How vertebrate communities affect quality and yield of macadamia farms in Levubu, South Africa

Thesis submitted to the Chair in Biodiversity Value and Change,
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requirements for the degree of

Doctor of Philosophy in
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by
Valerie M.G. Linden
Student No.: 15015310

Promoter: Professor Peter J. Taylor,
SARChI Chair on Biodiversity & Change, University of Venda, South Africa
Co-promoters: Professor Teja Tscharntke and Dr. Ingo Grass,
Department of Crop Sciences,
University of Göttingen, Germany
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“A smooth sea never made a skilled sailor.”

- Franklin D. Roosevelt

Declaration

I, VALERIE M.G. Linden, hereby declare that the thesis for the degree of Doctor of Philosophy in Mathematical and Natural Sciences at the University of Venda, hereby submitted by me, has not been previously submitted for a degree at this University or any other University, that it is my own work in design and execution and that all referenced material contained therein has been duly acknowledged.

Signature ____________________

Date ____________________

Publication timeline and disclaimer

Please note that chapters two to four of this dissertation are stand-alone papers (see below) and a certain degree of repetition was therefore unavoidable. The following chapters are submitted or in preparation for submission for publication in peer reviewed journals:

Chapter 2: Linden, V.M.G., Grass, I., Joubert, E., Tscharntke, T., Weier, S.M., Taylor, P.J., *Ecosystem services and disservices by birds, bats and monkeys change with macadamia landscape composition*
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Chapter 3: Linden, V.M.G., Grass, I., Tscharntke, T., Weier, S.M., Taylor, P.J., *Bat species diversity in South African macadamia orchards is driven by seasonality more than by spatial variation* (in preparation)

Chapter 4: Linden, V.M.G., Foord, S. H., Grass, I., Tscharntke, T., Weier, S.M., Taylor, P.J *Insecticide treatments and landscape simplification negatively affect honey bees (Apis mellifera) in macadamia orchards, possibly limiting ecosystem service provision* (in preparation)

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Summary

Ecosystem services and disservices are important features in agro-ecosystems and both can have relevant economic impacts on farmers. While there has been much research on the value of ecosystem services, especially that of pest control by bats and birds, ecosystem disservices are often overlooked or estimated separately. Both, services and disservices, however, change with landscape and may be supported by natural vegetation. It is hence inevitable to assess them together to uncover their relative value and importance. Habitat loss and fragmentation are major threats to biodiversity and ecosystem services. Agricultural intensification can cause habitat loss and can negatively affect natural ecosystems and their services. However, the removal of natural vegetation can also reduce ecosystem disservices that origin from natural areas.

This study focused on the economic trade-off between biocontrol by bats and birds and crop raiding by vervet monkeys in South African macadamia orchards, using vertebrate exclusion experiments. Crop quality and yield were assessed and extrapolated to income values. The study furthermore focused in more detail on the impact of orchard edge habitat and farm management on bats as ecosystem service providers as well as the arthropod community, which can provide both services (pollination, biocontrol) as well as disservices (crop damage). The macadamia industry is highly profitable and plantings are expanding worldwide. South Africa is currently the largest macadamia producer in the world and the study area, Levubu, holds some of the oldest macadamia plantings in the country. The subtropical climate and high annual rainfall make this area an intensively farmed landscape. Levubu lies at the foothills of the Soutpansberg, a centre of biodiversity and patches of natural vegetation wind through orchards of macadamia, avocado, banana and timber. Insect pest pressure is high in the macadamia industry, with several stink bug species (Hemiptera) and two moth species (Lepidoptera) accounting for most of the damage to the crop.

Chapter One provides a detailed overlook over the South African macadamia industry, describes the major pest insect species and their impact on the crop and highlights the role of ecosystem services and disservices and the potential importance of remaining natural areas. Over three consecutive seasons, between September 2015 and May 2018, bats, birds and monkeys were excluded, using cages with nets, from a total of 96 macadamia trees. Four treatments were applied (Full, Day, Night, Control) to distinguish between effects of the different functional groups. Exclusions took place at orchard edges with natural or human-modified edge habitat to assess the impact of vicinity to natural vegetation on pest control and crop raiding. Results presented in **Chapter Two** showed that biocontrol by bats and birds was stronger near

natural vegetation and significantly impacted crop quality as well as yield. Effects of bats and birds were still significant at human-modified edges, whereas crop raiding by monkeys is limited to the natural orchard edges. The economic impact analysis shows that the benefits of biocontrol through bats and birds outweighed the income losses due to crop-raiding monkeys. The value of bats and birds was as high as USD 5000 per hectare per year through prevented insect damage and a 60% crop increase. Crop-raiding affected the yield, which dropped by about 26% and resulted in losses of about USD 1500 per hectare. These results highlight the importance of integrating natural areas into agricultural landscapes, even if they incur the risk of being disadvantageous. Farmers need to be made aware of the enormous economic benefits. Effective crop raiding mitigation strategies still need to be researched to avoid negative association with natural areas. These can, however, possibly also limit access for biocntrol agents, like bats and birds and thereby reduce their economic impact. Especially the removal of natural areas or establishment of buffer zones of unpalatable crops between agricultural land and forests is not advisable. Integrative research in agro-ecosystems on trade-offs between a variety of ecosystem services and disservices is necessary in future, rather than assessing them separately.

The bat community on macadamia farms was monitored monthly and compared between orchard edges. Stationary bat detectors were placed at each set of exclosures for two consecutive nights a month, automatically recording from sunset to sunrise. Recorded bat calls were identified manually to species level and activity converted to Miller’s activity index, which counts the number of active minutes per species per night. We analysed the activity per feeding guild over season and landscape setting, estimated species richness and diversity (Hill’s numbers) and species turnover between farms, season and landscape setting, using diversity partitioning. The bat community was mostly influenced by seasonality with season turn-over accounting for 21% of total bat diversity (21.25 species). Edge habitat on the other hand only accounted for 5%. We found higher species richness and activity in the high season compared to the low. While there was no difference in diversity in the high season between the two orchard edge types, species diversity at the human-modified edge was lower than in the natural during the low season. Natural habitat might therefore be more important in the low season, while its effect is overwritten by high food availability during the high season. Clutter-edge species furthermore were more active at the natural orchard edges than open-air feeders, which were in turn more active at human-modified edges. Both activities dropped significantly during the low season.

Chapter Three concludes that the macadamia landscape is able to support a high bat species diversity, which is affected by seasonal differences, probably due to food availability. Natural areas are important to be maintained to support sensitive species, relying on clutter habitat and natural roosts.

Habitat features as well as farm management can also influence arthropod communities. Visual observations took place each month for 20 minutes per tree. Observations were counted and identified to at least order level. **Chapter Four** concentrates on the impact of orchard edge habitat and insecticide treatment on honey bees (83% of Hymenoptera observations) abundance. Honey bees were the only taxon significantly responding to both variables, with higher abundance close to natural areas and increasing abundance with increasing time since pesticide application. Honey bees furthermore seemed to recover slightly quicker from population crashes after insecticide treatments at natural edges than they did at human-modified edges. Hymenoptera can be highly beneficial to macadamia farmers, as farmers are heavily relying on pollination by honey bees and parasitoids are known to feed on major macadamia pest insect species. These ecosystem service providers were mostly affected by habitat and management practices, which may compromise their ecosystem service provision. Although commercial bee hives are exposed throughout macadamia orchards, they do not appear to fully replace the pollination and biocontrol services provided by feral species, which can be enhanced through resource supplementation by patches of nearby natural vegetation.

Chapter Five concludes with emphasizing the general importance of natural vegetation in landscape planning of agricultural areas. This study proved confidently that benefits through ecosystem services largely outweigh negative impacts of ecosystem disservices, both stemming from these natural areas. Through the inclusion, maintenance and restoration of such patches of natural vegetation, farmers can potentially increase the value and effectiveness of biocontrol by bats and birds or other services. Seasonality largely determined bat species diversity, and a general high species diversity was observed in the macadamia landscape, possibly due to a certain degree of landscape heterogeneity and high food availability. Activity patterns of clutter-edge and open-air feeding bats varied with edge habitat, while clutter-dependent bat species were mostly absent. The observed effects of landscape and farm management practices support other observations of insect, especially Hymenoptera declines, largely due to agricultural intensification and habitat loss. The intensive insecticide regime applied on macadamia orchards affected Hymenoptera that are pollination and biocontrol providers, and nearby natural areas functioned as refuge and source for regeneration of the population. The conservation of natural habitat can ensure the conservation of these beneficial ecosystem services and provides economically viable arguments for farmers and policy makers for integration and conservation of natural habitat patches in agricultural landscapes.

Chapter 1 – The macadamia agro-ecosystem

The macadamia industry in South Africa

The macadamia *macadamia integrifolia* Maiden and Betche, 1896 is a tree nut species native to Australia and was first cultivated in Hawaii in the early 1900s (Nagao et al., 1992). Biggest producers of macadamias are nowadays South Africa, Australia and the USA with China and some South American and African countries growing fast in production. Flowering occurs profusely on racemes (Figure 1a) after which roughly 0.3% of the 100-300 flowers per raceme result in nut set on the tree (Boyton and Hardner, 2002). Nut set (Figure 1b) is a function of cross-pollination, pollinator visits and nutrient status of the tree (Sedgley, 1983; Trueman and Turnbull, 1994). The embryo (kernel) developes and forms roughly 72% oil (Stephenson et al., 1989) until reaching full maturity. Most varieties of *macadamia integrifolia* drop their nuts after they reached maturity. Nuts are then manually collected from under the tree. The green husk is removed on the farm and nuts are delivered in shell to a local processing facility, where they are being dried, cracked and sorted and then sold as kernel to the food industry. Lately there has been an increase in the demand in dry-in-shell nuts, where especially big nuts are being sold uncracked to the Asian market. Cultivation in South Africa began in 1968 and today South Africa is amongst the biggest macadamia producers worldwide and steadily growing. The number of macadamia trees planted has increased from one million trees in 1996 (corresponding to a national kernel yield of 3 000 tons) to eight million in 2016 (corresponding to a national kernel yield of 38 000 tons), covering an area of ± 28 000 ha (Southern African Macadamia Growers' Association, 2017a). Simultaneously the sales value of macadamia nuts has increased from

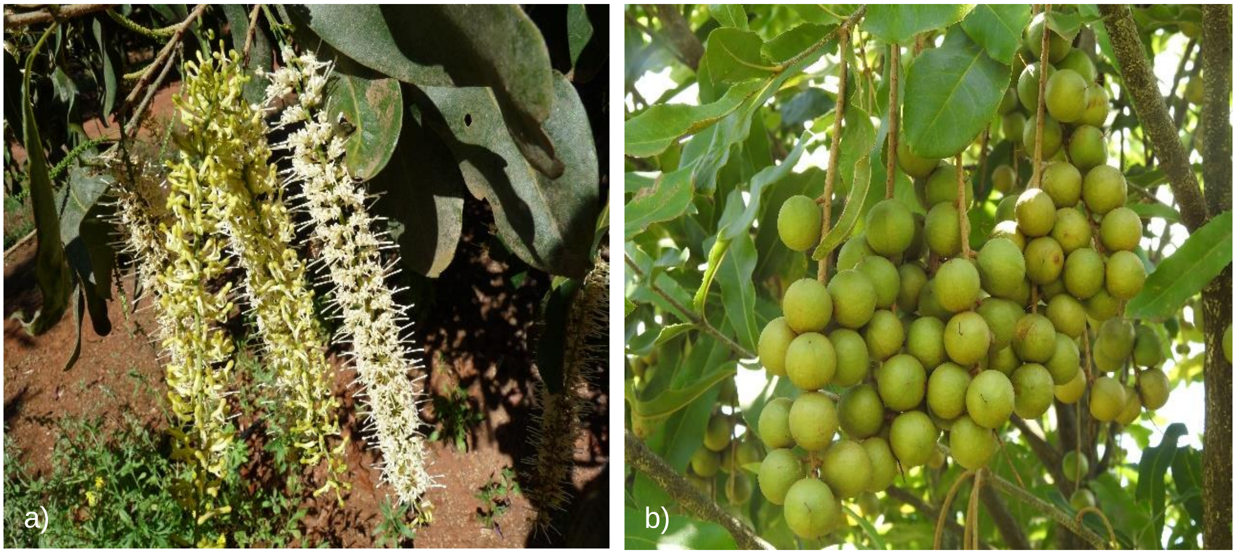

Figure 1 Pictures of a) macadamia flowers and b) fruit set of macadamia nuts in racemes

32mio ZAR (± 2.5 mio USD) in 1996 to 3.2bil ZAR (± 24.6 mio USD) in 2015 (Southern African Macadamia Growers' Association, 2017a). Macadamia production in South Africa is expected to double within the next five years. In 2016 approximately 36% of South Africa's crop was exported as nut-in-shell (NIS) to Asia. The USA and Canada are South Africa's largest markets for kernel, followed by Europe, Japan and the Middle East. One major threat to the macadamia production in South Africa is kernel damage by pest insect species resulting in a reduced nut quality (Nagao et al., 1992; DAFF, 2017).

Insect pests to macadamias

Major insect pests of macadamia include the stink bug complex Hemiptera; Linnaeus, 1758 and the nut borer complex Lepidoptera; Linnaeus, 1758. Stinkbug damages are generally divided into early (Figure 2a) and late (Figure 2b) stinkbug damage depending on the time of season or nut growth they have occurred. Since the macadamia shell is particularly hard, not all species of stinkbug can cause both types of damage. Early as well as late damage can be caused by e.g.

Figure 2 Different insect damages to macadamias with a) showing early stinkbug damage to the kernel, b) showing late stinkbug damage to the kernel and c) showing removed husks that have been damaged by mostly macadamia nutborer larvae

the coconut bug, *Pseudotheraptus wayi*, or the two-spotted stink bug (Figure 3) *Bathycoelia distincta*. The coconut bug is considered a pest insect in several subtropical crops, while its host plant is unknown (Schoeman and de Villiers, 2015). Damage to the nut by the coconut bug can cause the nut to drop prematurely or otherwise results in necrotic lesions and deformed kernel (Schoeman and de Villiers, 2015). The two-spotted stink bug can breed in macadamia orchards and feeds on macadamias during the early to late developmental stages of the nuts and can, like the coconut bug, cause necrotic lesions or white feeding marks (Schoeman and de Villiers, 2015). The short mouthed stinkbug complex, including the green vegetable bug, *Nezara viridula* and the yellow edged stink bug *Chinavia pallidoconspersa* feed on macadamias mostly during the early stages of nut development (Schoeman and de Villiers, 2015). Damage caused by these stink bugs is similar, but less severe than that of the earlier mentioned species (Schoeman and de Villiers, 2015) and is classified as “early stinkbug damage”. Despite the direct effect of spoiling and damaging the kernel, stinkbugs can also cause premature nut drop or fungal infestation. The South African Macadamia Growers Association estimated the loss due to stinkbug damage in 2016 to be as high as 190mio ZAR (Southern African Macadamia Growers’ Association, 2017b) but suggests a potential higher loss even, due to drought related reduced yields in 2016. Other insect pests include the nut borers from mainly two species: macadamia nut borer *Cryptophlebia batracopha* and false codling moth *Thaumatotibia leucotreta*. Adult moths lay eggs on the macadamia nut husks and the hatched larvae bore into the fruit and feed between the green husk and the hard shell, but can potentially even penetrate the shell and damage the kernel. Damage by borer larvae

Figure 3 a) Picture of the two spotted stinkbug on a macadamia tree stem and b) evidence of monkey damage with nuts and husks scattered under the tree can as well lead to premature nut drop (Schoeman and de Villiers, 2015). Evidence of nut borer on the kernel is only seldomly observed and estimations on losses or extent of damage are not existant, as nut borer evidence is mostly removed on farm with the husk (Figure 2c) and can hence not be assessed by the processing factories. Macadamia farmers use different approaches to control insect pests on their farms. Spraying of insecticides on the basis of scouting data, once a certain threshold of pest insects per tree is reached, is the most common, while others use a so called calendar method and spray unrelated to pest numbers. Despite extensive insecticide applications with tractors and helicopters, insect damages are still very high and farmers have started to observe a certain resistance in especially stinkbugs. Possible alternative pest control, like biocontrol agents, is hence growing in popularity in the macadamia industry. Other than insect pests, the macadamia industry is also facing damages caused by mammalian pests, like antilopes such as bushbuck *Tragelaphus sylvaticus*, bush pigs *Potamochoerus larvatus* or giant rats *Cricetomys gambianus* which feed on young leaves or dropped nuts. Most common and perceived are however damages caused by the vervet monkey *Chlorocebus pygerythrus*, which is hereunder more elaborated as an ecosystem disservice.

Ecosystem services and disservices for macadamia growers

Relevant ecosystem services for the macadamia industry are mainly pollination and natural pest control. While pollination is being managed through commercial honey bee hives that get distributed across the farms, there has been little awareness of the possible service of natural pest control through bats and birds. In recent years the research focus into this ecosystem service has grown and their economic value to the agricultural sector is evident. Several studies used theoretical or model-based approaches to determine the value of bats and/or birds to different crops (e.g. Boyles et al., 2011; Cleveland et al., 2006; Federico et al., 2008; López-Hoffman et al., 2014), while others used experimental approaches (Böhm et al., 2011; Kalka et al., 2008; Karp and Daily, 2014; Maas et al., 2013; Morrison and Lindell, 2012; Williams-Guillen et al., 2008). Taylor et al. (2018) recently estimated the economic value of bat predation to agriculture to range from USD 0 to USD757/ha/yr or to 0 to 47% of the annual production value. It can hence be assumed that there is substantial financial value of bats and birds as natural pest control service providers to this fast growing macadamia industry with steadily increasing crop prices.

Anecdotal evidence furthermore identifies a variety of mammals as pests to macadamias, which can be assumed to cause ecosystem disservices. As mentioned above vervet monkeys are very common in the area and inhabit natural savannas. From these natural areas they move into macadamia orchards and feed on premature nuts off the tree, before the shell begins to harden. This relation between monkey damage and vicinity to forest edges has further been confirmed by Saj et al. (2001). Evidence of monkey damage are broken off husks scattered under affected trees (Figure 3b). A survey by the Southern African Macadamia Growers Association amongst farmers in March 2018 resulted in an estimated loss to the industry due to monkeys and baboons of an annual USD 5,251,648, based on approximately 32 000ha planted in South Africa (Southern African Macadamia Growers' Association, 2018). Preventive measures to decrease losses due to monkeys include shooting of animals by farmers, the use of fire crackers, chasing and electric fences. While some farmers are very conservation minded, others are turning to even more drastic measures like the removal of natural forests. These areas are often viewed as lost area or even cost, where they promote ecosystem disservices like crop raiding by monkeys (Tscharntke et al., 2016), which inhabit these areas. It is not unique to the macadamia industry to experience disservices and crop raiding, but this can be observed in many other crops (also see Naughton-Treves et al., 1998; Saj et al., 2001; Sigwela et al., 2017; Tweheyo et al., 2005; Weyell et al., 2015).

Scientific rationale

Ecosystem services as well as disservices are highly dependent on and change with landscape structure (Kremen, 2005; Kremen et al., 2007; Tscharntke et al., 2005). With a highly profitable industry like macadamia farming which is growing rapidly it is important to investigate economic value of these (dis-) services and discover the limitations and possibilities of them. While there have been many qualitative surveys into the damage extent by monkeys, quantitative research on disservices are still lacking (Weyell et al., 2015; Zhang et al., 2007). With macadamia prices steadily increasing, crop raiding becomes increasingly concerning and natural vegetation is being removed to restrict monkey habitat and make space for more plantings. These natural areas, however, also provide habitat for ecosystem service providers like bats and birds, and also pollinators. A study in macadamia orchards in our study area showed that honey bee activity is higher near patches of natural vegetation (Grass et al., 2018). Likewise encouraged by natural and connected vegetation are bird and bat activities (e.g. Martensen et al., 2008; Weier et al., 2018). This study therefore aimed at determining the economic impact and trade-off between ecosystem services by bats and birds and ecosystem disservices by monkeys to the macadamia industry in different orchard settings (natural and human-modified) through exclusion experiments (Chapter 2), at specifying bat diversity and activity levels at natural and human-modified orchard edges (Chapter 3) and at assessing the effects of edge habitat and farm management on arthropod abundances (Chapter 4).

