 50 - 70 per cent of these monetary values can be attributed to honeybees *Apis mellifera* L. alone. Globally, the economic contribution of insect pollinators to food producing crops is estimated to be € 153 billion, representing 9.5% of the total value of food producing crops (Gallai *et al.* 2009). It is clear from these statistics that we would have considerably less crop varieties plus a loss in monetary value if insect pollinators were not present.

Ghazoul (2005a) argues against the importance of insect pollinators to food security, stating that the bulk of the world's staple foods (more than 60%) are wind pollinated and independent of insect pollination (see also Richards 2001; Klein *et al.* 2007). Furthermore, one has to take into account the degree to which a particular crop needs insect pollination, depending on flower morphology, level of self-fertilization and the arrangement of flowers (Delaplane & Mayer 2001). Most insect-pollinated crops are improved by, rather than totally dependent on, insect-pollination. Thus, if these pollinators went extinct, production would be reduced but not lost completely (Richards 2001; see Free 1993 for pollination requirements of different crops).

Nevertheless, pollinator-dependent crops such as fruits, nuts, vegetables and stimulant crops (e.g. coffee, cocoa and tea) contribute to a nutritional and balanced human diet beyond just caloric intake and therefore animal pollination is essential (Steffan-Dewenter *et al.* 2005). Furthermore, these pollinated crops are typically the low-acreage, high-value crops that are associated with the lifestyle of people eating for pleasure, rather than survival (Delaplane & Mayer 2001). They often are sold at five times the price per ton than non-insect pollinated crops (Gallai *et al.* 2009). It is not surprising that these crops are mainly planted and rapidly increasing in developed countries (Aizen & Garibaldi 2008). Where they are cultivated in developing countries (e.g. South Africa), a large portion is usually exported to developed countries which creates economic growth opportunities for the producing country.

To conclude, there are two reasons why pollinator-dependent crops, and therefore, pollinators, are important: firstly to maintain a healthy variety in the human diet, and secondly, for local or regional economies producing these high value crops. In the words of Delaplane & Mayer (2001): "Bees may not be necessary to human life, but they are necessary for life as we know it."

#### 1.3 Sources of pollinators for crop pollination services

It is important that differences be distinguished between two types of crop pollinators. Firstly, there are wild pollinators that are naturally occurring in the vicinity where the pollinated crop is grown. These pollinators usually reside in natural peripheries of crop fields (Kremen *et al.* 2007)

or larger areas of adjacent natural vegetation (Riketts 2004, Blanche *et al.* 2006). The pollination service provided by these animals (mostly insects) can be described as an ecosystem service in the true sense, as they are a natural service and do not rely on the management of humans. Secondly, there are managed pollinators. These are pollinators (mostly honeybees) that are commercially managed by beekeepers and deliberately placed at key times in crop fields for pollination purposes. In contrast to the wild pollinators, this study does not consider the managed colonies as an ecosystem service as they are a commercial service, dependent on the management actions of humans (Allsopp *et al.* 2008). From here on, 'pollination services' collectively refers to managed and wild (naturally occurring) pollinators, while the two types ('managed pollination services' or 'wild pollination services') will be referred to specifically.

In a given crop system, one or both of these sources of pollinators could be present. The specific dynamic and interaction of these sources can be termed the pollination system. This pollination system can differ between cultivars, countries, regions and even different fields or orchards in the same area. This will depend on the characteristics of the natural system and the management practises of the crop producer.

#### 1.3.1 Wild pollination services: the value, threats to and conservation of wild pollinators

Even though managed honeybees are the major pollinator of crops globally (McGregor 1976; Richards 2001), wild pollinators are particularly important for less intensively farmed crops with ample resources for these pollinators (Gazhoul 2005a,b). For example, coffee plants profited from a higher diversity in pollinating bees in Indonesia (Klein *et al.* 2003) and canola in Canada was 98% pollinated by non-honeybee pollinators (Morandin & Winston 2005). In the Western Cape of South Africa, Allsopp *et al.* (2008) have suggested that, of the 67% of deciduous fruit production that can be attributed to insect pollination, more than half can possibly be ascribed to wild pollinators. It must be noted that the honeybee is native to this area and is the primary wild pollinator in this case. They value this pollination service between US\$49.1–310.9 million, while managed pollination services (also honeybees) has a value between US\$28.0–122.8 million (Allsopp *et al.* 2008).

As agriculture intensifies and expands (Tilman et al. 2001), there is increasing evidence that wild pollinators are threatened by human land-use practises such as the introduction of and competition from, exotic species (Donaldson 2002; but see Allsopp & Cherry 2004), the use of harmful chemicals (Kearns et al. 1998) and the fragmentation of natural areas (Brosi et al. 2008). The value of and potential threats to wild pollinators have rekindled awareness of their conservation. Additionally, reports on managed honeybee declines in the Unites States have also added to research papers focussing on other potential crop pollinators and their conservation. Non-honeybee pollinators are less successfully managed, and the interest has spread to conserving their natural populations through habitat conservation to secure pollination of crops (Delaplane & Mayer 2001). Morandin and Winston (2006) have shown that there could be economic benefit to conserve natural areas near canola fields to sustain wild pollinator populations. The rationale for conservation of natural areas is that they provide nesting sites and supplemental forage to the wild pollinators. In reality, this is still a young research field (Klein et al. 2008) and very little is known about wild pollinator communities, consequences of their decline (Kevan 1999; Kevan & Philips 2001) or if habitat conservation would promote pollinator diversity and abundance (Klein et al. 2008). Except for a few studies, there is also a general lack in empirical evidence to show whether there are real benefits of wild pollinators in crop production on a monoculture, commercial scale (Ghazoul, 2005b). While a precautionary approach can prevent a crisis in many conservation issues, the resources that are available for these causes are often limited. It is therefore important that sufficient evidence is gathered to justify wild pollinator conservation for production of specific crops in specific areas.

# 1.3.2 Managed pollination services: the value, threats to and conservation of commercial pollinators

As the planting of ever increasing hectares of pollinator-dependent crops continue (Aizen & Harder 2009), the demand for pollinators is increasing beyond the capacity of wild pollinators residing in natural areas adjacent to crop fields. The result is growers becoming increasingly reliant on pollination by commercially managed honeybee colonies brought into orchards or fields (Richards 2001). Honeybees, mainly *Apis mellifera*, are the most important managed pollinators for economic crops globally, performing up to 90% of commercial pollination

(McGregor 1976; Free 1993; Richards 2001). The species has a very large native range extending over Africa, Europe and the Middle East and has spread further through commercial activities over the majority of the globe (Delaplane & Mayer 2001). The honeybee is a readily-managed species: it is tolerant to disturbance associated with apiculture, it is relatively adaptable to harsh climates and has favourable honey-making abilities (Delaplane & Mayer, 2001).

Since 1990, when reports of honeybee populations declining in the United States began, there has been an increased research focus on the threats to commercial honeybee colonies and the possible negative impacts such threats could have on agricultural production (Buchmann & Nabhan 1996; Ingram et al. 1996; Allen-Wardell et al. 1998; Kearns et al. 1998; Kevan & Phillips 2001; Steffan-Dewenter et al. 2005). The threats facing managed honeybee populations include diseases and parasites, pesticide poisoning, genetically modified crops, a lack of available forage resources, adverse weather conditions, political and economic factors as well as yet unexplained bee epidemics (Genersch 2010; see Van Engelsdorp & Meixner 2010 for a review). These factors (mostly in combination with one another) have caused dramatic declines in the United States and some European countries (Aizen & Harder 2009; Van Engelsdorp & Meixner 2010). Yet, if examined from a global scale the world honeybee population have actually increased by 45% in the last 50 years (Aizen & Harder 2009). Although several regions might experience colony die-outs, the honeybee is not a threatened species. However, Aizen & Harder (2009) do not discount the possibility of pollination problems for crops, as they simultaneously show a 300% global increase in pollinator-dependent crops over the last half century. It is thus clear that the global pollinator deficit is caused by the demand for pollinators increasing faster than the supply.

Even though managed honeybees are not a direct ecosystem service, they are also associated to the ecosystem in several ways. It has been suggested that natural vegetation plays an important role as a forage source for managed bees, with beekeepers placing their hives on natural vegetation to keep their colonies healthy and produce honey (Turpie *et al.* 2003; Allsopp & Cherry 2004). Naug (2009) examined the link between vegetation and managed honeybees in 40 US states. He showed that the proportion of managed colonies lost in a state is significantly related to the proportion of open land than has been developed between 2003 and 2007.

Moreover he discovered that the honey production of a state's hives is related to the amount of open land in a state (Naug 2009). It could thus be that vegetation conservation in the landscape will benefit managed honeybee colonies as it does wild pollinators.

In a young discipline with conflicting opinions and a lack of data, it is important to consider what information is needed for new research to help explain the importance of pollinators. A balanced view of both managed and ecosystem (wild) pollination services for crop production, is needed to give a clear perspective on the value of pollination services (Allsopp *et al.* 2008). A distinction must be made between the two, to be able to assess their separate contributions for a specific crop and ultimately make the management decisions which ensure crop pollination in the future.

The degree to which different crops and cultivars depend on pollinators for fruit set, size or quality can vary greatly from one to the other (Free 1993). Differences in land-use practises, pollinator species and whether honeybees are indigenous to an area or not, will all add to regional dissimilarities of pollination systems (Donaldson 2002). Therefore, studies on pollination services need to be more focused in regional terms (Donaldson 2002) as well as on specific crops and cultivars (see Allsopp *et al* 2008). It can be dangerous to extrapolate results from specific crops, cultivars or locations to others or to a global scale. Strategies for pollinator protection will also change, depending on the species composition and character of the surrounding vegetation and nesting sites. All of these factors highlight the need for detailed data on the pollinator systems of specific crops in specific areas.

#### 1.4 Deciduous fruit production and pollination research in South Africa

Pollination research in South Africa, have mostly focused on pollinators of indigenous plants with considerably less work done on crop plants (Donaldson 2002). Only recently, have pollination studies have been done on deciduous fruit, mangos and sunflowers (Allsopp *et al.* 2008; Shenkute 2009; Tesfay 2009; Carvalheiro *et al.* 2010). Furthermore, there is almost no literature on the value of other non-*Apis* pollinators to crop production in South Africa (Donaldson 2002). Yet, it is unlikely that they would be very effective in large monoculture

crops field (such as extensive areas of fruit orchards), where only strong flyers would be able to traverse the distances required. Indigenous pollinators are important however, for maintaining indigenous flora (Wright 1993; Johnson 1996). In this regard, they are important for agricultural systems such as livestock rangelands and wild flower farms that depend directly on resources from indigenous vegetation (Turpie *et al.* 2003), as well as other industries such as tourism and hospitality that rely on a beautiful environment as an attraction (Turpie *et al.* 2003).

The Cape Floristic Region, which falls mainly in the Western Cape province of South Africa, is a region of exceptionally high biodiversity (Cowling & Richardson 2000). Conservation of this rich fauna and flora often comes into conflict with economic growth of the agricultural sector. Agriculture has already converted more than 25% of the natural land in the CFR and it will continue as a threat in the future (Rouget *et al.* 2003). In such a region, where agriculture and biodiversity conservation are both imperative and sometimes opposing goals, constant trade-offs between these two are being made by policy makers, environmental practitioners and landowners. The Western Cape would thus benefit from knowing the economic value of their natural resources, for individuals and organizations to make informed decisions. Turpie *et al.* (2003) valued the CFR's marine and terrestrial ecosystem services at 10 billion ZAR per year. This value includes all naturally harvested products, tourism and beekeeping as well the value the public is prepared to pay for biodiversity conservation (existence value) (Turpie *et al.* 2003).

Several agricultural sectors in the Western Cape Province make use of such ecosystem services. The deciduous fruit industry is reliant on pollination services by wild and managed honeybees (Johannsmeier 2001; Allsopp & Cherry 2004) and if these services were unavailable, the replacement cost would be extremely high (Allsopp *et al.* 2008). Although South Africa is a relatively small deciduous fruit producer compared to Northern hemisphere countries, it is the third largest producer in the Southern hemisphere (DFPT 2009), thereby playing an important role in North-South trade agreements. South African deciduous fruit is largely cultivated in the Western Cape with 70% of the total hectares situated in this province (DFPT 2009). The managed honeybee colonies that Western Cape fruit farmers use for pollination are brought in by beekeepers during crop flowering, while wild honeybees come from natural areas adjacent to crop fields. The managed honeybee is the same subspecies as the indigenous one and is

commonly called the Cape Honeybee *Apis mellifera capensis* Escholtz. Interestingly, this subspecies' range corresponds closely with the extent of the CFR, indicating that the Cape Honeybee possibly has a close relationship with the associated floral resources and has adapted to the particular climatic conditions of the area (Hepburn & Crewe 1991). Consequently, Western Cape fruit producers can use one of three pollination systems. They either rely only on wild honeybees if their orchards are close to an intact natural area where the native bees reside, or they hire managed pollination services from beekeepers if too far from such a natural area. As a third option, fruit farmers can use both. Here they receive wild pollination services, but also hire honeybee colonies as extra insurance to ensure sufficient pollination.

#### 1.5 Objectives of the thesis

In light of the recent interest in crop pollination, the Global Environmental Facility undertook multiple projects in developing countries to determine if crops are experiencing pollination limitation and if crop production could be threatened by alleged declines in pollinators. The South African National Biodiversity Institute (SANBI) manages this project in South Africa under their Biodiversity and Ecosystem Services programme, under which this particular study also falls.

This study quantified the ecosystem services related to crop pollination for the Western Cape apple industry (Chapter 2) as well as the managed honeybee industry (Chapter 3).

The following questions were addressed in Chapter 2:

- Is apple production dependent on insect pollination? Production success was measured in terms of:
  - Number of fruit per branch
  - Fruit-set: number of fruit per 100 flowers
  - Seed-set: number of seeds per fruit
  - Fruit quality: whether or not the fruit meets the industry standards

- Do managed pollinators (M), natural pollinators (N) or a combination of managed and natural pollinators (MN) provide the most effective pollination service for the apple industry? Pollination efficiency was measured in terms of:
  - Number of foragers and foraging efficiency
  - Improvement in number of fruit per branch due to insect pollination
  - Improvement in fruit-set (number of fruit per 100 flowers) due to insect pollination
  - Seed-set (number of seeds per fruit) of insect pollinated fruit
  - Fruit quality: whether or not the fruit meets the industry standards

The outcomes of Chapter 2 will lead to a better understanding of the relative contributions of pollinator services in this specific agricultural sector.

The following questions were addressed in Chapter 3:

- To what extent are honeybee beekeepers using natural vegetation as a forage resource for their managed colonies?
- What percentage of managed colonies do beekeepers replace annually with wild colonies?

