SPATIAL AND TEMPORAL FLUCTUATIONS IN BIRD COMMUNITIES ALONG A FOREST-FARMLAND GRADIENT IN WESTERN KENYA

Dissertation

zur Erlangung des Doktorgrades

der Naturwissenschaften

vorgelegt beim Fachbereich Biologie

der Johann Wolfgang Goethe-Universitat

in Frankfurt am Main

von

Ronald K. Mulwa

aus Kitui, Kenya

Frankfurt 2011

(D 30)

vom Fachbereich Biologie der

Johann Wolfgang Goethe-Universitat als Dissertation angenommen.

Dekanin: Prof. Dr. Anna Starzinski-Powitz

Erste Gutachterin: Prof. Dr. Katrin Böhning-Gaese

Zweiter Gutachter: Prof. Dr. Rüdiger Wittig

Datum der Disputation: ____________________

To my dear family; wife Mercy and daughters Sara Ndethya, Lorna Msae and Sonia Mbithe for their support.

"Biodiversity is humanity's life-support system, delivering everything from food, to clean water and air, to recreation and tourism, to novel chemicals that drive our advanced civilization. Yet there is an increasingly well-documented global trend in biodiversity loss, triggered by a host of human activities."

Camilo Mora 2011

CONTENTS

1. ZUSAMMENFASSUNG

Der weltweite Rückgang der Waldbedeckung stellt eine der größten Bedrohungen für die globale Biodiversität dar (Sala *et al.* 2000) und ruft daher Besorgnis bei Ökologen und Naturschützern hervor (Tews *et al*. 2004, Butchart *et al*. 2010). Insbesondere in vielen tropischen Regionen haben Abholzungen zu einer Umwandlung der natürlichen Wälder zu artenarmen Waldfragmenten (Laurance and Bierregaard 1997), Sekundärwäldern, Weideflächen, Agrarland und anderen anthropogen geprägten Habitaten geführt (Myers 1992, Sala *et al.* 2000, Kammesheidt 2002). Diese Landnutzungsänderungen haben oft einen großen Einfluss auf die tropische Biodiversität, da eine Intensivierung der Landnutzung mit Veränderungen in der Vegetationsstruktur einhergehen. Diese wiederum wirken sich auf Diversität, Abundanz und Verteilung von Tierpopulationen aus (Hansen *et al.* 2001).

Obwohl unbestritten ist, dass ungestörte tropische Regenwälder die artenreichsten Ökosysteme der Erde darstellen (Myers *et al.* 2000), konnte gezeigt werden, dass tropische Agrarökosysteme eine hohe Biodiversität aufweisen können (Peh *et al.* 2006, Ranganathan *et al.* 2010). Allerdings wird der potentielle Wert von Agrarökosystemen für die Aufrechterhaltung tropischer Biodiversität noch vielfach diskutiert (Waltert *et al.* 2004). Während die meisten Strategien zum Schutz von Biodiversität in tropischen Ländern landwirtschaftliche Nutzflächen nicht in ihre Managementpläne einbeziehen (Millennium Ecosystem Assessment 2005), wird mittlerweile deutlich, dass die zunehmende räumliche Ausdehnung von Agrarökosystemen in den Tropen mehr Aufmerksamkeit bei der Planung von Naturschutzmaßnahmen genießen sollte (Ranganathan *et al.* 2010). So wurde festgestellt, dass es nicht ausreicht, Schutzmaßnahmen auf Schutzgebiete zu beschränken, um den globalen Rückgang der Biodiversität zu verlangsamen (Mora and Sale 2011). Das von Birdlife International betriebene Important Bird Areas (IBA) Programm berücksichtigt diese neue Auffassung und wählt auch landwirtschaftliche Nutzflächen als prioritäre Schutzflächen aus, allerdings nur, wenn diese Vogelarten beherbergen, die weltweit bedroht sind (BirdLife International 2007).