Study area

Levubu is one of the oldest and most productive macadamia growing areas (Schoeman and de Villiers, 2015; DAFF, 2017; Southern African Macadamia Growers' Association, 2017a) and is situated in the northern province of South Africa, Limpopo. This subtropical area (Figure 4), with an annual average rainfall of over 900mm, is a preferred fruit growing area and main crops are, next to macadamias, also avocados *Persea americana* and bananas (Zingiberales : Musaceae) as well as several timber plantations (Taylor et al., 2017).

Figure 4 a) macadamia orchards bordering a gum (*Eucalyptus*) plantation and mountainous landscape in the background with more timber, macadamia and avocado plantings, b) a view through rows of macadamia trees.

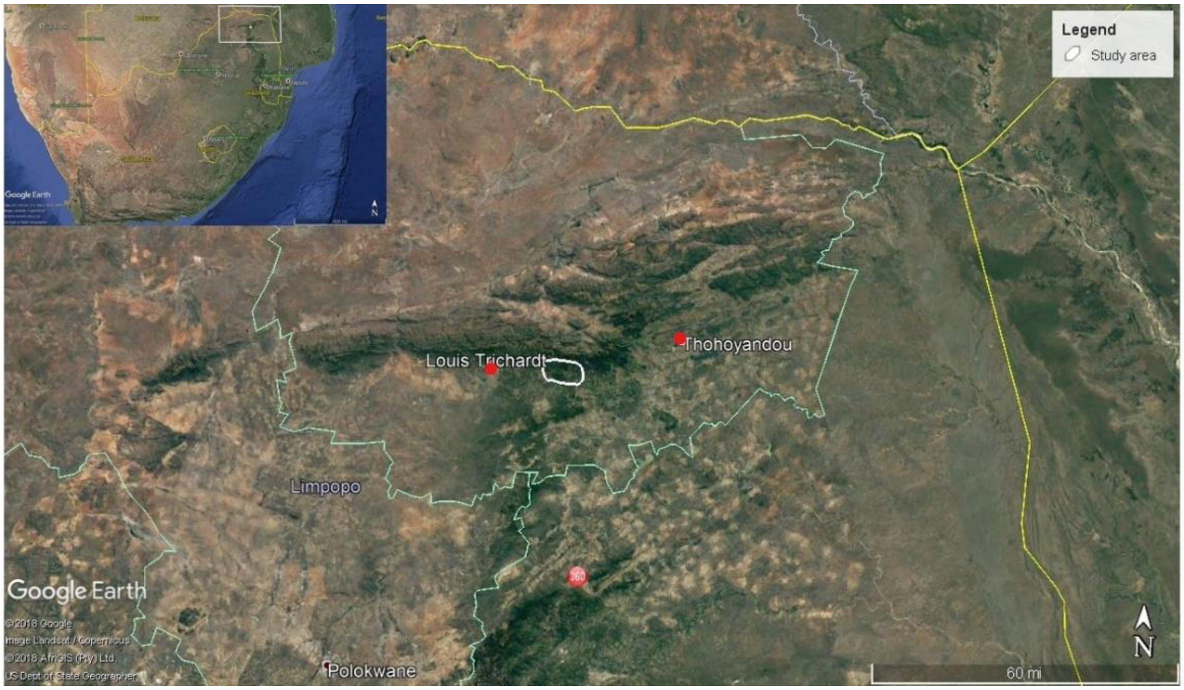

Figure 5 Map of the northern province of South Africa and the study area in the Soutpansberg encircled in white between the cities of Louis Trichardt and Thohoyandou (marked in red).

Levubu lies at the foothills of the Soutpansberg mountain range, which is proclaimed a centre of endemism and biodiversity (Mostert et al., 2008) and furthermore falls within the UNESCO Vhembe Biosphere reserve. Data collection for this study took part on several macadamia farms in the Levubu area (Figure 5) with a distance of about 11km between the two furthest sites (23° 3'33.31"S, 30° 4'32.01"E and 23° 4'48.96"S, 30°10'58.51"E).

Macadamia orchard settings

Macadamias are planted in rows with average spacing of 4m between rows and 8m between individual trees. Macadamia orchards are structured in blocks of various sizes and usually interplanted with up to three different varieties per block. The interplanting aids the fruit set due to benefits of cross pollination (Trueman and Turnbull, 1994). Areas that are not suitable for macadamia plantings due to e.g. slopes, soils or temperatures are often planted with other crops or left with natural vegetation consisting of woodlands and bushveld. These areas are classified as either Soutpansberg mountain bushveld or Tzaneen sour bushveld (Mucina and Rutherford, 2006). Our study compared two orchard edge habitats, a natural and a human-modified (Figure 6). Natural orchard edges consisted of macadamia trees bordering patches of natural vegetation, which made up 80% ±18% in a 250m half circle radius, while human-modified edges were continuous plantings of macadamias and other crops interrupted by farm roads. As mentioned previously, natural habitat is assumed to serve as source for biodiversity and with that as a source for ecosystem service providers as well as disservices. We hence looked into the difference between these orchard edges to determine whether or not the benefits or disadvantageous varied between them as described below.

Figure 6 Macadamia orchards at a) a human-modified edge and b) a natural edge.

Aims and objectives

The aim of this thesis was to gain insight into the ecosystem service provision by insectivorous bats and birds as natural pest control in macadamia orchards and to determine whether these are compromised by ecosystem disservices by crop raiding monkeys near remnants of natural vegetation. By taking a detailed look into effects of management practices on arthropod and bat abundances we aimed to gain insights into the underlying mechanisms and possible limitations of some ecosystem service provision. This data forms a first step to be able to advise farmers on optimal utilisation and improvement of beneficial services. The objectives for this study were:
Chapter 2: To determine the effect of bat and bird exclusion on macadamia nut quality and yield and calculate the economic impact of bats and birds as natural pest control to macadamia farming at natural or human-modified orchard edges, and compare these findings to the simultaneous exclusion of vervet monkeys and determine their effect on yield and income losses.

Chapter 3 aims at determining bat species richness and activities in macadamia orchards and looks into species turn-over between seasons, edge habitat and farms, to reveal potential limitations of insect pest control through bats.

Chapter 4 looks at the arthropod abundance on macadamia trees in response to insecticide treatments and landscape structure. We hypothesized that the abundance of pest insect species (Hemiptera and Lepidoptera) is greater on trees near natural vegetation, that abundance of beneficial taxa, like Hymenoptera (Linnaeus, 1758), is likewise greater in natural orchard settings and finally that abundances of all taxa are correlated with increasing time since insecticide applications.

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Chapter 2 – Ecosystem services and disservices by birds, bats and monkeys change with macadamia landscape heterogeneity

Abstract

The relative importance of ecosystem services and disservices can change with landscape structure, but the dynamics are poorly understood. We compare the impact of biological control, provided by bats and birds, with that of crop-raiding by vervet monkeys on yield in South African macadamia orchards. Insectivorous bats and birds are known to feed on major macadamia pest insect species, like the macadamia nut borer or the green vegetable bug. Vervet monkeys move into the orchards during the day to feed on premature macadamia nuts. Bats, birds and vervet monkeys benefit from patches of natural vegetation adjacent to the orchards. With exclusion experiments (four treatments: day, night, day + night, control) we quantified the relative importance of pest control and crop-raiding on yield, comparing two different orchard edge habitats, a more natural and a human-modified.

Crop-raiding occurred only close to natural vegetation and caused yield losses of about 26%. Biocontrol by bats and birds was higher near natural vegetation, but still significant in human-modified landscapes, at up to 530m distance to forest patches with yield loss protection of 60%. Effects of biocontrol by bats and birds were economically more important than the disservice of crop raiding. As both are linked to the vicinity of forest patches, the removal of natural vegetation to limit monkey abundances could also limit biocontrol service provision.

This study highlights the high economic impact of biocontrol by both bats and birds, which counterbalanced the disservice of crop raiding by monkeys, even with natural vegetation directly adjacent to orchards. Management practices to prevent crop damage, such as guarding, excluding vertebrates or destroying adjacent natural vegetation, would also limit access for bats and birds and the great economic benefits provided by their pest control. Services provided by bats and birds can be promoted by the exposure of artificial roost and nest sites, but research into species specific preferences is needed. The education of farmers is crucial, as many are unaware of the benefits from birds and bats and the fact that these benefits can outweigh the disadvantages of the monkeys' crop raiding.

Introduction

Nature provides well known ecosystem services (ES) as well as disservices (EDS). The interaction of the two is however less understood and further research into management strategies to enhance ES and to limit or even prevent EDS are necessary (Vaz et al., 2017). While affecting much more than our food production, both can have important economic impacts, especially in agriculture. Bennet et al. (2005) call for a better understanding of the relationship of different ES, not considering the potential role of EDS, while Saunders et al. (2016) recognize the interaction of both and the need for combined research. EDS in agriculture are defined as either reducing productivity or increasing production costs (Zhang et al., 2007). Primates are widely known crop-raiders and often cause EDS, as established in several qualitative surveys (Naughton-Treves et al., 1998; Saj et al., 2001; Sigwela et al., 2017; Tweheyo et al., 2005; Weyell et al., 2015), while quantitative research is scarce (Wallace and Hill, 2012; Weyell et al., 2015; Zhang et al., 2007). In Africa and Asia, where primates are believed to account for the majority of crop damages (Naughton-Treves et al., 1998), their impact can be especially high. It is believed that almost all primate species engage in crop raiding and old world monkeys (Cercopithecidae) are well known for crop raiding, due to their opportunistic foraging behavior (Lee and Priston, 2005). Damage by primates is related to vicinity to woodlands and decreases with increasing distance to forest edges (Ango et al., 2017; Lemessa et al., 2013; Saj et al., 2001; Wallace and Hill, 2012).

Insectivorous bats and birds provide important ES to agriculture (Kunz et al., 2011; Sekercioglu, 2006) and act, amongst others, as pest control agents (Boyles et al. 2011; Jones et al. 2003; Mols & Visser, 2002; Williams-Guillen et al., 2008). The economic impact of bats and birds in biological insect-pest control has been in the focus of scientific research. Based on a recent global review, estimates of the economic value of bat predation in different agro-ecosystems ranged from 0-757USD/ha/yr or 0-47% of the value of annual production (Taylor et al., 2018). These effects are mediated through trophic cascades in arthropod communities initiated by predation by both bats and birds (Maas et al., 2015a). Both ES and EDS change with landscape structure (Kremen, 2005, Kremen et al., 2007, Rusch et al., 2016; Tscharntke et al., 2005) and farmers often view remaining natural areas as lost area or even a cost, where natural habitats promote pests (Tscharntke et al., 2016). The loss of natural habitats and their fragmentation may result in the loss of service providers as well as higher crop raiding rates and there may be a trade-off between ES and EDS mediated by landscape composition.

In this study, we look into the trade-off between the ES of biological control by flying vertebrates and the EDS of crop raiding monkeys in macadamia nut orchards in South Africa. One major threat to the macadamia production in South Africa is kernel damage by pest insects (Schoeman and de Villiers, 2015). In 2017, Hemiptera caused an economic loss to the South African macadamia industry of USD 6,823,827 (Southern African Macadamia Growers' Association, 2017a). Farmers also experience high crop raiding pressure from the vervet monkey *Chlorocebus pygerythrus*, inhabiting patches of natural vegetation in and around agricultural land. A recent survey by the South African Macadamia Growers Association suggests that monkeys and baboons cause an annual loss of about USD 5,251,648 to South African growers (Southern African Macadamia Growers' Association, 2018).

We aimed to quantify not only the economic impact of insect-pest controlling services of flying vertebrates, but also the trade-off between their positive impact and the negative effects of crop-raiding vervet monkeys close to natural vegetation, by means of a three year long vertebrate exclusion experiment in two different orchard edge settings (natural and human-modified).

We hypothesized (Figure 7a) that (1) the absence of bats and birds increases insect damage to the macadamias, thereby decreasing nut quality, (2) macadamia yield decreases due to early abortion of damaged nuts where bats and birds are excluded, and, (3) the effect of bat and bird exclusion is stronger next to natural vegetation. In respect to crop raiding by monkeys we hypothesised (1) that macadamia yield increases significantly where monkeys have been excluded, but (2) that this is only true for the exclusions adjacent to natural habitats (where monkeys are present).

Materials and methods

Macadamias have been cultivated in Levubu, Limpopo, for more than 60 years. The macadamia *Macadamia integrifolia* is a tree nut native to Australia (Nagao et al., 1992). Macadamia trees are mass flowering, and flowering as well as nut developments takes place on racemes, where flowers are born in numbers of 100 to 300 along an axis (Trueman, 2013). Main insect pests are several Hemiptera species, namely the two-spotted stink bug *Bathycoelia distincta*, the green vegetable bug *Nezara viridula*, the yellow edged stink bug *Chinavia pallidoconspersa* and the coconut bug *Pseudotheraptus wayi*, as well as two Lepidopteran species, the macadamia nut borer *Cryptophlebia batracopha* and the false coddling moth *Thaumatotibia leucotreta* (Schoeman and de Villiers, 2015). Insect damage has not only the direct effect of spoiling the kernel, but also has indirect effects of promoting immature nut drop, kernel germination and fungus infestation (La Croix and Thindwa, 1986; Nagao et al., 1992; Schoeman and de Villiers, 2015).

Bats are known to be active in South African macadamia orchards and to feed on major insect pest species, like the green vegetable bug (Taylor et al., 2013a, Taylor et al., 2017). Unpublished data confirm the consumption of several more insect pests by bats (Weier et al., unpublished data), namely the macadamia nut borer, the two-spotted stink bug and the litchi moth *Cryptophlebia peltastica*. Sixty six percent of the local bat communities have been recorded inside macadamia orchards, with 14 identified species, while seasonal activity patterns of bats seem to be linked to pest insect abundance (Taylor et al., 2013b; Weier et al., 2018). Identified species were either classified as clutter-edge or open-air feeders (according to Monadjem et al., 2010), with clutter-edge feeding bat species being more restricted to landscape features with a certain degree of clutter, while open-air feeding bats fly and hunt above the vegetation. Common insectivorous birds in the study region are amongst others the Black-backed Puffback *Dryoscopus cubla*, Cape White-eye *Zosterops capensis*, Tawny-flanked Prinia *Prinia subflava*, Gorgeous Bush-shrike *Telephorus quadricolor*, Red-chested Cuckoo *Cuculus solitarius* or the Brown-hooded Kingfisher *Halcyon albiventris* (Symes et al., 2000; Symes and Perrin, 2008), which are presumably also foraging in macadamia orchards. Studies of bird species richness and activity in macadamia orchards in South Africa are lacking, but birds in Australia are known to feed on macadamia pest insect species like the green vegetable bug (Crisol-Martínez et al., 2016). In other agricultural systems, proximity to natural forests was one of the main drivers for bird diversity and predation success (Maas et al., 2015b). We can hence assume that birds play an important role for biocontrol of macadamia pests and that natural vegetation can influence its extent. Greyheaded parrots *Poicephalus fusciollis suahelicus*, which are frugivorous, have previously been observed in the study area, but do not feed on macadamia flowers or fruits or other commercially grown crops in the area (Symes and Perrin, 2003).

Lying at the foothills of the Soutpansberg mountain range, which has been declared a centre of endemism and biodiversity (Mostert et al., 2008), and part of the Vhembe Biosphere Reserve declared by UNESCO in 2011, Levubu is home to the chacma baboon *Papio ursinus*, the samango monkey *Cercopithecus albogularis* and the vervet monkey. A countrywide survey by the South African Macadamia Growers Association on problem animals showed that monkeys seem to be causing higher damages than baboons (Southern African Macadamia Growers' Association, 2018). Communications with farmers confirm this result and identified vervet monkeys as the most problematic animal to macadamia growers. In this study we therefore focus on the effect of monkeys as crop raiders, particularly vervet monkeys, as samango monkeys are rare and at this stage not considered a pest according to anecdotal evidence.

Baboons are only encountered on farms on the mountain and were absent from our study sites. Vervet monkeys are reported a crop pest in almost their entire range (Healy and Nijman, 2014). They are widely distributed throughout Africa and can be found in a variety of habitats (Estes and Otte, 2012; Skinner and Chimimba, 2005). Due to its relatively small size they are, however, dependent on trees and although they do come to the ground, they remain around forest edges for safety (Estes and Otte, 2012; Skinner and Chimimba, 2005). The vervet is diurnal and usually occurs in troop sizes of about 25 individuals and is mostly vegetarian (Estes and Otte, 2012; Skinner and Chimimba, 2005).

Study area, study organisms and the agro-ecosystem

The experiments were conducted on six commercial macadamia farms (see Appendix S1 for selection criteria). Macadamia orchards are planted alley like in rows, with typical spacing of 8m

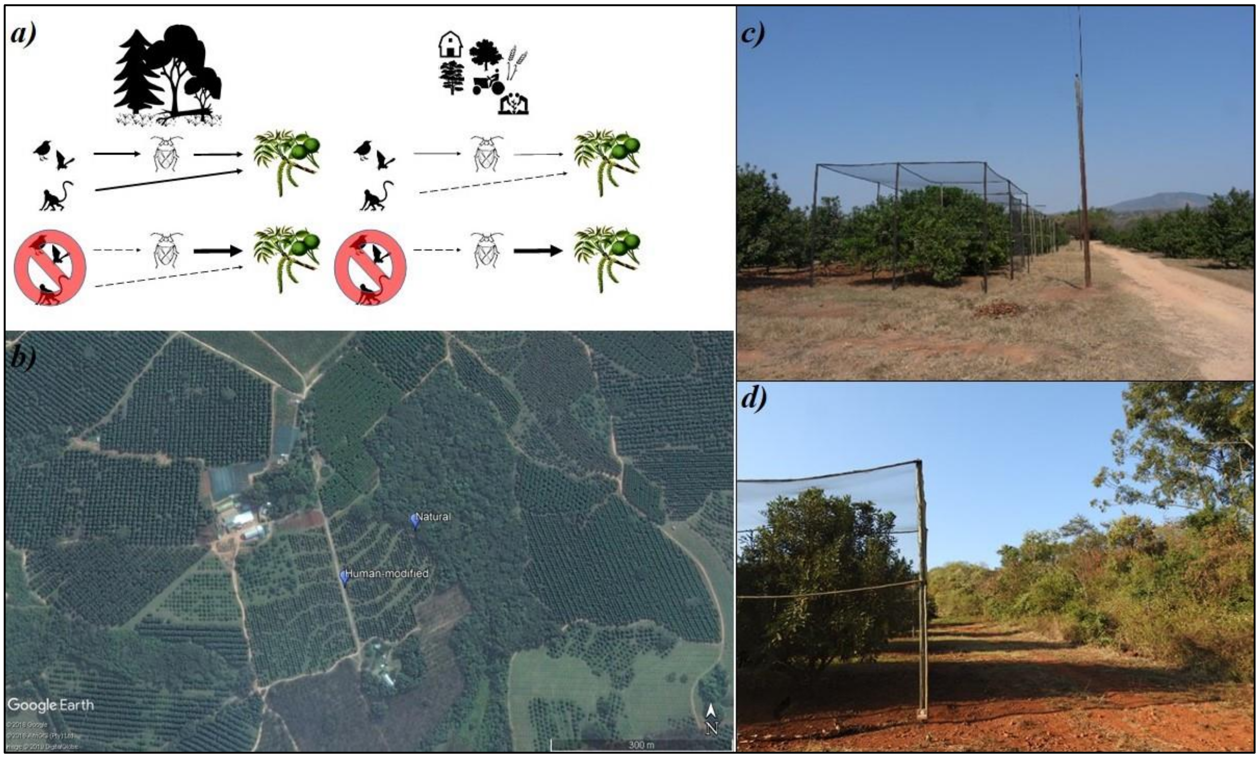

Figure 7 a) Graphical presentation of the main hypotheses expected from the exclusions of birds, bats and monkeys from natural versus human-modified landscapes. Solid arrows represent negative effects, thicker arrows indicate stronger effects, while dashed arrows reduced effects caused by the experiments; b) one of the experimental farm with natural and human-modified farm edges; c) Photo showing the four treatment cages at the human-modified edge; d) Treatment cages at a natural orchard edge.

between individual trees and 4m between rows. We compared natural to human-modified orchard edge habitats within each farm. Human-modified edge habitats included continuous crops of macadamias or other orchards (e.g. avocado Persea and pecan Carya), some disrupted by roads. Natural edges consisted of macadamia trees bordering patches of natural vegetation, which are dense corridors of natural bush, between 98m and 205m broad and up to 20 ha in extent. The dominant vegetation type at the natural edge habitat comprised 80% (SD: ± 18%) natural bushveld in a 250m half circle radius, while at the human-modified edge natural vegetation comprised only 27% ± 19% or less of the surrounding habitat (Grass et al., 2018). These natural areas still harbour wildlife, including several small antelopes, bushpigs *Potamochoerus larvatus* and vervet monkeys. As monkeys are very vigilant, they stay in the first few rows of the orchard, not moving far away from their natural refuge. Previous studies show that crop raiding of vervets is limited to forest edges with no records at or beyond 200m forest distance (Saj et al., 2001) or average maximum distances of 15m with a range of 3-90m (Wallace and Hill, 2012). Human-modified edges were located at distances between 156 and 527m away from natural vegetation and were therefore never visited by monkeys and no evidence of monkey damages were ever observed here.