There is a great void in pollination science research, and some fundamental questions on the specific regional requirements and pollinators of many crops are still to be answered (Donaldson 2002). This study will help to fill this void for the apple in industry in the Western Cape of South Africa. This study is novel in that pollination as an ecosystem service is conceptually broadened here, to not only include the traditional wild pollination services to crop production, but also those services that support managed pollination services, providing a more holistic overview of the dependence of crop pollination on the ecosystem. Should pollination ecosystem services prove valuable to crop production, it could provide an incentive for aligning ecosystem conservation with agricultural expansion on a farm, landscape and industry scale. For example, if natural vegetation is conserved, it could provide habitat for wild pollinators and forage for managed honeybees that could benefit pollination, but simultaneously other wild fauna and flora could also benefit. The overarching motivation for this study is thus two fold, both for the benefit

of crop production in the developing world as well as the preservation of valuable natural resources. In this particular case the motivation is for the production of apples and the preservation of pollination ecosystem services.

Chapters 2 and 3 are written as stand-alone research papers; consequently some necessary degree of repetition may be encountered. Chapter 4, the general discussion, explores the interaction of the services studied in the previous chapters. It incorporates an economic valuation of the ecosystem services to the deciduous fruit industry in South Africa to estimate their importance. Key recommendations for conservation of pollination services and future research opportunities are also discussed.

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#### Chapter 2

## Wild Pollination Services are Comparable to Managed Pollination Services in Terms of Apple Quantity, but Not Quality

#### 2.1 Introduction

Ecosystem services are the benefits received by humanity from various ecosystems and their interacting species (Daily 1997, MEA 2005). Insect pollination is an essential regulating service that adds substantial monetary value to crop production worldwide (McGregor 1976; Williams 1994; Roubik 1995; Carreck & Williams 1998; Jarvis *et al.* 2007; Gallai *et al.* 2009). Insect pollination can either be an ecosystem service (if from wild pollinators resident in adjacent natural areas) or a managed service (if from domesticated pollinators managed in hives). Because of its importance to crop production, insect pollination contributes significantly towards supplying diverse and healthy foods to humanity (Steffan-Dewenter *et al.* 2005; Klein *et al.* 2007); individual growers can increase their yield, quality and ultimately their revenue, with effective pollination services. Fruit cultivars are crops that are particularly dependent on pollinators for both production quantity and/or quality. To illustrate this, there would be 12% less fruit than consumption demanded in 2005 if insect pollinators were lost, despite the fact that fruit is currently produced in excess (Gallai *et al.* 2009).

Several wild pollinator species have been reported threatened as a result of habitat destruction and fragmentation (Brosi *et al.* 2008), the use of harmful chemicals in agricultural practices (Kearns *et al.* 1998) and various pests and diseases (Genersch 2010). However, managed honeybee colonies have increased by 45% in the last 50 years (Aizen & Harder 2009). The honeybee *Apis mellifera* L. is the major domesticated pollinator, responsible for 90% of commercial pollination globally (McGregor 1976; Free 1993, although see Allsopp *et al.* 2008).

Even though managed honeybees have increased globally, they are not exempt from having a threatened status at a local and regional scale. The threats to managed honeybees are in some cases similar to that of wild pollinators, such as insecticide poisoning, disease and the absence of forage resources (Ingram *et al.* 1996; Oldroyd 2007; Genersch 2010; Van Engelsdorp & Meixner 2010), although these may be exacerbated by the fact that pathogens and parasites are more easily transferred between colonies in an apiary (Fries & Camazine 2001). Other threats to regional and local industries include economic factors, such as lowering of beekeeping subsidies, cheap honey imports and a decreased demand for honey (Ingram *et al.* 1996; Delaplane & Mayer 2001; Van Engelsdorp & Meixner 2010). The differences in threats and responses between wild and managed pollinators necessitate the need to study both types of pollinator services to make conservation recommendations for pollinators. Apart from the threats, a threefold increase in pollinator-dependent crops in the last fifty years (Aizen & Harder 2009) places further demands on pollinators and highlights the need for their protection.

There is great variability among crops, cultivars and even regions and the pollination system at work in one cultivar or area might not be the same for another, thus extrapolations among them should be avoided (Free 1993; Richards 2001; Donaldson 2002; Allsopp *et al.* 2008). Yet, few specific crops in specific areas have been studied with regards to their pollination systems, and even fewer crops have sufficient data to make suggestions on landscape variables and their effect on pollination stability (Klein *et al.* 2007). The information available on the pollination requirements of most crops is usually not derived from primary data and is out of date (Klein *et al.* 2007). There is a need to understand pollination systems of individual crops at a local scale and the relative contributions of both managed and wild pollinators must be addressed to fully understand the pollination resources available to crops (Allsopp *et al.* 2008). Apart from their separate contributions, it is also possible that wild pollinators could enhance the effectiveness of managed pollinators when occurring together (Greenleaf & Kremen 2006).

Here I studied the pollination dependence of an apple cultivar *Malus domestica* Borkh. cv. 'Granny Smith', in the Western Cape region of South Africa. The apple is an economically important crop that is self-incompatible and must cross-pollinate to develop fruit (Free 1993). It is thus highly dependent on insect pollination for production (Roubik 1995), although this is

based on speculation and review data rather than empirical evidence, which is especially lacking in the case of specific cultivars (Allsopp *et al.* 2008). As honeybees are reported to be the main apple pollinators (Free 1993; Roubik 1995), and farmers are utilising honeybee hives for pollination of their apple orchards, I expected the major managed pollinator, as well as the wild pollinator, to be the indigenous honeybee subspecies of the Western Cape, the Cape honeybee *Apis mellifera capensis* Escholtz.

To clearly understand the pollination systems of apple orchards in the Western Cape this study addresses the following two questions. First, is Granny Smith apple production dependent on insect pollination? Four different levels of apple production are assessed in an exclusion experiment to determine this. Second, what pollination system provides the most effective Granny Smith pollination? To assess this, the study sites were classified into categories according to their source of pollinators (wild or managed). There were three categories termed the 'pollination system' of the orchard; they use either i) only wild pollinators, ii) only managed honeybees or iii) a combination of the two pollination services.

#### 2.2 Methods

## 2.2.1 Apple industry and study cultivar

The apple industry is an economically significant part of the agricultural sector in South Africa. With 20 736 ha apple orchards in 2008, South Africa is under the top 20 apple producing nations in the world, and fourth largest in the Southern Hemisphere after Chile, Argentina and Brazil (DFPT 2009). SA exported 44% of the total tons produced in 2008, mostly to European markets, amounting to a total sales value of R 4 733.77 million (DFPT 2009). The Western Cape contains 16600 (80%) of the total hectares under apple production, making it the most significant apple producing province in the country (DFPT 2009).

Granny Smith was chosen as the study cultivar, firstly, because it is reported to be particularly dependent on cross pollination (Delaplane & Mayer 2001) and secondly, because it is the most

produced cultivar in South Africa (25% of total hectares is Granny Smith, 5050 ha in 2008) (DFPT 2009). Using an abundant cultivar enhances how representative the research is of the Western Cape apple industry.

#### 2.2.2 Study area and sites

Twelve Granny Smith orchards were selected in the Western Cape as study sites. The sites are located in the Ceres and Grabouw areas, both situated in the Western Cape. I refer to the whole area around the towns of Villiersdorp, Grabouw and Vyeboom as the Grabouw area in this study. The Ceres and Grabouw areas are some of the most important apple producing areas in South Africa as they are collectively responsible for 60% of the country's production. In general, agricultural practices in Ceres are less intensive than in the Grabouw area. The Ceres farmers also hire less managed bees than farmers in Grabouw. Apple production in Ceres is mostly at high altitudes along the mountain ranges and in close vicinity to natural vegetation. This enhances the probability that wild pollination services are provided for apple production. The Grabouw area is characterized by a more intensively farmed landscape forming a large continuous transformed region, with only the landscape edges adjacent to large natural areas. In theory, the Grabouw landscape should be less favourable for ecosystem services for apple production. The study sites were selected to be representative of both areas and larger landscape systems. Each orchard was regarded as a homogenous unit with regard to cultivars planted, respective rootstocks and farming practices. Six sites were located in the Ceres area and six sites in the Grabouw area. The sites were difficult to find because it had to adhere to specific spatial criteria, but Granny Smith's abundance helped to make site selection achievable.

Wild honeybees and managed honeybees are the same subspecies (Cape honeybee). One would not be able to visually distinguish between wild and managed, yet we need to determine their separate contributions to apple pollination. Therefore, it was necessary to separate the two pollinator sources (natural vegetation vs. managed hives) on a spatial scale. For this to be possible, it is necessary to understand the foraging ranges of the honeybee. For example, if a site is chosen far enough from natural vegetation that it would be out of the foraging range for wild bees, it is relatively certain that the foragers observed there, are managed honeybees. On the

other hand, if a chosen site is isolated far enough from managed hives so that it would be outside of their foraging range, it is relatively certain that the foragers observed there, are wild honeybees.

Foraging honeybees use a series of decision makings to optimise the trade-off between effort to obtain nectar or pollen (flight distance) and the reward associated with floral resources (Schmid-Hempel 1987; Couvillon & Bitterman 1993; Greggers & Mauelshagen 1997). Additionally they have a recruitment system where scouts explore the area for patches of quality forage resources and communicate information on profitable forage patches to the other bees in the hive through an encoded dance routine (Visscher & Seeley 1982; Dyer 2002). In this way honeybees are able to fly further for resources than if every individual had to suffer the search costs (Schaffer et al. 1979). Flight distances are thus expected to be a function of the proximity of flowers to the hive and the quality of nearby patches relative to those farther away (Gary et al. 1972; Waddington et al. 1994). A study from the UK countryside have shown that during times of sufficient resources around hives, a mean foraging range of 1 km were observed (median = 0.68 km), but when there were poor foraging conditions around the hive, they could forage up to 14 km away (mean = 5.5km, median = 6.1 km) to large patches of good quality nectar sources (Beekman & Ratnieks 2000). Similarly, in an agricultural system, honeybee colonies on the periphery of fields, foraged locally (mean = 266 m), but distant colonies flew a mean of 1663 m to carrots and a mean of 557 m to onions (Gary et al. 1972). The flight difference between carrots and onions is related to their pollen quality (Gary et al. 1972). In a suburban area, where spring garden flowers are in abundance, honeybee colonies showed mean foraging distances from 534 meters to 1138 meters, with a maximum of 1251 meters (Waddington et al. 1994). Other modelled flight distances for honeybees is an estimated 663 m (maximum = 776 m) in Costa Rican coffee plantations (Lonsdorf et al. 2009) and an estimated 1091 m in Californian watermelon and sunflower crops (Lonsdorf et al. 2009). Honeybees observed foraging on fruit trees, foraged profusely on one tree and more readily flew to the next tree in the same row than over the between-row spaces to another row (Free 1960). This supports the notion that honeybees will not fly unnecessarily to other resources if the closest forage resources are reward for their effort. It has even been suggested that the role of the recruitment system is reduced in regions with abundant floral resources or during flowering seasons (Waddington et al. 1994; Dornhaus & Chittka 2004). To

conclude, honeybees can forage far from their hives when floral resources are scarce by using scouts and communication, but their resourcefulness makes them forage close to the hive when floral resources are abundant such as in a flowering crop field.

Schneider (1989) suggests there might be differences in foraging ranges of different Apis mellifera subspecies, but Waddington *et al.* (1994) cautions this outcome, by showing larger variation within one subspecies, because of differences in forage resources. Therefore, we can make general conclusions from the above observed or modelled foraging ranges, to help understand the foraging ranges of the Cape honeybee, as long as we have information about the floral resources available to them. Apple orchards are large homogenous areas with blossoms that are particularly attractive to honeybees (Somerville 1999) and it is expected that they be drawn to this forage resource or forage close to the hive when the hive is placed in an apple orchard. It seems that it is highly unlikely for a colony in an orchard with floral abundance to forage further than 1.2 km. In this study we used a 2 km as sufficient isolation from honeybee colonies. The above literature acts as a basis for the remainder of the section and will not be cited again.

**Table 2.1.** Selection of twelve study sites in three pollination systems, according to two parameters. The three pollination systems (M, MN and N) are defined by whether or not managed bees were present in the system and by the sites' position in the landscape. The landscape parameter (adjacency of natural vegetation) is used as a surrogate for the presence of wild pollinators.

		Management	practice parameter
		No managed bees	Managed bees present
Landscape parameter	Isolated from natural vegetation (> 2 km)	-	Managed pollination system Only managed pollinators 4 sites
Land parar	Adjacent to natural vegetation (< 1 km)	Natural pollination system Only wild pollinators 4 sites	Managed-natural pollination system Managed and wild pollinators 4 sites

The twelve sites were categorised into three sets (termed pollination systems) according to the two parameters that determine the site's pollinator source (Table 2.1). The first parameter is the presence or absence of managed bees. This is a management practice providing an unnatural input into the orchard to enhance pollination. Honeybees are very energy efficient nectar collectors (Schmid-Hempel 1987) and it is unlikely that managed honeybees would fly further than the 2 km used as isolation distance in a landscape filled with flowering fruit orchards.

The second parameter, a landscape parameter, is the orchard's proximity to a large natural area. Pollination studies show that closer proximity to a natural area generally increases the abundance of wild pollinators (Kremen *et al.* 2002; Chacoff & Aizen 2006; see Rickets *et al.* 2008 for a review of 23 studies; Carvalheiro *et al.* 2010). A 'large natural area' was mostly a mountainous area where agricultural production is not possible, and where it is large enough to be able to support honeybee colonies providing the wild pollination services. Also, mountains in the Western Cape have rocky crevices and nooks which are suitable nesting sites for wild honeybee colonies.

The wild honeybee abundance in the adjacent natural areas was not measured and there is no certainty that there are indeed honeybee colonies present, but that is not the issue in question. This assumption that natural vegetation is a surrogate for wild honeybees is made by the farmers who choose not to bring in managed honeybees. We are in fact testing this management practice against the management practice of using managed hives for pollination. Thus we are testing the assumption's validity by doing a forager survey (see section 2.2.4.1 for the methods) in the orchards. The question is not if there are wild honeybees in the natural vegetation, but whether natural vegetation's proximity enhances wild honeybee abundance in the orchard. We are testing pollination ecosystem services, which relates to the mechanisms inside the orchard, not the mechanism inside the natural vegetation or the factors influencing them to venture into the orchard. If there prove to be honeybee foragers in an orchard isolated from managed honeybees, then the assumption is valid that the only source they can come from is from the adjacent natural areas.