Obwohl viele Taxa durch die voranschreitenden Landnutzungsänderungen betroffen sind, wurden insbesondere für die Gruppe der Vögel viele wissenschaftliche Untersuchungen durchgeführt (Ormerod and Watkinson 2000). Dies liegt hauptsächlich daran, dass sie sich sehr gut als Indikatoren für Umweltveränderungen eignen (Bibby *et al.* 1992). Dank ihrer Mobilität reagieren Vögel unmittelbar auf Veränderungen in ihrem jeweiligen Lebensraum (Whelan *et al.* 2008), und ihre Diversität und Verteilung variiert sowohl räumlich als auch zeitlich (White *et al.* 2010). Daher sollten Artenreichtum und Häufigkeit von Vögeln gute Indikatoren für Veränderungen in anderen taxonomischen Gruppen sein (Bennun 1999, Gregory *et al.* 2003). Ökologisch gesehen spielen Vögel eine zentrale Rolle in der Aufrechterhaltung verschiedener Ökosystemfunktionen, z. B. bei der Bestäubung und Samenausbreitung von Pflanzen oder bei der biologischen Schädlingskontrolle (Sekercioglu 2006). Im Bereich der Ökosystemforschung wird zunehmend deutlich, dass die funktionale Diversität eine größere Rolle für Ökosystemfunktionen spielt als taxonomische Diversität (Diaz and Cabido 2001, Gamfeldt *et al.* 2008). Daher ist ein tieferes Verständnis der Verteilung von funktionellen Vogelgruppen auf Landschaftsebene sehr hilfreich, um effektive Management- und Planungsmaßnahmen aus Sicht des Naturschutzes und der Ökosystemdienstleistungen zu konzipieren.

1.1 Untersuchungsgebiet

Die Untersuchungen wurden im tropischen Regenwald Kakamega Forest, einem der Biodiversitätshotspots Kenias, durchgeführt (1520-1680 m, 0°10' - 0°21'N, 34°47' - 34°58'E). Der durchschnittliche jährliche Niederschlag in Kakamega beträgt ca. 2.000 mm, und im Jahresverlauf treten zwei Regenzeiten von März bis Mai und von Juli bis Oktober auf (Farwig *et al.* 2008). Die tägliche Durchschnittstemperatur schwankt zwischen 10,6°C (Regenzeit) und 27,7°C (Trockenzeit) (Tsingalia 1990). Kakamega Forest ist einer der östlichen Überreste des Guineo-Kongolischen Regenwaldes (Bennun and Njoroge 1999). Daher weist das hier vorkommende Artenspektrum viele Parallelen zu dem von zentral- und westafrikanischen Regenwäldern auf (Wagner et al. 2008). Kakamega Forest ist berühmt für seine diverse Vogelfauna. Mehr als 410 Vogelarten konnten innerhalb und in der näheren Umgebung des Waldes registriert werden (Shanni and de Bruinj 2006), davon zwei weltweit bedrohte Vogelarten (Turner's Eremomela *Eremomela tuneri* und Chapin's Flycatcher *Muscicapa lendu*) (BirdLife International 2011) sowie weitere 15 regional bedrohte Arten (Bennun and Njoroge 1999). Aufgrund seiner reichen Vogelfauna zählt Kakamega Forest zu den 60 in Kenia gelisteten „Important Bird Areas“ (Bennun and Njoroge 1999).

Kakamega Forest ist umgeben von einem der am dichtesten besiedelten Agrargebiete Kenias mit einer Bevölkerungsdichte von bis zu 643 Einwohner/km^2 (Schaab *et al.* 2010). Die Agrarlandschaft, die den Wald umgibt, ist geprägt durch ausgedehnte Zuckerrohrfelder und kleinräumiger Subsistenzwirtschaft mit hauptsächlichem Anbau von Mais, Bohnen und Gemüse. In den Agrarflächen sind häufig kleine Bereiche mit semi-natürlicher Vegetation zu finden, die sowohl aus einheimischen als auch exotischen

Bäumen bestehen und als kleine verstreute Wälder zwischen Weideflächen oder entlang von Bächen, Straßen oder Feldgrenzen auftreten. Insgesamt stellt die Landschaft ein Mosaik aus Flächen mit unterschiedlichster Landnutzungsintensität dar, das sowohl naturnahen Wald und Sekundärwald im Kakamega National Reserve umfasst als auch die Subsistenzwirtschaften und Zuckerrohrplantagen in den benachbarten Agrarflächen. Aufgrund dieser mosaikartigen Struktur eignet sich diese Landschaft hervorragend, um räumliche und zeitliche Fluktuationen in Vogelgemeinschaften entlang eines anthropogenen Landnutzungsgradienten zu untersuchen.