Experimental set-up

The experimental exclusion took place over three consecutive growing seasons, from September 2015 until May 2018. A total number of 48 cages were constructed, each enclosing two macadamia trees with nylon mesh net that would allow arthropods to access the trees but excluded flying vertebrates, monkeys and large herbivores (Appendix A1). We applied four treatments. The “Full” exclosure was closed at all times, thereby preventing all bats, birds and monkeys from feeding on the trees. The “Day” and “Night” exclosures were only closed either during the day or night excluding either diurnal birds and monkeys or bats and nocturnal birds (namely nightjars, Caprimulgidae, or small owls, Strigidae and Tytonidae) respectively. Additionally, “Control” cages were open at all times, consisting of a frame without nets. On each farm a set of four exclosures (Full, Day, Night, Open Control) was put up at a human-modified orchard edge and one at an orchard edge bordering natural habitat (Figure 7b, c and d). The design resulted in 12 sets of four treatment exclosures, hence 48 cages excluding a total of 96 macadamia trees. In the third year of this study, however, the sets were reduced to only full and control treatments, resulting in a reduced number of treatment cages of 20 over five farms in the final year (Appendix A1).

Yield

Macadamia nuts drop continuously over several months once matured and are then harvested off the ground (Nagao et al., 1992). To isolate the effect of vervet monkeys, which feed on immature nuts off the tree, from that of other animals, which feed on fallen nuts, we applied an indirect yield measure by counting and monitoring nut sets on the trees. In the season of 2016/17 we marked 50 racemes on each tree early in the season, counted all nuts per raceme and monitored the number per racemes until the nuts had completely matured. This resulted in a final nuts/50 raceme count prior to harvest. Nut set (final number of nuts) was analysed using generalized linear mixed models (GLMM, binomial error structure and logit link function), with treatment and edge habitat as fixed factor and farm as random factor, analysing the proportion of mature nuts of the initial nut set. In case of significant interaction, each edge habitat was then analysed separately to allow for multiple comparisons of means by treatment using Tukey contrasts. The final nut set was extrapolated to a yield in kg per hectare (Appendix A3).

Nut quality

All macadamia nuts were collected from within each experimental cage over the three consecutive seasons (2016–2018). As they drop continuously over several months (February till April), sites were visited weekly until no nuts were left on the tree. Samples of about 1,5kg were taken per experimental cage, cracked and the kernel checked for any quality defects. Total sample weight as well as shell and kernel weight were recorded. Total kernel weight was divided into sound (not damaged) and unsound (defected) kernel. The quality (mass unsound kernel within total sample mass) data were analysed using generalized linear mixed modelling (GLMM, binomial error structure and logit link function) with treatment and edge habitat as fixed factors and farm as random factor. Each edge habitat was again analysed separately to allow for multiple comparisons of means by treatment using Tukey contrasts. Quality refers to “Unsound kernel” or “Unsound kernel recovery”, a common measure of quality in the macadamia industry (Schoeman and de Villiers, 2015), which is the percentage of unsound kernel mass in the total in-shell sample weight.

All statistical analyses were performed in R (v. 3.5, R Foundation for Statistical Computing, Vienna, Austria) using packages ‘lme4’ version 1.1-14 (Bates et al., 2015) and ‘multcomp’ version 1.4-7 (Hothorn et al., 2008).

Economic impact

Income per hectare was calculated by using the mean yield and percentage unsound kernel per edge and treatment combination. Quality determined the price per kg, which was then multiplied by the yield per hectare (Appendix A4 – Income calculation).

Results

Since monkeys were absent from the human-modified edges, observed treatment effects were solely due to the exclusion of bats and birds, while effects at the natural edge included the impacts of crop raids by monkeys. Monkeys furthermore only affected the yield, but not the quality of nuts.

Table 1 Summary of results obtained from each edge and treatment combination, with mean nut set ±SE, estimated yield (as a function of mean nut set), mean % unsound kernel (UKR) ±SE and income/ha/yr (as a function of both mean yield and mean UKR).

Edge	**Treatment**	**Nut set (total/50 racemes)**	**Yield (kg/ha)**	**UKR**	**Income (USD/ha)**
Human-modified	Full	43.93 ± 5.86	862.76	7.69% ± 1.01	3065.45
	Night	77.88 ± 7.78	1529.52	7.17% ± 1.24	5587.45
	Day	59.26 ± 7.3	1163.83	7.83% ± 1.2	4078.78
	Control	107.06 ± 15.09	2102.60	6.13% ± 0.64	8035.15
Natural	Full	35.27 ± 8.81	1303.97	8.95% ± 2.42	4453.57
	Night	6.67 ± 3.16	246.60	6.31% ± 0.9	959.46
	Day	62.94 ± 10.95	2326.96	6.97% ± 1.1	8620.51
	Control	46.33 ± 8.24	1712.87	4.44% ± 0.59	7140.05

Yield

Final nut set was lower at the natural edge than the human-modified edge ($p<0.001$) and significantly ($p \leq 0.001$) influenced by the interaction of treatment and edge type (Table A1). Yield was 19% lower in the natural control than in the human-modified control (based on values in Table 1). In the human-modified edge setting, all treatments resulted in a significantly lower ($p \leq 0.001$) nut set relative to the control (Table 2 and Figure 8), with the full exclosure, where bats and birds were both excluded, resulting in the lowest nut set, followed by Day and then Night. The exclusion of both bats and birds resulted in a 60% decrease in yield compared to the control.

In the natural edge setting, where monkeys were present, the full exclosure did not significantly differ (p=0.87) from the control (Table 2 and Figure 8). In the day treatment on the other hand, we did observe a yield increase and nut set was significantly higher (p<0.001) than in the control (Table 2 and Figure 8) and yield increased by 26%. The night exclosure, where only nocturnal vertebrates were excluded, showed a significantly lower (p<0.001) nut set relative to the control (Table 2 and Figure 8).

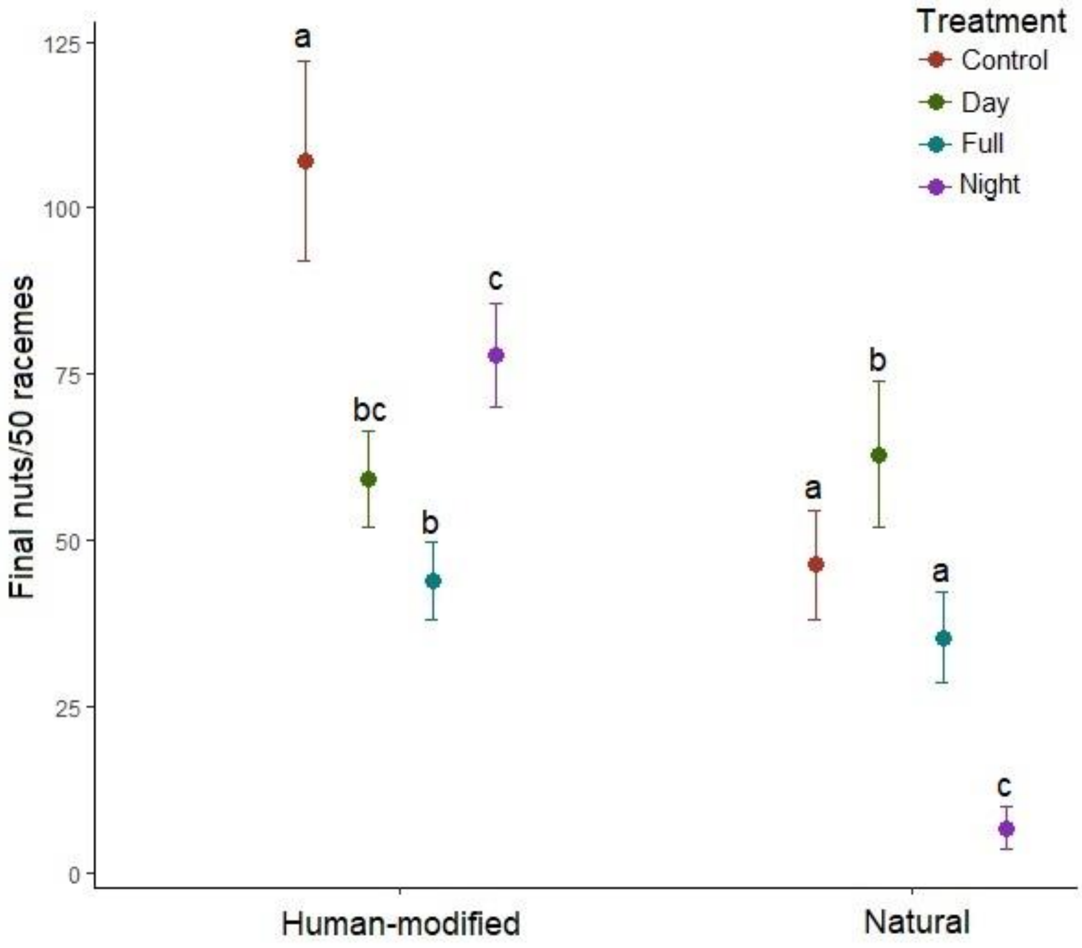

Figure 8 Mean final nut set ±SE per 50 racemes for each edge setting and treatment.

Nut quality

Quality of nuts was generally better at the natural edge, compared to the human-modified (p<0.001), with 4.44% unsound kernel compared to 6.13% in the two controls (Table 1 and Table A1; Figure 9). At both edges all exclusions resulted in significant increases in unsound kernel (p<0.001; Table 1 and Table 2). At the natural edge the combined effect of the full exclusion resulted in the lowest quality (highest percent of unsound kernel), followed by the day and then night treatment (Table A1; Figure 9). Treatment effects were stronger in the natural edge setting with higher differences in defect kernel between treatments.

Table 2 Tukey post hoc test results of nut set and quality effects separately for edge type

Edge	Treatment	Estimate	Std. Error	z-value	p-value
Nut set: *Fit: glmer(formula = cbind(Final.nuts, (Initial.nuts - Final.nuts)) ~ Treatment + (1 | Farm), family = "binomial")*					
Human-modified	Day – Control	-0.71	0.05	-13.78	<0.001
	Full – Control	-0.83	0.06	-14.34	<0.001
	Night – Control	-0.66	0.05	-13.49	<0.001
	Full – Day	-0.12	0.06	-1.97	0.198
	Night – Day	0.05	0.05	1.03	0.729
	Night – Full	0.17	0.06	2.98	0.015
Natural	Day – Control	0.52	0.06	8.76	<1e-05
	Full – Control	0.05	0.07	0.75	0.87
	Night – Control	-0.75	0.15	-5.07	<1e-05
	Full – Day	-0.46	0.07	-6.98	<1e-05
	Night – Day	-1.27	0.15	-8.75	<1e-05
	Night – Full	-0.80	0.15	-5.36	<1e-05
Nut quality: *Fit: glmer(formula = cbind (Unsound,(Total – Unsound)) ~ Treatment + (1 | Farm), family = "binomial")*					
Human-modified	Day – Control	0.25	0.04	7.14	<0.001
	Full – Control	0.201	0.03	6.48	<0.001
	Night – Control	0.14	0.04	3.78	<0.001
	Full – Day	-0.04	0.03	-1.12	0.68
	Night – Day	-0.12	0.04	-3.22	0.007
	Night – Full	-0.08	0.03	-2.31	0.09
Natural	Day – Control	0.49	0.04	11.46	<0.001
	Full – Control	0.72	0.04	18.14	<0.001
	Night – Control	0.32	0.05	6.60	<0.001
	Full – Day	0.23	0.04	6.01	<0.001
	Night – Day	-0.17	0.05	-3.69	0.001
	Night – Full	-0.40	0.04	-9.13	<0.001

At the human-modified edge the day exclosure resulted in the lowest quality, followed by Full and Night, while there was no significant difference between Full and Day (p=0.68) or Full and Night (p=0.09), but the night treatment resulted in significantly lower quality than the day treatment (p=0.001).

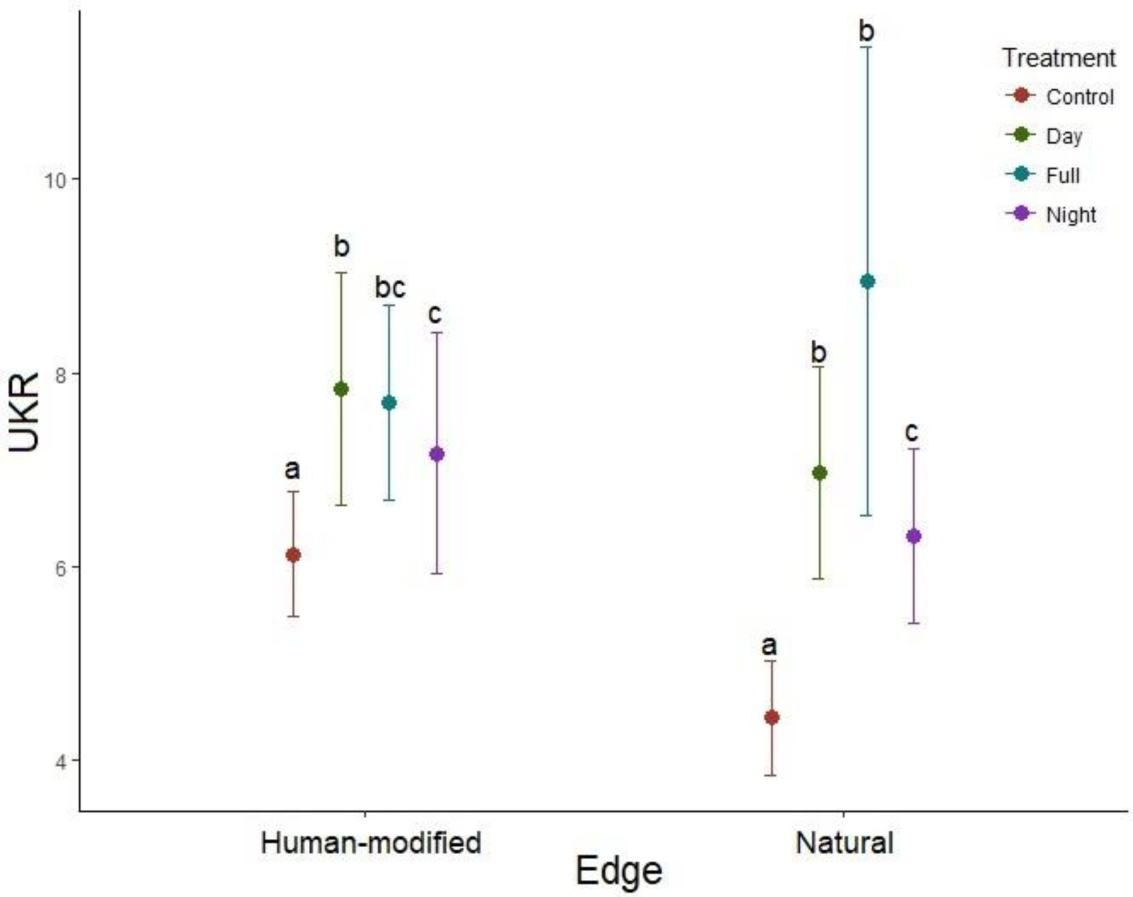

Figure 9 Proportion unsound kernel (%) per treatment amongst the total in-shell sample ±SE for the human-modified and natural edge.

Economic impact

All income values are expressed as kg/ha/year (Table 1) and combine both yield and quality effects (Figure 10). Income impacts generally followed the observed differences in yield. In the human-modified edge setting the exclusion of both bats and birds resulted in an income loss of USD 4969.70/ha and reduced income losses for the exclusion of either diurnal birds (USD 3956.37/ha) or bats and nocturnal birds (USD 2447.71/ha). At the natural edge the full exclosure resulted in an income loss of USD 2686.48/ha. Whereas the yield differences between full and control were not significant, a negative trend could still be observed where all vertebrates were excluded. The day exclosure resulted in an income gain of USD 1480.46/ha.

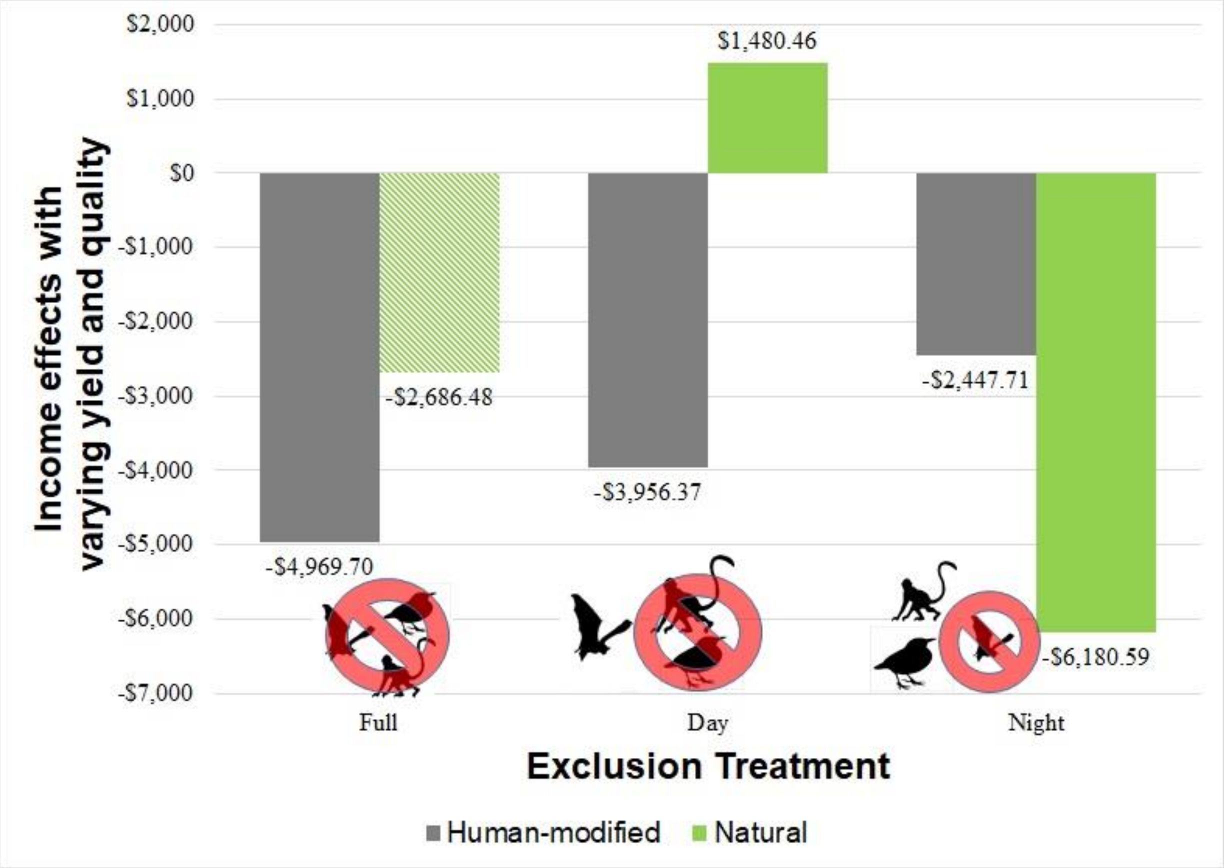

Figure 10 Income effects (losses and gains) resulting from varying average yield and quality over treatment and edge type, respective to each control. Solid fill for significant yield and quality difference to control and pattern fill for the full treatment in natural landscape, due to insignificant nut set effects.