Orchards separated by more than 2 km from a natural area can also be assumed to have no wild honeybees present. If wild honeybees are flying from natural areas into the agricultural area to forage, it is unlikely that they will travel further than 2 km from the edge where natural vegetation and apple orchards meet, as they would encounter profitable apple blossoms on the edge of the agricultural landscape and would not need to waste energy foraging further.

An explanation of how these two parameters interrelate to form each of the three pollination systems follows:

Four sites were selected that were closer than 1 km to a large natural area to allow access to the orchard for wild honeybees, most sites were directly adjacent. This pollination system is termed the 'natural' (N) system. The four sites were also isolated by minimum 2 km from any managed hives, so it can reasonably be assumed that all honey bees foraging and pollinating the apple blossoms are coming from the natural vegetation. Three sites were located in Ceres and one in the Grabouw area (near Villiersdorp). The site in Grabouw was isolated by only 1 km from managed bees. This might not be isolated enough, because Lonsdorf et al. (2009) estimated the foraging range for honeybees in watermelons and sunflowers to be 1091 m. Yet, it was the best site available in that area and there was a hill (with not fruit trees) between the site and where managed hives were kept, which probable aided in isolation. Also, De Marco and Coelho (2004) used 1 km as sufficient isolation in a coffee plantation while studying *A. mellifera* and crop production. Although this is a different system, it is similar to apple orchards in that it has abundant resources which are what mostly determines the foraging range of honeybees (Gary *et al.* 1972; Waddington *et al.* 1994).

The second pollination system was termed 'managed' (M) because all the pollination was assumed to come from managed honeybees. The orchards in these sites were isolated by at least 2 km from any large natural areas to be sure there are a negligible amount of wild honeybees. The orchards are pollinated by managed honeybee colonies that are hired from beekeepers and placed within the orchards. Three sites were located in the Grabouw area and one in the Ceres area.

The last pollination system selected was termed the 'managed-natural' (MN) set of sites. These four sites were closer than 1 km to natural vegetation (most were directly adjacent), but the farmer also hired managed bees for pollination. The assumption here is that pollination is done by both the managed and wild honeybees and they could possibly have a complimentary effect (Greenleaf & Kremen 2006). This third pollination system is representative of many orchards in the Western Cape and has to be included to obtain a full picture of the pollination systems active in this specific cultivar and region. The majority of farmers are aware of the pollination service provided by wild bees coming from natural areas, but managed bees are brought in as an extra insurance against low pollinator levels at crucial times of flower development. Two managed-natural sites were selected in Ceres with the other two sites in the Grabouw area.

Sites were carefully chosen to fit the geographical requirements by using 1:50 000 maps and Google Earth. Different sites were at least 2 km away from each other, to ensure independence from one another. I aimed to have at least one site of a specific pollination system in both areas. Site selection proved to be a difficult task, because apples are grown in narrow valleys or plateaus often only 5-10 km in width and surrounded by mountains, making it difficult to sufficiently isolate managed sites from wild pollinators. Additionally, the wide-spread use of managed honeybee hives made it again difficult to sufficiently isolate natural sites from managed honeybees. Nonetheless, all the spatial criteria for the sites were met, apart from the Grabouw natural site, in which 1 km isolation was accepted instead of 2 km. Therefore, I am confident that the distribution of sites used, is the best possible experimental selection given the circumstances and purposes of this study. All statistical analyses were performed using the software R (R Development Core Team 2010).

# 2.2.3 Question 1: Is Granny Smith apple production dependent on insect pollination?

### 2.2.3.1 Exclusion experiment setup

In each of the 12 study sites, five trees were selected in each of five rows, amounting to 25 trees throughout an orchard. For the insect exclusion experiment, I closed one branch on each of the trees with a 35 cm x 50 cm mesh bag and marked a similar branch on the same tree for the

control (see also De Marco and Coelho, 2004). I used a 2 mm mesh size to allow sufficient air flow and pollen grains passage for wind pollination, but at the same time exclude honeybee pollination. Caution was taken to select the branches not too close to the tree trunk where lack of sunlight will lower the productivity of the branch. I made certain a minimum of three flower clusters were included on an open or closed branch to ensure a sufficient sample size, with each flower cluster containing between three to five flowers. The mesh bags were put up in September 2008, just before flowering, so that the flowers on the enclosed branch would be excluded from insect pollinators throughout its whole flowering period. The apple production on the control branches could thus be compared to the production on the enclosed branches to determine how dependent apple production is on insect pollination. Caution was taken to remove the bags once the flower petals had fallen. If left too long, pesticides could be prevented from reaching inside the bag, a different microclimate could be created, and it could physically restrain growth, all which will alter normal fruit development.

# 2.2.3.2 Exclusion experiment measurements

Four production variables, related to pollination success, were measured on the enclosed and open branches for comparison. These were number of fruit, fruit-set, seed-set, and fruit quality.

## Number of fruit

All fruit that formed on the marked branches were counted, but only those that were greater than 2 cm in diameter were used for analyses. Anything smaller is likely to not to have been pollinated and would not be harvested or utilized for any purpose. The market minimum for a fruit's diameter is 6 cm, but smaller fruit are still harvested and used for juice. It is thus the total number of harvestable fruit that were counted. The number of fruit on the control branch of a tree was compared to the number of fruit on the insect excluded branch of the same tree to indicate dependence on insect pollination with regard to fruit formation. Even though initial fruit-set was measured, it was not used for analyses. The resources of a fruit tree support only a finite amount of fruit and thus aborts a large portion of its fruit as they mature. The aborted fruit are usually those that have not been pollinated sufficiently and therefore, counting all the initial fruit as if it

was pollinated fruit, could lead to overestimating the pollination benefits to crop yields (Bos *et al.* 2007).

#### Fruit-set

Fruit-set can be defined as the proportion of flowers that formed fruit. I therefore needed the number of flowers on each branch and compared that to the number of harvestable fruit on the same branch. With in-field observations it was determined that for the Granny Smith cultivar, a cluster of flowers consists of an average of four flowers and is collectively attached to the branch by a single stem. The number of flowers was determined by counting the markings on the branch where the stems of the flower-clusters had been and multiplying it by four to estimate the number of flowers there had been on the branch. Where there were bags over the branches, I simply counted the number of fallen flowers inside the bag to know how many flowers there were on the branch. For some of the bagged branches, I counted the number of cluster markings on the branch in the field as well as the flowers in the bags and the four flowers per clusters observed in the field held true. Fruit-set was expressed as number of fruit formed for every hundred flowers.

#### Seed-set and fruit quality

The first two production variables could be determined in the orchard, but seed-set and quality required further analyses in the laboratory. In order to analyse the fruit at harvestable size and quality, I wanted to collect it just before the grower would harvest the orchard normally. By keeping close communication with the grower, all fruit for the study were collected five days or less before the orchard was harvested. This was done during March/April 2009. All the fruit were counted for the number of fruit and fruit-set analyses, but a maximum of five fruit per branch were collected for lab analyses. Each fruit was carefully marked to indicate its origin and placed in cooling facilities to preserve it for further analyses.

Laboratory analyses included measuring the height (mm), diameter (mm) and weight (g) of each apple to determine its quality and whether it meets industry standards. The minimum standards

were obtained from the offices of the Deciduos Fruit Producers Trust (DFPT) in Stellenbosch. These factors are important for the marketability of the fruit. Furthermore, apples were visually observed for shape, if the shape was evenly round it was considered normal, but if it was very skew or lopsided it was considered malformed. The shape variable is included because fruit shape is related to the seed-set (Cuthbertson & Brown 2006) and a malformed fruit can often be traced back to inadequate seed-set because of insufficient pollination. Even though this observation is a subjective estimate, it was consistently done by the same person and therefore considered standardised. Afterwards the apples were cut open to count the number of seeds per apple. A distinction was made between seeds that were fully-formed or aborted. If a seed is aborted, it indicates that it was not pollinated and therefore only fully-formed, pollinated seeds were used in the analyses.

A marketability factor was compiled from two measurements indicating size (weight and diameter) and a third measurement indicating shape. Height was not included as there is no industry minimum for height and likely it is not important for the market. The weight and diameter of each apple was given a code to indicate if it met the industry standards or not. The minimum weight for a Granny Smith apple is 90 grams and the minimum diameter for an apple at the widest point is 60 millimetres. A specific apple had to adhere to both of these conditions as well as be of a standard shape to be considered a good quality, marketable apple. The three measurements were combined to form one factor to be used in statistical analyses that was termed the 'marketability' of the fruit.

#### 2.2.3.3 Analytical methods

To assess how insect pollination influences Granny Smith reproduction success, each of the four production variables were analysed in four separate mixed effects regression models, where the status of the branch (open or closed) were used as a fixed factor. Mixed effects model in R, allows for random factors to be included in the models. This makes it possible to exclude other sources of variation in the production data (e.g. between farms) not caused by the fixed factor in question (insect pollination in this case). Also it can reduce exaggeration effects of possible pseudoreplication, if (for example) trees were not entirely independent from each other in an

orchard. Farm, row and tree were set as random factors in all four of the models, with tree nested within row, and row nested within farm.

Linear mixed-effects models (LMM) were used for data that were normally distributed while generalised linear mixed-effects models (GLMM) were used for data that did not have a normal distribution. Where an analysis was done with a LMM the nlme R package was used, as opposed to the lme4 R package that was used for a GLMM (R Development Core Team 2010). The number of fruit variable was count data and were analysed with a GLMM (Poisson error distribution). The fruit-set data were separated in two columns for analysis, namely, 'number of flowers that formed fruit' and 'number of flowers that did not form fruit' and thus represent proportional data. The fruit quality data were categorised as 'marketable fruit' or 'not marketable fruit' and thus represents binary data. Both the fruit-set and fruit quality production variable were thus non-normal data and analysed with GLMMs (Binomial error distribution). The seed-set data were normally distributed and were analysed with a LMM (Gaussian error distribution).

General linear models (GLM) were used to analyse the relationships between seed-set and fruitquality variables (weight, diameter and shape).

# 2.2.4 Question 2: What pollination system provides the most effective Granny Smith pollination?

## 2.2.4.1 Forager survey data collection

A forager survey was undertaken to determine forager abundance under different pollination systems and to see what insects were pollinating apple orchards. Flower-visiting insects were surveyed at 25 trees, 5 trees in 5 rows, selected across the orchard. At each tree, the number of honeybees and other insects that visited flowers were observed and counted for one minute. Only insects that visited the flowers were counted, those that just flew past or sat on a leaf were not. Insects that were seen to visit an apple blossom can be assumed to be foraging on the blossom, and therefore the term 'forager' is used in this study. The reproductive parts of an apple blossom are very conspicuous (Fig. 2.1) and foragers inevitably will touch it, making foragers likely

pollinators. If any other flower visitor, other than a honeybee, was seen, it was recorded at family level. Additionally I followed a minimum of five honeybees per orchard for one minute each, to count how many flowers one honeybee visited during that time (visitation rate).



Fig. 2.1. A Granny Smith apple blossom, showing the conspicuous reproductive parts.

It was only possible to do the forager survey at 11 of the 12 sites in the study. One of the natural pollination system sites in the Grabouw area was lost in this respect, because it had an earlier bloom than expected. When the survey was to be done at this specific site, there was not sufficient flowering to survey foraging honeybees and it was decided to leave the site out of the forager survey. Despite this, the data for the exclusion experiment were still gathered.

Different trees were used in the forager survey than for the exclusion experiment. This was done to ensure that the white mesh bags used to cover the branches in the exclusion experiment did not interfere with the honeybees' natural foraging behaviour, and thereby compromise the forager survey data.

Adverse weather conditions can negatively influence bee activity by physically or physiologically hindering the honeybee's movements. Furthermore nectar production is dependent on photosynthesis and therefore influenced by sunlight and the lack of supply may also hinder foraging behaviour. Consequently it is of utmost importance to standardise for weather conditions as far as possible when observing honeybee behaviour. In addition to standardising, these environmental variables were also recorded and fed into the analyses to find out if I standardised correctly or if there were still an influence. The variables recorded were wind speed, temperature, relative humidity, time of day and percentage cloud cover. Clear, sunny days were selected to do surveys. Surveys were done in the morning from 09:00 until not later than 12:00. Temperature was selected as above 18°C, if this temperature had not been reached by 09:00, I would wait for it to rise to 18°C before surveying. Wind speeds of up to 15 km/h were tolerated as sufficient for bee surveys, but the majority of visitation surveys were conducted at wind speeds of less than 5 km/h. Although high humidity could affect honeybee behaviour, it was not necessary to standardise (except for rain), because of the relatively low spring/summer humidity associated with the Mediterranean climate of the Western Cape.

Beehives are usually brought in to orchards when about 10% of the flowers are open, but all surveys were performed as close to full bloom as possible. A greater number of flowers can create an attractive, concentrated resource which is more easily located by honeybees than a lesser number of flowers (Collevatti *et al.* 2000), and it is therefore important to standardize at what blooming stage observations are done. Farmers define full bloom as the situation where the number of unopened flowers is equal to the number of flowers that have finished flowering and I also used that standard. It was not possible to do surveys on all 12 sites exactly on full bloom as the blooming periods between orchards were more synchronized than anticipated and logistically it was impossible. To bring this into calculation I additionally counted the number of open flowers of 5 randomly chosen trees in the orchard. The average number of open flowers per tree was incorporated into the models to see if resource availability affected the results.

#### 2.2.4.2 Exclusion experiment

The number of fruit, fruit-set, seed-set and fruit quality data from the exclusion experiment were used again to answer question two. See the previous sections for information on the exclusion experiment setup and methods of data collection. The data from this experiment was analysed differently to determine what the effects of the pollination systems are.

#### 2.2.4.3 Analytical methods

To assess the influence of the three pollination systems on apple blossom foragers and production, mixed effects regression models were used with pollination system always set as a fixed effect. The reason for using mixed effects models (incorporating random variables), is the same as for question one; to eliminate variation not caused by the pollination systems and to account for possible pseudoreplication through spatial non-independence. Random variables were different for each model, depending on the character of the dataset. Akaike's information criterion (AIC) was used to select the best models (Appendix 1) in each regression sequence. Linear mixed-effects models (LMM) were used for data that were normally distributed and generalised linear mixed-effects models (GLMM) were used for data that did not have a normal distribution. Where an analysis was done with a LMM the nlme R package was used, as opposed to the lme4 R package that was used for a GLMM (R Development Core Team 2010).