1.2 Struktur und Ziele der Arbeit

1.2.1 Struktur der Arbeit

Im Anschluss an eine allgemeine Einleitung (Chapter 2) teilt sich meine Arbeit in zwei große Kapitel (Chapter 3 und 4), in denen der Kern meiner wissenschaftlichen Arbeit behandelt wird. Beide Kapitel sind in Form einer wissenschaftlichen Veröffentlichung geschrieben und strukturiert. Das abschließende Kapitel (Chapter 5) umfasst eine allgemeine Synthese meiner Arbeit mit übergreifenden Schlussfolgerungen und Perspektiven für die Wissenschaft und den Naturschutz. Alle Referenzen, die in der vorliegenden Arbeit zitiert werden, sind am Ende zusammengefasst. Abschließend folgen Appendixes, die zusätzliche Informationen enthalten.

1.2.2 Ziel der Arbeit

Landnutzungsänderungen stellen eine ernstzunehmende Bedrohung für die Biodiversität der Erde dar. In meiner Arbeit untersuche ich daher die räumlichen und zeitlichen

Beziehungen zwischen Vogelgemeinschaften und Ressourcenverfügbarkeit für unterschiedliche Landnutzungsintensitäten. Wenn sich die Diversität und Zusammensetzung von Vogelgemeinschaften substantiell zwischen Habitaten mit unterschiedlicher Landnutzungsintensität in diesem Wald-Agrarland-Mosaik unterscheiden, dann sollten Managementpläne zum Schutz der Vogelfauna in Kenia ein größeres Augenmerk auf das Landnutzungsmanagement sowohl in Wald- als auch in Agrarökosystemen legen.

Kakamega Forest und seine Umgebung bieten ein ideales Untersuchungssystem für meine Fragestellung, da es einen umfassenden Landnutzungsgradienten von intaktem Wald bis hin zu stark modifiziertem Agrarland aufweist. Um den gesamten Landnutzungsgradienten abzudecken, untersuchte ich die Vogelgemeinschaften in zwei Waldhabitaten (naturnaher Wald und Sekundärwald) und in zwei Agrarlandtypen (Subsistenzwirtschaft und Zuckerrohrplantagen). Ich führte meine Studien über einen Zeitraum von einem Jahr durch und konnte somit die zeitliche Variation der Vogelgemeinschaft als auch die Veränderungen der Ressourcenverfügbarkeit im Jahresverlauf erfassen.

In Kapitel 3 (Chapter 3) vergleiche ich Artenreichtum und Häufigkeiten von Vögeln entlang eines Wald-Agrarland-Gradienten mit unterschiedlichen Landnutzungsintensitäten. Zusätzlich untersuche ich den Einfluss von struktureller Diversität der Vegetation auf Artenreichtum und Häufigkeit von Vögeln innerhalb von Wald- und Agrarlandhabitaten, um landschaftliche Schlüsselelemente zu identifizieren, die eine hohe Vogeldiversität in den entsprechenden Habitattypen begünstigten. Abschließend betrachte ich die relativen Beiträge räumlichen und zeitlichen Turnovers der Vogeldiversität und quantifiziere die

Veränderungen in der Vogelgemeinschaft für verschiedene funktionale Vogelgruppen entlang des Wald-Agrarland-Gradienten.

Im Kapitel 4 untersuche ich die saisonalen Schwankungen im Frucht- und Insektenangebot im Kakamega Forest und den umgebenen Agrarflächen. Die Variabilität der Ressourcenverfügbarkeit setze ich in Beziehung zu Abundanz und Artenreichtum der entsprechenden Nahrungsgilden der Vögel (frugivore und insektivore Vögel). Dieser Ansatz soll Aufschluss darüber geben, ob (1) Schwankungen in der Ressourcenverfügbarkeit habitatspezifisch sind, und (2) wie die entsprechenden Nahrungsgilden auf diese Schwankungen reagieren. Da habitat- und gemeinschaftsübergreifende Beziehungen zwischen Vögeln und der Nahrungsvariabilität in Raum und Zeit bisher nur wenig Beachtung in wissenschaftlichen Studien gefunden haben, leistet die vorliegende Arbeit einen wichtigen Beitrag zu unserem Verständnis von saisonalen Fluktuationen in Vogelgemeinschaften. Dieses Verständnis gewinnt zunehmend an Bedeutung, da sich saisonale klimatische Schwankungen in näherer Zukunft weiterhin verstärken werden (Fischlin *et al.* 2007). Die Daten zur Ressourcenverfügbarkeit wurden über einen Zeitraum von einem Jahr erfasst; die Vogeldaten sind identisch mit denen aus Kapitel 3.