Discussion

In our study the profits of biocontrol by bats and birds at natural orchard edges exceeded the losses from crop raiding monkeys. The exclusion of bats and birds lead to a decrease in yield as well as quality for both edge habitats, while the exclusion of monkeys only resulted in yield gains close to natural vegetation. In the human-modified setting the exclusion of bats and birds resulted in yield drops of 60% or losses of about USD 5000/ha. The exclusion of monkeys in natural settings on the other hand led to an increased yield of 26% and income of about USD 1500/ha.

Nut quality values were generally realistic and comparable to the average of 4.5% defect kernel for 2017 in the study area, as given by the local processing facility (Green Farms Nut Company, personal communication, September 04, 2018). The exclusion of bats and birds resulted in all treatments and at both edges in reduced quality as expected, while the exclusion of diurnal birds (day treatment) had a larger impact than the exclusion of nocturnal birds and bats (night treatment). We found lower proportions of unsound kernel (-1.79%) for natural orchard edges compared to the human-modified one, which generally confirmed our expectation of stronger biological control by bats and birds near natural vegetation. The importance of these landscape features and connectivity within an agricultural landscape for bats has been highlighted in previous studies (Frey-Ehrenbold et al., 2013; Kelly et al., 2016; Weier et al., 2018; Wordley et al., 2017).

Yield effects at the human-modified edge followed a clear pattern and match our predictions that yield would decrease significantly where bats and/or birds were excluded. The combined exclusion of bats and birds, however, resulted in the largest effect and a yield drop of about 1240kg/ha (60%) compared to the control. The day exlcosure had again a larger effect than the night exclosure, which indicates a potentially larger role of diurnal birds in biocontrol for macadamias.

At the natural edge effects by monkeys greatly changed the pattern of yield differences. Pest control services by bats and birds seem to exceed crop raiding effects by monkeys and the exclusion of both, although not significant, still resulted in yield decreases, due to lacking biocontrol. The exclusion of monkeys in the day exclosure resulted in yield increases of 614kg/ha (26%). Although partially weakened by the simultaneous exclusion of diurnal birds, this effect is far less than the great impact bats and birds had at human-modified edges.

Our observations are in line with other studies (Naughton-Treves et al., 1998; Saj et al., 2001; Tweheyo et al., 2005) which showed that crop raiding by monkeys is limited to the vicinity of forest edges. This was also true in macadamia orchards as no positive yield effects could be observed in any exclusion experiments at the human-modified edge. Vervet monkeys and other primate species are, however, not only considered a pest to macadamias but also to many other crops in Africa (Ango et al., 2017; Mc Guinness and Taylor, 2014; Wallace and Hill, 2012). While the extent of damages caused by monkeys might differ in other crops, our results give a general indication on the possible threat by monkeys and the simultaneous compensation by beneficial insect pest control, both stemming from natural areas.

Since yield had a stronger impact on income calculations than had quality, profit differences roughly follow the pattern we observed in yield. Income is generally lower at natural edges compared to human-modified, due to extreme yield drops caused by monkeys. Prevented biological control of bats and birds combined (full exclosure) resulted in an income loss of about USD 5000/ha at the human-modified setting, whereas prevented monkey damage at the natural edge amounts to an estimated USD 1500/ha income gain. The exclusion of vertebrates near natural vegetation can hence enhance yield, but the loss of an ES like biological control would have a higher economic impact, assuming these natural arease serve as a source for biodiversity and ES. An avoided cost model estimates the value of bats in the South African macadamia industry to be up to USD 139/ha (Taylor et al. 2018). This is considerably lower than our estimations, even when just considering the effects of the night exclosure at human-modified edges of USD 2448/ha. This can be explained by the fact that our study includes effects of all pest insect species, while the model by Taylor et al. (2018) only considers one pest species. The model by Taylor et al. (2018) does furthermore not consider the effect of nocturnal birds or distinguished between quality and yield effects. This highlights the importance of experimental research as guideline and confirmation of theoretical models.

Our study assessed a trade-off relationship between specific ES and EDS of two independent functional groups. While previous work (Saunders and Luck, 2016; Saunders et al., 2016) already shows that ES can vary over season and with functional group and that ES can be compromised by EDS, we highlighted the contrasting impact of unrelated taxonomic groups, birds, bats and monkeys. Where farmers are encouraged to support ES, there is potential for disadvantages through EDS. The extent to which ES exceeded EDS in this scenario gives an indication that this will not compromise conservation efforts. It should therefore be the aim of future research to consider the interactions of ES and EDS of all participating functional groups as a whole (e.g. other mammals and herbivores, rodents, pollinators), to be able to assess the real value of biodiversity to agricultural systems.

While we observed high biocontrol services, which seemed linked to natural orchard edges, crop-raiding damages can be much more visible and more perceived by affected farmers, causing many farmers to view natural areas as loss or cost (Tscharntke et al., 2016). Studies looking into possible mitigation strategies are therefore highly advised, to avoid negative associations with natural areas.

One suggested mitigation strategy is the establishment of buffer zones between natural areas and palatable crops to prevent crop raiding (Naughton-Treves et al., 1998; Saj et al., 2001). By doing so, one potentially compromises the beneficial ecosystem services going out from natural habitats and in this case the highly profitable service of biological control by bats and birds. Other ES, like pollination, could also be enhanced by natural vegetation and be compromised by its removal or isolation. Primate proof fences are another alternative, which simultaneously exclude other herbivores and pest species. These are, however, associated with high costs and thereby only available to some commercial, large-scale farmers. Guarding of crops is a very popular mitigation strategy (Ango et al., 2017; Warren et al., 2007), which can, similar to the exposure of scare crows, also affect birds and their willingness to feed in the orchards. Education and the information of landowners about nature's valuable benefits, which can be more plentiful than its costs, can therefore be an important tool in protecting biodiversity in agricultural lands. To further promote bird and bat populations and thereby potentially increase the value of biological control, artificial nesting and roosting sites can be provided, as successfully done for great tits in apple orchards (Mols and Visser, 2002). This can be more cost efficient than pesticide treatments in keeping pest species under a certain threshold (Puig-Montserrat et al., 2015). Research towards species richness in agricultural areas and species specific preferences in artificial roosts is needed to be able to provide appropriate designs.

Conclusions

Our study showed the great impact of bats and birds as biocontrol agents in agricultural systems, which can be compromised, but not exceeded, by monkeys when bordering natural vegetation. While ecosystem disservices by monkeys are limited to only the close proximity of natural vegetation, ecosystem services by bats and birds still have substantial economic impacts at human-modified edges and outweighed negative impacts by monkeys. Remaining patches of natural vegetation, harbouring both ES and EDS, can therefore still be viewed as highly beneficial to agriculture. Since crop-raiding effects are more visible, it is still of high importance to research effective monkey mitigation strategies that can then be made available to farmers. Our findings are applicable to many agricultural systems, where monkey and primate species are considered a pest. Areas like the tropics and subtropical regions, where primate species are distributed are also areas with high general, but also bird and bat species richness and diversity. We can therefore assume similar counterbalancing effects between biological control and crop damages by monkeys, to what we have observed in macadamia orchards.

It is important to make growers aware of threats as well as economic benefits natural areas pose for them. By protecting surrounding natural bush and erecting low budget artificial roost and nest sites, these farmers can play an important role in species conservation, as it is a serious and affordable alternative to significantly increase your profits as a farmer.

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Chapter 3 – Bat species diversity in South African macadamia orchards is driven by seasonality more than by spatial variation

Abstract

Habitat fragmentation and habitat loss are two of the major threats to global bat populations with the agricultural sector causing much of this fragmentation. Bats, however, serve as natural pest control agents to agriculture and their economic value has repeatedly been proven. By consuming large amounts of pest insect species, bats improve crop yield and quality and can potentially decrease the need for insecticides. It is therefore of great importance, especially in a time when organic products are gaining popularity with consumers, to conserve and enhance bat populations in agricultural ecosystems. We conducted an acoustic monitoring survey over two growing seasons in South African macadamia orchards, comparing human-modified with natural orchard edge habitats and high with low insect pest seasons. We determined species richness of bats through additive partitioning of diversity and incicence based rarefaction and studied activity patterns of the two major feeding guilds, clutter-edge and open-air feeders. Observed alpha richness of 12.03 species made up about 60% of total bat species richness (γ) of 20.33. Our results show that there is higher turnover of species between seasons (22.6%) than there is between orchard edges (6.5%), while turn-over between farms accounts for 11.7%. Total bat activity as well as activity per feeding guild decreases in the low pest season, suggesting the need for alternative feeding grounds away from macadamia orchards when pest insect species inside the orchard are less abundant. We conclude that ecosystem services provided by bats depend on agricultural landscape management, as the spatial connection of agroecosystems with natural habitat is needed to ensure year-round foraging opportunities to maintain a diverse bat community.

Introduction

It is widely known that bats provide a number of important ecosystem services and their role especially in natural pest control has recently been the focus of a number of scientific publications (Boyles et al., 2011; Ghanem and Voigt, 2012; Karp and Daily, 2014; Kunz et al., 2011; López-Hoffman et al., 2014; Maas et al., 2016). Bats cannot only potentially reduce health risks by controlling for example mosquito numbers and limiting the distribution of diseases like malaria (Ghanem and Voigt, 2012), but can also have enormous economic effects through controlling pest insects in agriculture (Russo et al., 2018). Although bats can also pose risks and transmit disease (e.g. Schneeberger and Voigt, 2015), their beneficial economic value has been repeatedly proven through model based as well as experimental approaches and according to a recent literature review, their value ranges from USD 0-757/ha/yr or up to 47% of the annual production value (Taylor et al., 2018). Insectivorous bats can therefore be an important tool to enhance food security and they are gaining more importance in a society that is increasingly focusing on healthy and organic food. Bats are, however, under threat and populations are globally declining due to habitat loss and fragmentation, bush meat or most recently wind turbines and the North American White-nose syndrome (Arnett et al., 2016; Frick et al., 2016; Jones et al., 2003; Mickleburgh et al., 2002). Agricultural intensification is another cause for bat population declines and bats seem to prefer less intensive or even organic agricultural systems with remnants of natural habitat (Kelly et al., 2016; Park, 2015; Wickramasinghe et al., 2003; Wordley et al., 2017). The recently detected decline in arthropods, which is also being ascribed to agricultural intensification (Losey and Vaughan, 2006; Potts et al., 2010; Sánchez-Bayo and Wyckhuys, 2019; Stein et al., 2018; Vanbergen and the Insect Pollinators Initiative, 2013), can furthermore have cascading effects on insectivorous species, like many bat species (Hallman et al., 2017; Lister and Garcia, 2018).

Utilising bats and increasing their service of natural pest control to agriculture could be one way of conserving bat populations. Pest control services of predatory arthropods were found to be lower in simplified agricultural landscapes (Rusch et al., 2016). This could also be true for insect predation by bats, as they are known to be sensitive to habitat fragmentation (Frey-Ehrenbold et al., 2013; Starik, 2016). Natural vegetation serves not only as roost site provision for bats but also for orientation and bats are often found to use natural corridors and forest edges as flight paths (Downs and Racey, 2006; Verboom and Huitema, 1997). Especially in monocultural landscapes this could limit their dispersion range and potential pest control service to agriculture. In a study in northern Europe, woodlands and alleys of trees have resulted in highest bat activity in agricultural landscapes (Kalda et al., 2015). It is hence of great importance to fully understand bat communities and their activity patterns in agricultural systems and possible limiting or enhancing factors. This information can be used to make agricultural landscapes more attractive to bats and increase their activity and pest control services, which in turn may lead to a reduced need for chemical insecticides (Federico et al., 2008). Ecosystem services by bats are believed to be of higher impact in developing countries as the amount of remaining natural habitats and overall biodiversity is higher (Boyles et al., 2013; Maas et al., 2013). The need for alternative (natural) pest control is also potentially higher in countries where financial and mechanical limitations do not allow for extensive chemical treatments.

South Africa is currently one of the largest macadamia *Macadamia integrifolia* growers worldwide with an annual production of about 38 000 tons in 2016 (Southern African Macadamia Growers' Association, 2017a), and with continuously increasing macadamia prices, the industry is growing rapidly. Pest pressure on macadamias by mainly stinkbugs (Hemiptera: Heteroptera) and nut borers (Lepidoptera: Tortricidae) is particularly high (DAFF, 2017; La Croix and Thindwa, 1986; Nagao et al., 1992; Schoeman and de Villiers, 2015) and is believed to cause damage of over USD 6.5 million annually (Southern African Macadamia Growers' Association, 2017b) through kernel damage. One of the major pests, the green vegetable stinkbug *Nezara viridula,* has been found to form part of local bat species' diets (Taylor et al., 2017). In another study Taylor et al. (2013a) found 66% of local bat species to be active in macadamia orchards. Weier et al. (2018) was the first to study habitat preferences of bats in macadamia orchards over the whole annual cycle and suggests that bat activity is positively linked to natural vegetation as well as stink bug pest occurrences. In an experimental exclusion study the value of bats to the South African macadamia industry through natural pest control of stinkbugs and thereby improved nut quality was estimated to be at least USD 278.60/ha/yr (Linden et al., 2019). The effect of pest control was higher near natural vegetation compared to inside the orchards.

Our study focuses on the effect of semi-natural habitat on diversity partitioning, community composition and activity patterns of bats in commercial macadamia plantations in Levubu, South Africa throughout the year. With passive acoustic monitoring we sampled the bat community and activity in macadamia orchards over two growing seasons. We furthermore compared echolocation data from sites with natural edge habitat and sites with human-modified orchard edges. We hypothesized that 1) bat species diversity and activity are higher near natural areas compared to human-modified orchard edges, 2) the impact of natural vegetation differs between bat species and feeding guilds and 3) bat diversity and activity would be highest in months where insect pest pressure peaks.

Materials and Methods

Study area

The study took place in macadamia orchards in Levubu, one of South Africa's largest and oldest macadamia growing areas. Levubu is situated in northern South Africa on the southern slopes of the Soutpansberg mountain range.

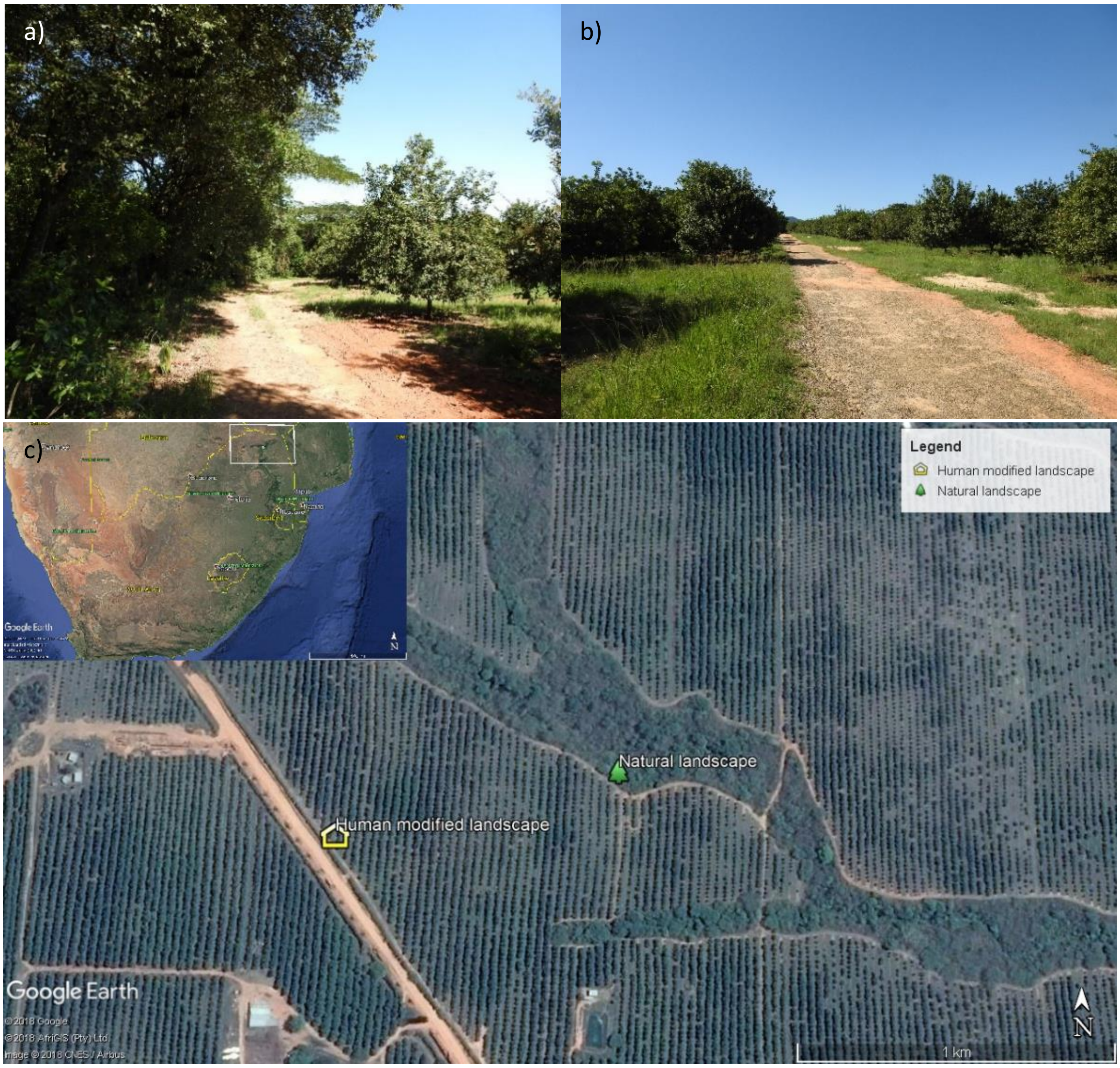

Figure 11 Study area, showing a) a natural orchard edge with macadamia orchards bordering natural vegetation, b) a human-modified orchard edge with continuous macadamia plantings and c) map showing an example of both natural and human-modified setting within one farm

Due to its subtropical climate and high annual precipitation (average of over 900mm) this area is very productive and other major crops planted here are banana (Zingiberales: Musaceae), avocado (*Persea*), timber (*Eucalyptus*) and to a lesser extent mango (*Mangifera*), pecan (*Carya*), Lychee (*Litchi*) or maize (*Zea*). We selected six farms in the Levubu area similar in abiotic conditions mostly growing macadamia nut trees. The farms were situated between the towns of Thohoyandou (22°59'03.7 S, 30°27'12.8 E) and Louis Trichardt (23°03'03.6 S, 29°55'12.7 E).

Each farm had remnants of natural vegetation bordering their macadamia orchards. We selected two sites on each farm with the same macadamia varieties and similarly aged trees, one bordering stretches of natural vegetation and one with continuous crops (human-modified edge). Sites with natural edge habitat (

Figure *11*a) consisted of macadamia orchards next to patches of natural woodlands of up to 20ha in size and about 100 – 200m deep. All but one of these patches were connected to further patches of natural vegetation. Human-modified sites (

Figure *11*b) consisted of orchards surrounded by more macadamia plantings in some cases crossed by farm roads and situated at a distance of 160 and 530m to the next natural vegetation patch (

Figure *11*c).