For the number of foragers and visitation rate regression analyses, the environmental variables (temperature, wind, humidity and cloud cover) were added as additional fixed factors with the pollination systems. Temperature, humidity and cloud cover were systematically removed from the analyses to improve the two models (lower AIC values) (Appendix 1). Wind was also removed from the visitation rate model, but kept as a fixed factor in the number of forager model. The variable, number of foragers, was count data and were analysed with a GLMM (Poisson error distribution) with farm and row (nested within farm) as random factors. The visitation rate data were normally distributed and were analysed with a LMM (Gaussian error distribution).

The improvement in number of fruit and fruit-set with insect pollination was calculated by subtracting the production of the closed branches from the production of the open branches. Thus the specific contribution that insect-pollinators make to apple production was quantified. There was not always fruit produced for each branch, especially on the closed branches and analyses could not be done, where no data was available. Therefore, the data for each row of five trees was added together and analysed per row instead of per tree. By adding the data together and not averaging it, there was less loss in the variation of the data and analysable outputs for each row was obtained. Three rows were not used in the analyses, because they had too few data available. Both the regression models of these two improvement variables were done with a LMM (Gaussian error distribution) as they had normal distributions, with pollination system as a fixed factor and farm as a random factor.

The formulas for the respective improvement variables are:

- 1) Improvement in number of fruit
  - = (#Open fruit per row #Closed fruit per row) / (#Open fruit per row + #Closed fruit per row)

The use of this formula for values recorded in each row result in a factor between -1 and 1. Positive values indicate improvement, where negative values indicate decline with insect pollination.

- 2) Improvement in fruit-set
  - = fruit-set per row (on open branches) fruit-set per row (on closed branches)
  - = [# fruit per row open branches / (# flowers per row open branches / 100)]
    - [# fruit per row closed branches / (# flowers per row closed branches / 100)]

In the seed-set analyses, I could not determine an improvement variable by subtracting the open branches results from the closed branches results as was done for number of fruit and fruit-set. This was because there was a large discrepancy between the number of fruit produced on the open and closed branches, the latter having far fewer fruit. If an improvement calculation for seed-set were to be done, a lot of variability in the data would be lost when seed-set of open branch apples would have to be averaged to compare with the closed branch apples. Thus, both the seed-set data from the open and closed branches were used as is, but the branch status (open

versus closed) was set as a random factor to exclude variability in the data caused the exclusion experiment. Thus, it was possible to determine the influence of the pollination systems on an apple's seed-set, apart from the fact that it grew on an open branch or not. The seed-set data were normally distributed and were analysed with a LMM (Gaussian error distribution) with pollination system fixed factor and farm and branch (nested within farm) as random factors.

The marketability factor (fruit quality) is categorical data and was analysed with a GLMM (binomial error distribution) to see if the three pollination systems were significantly different from one another. Only the variable 'branch-status' was set as a random variable, because it was the model with the lowest AIC value. There was no difference in the results of the fixed effect (pollination system) even if 'row' and/or 'farm' were set as random variables (Appendix 1). To further clarify the results, the marketability factor was disaggregated and the different components analysed separately to see if the compilation masked any trends. Pollination system was used as a fixed effect throughout. Both fruit diameter and weight variables had normal distributions and were analysed using a LMM (Gaussian error distribution). Also for both these models farm, row (nested in farm), tree (nested in row) and branch (nested in tree) were set as random factors. Fruit shape were categorised as 'normal' or 'not normal' and thus represents binary data. It was analysed using a GLMM (binomial error distribution) with branch-status as random factor.

#### 2.3. Results

# 2.3.1 Question 1: Is Granny Smith apple production dependent on insect pollination?

In every step of production, from the number of fruit to the marketability of the fruit there is a strong significant positive relationship with the presence of insect pollination on the open branches (versus the enclosed branches) (Table 2.2). Fruit production and fruit-set on the open branches were more than three times that on closed branches (Table 2.3 and 2.4). On average there were more seeds that developed per apple on the open, insect pollinated branches than on the enclosed branches (Table 2.5). A maximum of 12 seeds per fruit developed on the open

branches and a maximum of nine seeds per fruit developed on the closed branches. The number of seeds in a fruit had a strong correlation with the weight (P<0.001, General linear model, normal distribution), diameter (P<0.001, General linear model, normal distribution) and shape (P<0.001, General linear model, binomial distribution) of the fruit. At the open, insect pollinated branches almost 70% of the fruit were shaped normally, while half the fruit on the enclosed branches were malformed (Table 2.5). Of the 600 possible branches on the 300 trees studied, 42 branches were lost as a result of various factors such as the branches being damaged due to farming practices, the branch or tree markers were blown off by high pressure chemical spraying or in some cases there was tree mortality.

**Table 2.2.** Regression results for the reproductive success of Granny Smith apples in relationship to insect pollination. Positive z- or t-values indicate positive production response to insect pollination (open branches versus mesh enclosed branches). Regression analyses for three of the four production variables were done using GLMMs (M1, M2 and M4) and one were done using a LMM (M3). Fixed variable: branch (open *versus* closed). Random variables: farm (groups = 12 (M1-M4)), row nested in farm (groups = 58 (M1-M4)), tree nested in row (groups = 289 (M1&M2), 217 (M3&M4)). Number observation (M1,M2,M3,M4) = (558,551,553,551).

Model	Measures of Reproductive Success	Distribution	Branch treatment (open vs. closed)		
		Distribution	z-value	<i>t</i> -value	P-value
M1	Number of fruit per branch	Poisson	18.48		< 0.001
M2	Fruit-set: Fruit per 100 flowers	Binomial	18.03		< 0.001
M3	Number of seeds per fruit	Normal		13.51	< 0.001
M4	Marketability factor*	Binomial	2.67		< 0.01

^{*}A marketable fruit has a diameter  $\geq 60$  mm, weight  $\geq 90$  g and is shaped normal (see methods).

**Table 2.3.** Difference in fruit production when insect pollination is either excluded or allowed.

Treatment	Total # apples produced	Mean per branch	% of total fruit
Open branches	1034	3.6	77%
Closed branches	306	1.1	23%

**Table 2.4.** Difference in fruit-set: number of apples per hundred flowers when insect pollination is either excluded or allowed.

Treatment	Total # flowers	Fruit-set per branch	% of total fruit-set
Open branches	11284	9.16	75%
Closed branches	10278	2.98	25%

**Table 2.5.** Differences in seed-set (number of seeds per fruit), fruit size (weight (g) and diameter (mm)) and fruit shape, when insect pollination is either excluded or allowed.

Branch	Total # apples	Mean seed-set ±	Mean weight	Mean diameter	% Normal
treatment	analysed	SE	$(g) \pm SE$	$(mm) \pm SE$	shaped fruit
Open	409	$5.72 \pm 2.55$	$121.21 \pm 34.29$	$65.52 \pm 6.83$	68.21
Closed	203	$3.33 \pm 2.33$	$111.18 \pm 39.06$	$63.02 \pm 8.45$	48.28

# 2.3.2 Question 2: What pollination system provides the most effective Granny Smith pollination?

## 2.3.2.1 Foragers & visitation rate

By surveying 330 trees in 11 orchards a total of 587 honeybees where observed to visit apple blossoms. An average of two foraging honeybees on a tree per minute was seen with a maximum of 10 honeybees on a tree per minute. Apart from honeybees, there were only seven other insect visitors seen on the blossoms (one Lepidoptera, one Hymenoptera, four Diptera, one Coleoptera). The forager survey showed that more than 98% of apple flower foragers are honeybees (*Apis mellifera capensis*). By observing 66 honeybees in 10 orchards, it was found that the honeybees visited nine apple blossoms per minute on average and the maximum was 18 blossoms visited per minute.

The natural pollination system (N) had significantly less honeybee foragers observed than the other two (Table 2.6). At one orchard in Ceres, only one foraging honeybee was observed in the

whole study site even though it was good weather conditions and the orchard was directly adjacent to a large natural area. Considering the lack of honeybees here, it was not possible to record visitation rate at this site. The rate at which a honeybee visits apple blossoms was significantly higher at the combined, managed-natural pollination system (Table 2.7).

The recorded temperature and humidity during observations did not have an influence on honeybee activity, but honeybees were more sensitive to wind speeds than expected showing a significant decrease in activity with higher wind speed. The average number of open flowers present did neither influence the number of honeybees foraging nor their visitation rates significantly.

**Table 2.6.** Regression results for the number of honeybee foragers present in three pollination systems using a GLMM model with a Poisson distribution. The fixed variables are wind and pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 330 forager observations. The random variables are farm (groups = 11, intercept standard deviation = 0.73) and row (nested in farm, groups = 33, intercept standard deviation = 0.26).

Element	Value ± SE	z-value	<i>P</i> -value
Intercept	$0.79 \pm 0.38$	2.10	0.0360
Pollination system: MN	$-0.28 \pm 0.55$	-0.51	0.6097
Pollination system: N	$-1.72 \pm 0.61$	-2.80	0.0051
Wind	$-0.07 \pm 0.03$	-2.04	0.0411

**Table 2.7.** Regression results for the visitation rate (number of flowers visited per minute) of honeybee foragers in three pollination systems using a LMM with a Gaussian distribution. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). 66 Foragers were observed. Random variable (farm): groups = 10, intercept standard deviation = 0.00. Standardized within-group residuals: Q1 = -0.573, Median = -0.167, Q3 = 0.644.

Element	Value ± SE	d.f.	<i>t</i> -value	<i>P</i> -value
Intercept	$8.41 \pm 0.42$	56	19.91	0.0000
Pollination system: MN	$1.89 \pm 0.67$	7	2.78	0.0273
Pollination system: N	$-1.19 \pm 1.93$	7	-1.29	0.2386

# 2.3.2.2 Number of apples per branch

The improvement in number of apples per row did not show any significant differences when the three pollination systems were compared (Table 2.8). In other words, the different sources of insect pollination provided a similar service with regards to production.

**Table 2.8.** Regression results for the improvement* in number of apples per branch in three pollination systems using a LMM. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 57 observations (branches). Random variable (farm): groups = 12, intercept standard deviation = 0.25. Standardized within-group residuals: Q1 = -0.477, Median = 0.040, Q3 = 0.617.

Element	Value ± SE	d.f.	<i>t</i> -value	<i>P</i> -value
Intercept	$0.62 \pm 0.14$	45	4.56	0.0000
Pollination system: MN	$0.00 \pm 1.93$	9	0.01	0.9895
Pollination system: N	$0.02 \pm 1.93$	9	0.11	0.9171

^{*} Formula for improvement in apple production with insect pollination on a tree

^{= (#} open fruit per row - # closed fruit per row) /
(sum of apples from both the open and closed branches in a row).

#### 2.3.2.3 Fruit-set

Fruit-set gives a more realistic approximation of pollination services, as the influence flower abundance will have on fruit abundance is excluded. Still, the improvement in the fruit-set between a row of open and a row of closed branches also did not show any significant differences between pollination systems (Table 2.9). In other words, the different sources of insect pollination provided a similar service with regards to fruit-set.

**Table 2.9.** Regression results for the improvement* in fruit-set in three pollination systems using a LMM. Fruit-set is defined as the number of apples produced per 100 flowers. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 57 observations (branches). Random variable (farm): groups = 12, intercept standard deviation = 3.41. Standardized within-group residuals: Q1 = -0.496, Median = -0.118, Q3 = 0.306.

Element	Value ± SE	d.f.	<i>t</i> -value	<i>P</i> -value
Intercept	$6.38 \pm 1.93$	45	3.30	0.0019
Pollination system: MN	$0.73 \pm 2.74$	9	0.27	0.7968
Pollination system: N	$2.59 \pm 2.76$	9	0.94	0.3716

^{*} Formula for improvement in fruit-set with insect pollination on a tree

#### 2.3.2.4 Seed-set

Of the 1340 fruit produced on all the marked branches, about 45% were picked for laboratory analyses of which 409 were from open branches and 203 were from closed branches. The natural pollination system (N) showed significantly less seed per fruit than the other two where managed honeybees were introduced (M & MN) (Table 2.10). The managed pollination system showed

^{= [#} fruit per row open branches / (# flowers per row open branches / 100)]

^{- [#} fruit per row closed branches / (# flowers per row closed branches / 100)]

the best seed-set, but was not significantly different than the managed-natural pollination system (Table 2.10).

**Table 2.10.** Regression results for the number of seeds per fruit in three pollination systems using a LMM. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 553 observations (number of fruit analysed for seed-set). The random variables are farm (groups = 12, intercept standard deviation = 0.00) and branch (nested in farm, groups = 24, intercept standard deviation = 1.62). Standardized within-group residuals: Q1 = -0.675, Median = -0.044, Q3 = 0.712.

Element	Value ± SE	d.f.	<i>t</i> -value	<i>P</i> -value
Intercept	$5.33 \pm 0.61$	529	8.77	0.0000
Pollination system: MN	$-0.35 \pm 0.85$	9	-0.41	0.6890
Pollination system: N	$-2.11 \pm 0.87$	9	-2.43	0.0381

# 2.3.2.5 Fruit quality and marketability

There is no significant difference between pollination systems for the combined marketability factor (Table 2.11). When this factor is disintegrated and each factor analysed separately, it shows that pollination system has a significant influence on the shape of the fruit (Table 2.14), but not the diameter or weight (Tables 2.12 & 2.13, respectively). The fruit produced under the natural pollination system (N) were significantly more malformed than in the pollination systems where managed honeybees were introduced.

# **Marketability**

**Table 2.11.** Regression results for the marketability* the apple fruit produced in three pollination systems using a GLMM with a Binomial distribution. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 551 observations (number of fruit analysed for marketability). Random variable (branch): groups = 2, intercept standard deviation = 0.13.

Element	Value ± SE	z-value	P-value
Intercept	$0.00 \pm 0.12$	0.04	0.969
Pollination system: MN	$-0.13 \pm 0.12$	-1.08	0.278
Pollination system: N	$-0.15 \pm 0.12$	-1.25	0.210

^{*}A marketable fruit has a diameter  $\geq 60$  mm, weight  $\geq 90$  g and is shaped normal (see methods).

## **Diameter**

**Table 2.12.** Regression results for the diameter of the apple fruit produced in three pollination systems using a LMM with a Gaussian distribution. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 551 observations (number of fruit measured). The four random variables are farm (groups = 12, intercept standard deviation = 3.08), row (nested in farm, groups = 58, intercept standard deviation = 1.84), tree (nested in row, groups = 217, intercept standard deviation = 2.70) and branch (nested in tree, groups = 294, intercept standard deviation = 2.44). Standardized within-group residuals: Q1 = 0.546, Median = -0.020, Q3 = 0.596.

Element	Value ± SE	d.f.	<i>t</i> -value	<i>P</i> -value
Intercept	$63.36 \pm 1.70$	257	37.26	0.0000
Pollination system: MN	$0.93 \pm 2.40$	9	0.39	0.7090
Pollination system: N	$4.08 \pm 2.41$	9	1.69	0.1247

# Weight

**Table 2.13.** Regression results for the weight of the apple fruit produced in three pollination systems using a LMM with a Gaussian distribution. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 551 observations (number of fruit weighed). The four random variables are farm (groups = 12, intercept standard deviation = 13.75), row (nested in farm, groups = 58, intercept standard deviation = 8.07), tree (nested in row, groups = 217, intercept standard deviation = 12.59) and branch (nested in tree, groups = 294, intercept standard deviation = 11.57). Standardized within-group residuals: Q1 = -0.593, Median = -0.040, Q3 = 0.531.

Element	Value ± SE	d.f.	<i>t</i> -value	P-value
Intercept	$109.67 \pm 7.67$	257	14.29	0.0000
Pollination system: MN	$4.87 \pm 10.84$	9	0.45	0.6641
Pollination system: N	$24.10 \pm 10.89$	9	2.21	0.0541

#### Shape

**Table 2.14.** Regression results for the shape of the apple fruit produced in three pollination systems using a GLMM with a Binomial distribution. The fixed variable is pollination system: Managed (M) *versus* Managed-natural (MN) *versus* Natural (N). There are 551 observations (number of fruit analysed for marketability). Random variable (branch): groups = 2, intercept standard deviation = 0.13.

Element	Value ± SE	z-value	<i>P</i> -value
Intercept	$0.23 \pm 0.13$	1.83	0.0675
Pollination system: MN	$-0.17 \pm 0.12$	-1.40	0.1619
Pollination system: N	$-0.25 \pm 0.12$	-2.04	0.0413

#### 2.4. Discussion

# 2.4.1 Question 1: Is Granny Smith apple production dependent on insect pollination?

This study shows that Granny Smith apple production in the Western Cape of South Africa is highly dependent on insect pollination. When honeybees were excluded, there was a 70% reduction in the fruit-set. This provides clear empirical evidence in a research field where there is a lot of heterogeneity of the reported production dependence of apples (Gallai *et al.* 2009). The Granny Smith cultivar is of major importance to the apple industry (DFPT 2009) and the pollination services that honeybees perform is thus crucial for the future of the industry.

# 2.4.2 Question 2: What pollination system provides the most effective Granny Smith pollination?

Wild honeybees provided a vital ecosystem service to apple production in the natural pollination system where farmers were not using managed honeybees. These 'natural' orchards were receiving free pollination in the form of an ecosystem service, whereas farmers bringing in managed honeybees (in both the managed and managed-natural pollination systems) had to pay beekeepers for pollination services. On the other hand, by hiring managed honeybees, the number of honeybees foraging in the orchard was increased. Better pollination in these managed pollination systems was achieved, which meant significantly better quality fruit for growers and a higher price could be received for it. In natural pollination systems, however, there were less honeybee foragers, and flowers were not pollinated well enough to produce a good seed-set in the resulting fruit. Apples have five pistils, each with two ovules, creating the potential for 10 viable seeds if the fruit is fully pollinated (Cuthbertson & Brown 2006). Fruit growth and development is stimulated near fertilised, developing seeds (Cuthbertson & Brown 2006). If, for example, only a few seeds on the same side of the fruit were fertilised because of poor pollination services, a malformed, lopsided fruit would be formed. In the natural pollination system, this was the case, and the fruit was malformed and not up to standard. The managed and managed-natural pollination system thus provided the most effective pollination. It was expected that the managed-natural pollination systems would have a compounding effect on apple

production, having both wild and managed honeybee sources. However, apart from having a higher honeybee visitation rate, it showed similar results to managed pollination systems.

It is important to remember, that just because there were less honeybees foraging in orchards next to natural vegetation does not mean that there are less wild honeybees in natural areas than managed honeybees. It just means that whether there are many colonies in the natural vegetation or not, they are not sufficiently reaching the apple orchards and not providing a pollination ecosystem service that is up to standard with the managed colonies. There may a few mechanisms operating that could influence this, not withstanding competition from wild floral resources attracting honeybees away from apple orchards. This will depend on specific areas and the vegetation types present as well as the availability of nesting sites. More research is needed to clarify these mechanisms.

#### 2.4.3 Limitations

In the experimental design a 2 mm mesh size was used for the exclusion bags. This would have definitely deterred honeybees, but it might have let other smaller insects through that could influence pollination. Nevertheless, only 7 other individual insects were observed during the forager survey, making the above assumption acceptable.

Environmental variables were standardised during the forager survey. Wind speeds had a significant negative relationship with forager abundance, showing that the 15 km/h that I used is not a low enough standard, despite honeybees being relatively strong flyers. It is recommended that wind speeds of not more than 5 km/h be tolerated in a pollinator survey. Still, wind speeds were thus incorporated into the forager model, prohibiting it from altering the results. As previously mentioned, the forager surveys at the different sites were done at varying stages of bloom. It was suspected that this might compromise the forager abundance results as a greater resource of floral abundance might be a greater attractive force. However, the number of open flowers recorded at each site, was included in the regression models (Appendix 1) and it showed no significant effect on the forager abundance or visitation rates of the honeybees.

This study was done at the farm level, but pollinators can often be influenced on a larger landscape scale. To assess if the larger landscape influenced the variation in the data, the different sites were categorised into four areas. This landscape variable was incorporated in the models, but by using 'farm' as a random variable, it was clear that the variation was on farm level, rather than the larger landscape level. I thus conclude that the farm level is the appropriate level at which to study pollination systems in crops.

It is often suggested that pollination studies should use i) multiyear data, ii) whole plants as experimental units rather than branches and iii) hand pollination to create a control for optimum pollination (Vaissière *et al.* 2010). Unfortunately, the time frame of this study was not so that multiyear data could be collected, especially considering alternate bearing in deciduous fruit. The study would have been too extensive and unmanageable if whole apple trees were to be used, therefore branches were rather used. This enabled the research to rather incorporate more sites. As apples could experience over-pollination, a more realistic control was to leave the flowers to be pollinated as they normally would have been. The assumption is that the grower would farm for optimum production as his pollination system would allow him. Additionally, because I used branches as experimental units, hand-pollination could draw resources to that specific branch, inflating the production on the branch relative to a situation where the whole tree received pollination.

It must also be considered that even though there were no differences among pollination systems with regards to final fruit-set, this might not have been the case with initial fruit-set. It is possible that initially there were less fruit in the natural orchards, because there were fewer honeybees. Chemical and mechanical thinning activities, in orchards where managed honeybees are used, even the numbers. Farmers that use more intensive farming methods often both bring in managed honeybees and use intensive chemical and mechanical thinning methods. Initially, they make sure most of the flowers are pollinated well with an abundance of introduced honeybees. Under these unnatural conditions, over-pollination actually occurs, which then would result in many smaller fruit. Growers, however, prevent this by thinning the crop and keeping only the best quality apples. The logic here is that the cost of thinning is less than the opportunity cost lost in case of inadequate pollination, particularly given that nothing can be done once the fruit have set.

On the other hand, farmers that only rely on wild honeybee pollination, as a general rule, use less thinning. The inadequately pollinated fruit is aborted by the tree anyway, to avoid investing resources into fruit that will not guarantee reproductive success. Consequently the latter farming method is much less expensive, but it comes at the cost of quality as desired by the export market in particular.

#### 2.4.4 Conservation recommendations

South Africa's pollinator resources (both managed and wild honeybees) require protection from human- and environment-induced threats that could possibly jeopardise this important service. To ensure the provision of wild pollination services, the focus should be on protecting large natural areas adjacent to orchards that can act as habitats for these pollinators and sustain them with foraging resources when the orchards are not in flower. On the other hand, the conservation of managed pollination services should focus on protecting the species from pests and diseases, but should also focus on protecting the industry's viability. The service should be adequately valued, and the hiring price of the hives should more adequately reflect the value of the service, thereby financially securing the managed honeybee industry. Pests and diseases spread fast through an apiary and will also affects wild honeybees. It should be communicated that it also adversely affects the deciduous fruit industry and the necessary precautions should be taken to prevent new diseases to reach managed apiaries.

The interacting relationship between the environment, wild honeybees and managed honeybees should be taken into account if a comprehensive conservation plan for pollination services in South Africa is developed. Because the managed honeybees are the same indigenous subspecies as the wild honeybees, simultaneous conservation is to be expected. This can be considered a conservation opportunity for wild pollinators. Additional research on the ecosystem services provided to the managed honeybee industry is needed to better understand the connection between environmental protection and adequate crop pollination. For example, a healthy wild population is a source of genetic variability for managed honeybees enabling them to become resistant against pests and diseases. In some cases this interaction has negative repercussions, creating conflicting goals for wild and managed pollinator conservation. It has been suggested

that natural vegetation close to apple orchards, could act as competing bloom, luring pollinators away from orchards (Mayer & Lunden 1991, Delaplane & Mayer 2001). However, the managed pollination systems and the managed-natural pollination systems were not significantly different regarding forager activity and apple production success. The only difference between these two types of pollination systems is that the managed-natural orchards have natural vegetation in close proximity to them. It thus seems that the natural floral resources is not competing with the apple blossoms and it is not necessary to consider this competition if habitat for wild pollinators needs to be conserved.

Managed honeybees ensure that apples are nicely shaped through good pollination. Ultimately, it is thus the demand from the consumer's side to buy a satisfactorily shaped apple, which justifies the use of managed honeybees above the use of wild pollinators. Another conservation option is to do consumer education or promotion for wild pollination services at the point of sale. Only if the consumer could accept apples with a malformed shape, will it be economically viable to use wild pollination services. These free wild pollination services could be a key in reducing input costs for food production providing a step towards better food security. It would then also make economic sense for the producer to protect natural habitat for wild pollinators.

Overall, to guarantee the future of pollinator dependent crops, an inclusive view of the pollination systems must be taken. Firstly, both the managed honeybees and wild pollinators need to be taken into account. Secondly, an appeal for pollinator protection must be made at the farm scale. Thirdly, both biophysical factors (pollinator habitats and diseases) as well as economic factors affecting the different industries (price reflection and consumer awareness) should be considered. For now, managed pollinators should be made a conservation priority, but for long-term sustainability, wild pollinators (especially honeybees) should also be actively engaged in conservation activities.

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# Chapter 3

# **Ecosystem Services Supporting the Western Cape Managed Honeybee Industry**

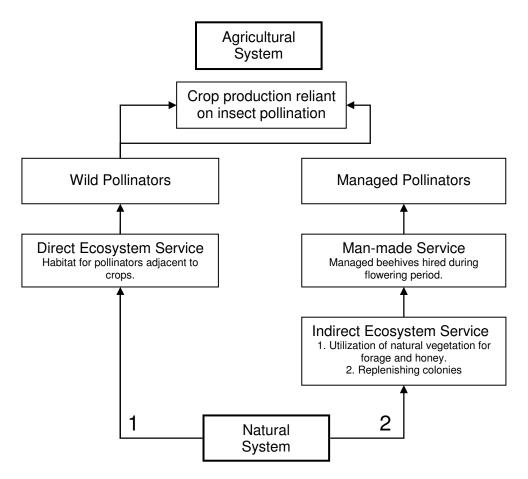
#### 3.1 Introduction

Ecosystem services are broadly described as the benefits provided by ecosystems and the species that make them up, to sustain and fulfil human life (Daily 1997; MEA 2005). Some of these benefits are directly presented to humanity, but ecosystem services are primarily conferred through indirect interactions (MEA 2005). There has been a growing recognition of the value of ecosystem goods and services, and this concept has created environmental awareness and conservation incentives in various sectors of society.

Agricultural landscape patches are in direct contact with natural patches, and together the two form an agri-environmental mosaic in which multiple interactions occur. While agricultural practices disturb natural ecosystems, they are also dependent on numerous ecosystem services such as pollination and pest control, as well as ecosystem goods such as water and nutrients (MEA 2005). Pollination services are typical of this interrelation between the natural and agricultural sectors. Crop production depends on pollination from insects, while agricultural practices, in turn, impact on pollinators through habitat degradation (Brosi *et al.* 2008) and through the use of harmful chemicals (Donaldson 2002).

Insect pollination is an essential part of commercial crop production, with 84% of European commercial crops being dependent on insect pollination (Williams 1996). While the bulk of the world's food volumes can be accredited to parthenocarpic crops and wind pollination, insect pollinated crops still account for a third of global food production (Buchmann & Nabhan 1996;

Klein *et al.* 2007). Gallai *et al.* (2009) calculated that the global economic contribution of insect pollinators to food producing crops to be €153 billion (9.5% of the total value of food producing crops).



**Fig. 3.1.** Hypothetical flow of ecosystem services from the natural system to the agricultural system via wild and managed pollination. Wild pollinators are directly linked to the natural system (1) as often described, but commercial honey bees are also linked to the ecosystem via an indirect pathway (2).

For any crop which is dependent on insect pollination, two types of insect pollination services can be distinguished in the agri-environmental system (Fig. 3.1). Firstly, there are naturally occurring pollinators (wild pollinators) residing in natural vegetation that perform pollination

services in adjacent cultivated lands. Secondly, there is the managed pollination component, which is the deliberate introduction of managed pollinators (such as honeybees) into orchards or fields to improve crop production (e.g. Allsopp *et al.* 2008). As the demand for pollinators increase, modern commercial crop production is becoming increasingly dependent on managed pollinators and less on wild pollinators (Richards 2001). Commercial honeybees *Apis mellifera* L. are used for 90% of commercial crop pollination (Free 1993). Beekeepers manage these honeybee colonies to collect and sell their honey and/or rent them out to crop producers for pollination purposes (Johannsmeier 2001). The managed honeybee industry has become an important industry in local and regional economies, and supports the global crop production industry via their pollination services (Allsopp *et al.* 2008; Aizen & Harder 2009).

Pollination services to crops often only relate to wild pollinators (De Marco & Coelho 2003; Kremen *et al.* 2004; Ricketts 2004). Managed pollination services are generally regarded as manmade services unrelated to the natural environment (Richards 2001, Winfree *et al.* 2007). Consequently, environmental degradation can then be considered to only impacting pollination from wild pollinators (not managed pollinators). In turn, this means that there would be little effect on production from most pollinator-dependent crops (Richards 2001; Ghazoul 2005).