Data collection

We used passive acoustic recording to assess bat activity on six different macadamia farms in a paired design over two seasons. Simultaneously we surveyed a natural as well as a human-modified landscape setting per farm, resulting in 12 sites. With six stationary bat detectors (Song Meter BAT2+) from Wildlife Acoustics we recorded from sunset to sunrise for 12 hours over two consecutive nights every month. We sampled monthly in the first season (September 2015 until August 2016) and in the second season only every three months starting with August 2016 until the end of the season in March 2017. Each site was sampled in 14 months over two nights, adding up to a total 336 nights. Due to technical faults and uncomplete samples the sample size was reduced to 265 nights. Microphones were erected on 4m high flagpoles facing downwards at an angle of approximately 45°. The six bat detectors were moved randomly between sites. Recording only took place on dry nights due to logisitical restraints.

Data analysis

All calls were identified manually to species level using AnalookW version 0.3.7.23 (www.titley-scientific.com) after being converted to zero-crossing (ZC) files with Kaleidoscope version 1.1.15 (www.wildlifeacoustics.com). Frequencies (minimum, maximum, characteristic and frequency of the knee), duration and slope of each call sequence were used to assign recordings to a certain species according to reference libraries of Southern Africa (Monadjem et al., 2010; Monadjem et al., 2017; Taylor et al., 2013b). Recordings that could not be assigned to a species with confidence were labelled “Unknown” and excluded from further analysis.

Identified bat calls were then converted into Miller’s activity index (Miller, 2001), accounting for species specific activity patterns and counting the number of active minutes per species rather than the number of bat passes. Each bat species was furthermore assigned to a foraging guild (Appendix A5: Table A5) as being either “Clutter-dependent”, “Clutter-edge feeder” or “Open-air feeding” (Monadjem et al., 2010). For each night the edge type, moon phase, average temperature and date were recorded. The months of recording were then divided into high (December until and including May) and low (June until and including November) season. Macadamia fruit development takes place during the high season and with that increases pest insect pressure (De Vielliers and Joubert, 2003). The high season furthermore coincides with the rainy season in the study area.

Generalized linear mixed models were used to assess differences in activity patterns per night, using the sum of active minutes. Due to overdispersion of the count data we used the “lmer” function with a log transformation. The global model included edge type, season, feeding guild, moon phase and temperature as explaining variables with year, month and farm as random factors. The “dredge” function from the “MuMIn” package v. 1.40.0 (Barton, 2017) was used for the final model selection based on Alkaike’s Information Criterion, resulting in a final model with edge, season and feeding guild (Table 3). All analysis was done using R v. 3.5 and packages “lme4” version 1.1-14 (Bates et al., 2015), “multcomp” version 1.4-7 (Hothorn et al., 2008).

We used an incidence-based measure to calculate species richness and diversities per season and landscape setting, as this approach is appropriate for repeated sampling techniques (Hsieh et al., 2016). The incidence-based approach is based on presence-absence data per species for each site, while the abundance-based approach is calculated using levels of activity per species at each site. Number of presences per species across all sample sessions for each site were used to calculate Hill numbers of species richness and diversity based on an incidence-based rarefaction approach using the iNext function (Chao et al., 2014; Hsieh et al., 2016) in R v. 3.5 (R Foundation for Statistical Computing, Vienna, Austria) using packages “iNext” v. 2.0.17 and “ggplot2” v. 2.2.1 (Wickham, 2009). This outcome produces Hill numbers or effective numbers of species, which are diversity estimates in respect to the sample coverage, namely Species richness (q=0), the exponential of Shannon’s entropy index (q=1) and the inverse of Simpson’s concentration index for q=2 (Chao et al., 2014).

Additionally we used additive diversity partitioning using the “vegan” package v. 2.5-3 (Oksanen et al., 2018) following methods of Crist et al. (2010) to assess turnover of species and compare average alpha richness of samples to the gamma richness of the entire dataset. Additive diversity partitioning accounts for the possibility of random placement of individuals at hierarchical higher levels (Christ et al., 2010). Through a randomization function, which randomly places individuals of different species in samples and then pooling these samples according to the hierarchical structure, diversities are partitioned and result in a gamma diversity comprised of one α- and several β-diversities, divided in each level. We nested the data set in a hierarchical order with Season within Edge (natural or human-modified) and Farm and in highest order, resulting in

$\gamma_{obs} = \alpha + \beta_{Season} + \beta_{Edge} + \beta_{Farm}$.

Results

The passive monitoring and conversion to Miller’s activity index resulted in 43,394 active minutes over 265 nights of which 450 were labeled “Unknown” (1%). These unknown calls mostly belonged to some of the identified species, but calls were either unclear or too overlapping with other species’ as to assign them to one with certainty. A total of 25 species were identified (Appendix A5: Table A5), however, three *Myotis* species were grouped and treated as one, due to largely overlapping call parameters and few available reference calls and parameters. Two open-air feeding bat species were dominant, namely *Chaerephon cf. ansorgei* and *Tadarida aegyptiaca,* with 12360 active minutes. Of the clutter-edge feeding guild *Laephotis botswanae* and *Pipistrellus hesperidus* as well as *Neoromica nana* accounted for the majority of active minutes with 11787 minutes. Activity of clutter-dependent species was generally low with seven species accounting for only 127 active minutes.

Activity

Overall bat activity did not respond significantly to any individual predictor, but only to the interactions (Table 3). Feeding guilds responded significantly different, with clutter-edge and open-air feeding bat species being generally more active than clutter-dependent bats ($p<0.001$; Table 3; Figure 12). Clutter-edge activity was furthermore higher at natural edges ($p=0.009$), while open-air activity was lower here, but only marginally significant ($p=0.084$; Table 3; Figure 12). Both, clutter-edge ($p=0.004$) and open-air ($p<0.001$) feeding guilds were furthermore less active during the low season compared to the high season (Table 3; Figure 12). The final model explained about 75% of the variation ($R^2 = 0.73$, $R^2c = 0.76$). Moon phase and Temperature were not included in the final model.

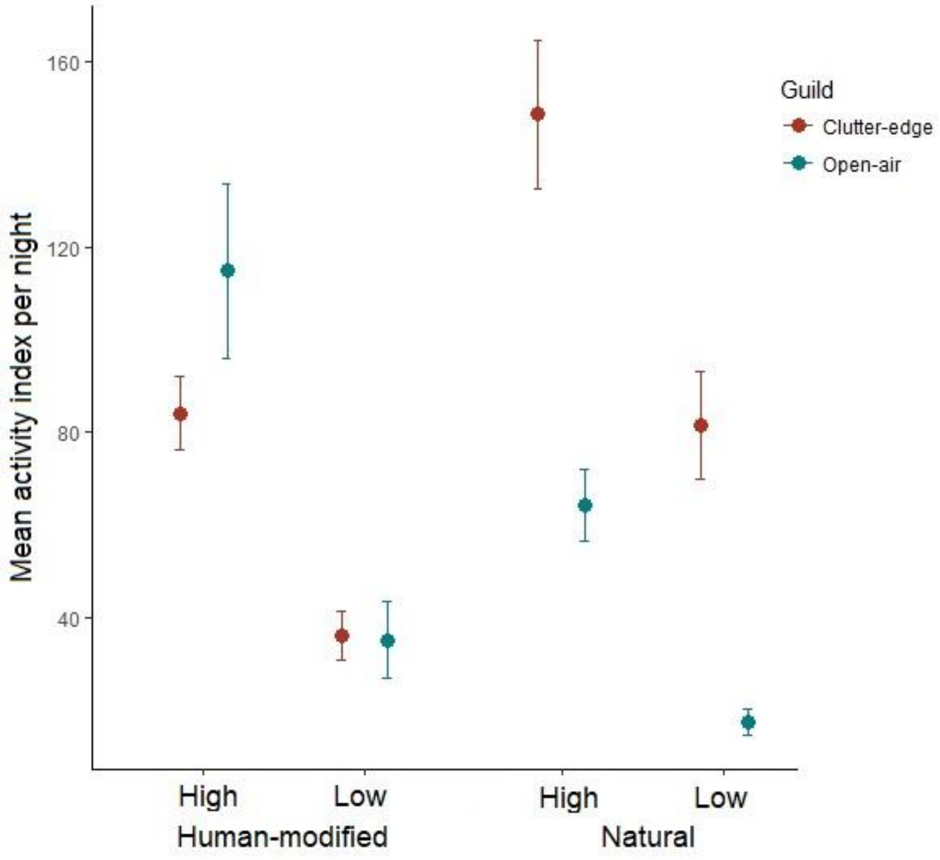

Figure 12 Mean active minutes ± SE for Clutter-edge and open-air feeding bat species in the high and low macadamia season and for the natural and human-modified edge habitat.

Table 3 Bat activity index (AI), summed per night in response to edge type (natural and human-modified), Season (high and low) and feeding guild

	Estimate	SE	Z	P
AI (log + 1) ~ Edge * Season * Guild + (1|Farm) + (1|Month)				
Intercept	0.19	0.21	0.93	0.354
Natural edge	-0.05	0.16	-0.35	0.728
Low Season	-0.16	0.21	-0.75	0.454
Clutter-edge guild	3.81	0.15	24.74	<0.001
Open-air guild	3.76	0.15	24.42	<0.001
Natural Edge : Low Season	0.12	0.26	0.45	0.652
Nat. edge : Clutter-edge	0.57	0.22	2.61	0.009
Nat. edge : Open-air	-0.38	0.22	-1.73	0.084
Low season : Clutter-edge	-0.76	0.26	-2.89	0.004
Low season : Open-air	-1.22	0.26	-4.65	<0.001
Nat. edge : Low : Clutter-edge	0.08	0.36	0.23	0.817
Nat. edge : Low : Open-air	-0.22	0.36	-0.59	0.554

Richness and diversity

Hill numbers of the incidence-based species richness (SR) do not differ between any season and landscape combinations (Figure 13a).

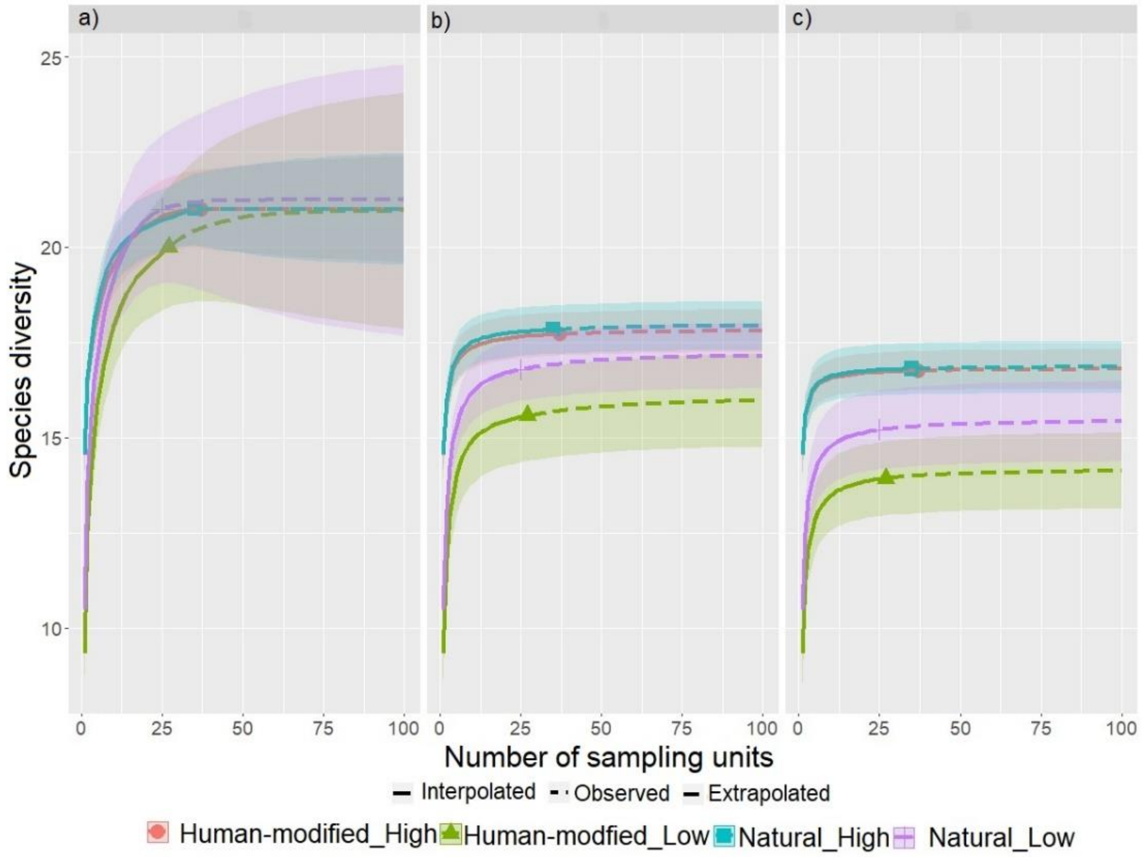

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Figure 13 Incidence based diversity estimates with respect to sample coverage (Hill numbers). a) Species richness, b) the exponential of Shannon's entropy index and c) the inverse of Simpson's concentration index

Shannon as well as Simpson diversity show that there is no difference in diversity during the high season for neither edge, while Simpson's concentration index generally shows slightly lower species diversity than Shannon's entropy index. In the low season however both edge settings show lower species diversity than in the high season (Figure 13b,c). Species diversity was lowest in the human-modified edge setting during the low season.

Diversity partitioning

The diversity partitioning shows an alpha richness with observed mean of 12.03 species which comprises about 60% of total bat species richness with 20.33 species (Figure 14). The highest species turn-over could be observed on a temporal scale, with a β-richness of 4.6 (22.6%) species between seasons (Figure 14). We can hence assume that seasonality and varying climate as well as food availability influences bat community composition and diversity. On a spatial scale we could in turn observe lower species turn-over rates with a β-richness of 2.38 species (11.7%) for “Farms” and the lowest turn-over on the smallest scale with a β-richness of only 1.33 (6.5%) between orchard edges. Total beta-diversities of all levels (8.31 species) account for 41% of total gamma diversity. Turn-over between farm edges and season was furthermore restricted to Rhinolophous species, with *Rhinolophus smithersii* being only present during the high season and *Rhinolophus clivosus* and *R*. *darlingi* only during the low season, while *Rhinolophus Rhodesia* was furthermore only detected at the natural edge and *R.darlingii* only at the human-modified edge.

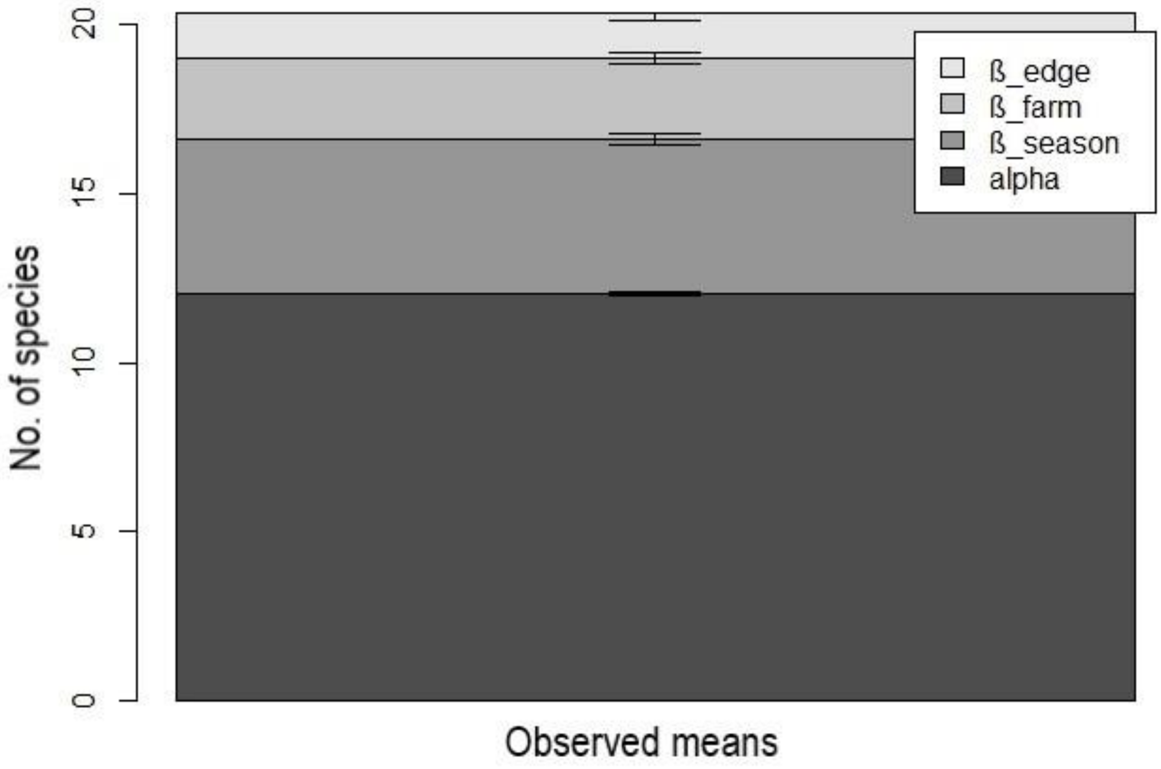

Figure 14 Bar graph with obeserved means ± SD of diversity partioning outcomes, with gamma diversity split into alpha and the three levels of beta diversity (season, farm and edge, from dark to lighter grey levels)

Discussion

Our results showed a large impact of seasonality on bat activity and species diversity. Seasonality caused the highest species turn-over in the diversity partitioning and both spatial scales, farm and orchard edge, had little impact. We can hence assume that seasonality and varying climate as well as food availability influences bat species richness. Edge habitat potentially still influences bat diversity, especially in the low season as Hill numbers suggest a greater response to seasonality at human-modified orchard edges. Activity indices furthermore indicate feeding guild specific edge preferences and likewise decreased activity rates during the low season.

In total we could positively identify 25 different bat species active at our study sites. This and the observed gamma richness of about 20 species, according to both the diversity partitioning and Hill numbers, attest to a high local bat species richness in macadamia orchards. Our estimations are higher than previous studies in local macadamia orchards (14-15 species), but are in line with estimations from surrounding areas as well as local species richness from other studies in Southern Africa (Cooper-Bohannon, 2016; Linden et al., 2014; Monadjem et al., 2010; Schoeman et al., 2013; Taylor et al., 2013a, 2013b; Weier et al., 2017, 2018). This shows that an intensively farmed agricultural landscape is still able to support high bat diversity. Outcomes of the diversity partitioning show that season has a high effect on species richness, accounting for over 22% of species turn-over. This high impact of seasonality is supported by our activity data, which shows lower levels of activity for both clutter-edge and open-air feeding guilds in the low season. This could be due to prey availability and pest insect abundances (Taylor et al., 2013a; Weier et al., 2018), but can also be explained by weather dependent generally lower activity levels in winter (Monadjem et al., 2010).

The turn-over between seasons was restricted to a few *Rhinolophus* species. All other species have been detected throughout the year. There was very little turn-over between the natural and the human-modified orchard edges and only slightly higher β-richness between farms. This could be due to the generally low amount of clutter-dependent bat species and the nature of macadamia orchards, catering well for both clutter-edge and open-air feeding species, as suggested by Kalda et al. (2015), who found that bats prefer alley-like tree plantings as a second option after woodlands. Taylor et al. (2013a) found similarly no effect of natural riparian habitat in comparison to bat activity in macadamia orchards and likewise concluded, that this might be due to the similarity of vegetation structure. The low β-richness between edges within macadamia orchards might, however, also be due to the presence of a certain degree of heterogeneity in the general landscape, since β-richness, although low, is still higher than that recorded at nearby villages (Foord et al., 2018). All farms sampled in this study furthermore had remnants of natural vegetation and the human-modified orchard edges were possibly not completely independent from these, considering the large homerange of bats, which can travel several kilometres a night (e.g. Monadjem et al., 2010; Noer et al., 2012).

Hill numbers from our incidence-based analysis also resulted in lower species diversitiy in both landscape settings during the low season, with stronger effects at human-modified orchard edges. Natural habitats could hence be potentially more important in the low season, where food is less abundant in the agricultural landscape, while high food availability in the high season overwrites a potential landscape effect.