Here I use a case study to show that this definition of managed pollination services is invalid. I hypothesised that the Western Cape beekeeping industry in South Africa receives essential ecosystem goods and services, which, in turn, enable beekeepers to service the deciduous fruit producing sector of the province (Fig. 3.1). The Western Cape presents a system where there are still relatively high proportions of natural areas as opposed to areas such as Europe and the United States where most pollination related studies are done. An extensively modified countryside in Europe has resulted in significantly lower densities and genetic diversity of wild honeybee colonies compared to South Africa (Moritz *et al.* 2007; Jaffe *et al.* 2009). An environment which supports more viable wild honeybee populations is also likely to better support commercial honeybees by means of ecosystem services, especially since the indigenous Cape honeybee *Apis mellifera capensis* Escholtz is the same subspecies which is used commercially. These factors make the Western Cape of South Africa an ideal system to study ecosystem goods and services flowing to the managed honeybee industry.

It is thus proposed that the pollination services provided by managed honeybees are indirectly dependent on the natural environment. If these ecosystem goods and services prove to be vital to the managed honey bee industry, then a much larger portion of crop pollination and production must be attributed to this supporting ecosystem service provided by a relatively intact ecosystem.

Two ecosystem services supporting the managed honeybee industry are explored in this case study. Firstly I looked at the extent to which managed honeybees depend on forage from natural vegetation to sustain the colony and to produce honey. The second service has to do with replenishing the beekeeper's colony stock. The beekeeper often loses colonies during the year, but especially during pollination season, either through migration (absconding) or mortalities caused by pesticide poisoning or harsh weather conditions (Johannsmeier 2001). These colonies have to be replaced by wild honeybee colonies by either catching swarms in trap boxes or removing them from habitats where they are unwanted or problematic. Both trapping and removing were seen as a source of wild, unmanaged honeybee colonies, even though it could be in an urban area. These wild colonies are indigenous and part of either a natural or semi-natural environment and are therefore seen as an ecosystem service (see definition of ecosystem service in first paragraph). This particular ecosystem service has not been investigated before relative to its contribution to pollination ecosystem goods and services. Specifically, I ask: 1) To what extent are beekeepers using natural vegetation as a forage resource for their managed colonies? 2) What percentage of the total honey production in the local area is derived from natural vegetation? 3) What percentage of managed colonies do beekeepers replace annually with wild colonies?

#### 3.2 Methods

#### 3.2.1 Study area and industry

Although the importance of insect pollination for pollinator dependent crops have been well studied (e.g. Klein *et al.* 2007), the specific contributions of different cultivars or different

farming systems is not known. There is great variability and uncertainty among fruit crops and cultivars with regards to the degree to which they depend on insect pollination (Richards 2001). This makes it difficult to determine the significance and value of the ecosystem services in question. Nonetheless, with existing information, a generalised conclusion can be made that fruit production in the Western Cape is dependent on both wild and managed insect pollination services (Allsopp & Cherry 2004; Allsopp *et al.* 2008). South Africa is the third largest deciduous fruit producing nation in the Southern hemisphere, with 70% of the area under deciduous fruit tree production in the Western Cape Province (DFPT 2009).

#### 3.2.2 Questionnaire survey

The use of natural vegetation by beekeepers in comparison with other forage sources was obtained from a questionnaire that was undertaken by Allsopp and Cherry (2004). A total of 173 beekeepers (19% of Western Cape beekeepers) responded to the questionnaire, although they represented 33,796 managed honeybee colonies, an estimated 80% of colonies in the area. The questionnaire data was reanalysed here to determine forage sources present at apiary sites and percentage of honey produced at apiary sites with natural vegetation.

An additional questionnaire was posed to the beekeepers in January 2009 to quantify the annual replacement of their colonies. I asked what their total amount of colonies was and how many additional colonies they caught each year by putting out trap boxes or by removing colonies from urban environments. They also had to indicate on what vegetation the empty trap boxes were placed to catch colonies. The questionnaire was viewed suspiciously by some beekeepers, as they were reluctant to release sensitive information on their apiary sites. Therefore only 18 beekeepers responded, but this still comprised of about 10% of the total number of colonies in the Western Cape, and it was deemed a representative report. Nevertheless, the questionnaire data was combined with an opinion of the Agricultural Research Council (ARC) to reach a more accurate estimate.

#### 3.3 Results

#### 3.3.1 Natural forage use for colony maintenance and honey production

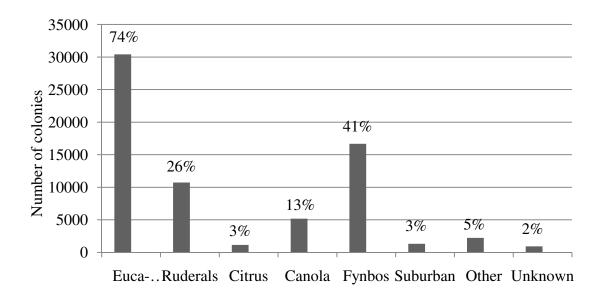
From analysing the questionnaire data from Allsopp and Cherry (2004) it was found that 49.41% (16 699 hives) of all colonies reported are being intentionally placed on apiary sites that are fully or partially natural vegetation (fynbos) as a forage source for honeybees (Fig. 3.2). Included in this percentage is the 11.03% of the total colonies that are placed on apiary sites that contain no forage source other than natural vegetation.

Combined, the colony forage-use percentages (Fig. 3.2) add to more than a 100%. The reason being, that hives are moved around by the beekeeper to favourable forage when it becomes available during specific times of the year. Alternatively, some sites can have more than one forage resource present, although often flowering at different times of the year. Therefore, some colonies forage at multiple apiary sites and are reported to be on more than one forage type during the year, and thus accounted for more than once.

The beekeepers reported that 18% of their honey production is from the nectar and/or pollen of natural vegetation while 66% can be attributed to foraging on *Eucalyptus* species (Table 3.1).

**Table 3.1.** Annual honey production (kg) in the Western Cape from different sources of honeybee forage, as reported by Western Cape beekeepers in 2004 (Allsopp & Cherry 2004).

Forage source	Honey produced (kg)	%
Eucalyptus	299 882	66.1
Canola	12 251	2.7
Fynbos (indigenous vegetation)	81 992	18.1
Ruderals	31 964	7.0
Citrus	13 549	3.0
Other	14 243	3.1
Total kg honey produced	453 881	100



**Fig. 3.2.** Number of honeybee hives Western Cape beekeepers place on each type of forage source at apiary sites (for the whole year or part of the year). Collectively the percentages add to more than 100%, because some hives are moved around apiary sites and therefore accounted for more than once. The figure indicates the number of colonies that fully or partially use a particular forage source. The proportion of total number of colonies, represented at each forage source is indicated in percentage above each bar. Data was adapted from Allsopp & Cherry (2004).

#### 3.3.2 Colony replenishing

The 18 beekeepers that answered the questionnaire kept a total number of 3,762 colonies. The smallest beekeeper owned 1 beehive and the largest beekeeper owned 1,300 hives. The dataset has a median of 100 and an average of 221 hives per beekeeper. The beekeepers indicated that 1,177 (31%) of their colonies were replaced annually from wild honeybee colonies (Table 3.2). Of those replaced, 922 (78%) were swarming colonies trapped in empty hives, and 255 (22%) were removed from buildings or trees in urban areas (Table 3.2). The expert opinion from the ARC agreed with this by estimating that between 20 - 30 per cent of colonies are replaced. The lowest percentage (20%) was chosen as a conservative value so as not to inflate the importance of the ecosystem service in question.

**Table 3.2**: The number of wild honeybee colonies collected annually by Western Cape beekeepers to replenish their managed colony stock. Colonies are collected either by removal from urban areas or by placing empty trap boxes in specific areas with forage sources that are attractive to honeybees.

	Source area	Number of colonies	%
	Eucalyptus Stands	319	27.1
	Canola Fields	213	18.1
	Fynbos (indigenous vegetation)	171	14.5
	Urban Areas	99	8.4
Trapped	Westcoast-sandveld (indigenous vegetation)	89	7.6
	Ruderals	15	1.3
	Citrus Orchards	10	0.8
	Other	6	0.5
Removed	Urban Areas	255	21.7
	Total number of colonies replaced	1177	100

#### 3.4 Discussion

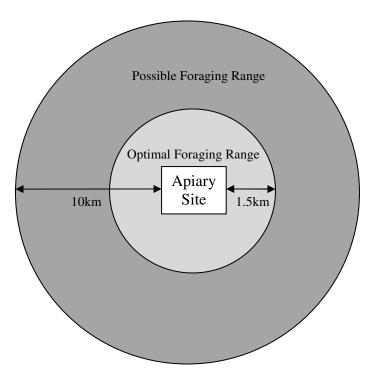
#### 3.4.1 Use of natural vegetation

From the beekeepers' reports, it can be concluded that a large portion of the Western Cape managed honeybee industry is reliant on fynbos vegetation as a forage source. Specifically, half of the managed bee colonies are reliant on fynbos forage for at least some parts of the year, and a substantial portion of honey is produced from fynbos nectar or pollen. However, fynbos vegetation might play an even more important role than the results show. Especially, seeing as there is such high floral diversity in the fynbos vegetation, that there are plants flowering all year round. Many fynbos species flower during winter and provide pollen and nectar food resources during a time of year when other resources are scarce. This implies three major factors

contributing to the managed honeybee industry. Firstly, fynbos can sustain populations through periods of otherwise low forage. Secondly, bee colonies start their spring pollination season in better condition, and are less prone to stress and associated die-outs. Thirdly, winter forage provides a more continuous flow of honey production that enhances the beekeepers income.

#### 3.4.1.1 Fynbos can sustain populations through periods of otherwise low forage

Eucalyptus is reported to be the most frequently used forage resource to sustain managed honeybees. Almost three quarters of all colonies are placed on *Eucalyptus* during some part of the year, and 35% of colonies are placed only on *Eucalyptus* for the whole year. Although this is how the beekeepers interpret this information, most *Eucalyptus* species flower only in summer (Johannsmeier 2005). It is thus impossible that managed bees can forage only on *Eucalyptus* for the whole year. What then is the explanation that the beekeepers reported year-long foraging? The answer is a very large foraging range (up to 10 km) of honeybees around the apiary site (Fig. 3.3) (see explanation of foraging ranges with references in chapter 2, methods). In winter, when the Eucalyptus species are not flowering, it is likely that the bees will fly away from their apiary sites to forage on nearby natural fynbos patches. In this case, the value of fynbos could be underscored in the questionnaire results. Alternatively, some colonies could gather all their resources on Eucalyptus during summer and store the honey for winter use. Consequently, little honey can be taken out for commercial use, otherwise the colonies will starve, which is not a feasible option for the beekeeper. Therefore, even though Eucalyptus seems to be the most important forage resource, it alone cannot sustain managed honeybee colonies. Apart from fynbos, there are also other important honeybee forage sources, such as canola, lucerne and ruderals, but their flowering times are mainly from August to March, and thus do not provide winter forage (Johannsmeier 2005). Fynbos is thus an essential winter forage component for managed colonies to remain in good condition and commercially viable for the beekeeper.



**Fig. 3.3.** Hypothetical foraging range of a honeybee colony around the apiary site. The bees of a colony stationed at a beekeeper's apiary site can forage optimally up to 1.5km from their hive but have been recorded foraging up to 10km from the hive. Colonies often forage on other vegetation types when the dominant forage source at the apiary site is not flowering.

#### 3.4.1.2 Improved colony condition prior to crop pollination

All deciduous fruit crops flower during spring (August-October). Honeybee colonies are used for pollination and placed in the fruit orchards, where they are exposed to many flowers, but with generally low nutritional value. They can also lose condition due to between-colony competition during high stocking densities or due to being transported for long distances. They often experience stress under these harsh conditions. If the colonies that are being brought in are in a weak condition, they will not be able to provide a pollination service of sufficient quality due to rapid die-off of the colony. Winter flowering fynbos helps these colonies to maintain their viability during the winter months, and subsequently they provide a better pollination service to the deciduous fruit industry during spring. Thus, not only the beekeeper directly, but also the deciduous fruit farmer indirectly, will benefit greatly from a winter forage source such as fynbos.

Fynbos vegetation resources can thus be seen as providing an indirect ecosystem service to the deciduous fruit industry through the managed honeybee industry (Fig. 3.1), contributing to a large sector of the Western Cape economy.

#### 3.4.1.3 Income for beekeepers from fynbos honey

Commercial beekeepers hire out their colonies for pollination services as well as sell honey. Apart from needing healthy colonies to pollinate fruit orchards, they also need colonies that produce as much honey as possible. The majority of honey produced during summer is from *Eucalyptus* species (Table 3.1), but having fynbos as a forage source also enables honeybee colonies to produce honey during winter. Beekeepers can thus provide a sustained flow of honey to buyers and also stabilize their income throughout the year rather than having income for a single season. As the local market for all things organic and eco-friendly grows, the trend for fynbos honey will also likely increase.

#### 3.4.2 Colony replenishing

The results here indicate that beekeepers on average replenish more than a fifth of their colonies with sourced wild colonies every year. What this means is that all managed honeybees colonies experience a complete turnover with wild colonies within five years. If the ecosystem is damaged in such a way that it can no longer support the demand for wild colonies, both the deciduous fruit and the managed honeybee industries could therefore suffer losses within relatively short time.

Catching wild colonies is not the only option for replacing dwindling colonies numbers. To import honeybees is illegal in South Africa, but has been done in the USA and South America to guarantee pollination of crops when local populations crashed. In SA it is most likely to stay illegal, because it can have far reaching implications. The introduced subspecies could hybridize with the indigenous South African subspecies, or be a carrier of honeybee diseases both of which is likely to compromise the indigenous population's ecological integrity. Furthermore, the ecosystem of the country from where the bees have been imported, will be under increased

pressure if having to supply additional honeybee colonies to South Africa's beekeeping and fruit producing industries. Queen-rearing is a method where beekeepers split existing colonies by identifying new queens and adding them to a part of the colony (few frames) to grow to a new separate colony in a new hive box (Johannsmeier 2001). This is a more feasible alternative than importing honeybees, but it must be noted that catching wild colonies holds additional genetic benefits, not applicable with queen-rearing. An inflow of genes from an outside source, would increase genetic diversity and improve resistance to diseases. In conclusion, there is a lack of better alternatives to replenish South Africa's managed colonies other than from local wild populations. It is thus important for all role players and beneficiaries of the managed honeybee industry to protect our natural honeybee populations and the habitats in which they occur.

#### 3.5 Conclusions

Almost all managed bees are dependent on natural vegetation, or at least would be better off foraging on it, either for good health or better, more valuable honey production for the beekeeper. Furthermore, beekeepers replenish a fifth of their colonies with wild honeybees each year. Ecosystem goods and services are thus important to sustain the Western Cape beekeeping industry with far reaching implications. Deciduous fruit production is in turn largely reliant on the managed honeybees for commercial crop production. This relationship between the ecosystem, beekeeping industry and agriculture has to be viewed from an ecosystem service perspective to appreciate how dependent agriculture is on the ecosystem. If not done, environmental neglect could have serious economic and food security implications.

Large emphasis is currently being placed on the economic value of pollination services (e.g. Allsopp *et al.* 2008; Gallai *et al.* 2009). It is clear from this study that the ecosystem goods and services used by Western Cape beekeepers is of great economic value to the South African economy. It can be argued that an uncultivated piece of land is of economic value because it provides not only potential wild pollinators (Kremen *et al.* 2004) but also ecosystem goods and services to managed honeybees that improve crop production (Morandin & Winston 2006). Such

economic valuations could be used as incentives for conservation of natural areas around cultivated fields in the agricultural landscape of the Western Cape.

Further research should focus on practical solutions to sustain these connections between the agriculture and the ecosystem. These should include farming practices that are less harmful to pollinators and their associated resources and the market potential for pollinator conservation from a fruit production perspective. In future, existing guidelines for good agricultural practices and certification of agricultural products should be evaluated explicitly for their efficiency in securing ecosystem goods and services to agriculture as illustrated for this component here. Maximising the benefit of ecosystem services to agriculture is likely to increase in importance for both humans and nature.

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# Chapter 4

#### **General Discussion and Conclusions**

# 4.1 Overview of the direct and indirect pollination ecosystem services to the Western Cape apple industry

Insect pollination leads to a marked improvement in Granny Smith apple production in the Western Cape. Pollination ecosystem services to Granny Smith apple production in the Western Cape can follow a direct or indirect pathway. The direct ecosystem service derives from wild honeybees visiting orchards for nectar and pollen while pollinating the apple blossoms in the process. In certain orchards, growers relied only on wild pollinators for their pollination needs. For this to be effective the orchard has to be close to a source of wild pollinators, namely a large area of intact natural vegetation with suitable honeybee nesting sites.

Since apple orchards are not always close to such a source, beekeepers provide managed honeybees which are thus more frequently used for pollination services than wild pollinators. Managed honeybees were more abundant in these orchards than the occurrence of wild honeybees in orchards where no managed honeybees were used. This resulted in managed honeybees delivering more effective pollination services, and ultimately a better quality crop was produced compared to when only wild pollinators were relied on.

Even though pollination services by managed honeybees are a managed service and not an ecosystem service, they are not totally isolated from the ecosystem. There are other ecosystem services supporting the managed honeybee industry in the Western Cape. Areas of intact natural vegetation provide essential winter forage for managed honeybees, vital to maintain colony health and honey production. Furthermore, the wild honeybee population is a source of colonies for beekeepers to uphold their stock, and the inflow of genetic variation from wild honeybees

could help domestic colonies become resistant against diseases. These ecosystem services described above, following an indirect pathway to enhance and support the pollination of deciduous fruit.

It is clear that intact ecosystems are supporting the indigenous honeybee, *Apis mellifera capensis*, whether it is directly through a natural system or indirectly through a managed system. By upholding the abundance and health of this important pollinating insect, the ecosystem is supporting all pollination-dependent crop production in the Western Cape, especially deciduous fruit.

#### 4.2 Financial considerations of pollination services

Financial valuation of ecosystems and their services is supported by a growing body of literature on conceptual approaches, technical valuation methods and operational issues (Simpson 1998; Costanza 2003; Turner *et al.* 2010). Despite these advances, ecosystems remain difficult to value given their complex behaviour, non-linear responses and their potential to undergo irreversible change (Chavas 2000; Ludwig 2000; Norgaard *et al.* 2007). The services they produce are also multiple and interdependent, and differ in terms of their ease of valuation (Turner *et al.* 2003), leading to a risk of excluding or undervaluing key ecosystem services (Redford & Adams 2009). Added to these concerns, and of central interest here, is the influence that the type and location of beneficiaries will have on the value calculated. The values people place on ecosystem services are considered to be highly dependent on social and environmental factors (Carpenter & Folke 2006). Valuation therefore requires an understanding of the spatial scales at which services are generated and flow, where benefits are realised and to which beneficiaries, to which components of their wellbeing, and taking into account the beliefs and value systems of the owners, managers and beneficiaries of ecosystem services (Turner *et al.* 2003; Hein *et al.* 2006; Brauman *et al.* 2007; Norgaard *et al.* 2007; Tallis & Polasky 2009).

This thesis focused on pollination as a specific ecosystem service to the deciduous fruit industry. The deciduous fruit value chain is therefore of importance to identify beneficiaries and estimate a monetary value for pollination services in this industry. However, the distinction between pollination as a "true" ecosystem service and pollination as a "managed" service becomes important in the valuation process since different beneficiaries are involved and hence different value attributes are at play. The following section presents a first effort to estimate the value of pollination services. It was not the main focus of the study and cannot be regarded as a fully inclusive estimate of the value of the service.

#### 4.2.1 Financial valuation of pollination services to Granny Smith apple production

The difference in fruit-set between the open and closed branches shows that 32.53% of the production will be achieved without pollination (Chapter 2). The pollination dependence factor of Granny Smith apples that this study reveals is thus 0.67. This factor is relevant if a farmer aims to achieve abundant crop production and does not take into account fruit quality. On the other hand, if one looks at the marketability of the fruit produced it results in a dependence factor of 0.81. This higher dependence factor is because more pollination is needed to produce a good quality, marketable fruit. This means that 67% of the production, in terms of apple-quantity, is dependent on insect pollination, whereas 80% of the production, in terms of apple-quality, is dependent on insect pollination. The dependence factor is lower than expected, because most comprehensive studies show a 0.9 dependence factor (Soltész 1997; reviewed by Allsopp *et al.* 2008).

To explain the production benefits in economic terms, the income figures received from apple production for the 2007/2008 season is used (DFPT 2009). The average price reported for the local fresh market is R 4 243 per ton while the export price is quoted at R 5 167 per ton (DFPT 2009). By combining these two prices, an average price per ton for marketable fresh apples is determined to be R 4 705 per ton. In comparison, processing apples (mainly for juice, canning and pulp) were sold for R 1 056 per ton. It is assumed that all apples that were marketable according to the weight, diameter and shape standards (see Chapter 2) were sold fresh, while all apples that were under the standard were processed.

To illustrate the contribution of insect pollination to apples in monetary terms, two scenarios are explored (Table 4.1). The first scenario is the control scenario, where branches were left open to be pollinated by insects. This scenario is representative of the current state of apple production. The second scenario is the exclusion scenario where insect pollination is excluded. This scenario is representative of a landscape where all insect pollinators have been eliminated and there is no other pollination replacement available. An average yield of 55 tons per ha was used as the control (when insect pollinators are present) (DFPT 2009). The yield for the exclusion scenario was calculated at 18 tons per ha. It must be noted that the yield value and sale prices are for apples in general and it is assumed that it is relevant for the Granny Smith cultivar. Granny Smith is the largest player in the apple industry (25% of total planted area and 24% of exports) (DFPT 2009) and therefore this assumption is not unfounded. The difference between the incomes of the two scenarios was R125 028 per hectare (Table 4.1), showing that insect pollination make sense from a financial perspective.

**Table 4.1.** The financial valuation of pollination using the comparison of two scenarios: Scenario 1 depicts Granny Smith apple production with insect pollination and scenario 2 depicts Granny Smith apple production without insect pollination. Both the quantity (yield) and quality (marketable *versus* processed) is taken into account for the monetary valuation. The proportion of the production value (R / ha) attributed to insect pollination is obtained.

	Scenario 1 (with insect pollination)		Scenario 2 (insect pollination excluded)	
	Yield = 55	ton per ha	Yield = $18$ ton per ha	
Fruit quality category	Marketable	Processed	Marketable	Processed
% production	53.17 %	46.83 %	31.61 %	68.39 %
Ton produced	29.24 ton	25.76 ton	5.69 ton	12.31 ton
Sales value per ton	R 4 705	R 1 056	R 4 705	R 1 056
Income per ha	R 137 591	R 27 199	R 26 762	R 13 000
Total income per ha	R 164 790		R 39	762

The monetary value (R / ha) of the contribution of insect pollination: R 125 028

In reality, if the pollination sources would be lost, an alternative or replacement would be sought out to continue production. Allsopp et al. (2008) valued the cost to replace pollination services with hand pollination for apple production in the Western Cape, to be between R 199.1 million – R 262.3 million (not including their conservative estimate). Hand pollination is the most costeffective replacement that is able to deliver the same yield as compared to insect pollination. Allsopp et al. (2008) used data from the 2003/2004 production season and there were 18 873 hectares under apple production during that season (see Allsopp et al. 2008 supplementary material). The replacement costs can also be converted to a value per hectare to be compared with our previous direct valuation method (see Table 4.1). It would cost between R 10 549 – R 13 898 per hectare to replace insect pollination services with hand pollination. To clarify, if insect pollination services are lost for some reason, an apple farmer will lose R 125 028 per hectare if he does nothing, but if he tries to replace it, he will only lose about R12 000 per hectare to extra costs associated with hand pollination. This replacement cost method of valuating insect pollination achieves a lower value, but one that is more likely to occur in reality. Yet, it is still unlikely that a farmer would be able to absorb these extra costs as input costs are already high and profits are marginal in agriculture (see DFPT 2009 for an outline of apple production costs).

#### 4.2.2 Valuation of wild pollination services to apple production

Allsopp *et al.* 2008 determined that the proportion of managed honeybees used in apple production, is 0.418 of the total number of colonies required (stocking density of 2 colonies per ha). Therefore, it can be assumed that wild honeybee colonies does the remainder of the pollination service (although other possible reasons are also given; see Allsopp *et al.* 2008). These proportions of wild and managed honeybees will change, among different pollination systems, but the current proportions can be used to estimate the situation for the Western Cape. The total production value that can be attributed to insect pollination is thus divided into the following proportions managed:wild = 0.418:0.582. Keeping to the estimate as per Table 4.1, the contribution from managed honeybees is estimated to be R 52 261 per hectare, while wild honeybees are contributing R 72 766 per hectare. To replace wild honeybee pollination for apples in the Western Cape with hand pollination would add between R 11 424 and R 15 062 per

hectare to the current production cost of apples; whereas it would cost between R 8 205 and R 10818 per hectare to replace all managed honeybee pollination. There are 4020 ha Granny Smith in the Western Cape (DFPT 2009). Total annual production contribution of wild honeybees to Granny Smith cultivar in the Western Cape is estimated to be: R 72 766 / ha x 4020 ha = R 292 501 129 per year.

#### 4.2.3 Valuation of ecosystem services supporting the managed honeybee industry

The ecosystem supports the managed honeybee industry, which in turn supports the deciduous fruit industry (Chapter 3). Managed honeybees are neither independent from natural vegetation nor from the wild honeybee population. Therefore conservation of these ecosystem services is still essential for deciduous fruit production. The three ecosystem services provided to beekeepers as studied are 1) the use of natural vegetation as a forage source for colonies, 2) honey production from natural vegetation and 3) wild colonies provided to replace depleted managed colonies (Table 4.2). This section presents a systematic value-based aggregation of these three prominent ecosystem services which support the honeybee industry. It is a somewhat contentious area where very little research has been done, and the following valuation must also be seen as a first contribution. The quantities used in this section are obtained from chapter 3 of the thesis.

**Table 4.2.** A summary of the annual flow value of the ecosystem services (ES) for the managed honeybee industry. At ES 1 the cost of replacement was used for valuation, and at ES 2 and ES 3 the direct market values were used.

	Quantity (units)	X	Price / unit	=	Value (R)
ES 1: Forage	16 699 colonies	X	R 1 244.30 / colony*	=	R 20 778 566
ES 2: Honey	81 922 kg	X	R 70.00 / kg	=	R 5 734 540
ES 3: Colonies	8400 colonies	X	R 500.00 / colony	=	R 4 200 000
				Total	R 30 713 106

^{*} The amount it would cost to feed one colony artificially for 22 weeks.

The value of natural vegetation as a forage source was determined by looking at the cost to replace it with artificial feed, as the most feasible alternative. Beekeepers reported that for at least some part of the year there were 16 699 hives (49.41% of Western Cape colonies) placed on natural vegetation. It is assumed that this is mostly during winter, from May – August (22 weeks) as this is the part of the year when other forage sources are not readily available. To support a colony for 22 weeks on sugar syrup and pollen supplement, it would cost the beekeeper R 1 244.30. If it were to be done for all the colonies placed on fynbos in the Western Cape it would cost the industry R 20 778 566 annually. This is still a moderate estimate, because spin-off effects, such as the cost of reduced honey production and pollination services, as well as increased labour costs are not included.

The pollen and nectar of natural vegetation not only sustains colonies, but as a secondary, related ecosystem service it also provides the beekeeper with a product that can be sold, honey. The direct market price for honey, estimated at R 70 per kg, was used to value this ecosystem service. The questionnaire data revealed that 81 922 kg honey is produced from honeybees foraging on natural vegetation and the total industry value of the honey is estimated on R 5 734 540 per annum.

The third ecosystem service is when beekeepers trap and remove wild colonies to replace their own managed colonies that have died-out or absconded during times of stress. A beekeeper replaces at least 20% of his colonies with wild colonies each year, which amounts to a total of 8400 colonies being brought into management each year (Chapter 3). Colonies are sometimes sold between beekeepers for an estimate market value of R 500 per colony. The total market value of the colonies replaced annually is thus R 4 200 000. Additionally it must be noted that this ecosystem service is more valuable as it supplies the species around which this whole industry revolve and from which all its income is derived.

A first estimate on the total annual flow value of the ecosystem services for the Western Cape managed honeybee industry thus amounts to almost R 31 million (Table 4.2). This means that if the ecosystem is damaged in such a way that these services will not be provided anymore, the industry would suffer a loss of R 31 million annually, either by means of reduced turnover or

increase production cost. This is quite a significant amount, considering that in the Western Cape, the total annual industry income from honey sales and pollination services is R 52 161 000 (Allsopp & Cherry 2004).

#### 4.3 Conservation and management recommendations

To effectively characterise and value ecosystem services, it has to be separated into quantifiable components that can be researched. In the preceding chapters, different components of the services have been carefully characterised and in this chapter a valuation of these components were performed. This method can give one an understanding of what part of the system is more important than others and if conservation resources are limited, can help with prioritization. If the pollination system is not subdivided into compartments, it will not be possible to do monetary valuation. Monetary valuation is important when decision makers are faced with a limited budget and conflicting goals as is often the case in conservation of ecosystem services. Nevertheless, it is of utmost importance that the interconnectedness of the system not be forgotten when considering conservation and management practises (Fig. 4.1). An action to protect or neglect one component of the pollination system, will inevitably affect the others. This necessitates the need to assess the situation on a farm, landscape and industry scale.