Total bat activity was not affected by the orchard edges. The two feeding guilds separately responded as expected to the edge settings, with clutter-edge feeding species being more active at natural edges and open-air feeding species being more active at human-modified edges. Clutter-dependent bats were hardly recorded during our study. Aside from their preference for dense, cluttered vegetation, this could also be due to farm management practices. A study in Britain comparing bat activity on organic farms to that on conventional farms found that *Rhinolophus* species' are only active on organic farms (Wickramasinghe et al., 2003). Macadamia orchards are extensively sprayed with pesticides and could deter sensitive species like the Rhinolophidae.

Our study furthermore did not account for detectability of different species according to Monadjem (2017). High frequency calls, like those of the Rhinolophidae, could hence be undersampled. Due to the standardised set-up of detectors, habitat should not have affected the detectability. We also did not focus on the species level or community composition in detail, where detectability of different species plays a more important role. Clutter-edge bats could potentially be under-detected compared to open-air, which would result in a consistent effect in turn-over and should not influence our results. Our statistical model explained about 75% of the variation and could potentially be improved by the inclusion of arthropod abundance data and other weather data, like rainfall and wind speeds. To complement the acoustic data it is furthermore advisable to use additional catching of bats (e.g. Ahlén and BaagØe, 1999; Flaquer et al., 2007) in the orchards and the adjacent natural areas, to control for the detection bias of the purely acoustic recording, which might undersample certain species.

Concluding we can say that our study confirmed previous observations of bat activity in and around macadamia orchards. Seasonality had a larger influence on bat activity than had edge habitat. The agricultural landscape in Levubu seems to be supporting a high bat species richness throughout the year. The near absence of highly sensitive species, like *Rhinolophus*, is a concern, but must be further looked into as this could also be due to detection limitations. Previous studies in Europe suggest the importance of connectivity and heterogeneity in an agricultural landscape to conserve bat species richness, diversity and activity (Frey-Ehrenbold et al., 2013; Kalda et al., 2015). Due to its location at the foothills of a large mountain range, Levubu still maintains a large degree of natural habitat amongst and around agricultural farms, which could be the reason why this area is able to support such a high species richness.

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Chapter 4 – Insecticide treatments and landscape simplification negatively affect honey bees (*Apis mellifera*) in macadamia orchards, possibly limiting ecosystem service provision

Abstract

The observed worrying trend in insect population declines, which is often linked to agricultural intensification, could potentially affect ecosystem services. Hence, it is of great importance to better understand the impact of agricultural management on insect abundance. We aimed to determine the effect of insecticide treatments and landscape simplification on arthropod abundance in macadamia orchards in South Africa, which make up a fast growing, highly profitable industry. In a paired design, we compared insect abundance on macadamia trees with human-modified and natural orchard edge habitat. The only insect order that responded significantly to both edge habitat and insecticide application were the Hymenoptera (excluding ants). Observations of Hymenoptera were to a large extent honey bees and wasps with few observations of stingless bees. Hymenoptera abundance decreased after insecticide treatments and was higher at natural orchard edges and recovered quicker after insecticide treatments than they did at the human-modified edge. This can potentially limit or hinder ecosystem service provision, since macadamias are dependent on pollination by honey bees and also benefit from natural pest control by parasitoids. Farm management needs to be reconsidered to facilitate beneficial and yield-promoting insect species such as Hymenoptera with the help of closely connected natural habitat.

Introduction

While many insects are considered a pest in agricultural systems, they also provide important ecosystem services to agriculture. The value of services provided by wild insects in the United States of America has been estimated to be as high as USD 57bn annually (Losey and Vaughan, 2006) and the worldwide value of pollination alone was estimated to €153bn (Gallai et al., 2009) and even as high as USD 235bn – 577bn (IPBES, 2016). Some of nature's services such as pollination are being used as management tools, through artificial hives and their strategic placements in crop lands to enhance pollination. The origin of these services is quickly forgotten and only recently concerns have risen, also in the public, about the potential decline of wild insect populations, which could affect natural systems, but also agriculture and food security. Several studies have looked into this trend and its causes and estimations of the insect biomass decline have been found to be as much as 80% over 27 years (Hallmann et al., 2017). One of the major reasons for insect biodiversity decline is the loss and fragmentation of natural habitat, much of which is due to agricultural developments (Losey and Vaughan, 2006; Potts et al., 2010; Sánchez-Bayo and Wyckhuys, 2019; Stein et al., 2018; Vanbergen and the Insect Pollinators Initiative, 2013). Another concern is the extensive use of insecticides to chemically control insect pests to crops (Losey and Vaughan, 2006; Potts et al., 2010; Sánchez-Bayo and Wyckhuys, 2019), which can, however, not only affect the target species. Their estimated value and the potential impact of their decline is reason to further investigate factors limiting or enhancing insect abundance and to make serious efforts of conserving insect diversity and ecosystem service provision. With a growing human population and the increasing demand for food security, the pressure on remaining natural areas, harboring many important ecosystem services, is high.

Macadamias *macadamia integrifolia* are one of the most highly priced nuts on the market and the industry is growing quickly. South Africa, the currently largest macadamia nut producer has approximately ± 28 000 ha planted with macadamia trees (Southern African Macadamia Growers Association, unpublished data). The area planted with macadamias is steadily increasing, and other crops, but also natural areas, have to give way. The industry is experiencing high pest pressure of mostly Hemiptera: Pentatomidae and Lepidoptera: Tortricidae, which feed on the outer husk as well as inner kernel of the macadamia nuts. These are being controlled by extensive use of chemicals. However, stinkbugs still cause an estimated damage to the South African macadamia industry of approximately of USD 6 823 827 annually (Southern African Macadamia Growers Association, unpublished data). Macadamia farmers are furthermore heavily relying on insect pollination (Howlett et al., 2015), mostly by wild honey bees (*Apis mellifera*), however often enhanced through additional commercial hives placed around the farm (Grass et al., 2018).

There is a certain controversy in the macadamia sector. Ecosystem services, provided by insects, are highly valued and hardly replaceable, but they are being threatened by the extensive agriculture and the expansion into their natural habitats. In a highly profitable, growing industry like macadamia farming, we looked into the effects of farm management on arthropod abundance on macadamia trees. Through an observational study we assessed the response of the arthropod community to insecticide treatments and orchard edge habitat. We compared natural orchard edges, bordering remnants of natural vegetation, with human-modified edges, being surrounded by continuous crops. We hypothesized that 1) pest pressure of hemipteran and lepidopteran pests would be greater on trees near natural vegetation, 2) abundance of beneficial hymenopteran species is likewise greater at natural orchard edges and that 3) abundances of all taxa respond negatively to insecticide treatments and increase with increasing time since last application.

Figure 15 a) example of macadamia trees bordering a natural landscape setting and b) example of a human-modified landscape setting.

Materials and Methods

This insect abundance study was part of a predator exclusion experiment, which is not presented in detail here. Bats and birds have been excluded from macadamia trees to assess their role as natural pest control and effect on macadamia nut quality. The experiments did not result in a detectable effect on relevant arthropod taxa (Appendix A6 – Vertebrate exclusion context).

Study site

The study took place in the South African province of Limpopo, in Levubu, one of South Africa's oldest and largest macadamia growing areas (DAFF, 2017). It is an area of high rainfall with an average annual precipitation of over 900mm (Taylor et al., 2013), which makes it specifically attractive for agriculture. It is situated at the foothills of the Soutpansberg mountain range which is considered a biodiversity hotspot (Mostert et al., 2008). The area around Levubu retains remnant natural bush in the agricultural matrix. On six commercial farms we selected 96 macadamia trees that were between seven and 11 years of age. On each farm we had 16 trees, of which eight were situated at a natural orchard edge (Figure 15) bordering natural bush and another eight at a human-modified edge, inside the orchard with continuous crops or interrupted by farm roads.

The patches of natural bush were up to 20ha in size and in all but one case connected to further natural vegetation. Orchard borders next to these natural areas were used in our experiments as "natural landscape" and compared to trees at "human-modified landscapes" which consisted of continuous crops or roads. The two landscape settings per farm were between 156 and 527m apart. Dominant vegetation type at the natural landscapes were woodlands or bushveld, classified by Mucina and Rutherford (2006) as 'Soutpansberg Mountain Bushveld' and 'Tzaneen Sour Bushveld', covering 80% (SD: ± 18%) of the surrounding edge habitat (250m half circle radius), while this was only true for 27% (SD: ± 19%) at the human-modified edge (Grass et al. 2018).

Prominent insect species related to macadamia cultivation

Macadamias (Family: Proteaceae) are a tree nut species native to Australia (Nagao et al., 1992). Our study focused exclusively on smooth shell macadamia (*Macadamia integrifolia*), which is the dominant commercially planted cultivar. Macadamia nuts develop after flowering in early spring until the late summer months. They grow in racemes and drop continuously once matured and are then harvested off the ground. Once the husk is removed by the farmer, they are then dried and processed in local factories and are mostly exported to USA, China and Europe. The greatest natural threat to the macadamia industry is pest insect damage. Major pest species include several Hemiptera species from the stink bug complex as well as lepidopteran pests from the nut borer complex (Schoeman and de Villiers, 2015). Most common and responsible for the most damage in the industry are the two-spotted stink bug (*Bathycoelia distincta*), the green vegetable bug (*Nezara viridula*), the yellow edged stink bug (*Chinavia pallidoconspersa*) as well as the coconut bug (*Pseudotheraptus wayi*). The two main nut borer pests are the macadamia nut borer (*Cryptophlebia batracopha*) and the false codling moth (*Thaumatotibia leucotreta*). While the stink bugs and coconut bug are able to damage the kernel through the shell, nut borers mainly feed on the husk, but can also damage the kernel of immature nuts. Defects to the kernel, known as unsound, make them unusable for the kernel market. Insect damage hence mainly affects the quality of the nut, which reflects in prices farmers are able to achieve with their product, but can also affect the yield, through higher rates of premature nut drop (Blanco-Metzler, Watt and Cosens, 2007; La Croix and Thindwa, 1986; Nagao et al., 1992; Schoeman and de Villiers, 2015).

The main pollinator of South African macadamia flowers is the honey bee (Howlett et al., 2015). While these are native and naturally occurring in the area, many farmers make use of commercial bee hives. Other arthropods have previously been observed at the flowers of macadamias and in Australia stingless bees (Meliponini) are believed to be the original pollinators (Howlett et al., 2015).

Data collection

The arthropod abundance on each tree was assessed in 14 months over two macadamia growing cycles between September 2015 and March 2017 by means of visual scanning. As the arthropod monitoring was part of a vertebrate exclusion study the scanning was chosen as to not interfere with the arthropod community and experimental outcomes of the exclusion experiments. Our methods followed approaches of other exclusion studies like Maas et al. (2013). Each tree was scanned for 20 minutes starting at the stem and gradually moving up towards the foliage. A ladder was used to allow for scanning from above and for the top parts of the tree. All arthropods were recorded and identified to the highest taxonomic level possible, but at least to order level. Pictures were taken where possible to allow for identification later on using Picker et al. (2004). Sampling took place in the mornings between 7am and 1pm on clear days. We sampled all trees of one farm within the same day. A sampling period (all 96 trees), unless interrupted by rainy days, would usually be completed within one week. Great care was taken not to disturb the arthropod community on the trees and we refrained from any beating of branches. For each sample we recorded the date, the number of days since the last insecticide treatment of the surrounding plots as well as the edge habitat (natural or human-modified). Although trees were not directly sprayed with insecticides (to not interfere with the previous mentioned exclusion experiments), we recorded each date of chemical insecticide treatment for that farm to account for possible effects on the general arthropod abundance caused by insecticides sprayed on surrounding blocks or rows (Table 4). Insecticide application schedules varied per farm with two to over 10 sprays per season. Most chemicals were applied with tractors and two farms also used aerial sprays by helicopter (twice/season). Kohinor is applied by drenching the soil around the tree stem for intake through the root system.

Table 4 Insecticides used on experimental macadamia farms in Levubu, South Africa

Product	Active ingredient	Dosage	Withholding period	Pest
Ampligo	Chlorantraniliprole / lambda-cyhalothrin	400ml/ha	14 days	African bollworm, litchi moth, codling moth, false codling moth, stinkbug
Karate Zeon® 10 CS	Lambda-cyhalothrin	5ml/100L	30 days	Stinkbug
ACE® 750 SP	Acephate (Organophosphate)	75g/100L	35 days	Stinkbug
Klartan 240 EW	Tau-fluvalinate 240 g/L	30ml/100L	30 days	Stinkbug
Pyrinex 250 cs	Chlorpyrifos (organophosphate)	200ml/ 100L	83 days	Thrips, stinkbug, cotton aphids
Lannate	Methomyl (carbamate)	200ml/ 100L	14 days	Stinkbug
Polythrin 200 EC	Terbufos (organophosphate)	400ml/ 2000L	30 days	Stinkbug
Alpha-thrin 100 SC	Alpha-cypermethrin (pyrethroid)	10ml/100L	30 days	Stinkbug
Cyperfos 500 EC	Chlorpyrifos (Organophosphate) / Cypermethrin (Pyrethroid)	105ml/ 100L	83 days	Stinkbug
Cyperin 200 EC	Cypermethrin (Pyrethroid)	20ml/100L	30 days	Stinkbug
Kohinor 350 SC	Imidacloprid (neonicotinoids)	400ml/20L	112 days	Thrips
Vantex 60 CS	Gamma-cyhalothrin (pyrethroid)	100ml/ 2000L	82 days	Stinkbug
Avalanche	Alpha-cypermethrin (pyrethroid)	200ml/ 2000L	30 days	Stinkbug
Rossi 200 SC	Fipronil (phenyl pyrazole)	200ml/ 1000L	30 days	Thrips
Bulldock Beta 125 SC	Beta-cyfluthrin (pyrethroid).	120ml/ 2000L	30 days	Stinkbug
Sipermethrien	Cypermethrin	400ml/ 2000L	30 days	Stinkbug

Data analysis

Each month of sampling resulted in a count of individuals per taxon per tree. Lepidoptera were split up into Rhopalocera (butterflies) and Heterocera (moths), since it is species of the Heterocera complex that are mainly considered a pest to macadamias. Due to short term outbreaks of Stenorrhyncha (mostly aphids) these were analysed separately from the remaining Hemiptera complex. The family Formicidae was also analysed separately of the remaining Hymenoptera. We used a two-step approach to analyse significantly responding taxa, first identifying most important and strongest responding taxa by means of a multivariate generalised linear model and then performing separate generalized linear mixed models on significantly responding taxa only. We first fitted multivariate generalised linear models (GLMs) to abundance of taxa in the R package “mvabund” v. 4.0.1 (Wang et al., 2012; 2019) using the functions “manyglm” and “anova.manyglm”. This model-based method is superior to a distance-based approach, as multivariate GLMs account for confounding mean-variance relationships, that commonly arise in abundance data that contain many zeros (Warton et al., 2012; 2015). We used this method to test for an effect of edge habitat (natural vs. human modified), treatment (vertebrate exclusion) and days since insecticide spray on invertebrate assemblages, by summing likelihood ratio statistics for each taxon, yielding a community-level measure of days since insecticide spray and each edge and treatment- category. The log-ratio statistic was calculated for each taxon as a measure of effect for each predictor and summed. Correlation between species was accounted for by using Wald statistics with 50 permutations. The PIT-residual bootstrap method (Warton et al., 2017) was used to derive p-values by resampling 999 rows of the dataset. We first explored conditional responses of date, farm, days since insecticide spray, edge and treatment. Then we accounted for temporal autocorrelation by resampling residuals across sampling times within farms, which controls for unaccounted cross-farm variation. This was done by specifying farm in the block argument of the “anova.manyglm” function. Models were checked for departure from model assumptions by visually examining Dunn-Smyth residuals plotted against the fitted values.

Significantly responding taxa, as identified by the multivariate analysis, were furthermore explored using generalized linear mixed effects models (GLMM) with sampling month and farm as random factors and treatment, landscape and days since spray as explaining variables using dedicated packages ‘lme4’ v. 1.1-14 (Bates et al., 2015), and ‘multcomp’ v. 1.4-7 (Hothorn et al., 2008). We accounted for overdispersion of the data by using a negative binomial distribution. All statistical analyses were performed in R (v. 3.5, R Foundation for Statistical Computing, Vienna, Austria). While treatment effects were included in the analysis of our data to account for possible effects of vertebrate exclusion, these results were negligible compared to the effects of insecticide application and landscape context and are only presented in the Appendix (Figure A1 and Table A6). Variables were checked for collinearity using the ‘vif’ function in the ‘cars’package v. 0.2 (Wang, 2017) with no correlation detected between variables.

Results

In total 52 191 individuals were assigned to 19 taxa during this study (Table 5), plus few observations of unidentified insect larvae. The most abundant taxa were Formicidae and Stenorrhyncha accounting for 88.5% of all observations and were analysed separately from their remaining order, due to these large abundances. Next most common abundant orders were Hemiptera, Diptera, Aranea and other Hymenoptera. Of all remaining Hymenoptera (excluding ants) 83% observations were in fact honey bees and results are discussed accordingly as responses of honey bees, although few observations of *Vespidae* and stingless bees were made as well.

Table 5 Invertebrate taxa observed on macadamia trees during the study period, the count of individuals per taxon and their percentage of total observations

	Count	**%**
Formicidae	34220	65.57%
Stenorrhyncha	11950	22.90%
Hemiptera	1899	3.64%
Diptera	1881	3.60%
Araneae	704	1.35%
Hymenoptera	686	1.31%
Heterocera	228	0.44%
Rhopalocera	202	0.39%
Coleoptera	112	0.21%
Isoptera	85	0.16%
Odonata	43	0.08%
Myriapoda	41	0.08%
Orthoptera	40	0.08%
Larvae	39	0.07%
Mantodea	28	0.05%
Ephemeroptera	13	0.02%
Neuroptera	11	0.02%
Blattodea	4	0.01%
Psocoptera	3	0.01%
Megaloptera	2	0.00%

Conditional responses of the invertebrate assemblages (Table 6) from the multivariate analysis suggest that seasonality (date) and farm accounted for most of the variation. These variables are accounted for as random factors in further analysis (GLMM). The time since the last chemical treatment (days since spray) was also of great importance and explained even more of the variation than treatment and edge.

Table 6 Conditional responses of overall invertebrate assemblages to date (when sampling took place), farm, insecticides (days since spray), edge (natural, human-modified), treatment (control, day exclusion, night exclusion, full exclusion). With Wald statistics representing the variation accounted for by each variable and the p-value the respective significance.

	Date	Farm	Insecticides	Edge	Treatment	Edge* Insecticides	Treatment* Insecticides	Treatment* Edge	Treatment* Edge*Insecticides
Wald statistic	23.16	16.81	11.88	6.52	8.82	6.37	6.7	7.5	6.17
p-value	0.001	0.001	0.001	0.002	0.011	0.02	0.41	0.04	0.55

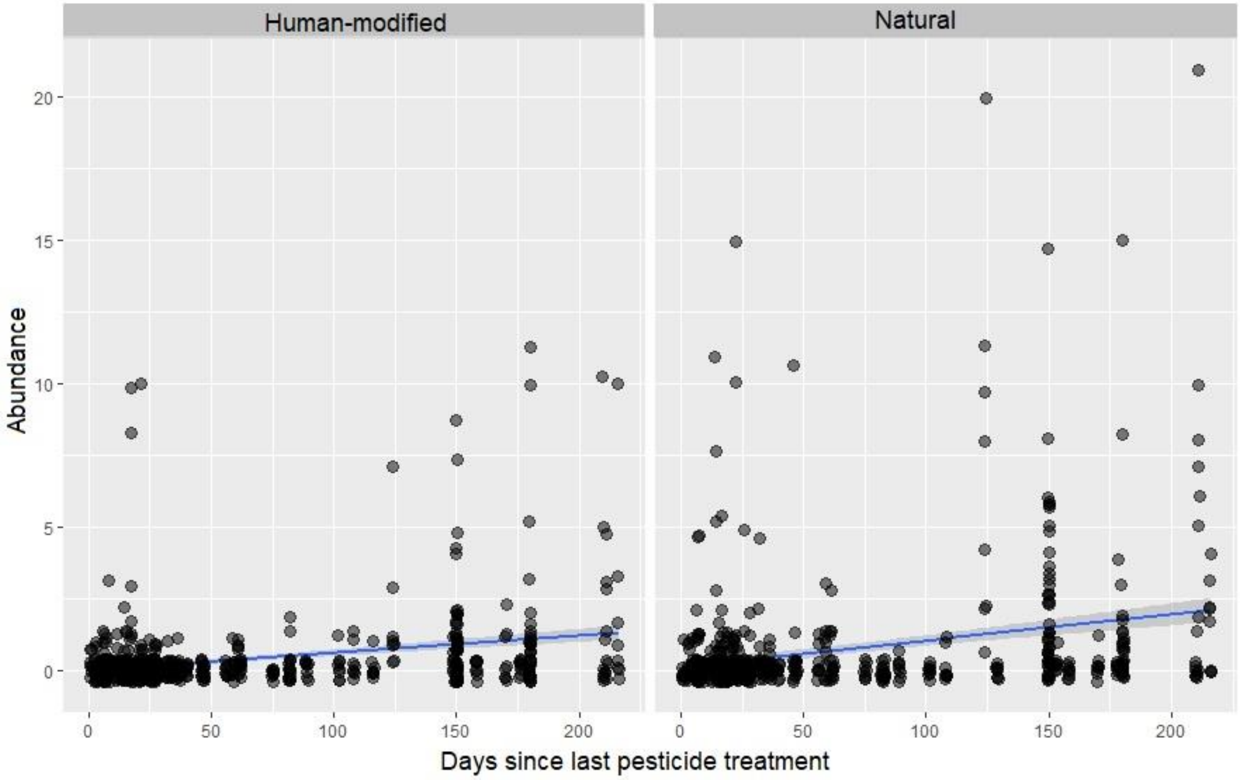

Figure 16 Honey bee observations and mean abundance over time (blue line) per tree at human-modified and natural edges with increasing number of days since last insecticide treatment and 95% confidence interval (in grey)

The edge factor furthermore showed significant interaction with the days since spray (Table 6), suggesting the effect insecticides have varied between the two edge settings. Although there were significant overall multivariate responses of the arthropod community, only certain taxa contributed to this overall response (Table 7).

The only taxon that responded significantly to both days since spray as well as the edge type effect (

Table 7), according to the multivariate analysis, were Hymenoptera, or honey bees, which increased in numbers with time since chemical treatment (Appendix A7: Figure A2). Honey bee abundance furthermore recovered more rapidly at natural edges than at human-modified edges (Figure 16).

Table 7 Model outcomes of the anova.manyglm analysis for the five taxa that contributed the most to test statistics and the significance of their contributions for days since spray, treatment and edge. Data was blocked by farm to control for unaccounted cross-farm variation during significance testing.

	Days since spray		**Treatment**		**Edge**	
	Cumulative contribution to test statistic	p-value	Cumulative contribution to test statistic	p-value	Cumulative contribution to test statistic	p-value
Hymenoptera	0.75	0.02			0.41	0.003
Orthoptera	0.82	0.09			0.85	0.64
Diptera	0.86	0.35	0.65	0.73	0.79	0.6
Rhopalocera	0.90	0.37			0.57	0.18
Mantodea	0.93	0.37				
Hemiptera			0.45	0.33		
Formicidae					0.70	0.28
Heterocera						
Coleoptera						
Araneae			0.30	0.04		
Blattodea						
Psocoptera						
Stenorrhyncha			0.72	0.98		
Isoptera			0.56	0.63		

The GLMM for honey bees, analysing previously identified significant predictors and including month, treatment and farm as random factors, confirmed these findings and resulted in significant effects for edge and days since spray. Honey bees were hence more abundant at the natural edge compared to the human-modified edge (

Table *8*; Figure 17) and their abundance was positively correlated with days since spray. The interaction of edge and days since spray was, however, not significant.

Table 8 GLMM results for Honey bee (Hymenoptera) abundance with edge type, treatment (Appendix A6) insecticide application as explaning variables

Linear Hypotheses	**Estimate**	**SE**	**Z**	**P**
*Hymenoptera ~ Edge * scale(Days.since.spray) + Treatment + (Month|Farm),data=agginsects ,family = negative.binomial*				
Intercept	-1. 34	0.27	-4.96	<0.001
Edge (natural)	0.58	0.17	3.35	0.0008
Days since spray	1.26	0.23	5.43	<0.001
Day Exclusion	0.17	0.22	0.78	0.4329
Full Exclusion	-0.0004	0.22	-0.002	0.9984
Night Exclusion	0.33	0.22	1.49	0.1364
Edge(nat):Days since spray	-0.19	0.14	-1.38	0.1662

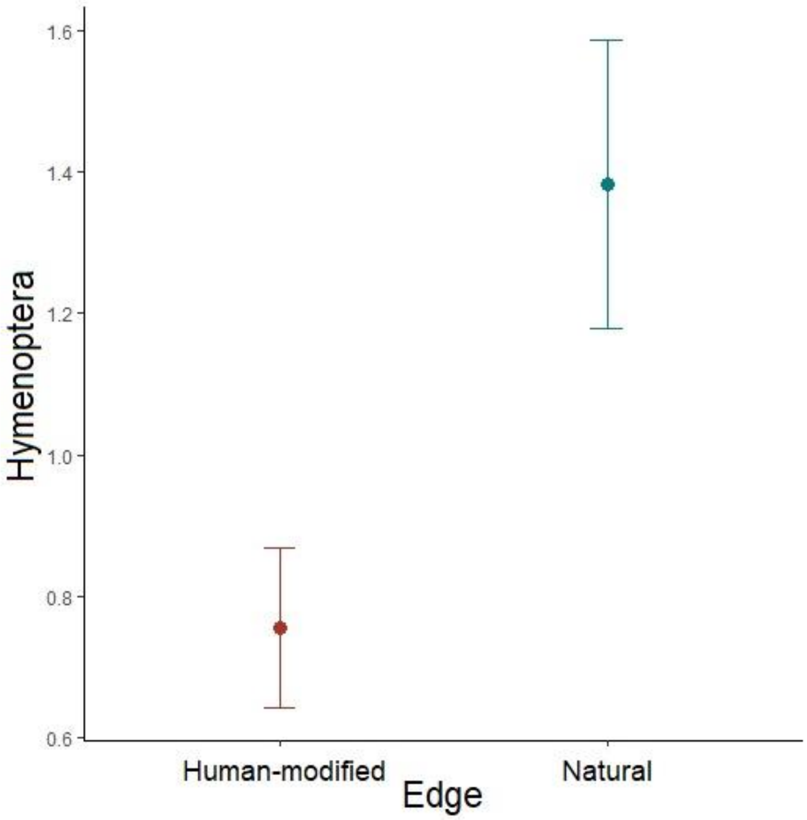

Figure 17 Mean honey bee (Hymenoptera) counts ± SE per tree at human-modified and natural orchard edges

Discussion

Honey bees were the only taxon that responded to insecticide treatments and orchard edge habitat, making this taxon the most vulnerable in an intensely farmed macadamia landscape, thereby potentially reducing beneficial ecosystem services.

Honey bees are considered the main pollinator of macadamias (Howlett et al., 2015) and are commercially farmed and distributed around macadamia orchards to provide pollination services. Despite these commercial hives, honey bees in our study seemed to have been influenced by edge habitat and are most abundant at natural orchard edges, which is in line with previous studies (Fabian et al., 2013; Watson et al., 2011). A pollination study specifically on macadamias found a similar, yet weaker, effect of edge habitat on honey bee flower visitation (Grass et al., 2018). Honey bees are also responding strongest to insecticide treatments with increasing abundance with increasing time since pesticide application. Although not significant, our results indicate a slower recovery from the resulting decline in abundance at human-modified edges than at natural edges. This is of great concern not only from a conservation perspective but also considering economic losses to farmers or bee keepers. Sánchez-Bayo and Wyckhuys (2019) advise a rethinking and adaptation of insecticide regimes in agriculture. Not only pollinators are potentially affected by edge habitat but also parasitoids which are dependent on natural or semi-natural areas (Krewenka et al., 2011; Mody et al., 2011; Steffan-Dewenter, 2002; Tscharntke et al., 1998). Parasitoids feed on a variety of macadamia pest species as shown in studies from e.g. Malawi, Costa Rica and Australia (Blanco-Metzler et al., 2008; Chambers et al., 1995; Jones, 1988; Sands and Coombs, 1999) and their response to insecticide applications could potentially limit their role as biocontrol agents.

One possible reason why other taxa, especially pest species are not responding as strongly to insecticide treatments is that their numbers are kept low throughout the year. Through scouting, a method to determine pest pressure on the crops, farmers time their insecticide applications accurately to prevent pest outbreaks in time and keep pest levels under a certain threshold. Hemiptera did in fact show a delayed response to pesticide application and a decreasing abundance with increasing time since spray, however, not significant. This could indicate a higher resistance to insecticides due to this targeted spraying regime. All experimental trees were furthermore excluded from direct chemical applications, while the surrounding block was sprayed as part of the vertebrate exclusion set-up. The high mobility of honey bees might expose them more than other species to the pesticides applied in the orchard, while the experimental trees remain untreated. Honey bees are not known to show higher sensitivities to insecticides than other arthropods (Hardstone et al., 2010).

Hymenoptera only accounted for 1.3% of all observations in this study and yet were the only ones with significant responses. The most abundant taxa were Formicidae and Stenorrhyncha (aphids), which did not respond significantly to any tested variables. This is most likely due to their ecology and their general occurance in large numbers, like the random outbreaks of aphids and the rapid but short term increase in individuals, which can mask possible effects that were tested here. As many species of ants have nests underground, pesticide effects on the reproduction in these nests are potentially prevented. Similarly, ants could often be observed in large numbers on the stem of the trees. These large numbers are most likely related to this family’s ecology rather than to any external influences and by far exceed numbers of any other observed taxa. What triggers such outbreaks and determines their occurrence should be subject of future research. Apart from these two taxa, Hymenoptera were the fourth most abundant taxa observed in this study. Although we were able to pick up significant responses of honey bees, our study surveyed general arthropod abundance and does potentially not fully represent a survey of Hymenoptera. Our results indicate the sensitivity of this order to farm management practices and provide reason for further research into Hymenoptera responses to management practices in agricultural systems. Another limitation of our study is the visual sampling method. This was chosen as any interference to the arthropod community should be kept to a minimum to not influence the impacts of the vertebrate exclusion. Our observations are hence potentially not representing the actual arthropod community, as individuals might have been overlooked, which are difficult to spot or well camouflaged. It is therefore important to interpret these findings as an indication and trend, which needs to be further looked into using more accurate methods like beating or knock downs. A standardised survey specifically on insecticides is furthermore advisable, which looks into responses of the arthropod community to type, time and application method of insecticides.

Concluding we can say that the clear and strong negative effect of insecticides as well as the positive effect of natural landscapes on Hymenoptera abundance is of great concern considering the increased use of insecticides, and the continuous removal of natural vegetation, which are the main drivers for biodiversity loss, from which Hymenoptera are especially affected (Sánchez-Bayo and Wyckhuys, 2019). This can potentially counteract the effectiveness of parasitoids as well as pollinators. Further research into integrated pest management is needed, to prevent interference of chemical insecticides with this ecosystem service and potentially increase its effectiveness. Our results furthermore emphasize that the artificial bee keeping does not replace their natural environment and it is important to combine the two to ensure for successful and effective pollination of crops. Research into Hymenoptera responses, arthropod diversity and insecticide responses is furthermore needed to confirm findings indicated in this study and to be able to identify important ecosystem service providers and to protect and restore their natural habitat.

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Chapter 5 – General discussion and conclusion

This study provides important insights into the relationship of ecosystem services and disservices and the role of natural habitats in South African macadamia orchards. By excluding vertebrates from macadamia trees, we found that ecosystem service provision by bats and birds varied with orchard edge and was stronger at natural edge habitats (Ch.2). Their impact at human-modified edges was, however, still significant and exceeded the negative impact of crop-raiding monkeys, which were restricted to orchard edges near natural vegetation (Ch.2). Seasonality mostly determined bat species richness and activity, but natural vegetation might still serve as important alternative habitat for the diverse bat community (Ch.3). Honey bees, which are important ecosystem service providers, were also more abundant at natural orchard edges and were negatively affected by insecticide treatments. Other taxa remained unaffected by as well the edgee factor as the insecticide treatment (Ch. 4). We conclude with recommendations on landscape and farm management practices to possibly enhance ecosystem service provision and limit impacts of ecosystem disservices and provide a research outlook resulting from our findings.

Benefits of biological control counterbalance disadvantageous of crop raiding

Agricultural intensification is one of the major drivers of habitat loss (Stoate et al., 2001) although the agricultural sector benefits hugely of ecosystem services (ES). Especially biocontrol by flying vertebrates, which can consume large amounts of pest insect species, has been in the scientific focus with several studies measuring and estimating their economic impact (e.g. Böhm et al., 2011; Kalka et al., 2008; Karp and Daily, 2014; Maas et al., 2013; Morrison and Lindell, 2012; Russo et al., 2018; Williams-Guillen et al., 2008). Their impact can however depend on local and landscape factors, which need to be further assessed (Maas et al., 2016). Biodiversity and with that ecosystem services are enhanced and originating from natural areas. These are, however, often viewed as lost land or even threat by farmers (Tscharntke et al., 2016). Ecosystem disservices (EDS), like crop damages or raids, can cause income losses to growers or decrease productivity (Zhang et al., 2007). Both ES and EDS are enhanced by natural areas (Tscharntke et al., 2016). It is therefore inevitable to also assess the impact of both in one agro-ecosystem to be able to tell the true economic value of ES or EDS.
One of the key findings of this study was the enormous economic impact of bats and birds as biocontrol agents, which counterbalanced the impact by crop-raiding monkeys. The exclusion of bats and birds resulted in higher profit losses than monkeys caused through crop raiding. Birds

seemed to have a higher effect as biocontrol than did bats, with higher income losses in the day exclosure. However, only the combined effect of all birds and bats could compensate the effect of crop-raiding monkeys. Vervet monkeys are considered a crop pest throughout their range and are associated with patches of forests close by or bordering agricultural areas and can cause devastating losses, especially for small-holder growers. Mitigation strategies, including the removal of natural areas, establishment of buffer zones or the guarding of crops, as identified by the literature (Ango et al., 2017; Naughton-Treves et al., 1998; Saj et al., 2001; Warren et al., 2007), could, however, also compromise the benefits of biological control by bats and birds. Our results are of critical importance from an agro-ecological point of view. Although damages by crop-raiders may seem like a huge loss economically, they might be outbalanced by simultaneous beneficial effects like prevented insect crop damage, which needs to be considered in management practices. In future research it is furthermore important to consider a variety of ES as well as EDS when assessing economic impacts, instead of only concentrating on one or the other (Saunders et al., 2016). The continuous degredation of natural habitats can potentially limit the ES provision and cause not only economic losses, but also endanger food security for an ever growing human population.

The importance of natural vegetation in an agro-ecosystem

Although remnants of natural woodlands in the study region constitute habitat for crop raiding monkeys, they do so also for beneficial ecosystem service providers. While the effect of bats and birds on yield was masked by the effect of simultaneous monkey exclusion, the nut quality assessment clearly showed that bats and birds had higher biocontrol impacts at natural orchard edges than they did at human-modified. Nut quality was generally better near natural vegetation, due to lower insect damages and the exclusion of bats and birds caused larger quality decreases at these natural edges. The measured economic benefit of biocontrol by bats and birds at the human-modified edge is counterbalancing the conomic loss of crop-raiding monkeys measured at natural edges. To fully separate the economic benefits of flying vertebrates and losses of monkeys at natural edges, extensive research and further exclusion experiments would be needed that distinguish between all ES or EDS providers. It is, however, not only vertebrates that are more abundant near natural vegetation, but we also expected arthropod abundance to increase compared to human-modified edges. We already discovered that insect damage to the kernel did not increase, but instead decrease at natural edges. This, however, presumably due to higher pest control by bats and birds. We furthermore could not find an effect of edge habitat on any other taxon than honey bees, which abundance was higher at natural orchard edges than at human-modified ones. Hymenoptera are a highly beneficial insect order to the macadamia industry. Macadamias are reliant on pollination by honey bees (Howlett et al., 2015; Grass et al., 2018). Other possible pollinators include stingless bee species (Howlett et al., 2015). Parasitoids furthermore are known to prey on certain macadamia insect-pest species (Blanco-Metzler et al., 2008; Chambers et al., 1995; Jones, 1988; Sands and Coombs, 1999). The higher occurance at natural habitats could potentially increase ES provision by honey bees in orchards bordering these areas. It could hence be of high interest to farmers and landowners, who wish to benefit from ES by Hymenoptera, to increase the amount and connectivity of natural vegetation on their farms and with that make more sections accessible for biocontrol and pollination providers, but more research into the exact impacts of habitat preference of Hymenoptera in agricultural areas is needed, to be able to advise more concretely.

Agricultural intensification and with that the loss and fragmentation of habitat is believed to be one of the main drivers of insect losses (Losey and Vaughan, 2006; Potts et al., 2010; Stein et al., 2018; Vanbergen and Initiative, 2013). Intensive insecticide applications, to control pest insect abundance, is another factor (Losey and Vaughan, 2006; Potts et al., 2010) that can potentially harm other insect species like pollinators. Honey bees were the only taxon in our study that responded significantly to insecticide applications. They were also more abundant at natural orchard edges, which potentially caused a faster recovery after insecticide sprays. This emphasizes how important natural areas can be as refuge and also as source for important ecosystem service providers like Hymenoptera and that artificial, commercial bee hives, like they are being used in agriculture, cannot replace or compensate for the loss of natural areas. Farmers are advised to consider all beneficial arthropod species, including pollinators and biocontrol agents and be aware of the impact their pest and land management has on ecosystems and with that potentially on their crop.

Seasonality affects bat species richness and activity in the agricultural landscape

The orchard edge factor did not have the expected effect on species diversity. Seasonality was of greater importance and affected species richness and diversity more than any spatial factor. We observed higher species richness in the high season (summer month), which is coinciding with high insect pest pressure in the macadamia orchards (De Villiers and Joubert, 2003). These findings were in line with previous observations (Taylor et al., 2013a). Lower richness as well as activity in the low season can be explained by lower food availability as well as weather dependent behaviour, which causes bats to generally be less active in winter (Monadjem et al., 2010; Taylor et al., 2013a). Although orchard edge caused the lowest species turn-over and with that hardly contributed to bat species diversity according to the diversity partitioning, Hill numbers as well as activity indices indicate that season specific differences do in fact depend to a certain degree on edge habitat, with higher drops of species diversity at the human-modified edge during the low season, than at the natural edge. Bat species richness was generally high and it is hence of great importance to maintain current level of landscape heterogeneity in the macadamia agricultural landscape, which is in line with recommendations by e.g. Wordley et al. (2017). Some African bats, like *Chaerephon pumilus* and *Mops condylurus*, are furthermore known to fly several kilometres between roosting and feeding grounds a night (Monadjem et al., 2010; Noer et al., 2012). The distance between edges might have hence been too small, to detect real differences in species turn-over. A larger effect could possibly be expected when extending the range of the study and including e.g. local villages (Foord et al., 2018). Bat abundance generally has been known to be supported by natural areas and corridors within farmland (Downs and Racey, 2006; Frey-Ehrenbold et al., 2013; Kelly et al., 2016; Verboom and Huitema, 1997) and a study in Australian macadamia orchards also suggest preferences for edges close to woodland compared to isolated orchards (Crisol-Martínez et al., 2016). In general we observed a high species richness in macadamia orchards, which is higher than observed previously and similar to observations from local natural areas and reserves (Linden et al., 2014; Taylor et al., 2013a, 2013b; Weier et al., 2017). To maintain this high species richness and diversity, which seems largely influenced by seasonality, it is important to protect food sources, natural habitat and roost sites (Kelly et al., 2016). With artificial roosts one can potentially further support bat abundance (Weier et al., 2018) and with that ecosystem service provision. Further research into roost preferences of local bat species is, however, necessary, to be able to provide suitable roosts for all species.