#### 4.3.1 Farm scale

Managed honeybees performed better pollination services than wild pollinators, because there are more pollinators present in an orchard using managed honeybees. But wild pollinators also play a significant role in apple pollination. At the managed-natural system it was generally observed that farmers often used less managed honeybee hives than in the pollination systems far away from natural systems. This could suggest that farmers close to natural areas have realised that they need less hives per hectare to achieve a satisfactory harvest, because wild honeybees are helping to pollinate the orchards. If measures could be taken to increase wild honeybees in or facilitate them into orchards, farmers could save on pollination costs and thus they might play a role in conservation too. For example, intact natural vegetation adjacent to or in between

orchards should be left unscathed and not be further converted to farmland. A buffer zone could be created to avoid edge effects from the orchards into the natural areas, for example pesticide-drift could harm wild pollinators. Furthermore, they could create nesting sites for wild honeybee colonies, by placing elevated (for protection from badgers), empty hives or old tyres throughout the orchard. Other attractive flowering resources could aid in attracting honeybees and so it is also suggested that ruderals within rows should rather be left than mowed or ploughed.

#### 4.3.2 Landscape scale

The responsible party for the protection of the pollination resources on a landscape scale is difficult to isolate, because it stretches across multiple landowners and industries. Ideally it should be a combination of local government (municipalities, Western Cape Department of Agriculture), regional conservation agencies (Cape Nature in the Western Cape) and industry bodies (e.g. the Deciduous Fruit Producers Trust, collective fruit pack-houses and the Western Cape Bee Industry Association). On a landscape scale it is important to protect the main area where wild honeybees are sourced from, which is usually the mountainous areas. Fire management is crucial in fynbos vegetation to maintain the natural balance of floral species that can support wild pollinators. Where these areas are formally conserved already, there has been conflict between conservation managers and beekeepers. The conflict is centred around beekeepers that want to put their managed hives on natural vegetation for forage and the trapping of wild colonies. More research is needed with regards to the effect a larger concentration of honeybees may have on natural vegetation as well as the extent of the wild population. Corridors of native vegetation connecting the agricultural land to natural land could increase the presence of wild honeybees in orchard, provide forage sources for managed honeybees and could also increase the genetic flow between the wild and managed populations. If new corridors are created in the landscape, rocks (or any natural, hollow objects) should also be added to create suitable nesting sites for wild pollinators.

#### 4.3.3 Industry scale

If we want to address pollinator conservation on an industry level, a crucial point to remember is that industries are often only moved by monetary gain. Hence, economic valuation of pollination services could play a large part in convincing industries to take conservation action. Another characteristic of industries is that it could often traverse a whole country or even the globe.

Probably the biggest threat to managed honeybee populations is pests and diseases. To prevent the spread of honeybee pests and diseases, import regulations must be strictly adhered to. Two of the most destructive forces that the South African managed honeybee industry has been facing, the *Varroa* mite and the American foulbrood disease have both been introduced through imports. Managed honeybees are providing a very important service to apple production, especially in orchards that are far away from a source of wild honeybees. The pollination services beekeepers are providing to fruit producers are undervalued (Allsopp *et al.* 2008). The price at which these colonies are hired out to fruit producers should be raised, to more accurately reflect the value they add to apples. This would improve the perceived value and conservation awareness of all pollinators.

Another industry initiative to conserve pollinators is to develop a best practice guideline for deciduous fruit production that can include farm scale methods to enhance pollinator abundance in the orchard. Although practise change will be on farm scale, such an initiative needs to be driven from the industry to be effective and sustainable. Yet, ultimately it is the consumer that will drive fruit production to adopt more ecologically friendly methods. Especially in the overseas market, such a consumer market exists. But the consumer will still not accept a poor quality apple as a trade-off for environmental protection.

#### 4.4 Future research

A critical assumption that is made in this study is that natural vegetation supports wild honeybee colonies. Furthermore it is assumed that the closed proximity of natural areas to orchards would

provide the orchard with wild pollinators. This assumption needs validation. Some of the research questions that could address this are: What is the density of honeybee colonies in mountain fynbos? What colony density is needed to perform good pollination services in orchards? What biological factors, such as the presence of a competing flowering species, or environmental factors (altitude) will inhibit wild honeybees from pollinating orchards? Also, some of the conservation recommendation needs to be implemented and then assessed. Relevant research questions could be: What conservation actions will improve crop production? What actions will actively contribute to the protection of pollinators? This study only focuses on Granny Smith apples, but other cultivars and crops needs to be assessed in a similar fashion to understand the pollination requirements of the larger landscape.

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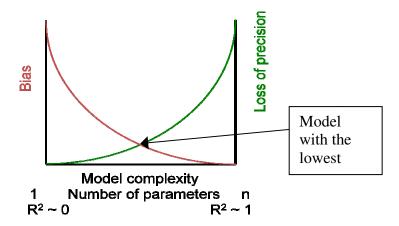
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# **Appendix A: Model Selection for Question 2 of Chapter 2**

The model selection is done by using Akaike's Information Criterion (AIC). The best model is the one with the lowest AIC value. If the number of parameters are decreased (by removing factors), the model's precision is increased. This can result in a bias model. The optimum point between precision and bias of a model is where the AIC value is at its lowest (Fig. A1).



**Fig. A1.** Model selection was done by using Akaike's Information Criterion. The model with lowest AIC value is the model where the relationship between the bias and precision of the model has been optimized.

In Table A1 and Table A2 the model selection process for the number of foragers and visitation rates are depicted. For the environmental variables, the least significant factor is removed one at a time from the analyses. The factors that are excluded are listed for each model. Model selection for the number of fruit and fruit-set variables are not shown in this Appendix, as there were only one possible combination of variables (see Tables 8 and 9 respectively). In Tables A3-A7 it shows the model selection process for the remaining production variables. The best model was selected by exploring different combinations of random variables and selecting the model with the lowest AIC value once again. The nestedness of the random variables are indicated by the

forward slash sign (/), where the variables after the sign are nested within the variables before the sign in the sequence indicated for each data set (see Table A3-A7).

**Table A1.** Model selection for the number of foragers (honeybees) data. A GLMM was used to analyse the data. The following factors were modelled against the number of foragers: pollination system, wind, temperature, relative humidity, percentage cloud cover and average number of open flowers per orchard. The factors farm and row were set as random variables, with row nested in farm. Model 5 was selected as the best model. All the variables that were removed from the model 5 did not have a significant influence on the dependent variable.

	Excluded factor(s)	AIC
Model 1	-	451.4
Model 2	Flowers	449.4
Model 3	flowers; cloud cover	448.1
Model 4	flowers; cloud cover; relative humidity	446.6
Model 5	flowers; cloud cover; relative humidity; temperature	445.2
Model 6	flowers; cloud cover; relative humidity; temperature; row (random)	450.7
Model 7	flowers; cloud cover; relative humidity; temperature; farm (random)	647

**Table A2.** Model selection for the honeybee visitation rate data. A LMM was used to analyse the data. The following factors were modelled against the visitation rate: pollination system, wind, temperature, relative humidity, percentage cloud cover and average number of open flowers per orchard. The factors farm was set as a random variable. Model 6 was selected as the best model. All the variables that were removed from the model 6, except for relative humidity, did not have a significant influence on the dependent variable.

	Excluded factor(s)	AIC value
Model 1	-	339.8
Model 2	Wind	336.0
Model 3	wind; cloud cover	329.1
Model 4	wind; cloud cover; temperature	325.8
Model 5	wind; cloud cover; temperature; flowers	312.8
Model 6	wind; cloud cover; temperature; flowers; relative humidity	311.2

**Table A3.** Model selection for seed-set data. A LMM was used to analyse the data. Pollination system is the only variable modelled against seed-set. The random variables were selected by using the AIC method. Model 8 was selected as the best model.

	Random factor(s) included in model	AIC value
Model 1	farm / row / tree / branch	2589.2
Model 2	farm / row / tree	2621.0
Model 3	farm / row / branch	2541.0
Model 4	farm / tree / branch	2554.2
Model 5	row / tree / branch	2576.5
Model 6	farm / row	2620.1
Model 7	farm / tree	2621.4
Model 8	farm / branch	2488.1
Model 9	farm	2619.4
Model 10	row / tree	2643.9
Model 11	row / branch	2542.3
Model 12	row	2642.2
Model 13	tree / branch	2543.3
Model 14	tree	2642.2
Model 15	branch	2518.3

**Table A4.** Model selection for the fruit-quality (marketability factor) data. A GLMM was used to analyse the data. Pollination system is the only variable modelled against the marketability of the fruit. The random variables were selected by using the AIC method. Model 7 was selected as the best model.

	Random factor(s) included in model	AIC value
Model 1	farm / row / branch	196.7
Model 2	farm / row	194.7
Model 3	farm / branch	194.7
Model 4	row / branch	194.8
Model 5	farm	192.7
Model 6	row	192.9
Model 7	branch	189.9

**Table A5.** Model selection for the fruit-quality (diameter) data. A LMM was used to analyse the data. Pollination system is the only variable modelled against the fruit diameter. The random variables were selected by using the AIC method. Model 1 was selected as the best model.

	Random factor(s) included in model	AIC value
Model 1	farm / row / tree / branch	3569.9
Model 2	farm / row / tree	3571.7
Model 3	farm / row / branch	3600.8
Model 4	farm / tree / branch	3617.4
Model 5	row / tree / branch	3686.5
Model 6	farm / row	3598.8
Model 7	farm / tree	3617.0
Model 8	farm / branch	3623.0
Model 9	farm	3621.4
Model 10	row / tree	3684.5
Model 11	row / branch	3691.8
Model 12	row	3690.7
Model 13	tree / branch	3693.7
Model 14	tree	3693.3
Model 15	branch	3689.2

**Table A6.** Model selection for the fruit-quality (weight) data. A LMM was used to analyse the data. Pollination system is the only variable modelled against the fruit weight. The random variables were selected by using the AIC method. Model 1 was selected as the best model.

	Random factor(s) included in model	AIC value
Model 1	farm / row / tree / branch	5354.7
Model 2	farm / row / tree	5355.2
Model 3	farm / row / branch	5375.0
Model 4	farm / tree / branch	5385.8
Model 5	row / tree / branch	5444.5
Model 6	farm / row	5374.3
Model 7	farm / tree	5385.5
Model 8	farm / branch	5389.6
Model 9	farm	5388.7
Model 10	row / tree	5442.5
Model 11	row / branch	5444.6
Model 12	row	5442.7
Model 13	tree / branch	5446.0
Model 14	tree	5444.2
Model 15	branch	5441.9

**Table A7.** Model selection for the fruit-quality (shape) data. A GLMM was used to analyse the data. Pollination system is the only variable modelled against the fruit shape. The random variables were selected by using the AIC method. Model 15 was selected as the best model.

	Random factor(s) included in model	AIC value
Model 1	farm / row / tree / branch	189.4
Model 2	farm / row / tree	187.4
Model 3	farm / row / branch	187.4
Model 4	farm / tree / branch	187.4
Model 5	row / tree / branch	187.6
Model 6	farm / row	185.4
Model 7	farm / tree	185.4
Model 8	farm / branch	185.4
Model 9	farm	183.4
Model 10	row / tree	185.6
Model 11	row / branch	185.6
Model 12	row	183.6
Model 13	tree / branch	185.6
Model 14	tree	183.6
Model 15	branch	180.3

# **Appendix B: Questionnaire on Colony Replacement**

Questionnaire for Western & Southern Cape Beekeepers

Theme: Colony Replacement

As a continuation of the Gums & Beekeeper Survey, we (ARC-PPRI and the South African National Biodiversity Institute, Kirstenbosch) are collecting information relating to the importance of 'wild bees' and natural forage to the beekeeping industry of the Western Cape. We hope this information will prove valuable in the preservation of important natural forage for bees, and possibly, in improving access to this forage for beekeepers.

We therefore ask that ALL beekeepers in the Western and Southern Cape (anywhere in the province of the Western Cape) please take 5 minutes to assist us by completing the questions below and emailing the response to Madelé Rademan at Rademan@sanbi.org

All data will be treated confidentially, and will not be passed on to any third party. All respondents are sincerely thanked for their time and information. If there are any questions, please contact Madele Rademan at 021 799 8861 or 082 926 1855.

Mike Allsopp (ARC-PPRI, Stellenbosch) Madele Rademan (South African National Biodiversity Institute, Kirstenbosch

#### Questions

- 1. Beekeeper name and surname:
- 2. Number of colonies:
- 4. Please indicate in the table below how many colonies you trap annually on different primary forage sources. If colonies are trapped on the same forage in more than one place, please indicate, up to a maximum of six sites for each forage source.

Forage source:	Closest town:	Distance to closest town:	Number of colonies trapped:	During what months of the year?
Gums	1.	1.	1.	1.
	2.	2.	2.	2.
	3.	3.	3.	3.
	4.	4.	4.	4.
	5.	5.	5.	5.
	6.	6.	6.	6.
Weeds	1.	1.	1.	1.
	2.	2.	2.	2.
	3.	3.	3.	3.
	4.	4.	4.	4.

	5.	5.	5.	5.
	6.	6.	6.	6.
Citrus	1.	1.	1.	1.
Citius	2.	2.	2.	2.
	3.	3.	3.	3.
	4.	4.	4.	4.
	5.	5.	5.	5.
	6.	6.	6.	6.
Canola	1.	1.	1.	1.
C 4111014	2.	2.	2.	2.
	3.	3.	3.	3.
	4.	4.	4.	4.
	5.	5.	5.	5.
	6.	6.	6.	6.
Fynbos	1.	1.	1.	1.
•	2.	2.	2.	2.
	3.	3.	3.	3.
	4.	4.	4.	4.
	5.	5.	5.	5.
	6.	6.	6.	6.
West-coast Sandveld	1.	1.	1.	1.
	2.	2.	2.	2.
	3.	3.	3.	2. 3.
	4.	4.	4.	4.
	5.	5.	5.	5.
	6.	6.	6.	6.
Suburban	1.	1.	1.	1.
	2.	2.	2.	2.
	3.	3.	3.	3.
	4.	4.	4.	4.
	5.	5.	5.	5.
	6.	6.	6.	6.
Other (specify)	1.	1.	1.	1.
	2.	2.	2.	2.
	3.	3.	3.	3.
	4.	4.	4.	4.
	5.	5.	5.	5.
	6.	6.	6.	6.
Other (specify)	1.	1.	1.	1.
	2.	2.	2.	2.
	3.	3.	3.	3.
	4.	4.	4.	4.
	5.	5.	5.	5.
	6.	6.	6.	6.