Conclusion

This study highlights the importance of heterogeneity in an agricultural landscape and the value and necessity of remaining natural areas within intensely farmed areas. Bat diversity and activity was mostly influenced by seasonality, probably caused by food availability and natural season dependent activity patterns. Open-air and cluter-edge dependent bat species furthermore showed higher levels of activity at human-modified and natural orchard edges respectively. The provision of a heteregenous landscape and natural areas is hence important to maintain a healthy and stable bat community, which in turn benefits farmers and ensures a high level of biocontrol services. Bats and birds had a higher impact as biocontrol at natural edges and generally outbalanced negative effects of crop-raiding monkeys. This highlights the need for integrated research when assessing ecosystem service and disservice providers. The natural orchard edge played a likewise important role for honey bee abundance, which was generally higher close to natural vegetation and recovered quicker from population crashes caused by insecticide applications. This shows that ecosystem services by arthropods (e.g. pollination) also rely on remaining natural habitats, despite commercially managed honey bee hives. The findings of this study can impact future land management and can be applied to a variety of agro-ecosystems, where farmers need to be aware of the beneficial and economically relevant impacts of remaining natural vegetation and the impact of farm management on ecosystem service providers.

Practical recommendations and research outlook

Ecosystem services and disservices are both enhanced by natural vegetation (Kremen, 2005; Kremen et al., 2007; Rusch et al., 2016; Tscharntke et al., 2005). We can assume that where there are high levels of services, there might also be an increased disservice and vice versa. To make a meaningful estimation of the economic impact it is hence of critical importance to simultaneously assess both services and disservices to a system (Saunders et al., 2016). Our study showed that, although highly perceived and a great concern to the industry, damage by crop-raiding monkeys was largely counter-balanced by beneficial effects of biocontrol through bats and birds. Future research should aim at including a variety of economic ecosystem service and disservice providers to agriculture and rather than assessing the value of one single service provider, assess the value of landscape features, like nearby forests, which are the origin of these services. Vertebrate exclusion experiments should hence ideally distinguish between the different service providers, to allow for specific effect attributions. Exclusion experiments should also be accompanied by detailed community and activity assessments of all functional groups, as one group or in fact one species can provide both services and disservices in different stages of one crop (Saunders and Luck, 2016). This can also be true for bats, where insectivorous species could act as biocontrol, while frugivorous species actually consume the crop. We furthermore observed higher abundance of hymenoptera on macadamia trees close to natural vegetation. This could potentially be due to flight range limitations, but also different food preferences for e.g. wild plants. Whether natural areas in fact increase pollination services to agriculture by hymenoptera should be assessed, by arthropod exclusion from crop flowers (Grass et al., 2018) or pollination efficiency and food preferences of honey bees. Hymenoptera were furthermore the only arthropod order responding significantly to the insecticide treatments. While the lacking effect on actual pest species was surprising, it is rather concerning that this mainly beneficial order was so strongly impacted. Insecticides could therefore potentially decrease important ecosystem services, by limiting abundance of pollinators like honey bees. Which factors determine the abundance of other orders is furthermore of interest, to be able to explain especially outbreaks of possibly crop damaging aphids. A standardized pesticide survey, which takes into account the type of chemical, spraying regime and method and monitors arthropod abundance and diversity at set, increasing periods after application, which can furthermore be compared to natural areas at increasing distances to the orchard can be of high interest and fill in knowledge gaps and questions left after our experimental survey. The impact of insecticides on other ecosystem service providers can be of high interest. Bats are known to prefer low intensity or organic agricultural areas (Park, 2015; Wickramasinghe et al., 2003), which could be due to lower levels of insecticides and hence potentially higher food availability. Detailed dietary and toxicological analysis of service providers like bats and birds is advisable, especially considering the increasing use of artificial roost and nest boxes. If management practices are potentially harming flying vertebrates which are attracted to agricultural areas, this could in turn have negative impacts on populations and conservation status. Finally and since the effects of diurnal birds as biocontrol seemed to be much larger than the effects of bats and nocturnal birds, research into the community structure of insectivorous birds in African agricultural landscapes is highly desirable. Studies into activity patterns, species richness and diet of insectivorous birds, comparative to previous studies on bats (Taylor et al., 2013a; Weier et al., 2018) or other agro-ecosystems (Crisol-Martínez et al., 2016; Maas et al., 2015), to complete the picture of ecosystem service provision by flying arthropods.

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Appendices

Appendix A1: Experimental set-up

The six commercial orchards selected were all in the same altitudinal range, had planted the species *Macadamia integrifolia* and were similar in abiotic conditions. Willingness of the landowner to host and cooperate with the project was an important criterion, as management practices had to be altered and adapted, to limit interference with the experiments. All trees were of similar age, between seven and 16 years old, so that the trees were all in full production but still manageable in size. The rows of trees where the experimental trees were situated, were excluded from all insecticide treatments to prevent alteration of the arthropod community within the cages. The cage frames were constructed of pine wood, measuring 5 x 10 x 5 m and were covered with 2 x 2 cm black nylon mesh net, which allows arthropods and other small animals to move freely, but forms a barrier for flying vertebrates, primates and large herbivores. The trees were trimmed to and maintained at a 0.5m distance from the exclosure cage to form a sufficient buffer for pest insects as well as other outside factors.

The opening of day and night treatments was limited to only the side panels, as the size of the cages did not allow for opening and closing roofs. The roofs were as well constructed of the same nylon mesh net, which was permanently closing the roof, limiting access to only the sides of the cages. On each experimental farm a trained assistant opened/closed the side panels of day and night treatments at 7am and 5pm every day. The Control treatments consisted only of the wooden frame and netted roof to control for any interfering effect the cage structures could possibly have.

In the third year of this study however the sets were reduced to only full and control treatments as the operation of the night and day treatments was not manageable anymore. Also due to the growth of trees the cages had to be removed from one farm, as a repeated trimming of the trees would have had a too great effect, resulting in a reduced number of treatment cages of 20 over five farms in the final year.

Appendix A2 – Analysis of nut set and quality

Table A1 Binomial model outcomes for nut set and quality with Treatments and landscape as fixed factors

Nut set/raceme:

glmer(cbind(Final.Nuts, (Initial.Nuts – Final.Nuts)) ~ Treatment * Edge + (1|Farm), family="binomial")

Fixed effects	***Estimate***	***Std. Error***	***z-value***	***p-value***
Intercept	-0.344	0.25	-1.39	0.163
Day exclosure	-0.69	0.05	-13.92	<0.001
Full exclosure	-0.81	0.06	-14.22	<0.001
Night exclosure	-0.66	0.05	-13.87	0.001
Natural Landscape	-1.21	0.06	-21.52	<0.001
Day:Natural	1.24	0.08	16.41	<0.001
Full:Natural	0.82	0.09	9.35	<0.001
Night:Natural	-0.58	0.15	-3.87	0.001

Nut quality:

glmer(cbind(Mass.unsound), (Mass.total – Mass.unsound)) ~ Treatment * Edge + (1|Farm), family="binomial")

Intercept	-2.73	0.116	-23.59	<0.001
Day exclosure	0.26	0.035	7.32	<0.001
Full exclosure	0.22	0.033	6.63	<0.001
Night exclosure	0.14	0.036	3.96	<0.001
Natural landscape	-0.35	0.040	-8.75	<0.001
Day:Natural	0.23	0.056	4.16	<0.001
Full:Natural	0.52	0.052	10.06	<0.001
Night:Natural	0.19	0.060	3.29	<0.001

Appendix A3 – Calculation of yield

To extrapolate the nut set (number of nuts/50 racemes) to a yield value (kg/ha), we obtained the actual farm yields of each experimental block. Assuming our control cages are a true representation of nut set, we used these actual yields and nut sets of control trees to calculate a multiplication factor to extrapolate the nut sets of the remaining treatments to a yield per hectare. All experimental blocks had similar tree spacing and we therefore assumed an equal number of trees per block (312.5 trees/ha) as well as an equal number of nuts/kg (130). We then averaged the actual farm yields (Table A2) per landscape setting (human-modified: 2103.7kg/ha; natural: 1712.5kg/ha). In all but one case the treatments of the two landscape structures were in the same block. By multiplying the actual yield with the number of nuts/kg and then dividing this product by the tree spacing, we calculated a value representing the average number of nuts per tree. We then divided that number by the nut set of the two controls to obtain multiplication factors that could be applied to the nut sets per treatment to calculate the yield effects. Nuts are harvested and summed per block and then divided into a value per hectare.

Table A2 Farm yields (kg DIS/ha) of the year 2017 provided by each landowner.

	Yield (kg DIS/ha)
Farm 1	781
Farm 2	3447
Farm 3	583
Farm 4	1750
Farm 5 Human-modified	4740
Farm 5 Natural	2393
Farm 6	1321

Table A3 Variables used to calculate Yield (kg DIS/ha). Actual farm yields from all six farms were averaged. Nut set (Number of nuts per 50 racemes) derived from the final nut counts taken from the two control treatments (at the two landscape settings). Number of trees/ha and Number of nuts/kg DIS are constant over landscape settings and treatments.

	Average actual farm yield (kgDIS/ha)	**Nut set at Control (No. nuts/50 racemes)**	**No. Trees /ha**	**No. Nuts /kg DIS**
Human-modified	2103.67	46.33	312.5	130
Natural	1712.5	107.06	312.5	130

Calculation of multiplication factor, applying the average of actual farm yields/ha of each landscape setting.

Multiplication factor $_{\text{Human-modified}}$ = ((2103.67 * 130) / 312.5) / 107.06 = **8.17**

Multiplication factor $_{\text{Natural}}$ = ((1712.5 * 130) / 312.5) / 46.33 = **15.38**

This multiplication factor was then used to calculate yields per treatment with the following function:

Yield = ((a * b) * c) / d

where a = nut set; b = multiplication factor; c = 312.5 (trees/ha); d = 130 (Nuts/kg DIS)

Step by step calculation of yield demonstrated with the example of the Day treatment in the human-modified landscape setting:

Nut set (No. nuts/50 racemes)	= 59.26	No. Trees/ha	= 312.5
Multiplication factor	= 8.17	No. Nuts/kg DIS	= 130

Nuts/tree = 59.26 * 8.17 = 484.15

Nuts/ha = 484.15 * 312.5 = 151298.19

Kg/ha = 151298.19 / 130 = **1163.83**

Table A4 Nut set and yield per treatment and landscape setting

	Nut set **(No.nuts/50 racemes)**	**Yield** **(kg DIS/ha)**
Human-modified		
Control	46.33	2102.6
Day	59.26	1163.83
Full	43.93	862.76
Night	77.88	1529.52
Natural		
Control	107.06	1712.87
Day	62.94	2326.96
Full	35.27	1303.97
Night	6.67	246.6

Appendix A4 – Income calculation

To calculate the total income/ha, the price of macadamia nuts was based on 2017 sound kernel prices per style (kernel size) with an average style distribution from the Levubu growing area made available by a local processor. This resulted in an average price of USD 17.26/kg kernel and USD 4.60/kg dry-in-shell. A total kernel recovery (TKR = percentage kernel within total sample) of 32% was assumed as realistic average for all calculations (Green Farms Nut Company, personal communication, September 04, 2018) and unsound kernel varied according to landscape and treatment combination. Costs for the more labour intensive processing of unsound kernel was deducted, also according to unsound kernel variation over treatments. The resulting price/kg was then multiplied by the yield of each landscape/treatment combination to get the total income/ha/yr. Conversions from South African Rand into US Dollars in this study are calculated at a set exchange rate of 1:13 (average exchange rate achieved by the local factory in oversea sales for 2017 was 1:13.67; Green Farms Nut Company, personal communication, September 04, 2018).

Appendix A5 – Bat species list and activity index

Table A5 Species list of all positively identified species, the Miller's activity index per species with the sum of active minutes per species throughout the study period and the assigned feeding guild per species according to Monadjem (2010)

Species	Activity index	Feeding guild	Season present	Edge present
Chaerophon ansorgei	6758	Open-air	High & Low	Both
Chaerophon pumilus	814	Open-air	High & Low	Both
Eptesicus hottentotus	99	Clutter-edge	High & Low	Both
Hipposideros caffer	27	Clutter-dependent	High & Low	Both
Kerivoula argentata	18	Clutter-dependent	High & Low	Both
Laephotis botswanae	4291	Clutter-edge	High & Low	Both
Mops condylurus	1420	Open-air	High & Low	Both
Mops midas	1877	Open-air	High & Low	Both
Myotis bocagii, tricolor, welwitschii	323	Clutter-edge	High & Low	Both
Neoromicia capensis	573	Clutter-edge	High & Low	Both
Neoromicia nana	3748	Clutter-edge	High & Low	Both
Neoromicia zuluensis	2813	Clutter-edge	High & Low	Both
Otomops martiensseni	885	Open-air	High & Low	Both
Pipistrellus hesperidus	9451	Clutter-edge	High & Low	Both
Pipistrellus rusticus	2252	Clutter-edge	High & Low	Both
Rhinolophus clivosus	37	Clutter-dependent	High & Low	Both
Rhinolophus darlingi	1	Clutter-dependent	Low	Human-modified
Rhinolophus rhodesia	13	Clutter-dependent	Low	Natural
Rhinolophus simulator	27	Clutter-dependent	High & Low	Both
Rhinolophus smithersii	4	Clutter-dependent	High	Both
Scotophilus dinganii	1729	Clutter-edge	High & Low	Both
Tadaria aegyptiaca	5602	Open-air	High & Low	Both
Taphozous mauritianus	182	Open-air	High & Low	Both
Unknown	450			
Grand Total	**43394**			

Appendix A6 – Vertebrate exclusion context

A vertebrate exclusion experiment took place on the six commercially managed macadamia farms in Levubu, South Africa, to assess the effect of bats and birds as natural pest control of macadamia pest species. In four treatments, bats and/or birds were excluded from macadamia trees in either a human-modified or natural landscape. The full exclosure was closed at all times, excluding bats as well as birds, while the Day and Night exclosures were only closed during the day or night respectively, to be able to distinguish between effects of diurnal birds and bats and nocturnal birds. Later effects of the exclusion treatments on nut quality and yield were assessed. During the time of the exclusion experiments, insect abundance on the experimental trees was monitored monthly and analyzed as described in the main text. The exclusion of bats and/or birds had only a significant impact on aranea abundance, which were higher on trees, where both bats and birds were excluded, compared to unmanipulated control trees. Although one could expect a cascading effect of this meso-predator release, no responses of any other taxon could be observed. Aranea on the other hand did not respond to the landscape or spraying context. The only taxon significantly affected by these factors was Hymenoptera, which is discussed in the main text. However, one can assume, that these effects on Hymenoptera are unaffected by the vertebrate exclusion experiments.

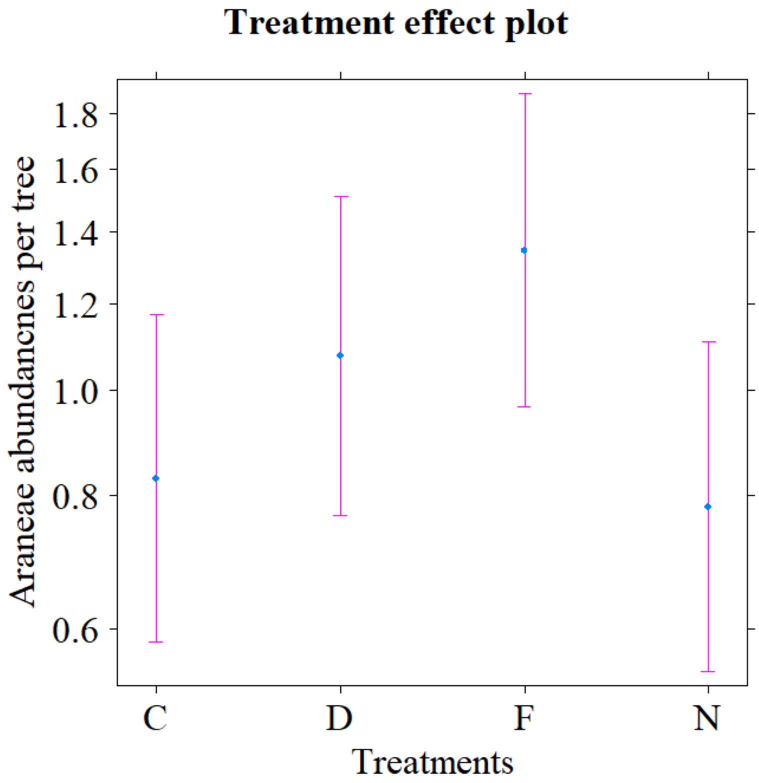

Figure A1 GLMM output of Aranea abundance at each treatment: Control (C), Day (D), Full (F) and Night (N)

Table A6 GLMM model results for Aranea responses to treatment, landscape and insecticide treatments

Linear Hypotheses	**Estimate**	**SE**	**Z**	**p**
Aranea ~ Treatment + Landscape + scale(Days.since.spray) + (1|Month) + (1|Farm),data=agginsects,family=negative.binomial				
Intercept	-0.185	0.184	-1.003	0.316
Day Exclusion	0.261	0.141	1.850	0.064
Full Exclusion	0.486	0.138	3.531	<0.001
Night Exclusion	-0.059	0.148	-0.400	0.689
Landscape (natural)	-0.009	0.098	-0.095	0.924
Days since spray	0.062	0.069	0.906	0.365

Appendix A7 – Response of Hymenoptera and Orthoptera to insecticide use

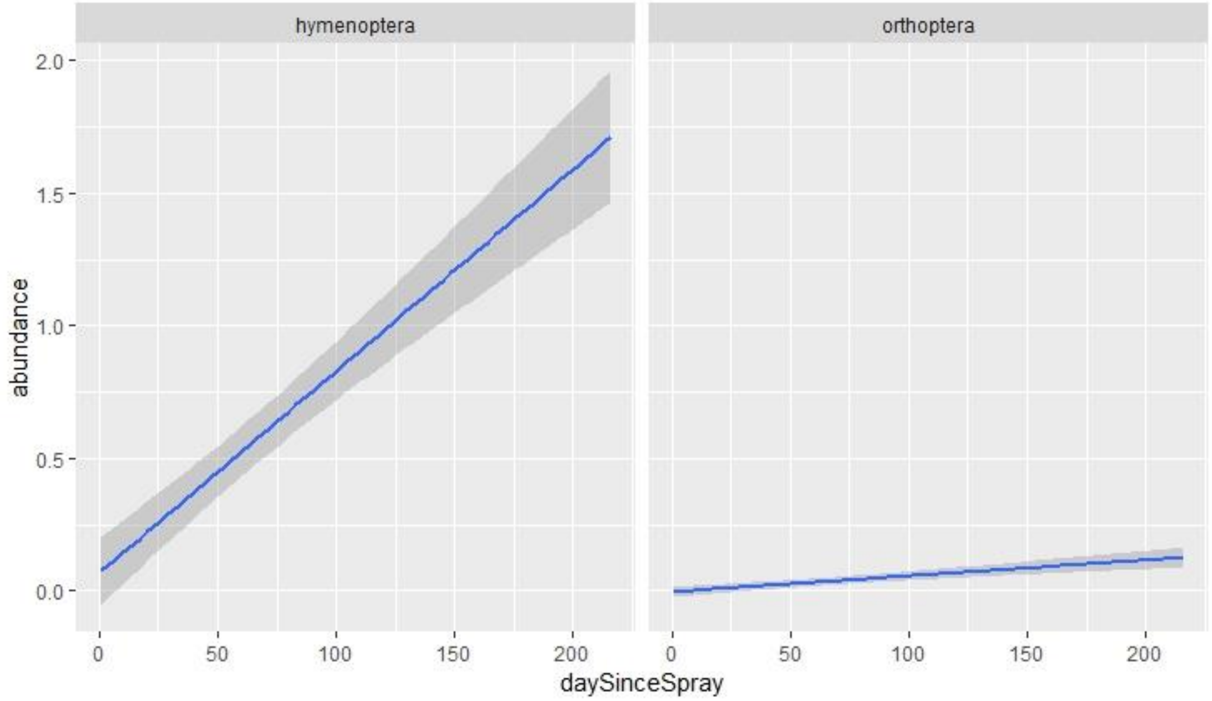

Figure A2 Abundance per tree of Hymenoptera and Orthoptera with increasing numbers of days since last insecticide treatment