1.3 Hohe Vogeldiversität in strukturell heterogenem Agrarland im westlichen Kenia

Tropische Ökosysteme sind wichtig für die weltweite Vogeldiversität. In vielen tropischen Regionen hat die Intensivierung der Landnutzung zu einer Umwandlung von natürlichen Wäldern in anthropogen modifizierte Habitate wie Sekundärwälder und heterogene Agrarlandschaften geführt. Trotz einiger vorhergehender Studien ist das Verständnis um

die Verteilung von Vogelgemeinschaften in diesen Wald-Agrarland-Mosaiken gering. Um die Vogeldiversität in einer anthropogen modifizierten kenianischen Landschaft zu untersuchen, erfassten wir Vogelgemeinschaften durch Punkt-Stopp-Zählungen und Distanzmessung an 20 Orten entlang eines Habitatgradienten ausgehend von Wald- (naturnaher Wald, Sekundärwald) bis hin zu Agrarlandhabitaten (Subsistenzwirtschaft, Zuckerrohrplantagen). Vogeldichten und –artenreichtum waren im Agrarland im Schnitt höher als in Waldhabitaten. Innerhalb von Wald und Agrarland stiegen Vogeldichten und –artenreichtum mit steigender struktureller Diversität der Vegetation, d. h. waren höher im naturnahen Wald als im Sekundärwald und höher in Subsistenzwirtschaften als in Zuckerrohrplantagen. Vogelgemeinschaften in Wald- und Agrarlandhabitaten waren sehr distinkt, und nur wenige Waldspezialisten konnten auch in Agrarlandhabitaten beobachtet werden. Außerdem ging die Anzahl insektivorer Vogelarten in Agrarlandhabitaten zurück, während karnivore und herbivore Vogelarten zunahmen. Unsere Studie bestätigt, dass das tropische Agrarland nur bedingt als Ersatzhabitat für auf Wälder spezialisierte Vogelarten geeignet ist. Im Gegensatz zu vielen vorherigen Studien zeigen unsere Ergebnisse, dass strukturreiches tropisches Agrarland eine reiche und distinkte Vogelgemeinschaft aufweist, die von der Umwandlung von Subsistenzwirtschaften zu Zuckerrohrplantagen bedroht ist. Wir schlussfolgern, dass Schutzstrategien in den Tropen über den Schutz von natürlichen Regenwäldern hinausgehen müssen und strukturell heterogene Agrarökosysteme in Schutzpläne integriert werden sollten, um artenreiche Vogelgemeinschaften in tropischen Wald-Agrarland-Mosaiken zu erhalten.

1.4 Saisonale Schwankungen von Ressourcenverfügbarkeit und Vogelgilden in verschiedenen Habitaten im westlichen Kenia

Aktuellen Prognosen zufolge wird in den nächsten Jahrzehnten eine Zunahme an saisonalen klimatischen Schwankungen erwartet. Dennoch ist nur wenig darüber bekannt, wie tropische Artengemeinschaften auf saisonale Schwankungen von Klimafaktoren und Ressourcenverfügbarkeit reagieren, insbesondere über Habitatgrenzen hinweg. Wir untersuchten die Beziehung zwischen räumlich-zeitlichen Fluktuationen in der Verfügbarkeit von Früchten und Insekten und den zwei entsprechenden Nahrungsgilden, d. h. frugivore und insektivore Vogelarten, in Wald- und Agrarlandhabitaten im westlichen Kenia. Das Angebot an Früchten und Insekten fluktuierte substantiell über das Jahr, aber die saisonalen Schwankungen waren asynchron zwischen den zwei Habitattypen. Artenzahl und Häufigkeit der Frugivoren und Insektivoren schwankten ebenfalls sehr stark und waren eng gekoppelt an die Verfügbarkeit der entsprechenden Nahrungsressource. Der Artenreichtum bei den Frugivoren schwankte antizyklisch in Wald- und Agrarlandhabitaten, was vermuten lässt, dass frugivore Arten ihren Fruchtressourcen über Habitatgrenzen hinweg folgen können. Im Gegensatz dazu fluktuierte der Artenreichtum insektivorer Vögel synchron in den zwei Habitattypen, was darauf hindeutet, dass bei dieser Nahrungsgilde Flüge über Habitatgrenzen hinweg selten stattfinden. Wir schlussfolgern daraus, dass Vogelgemeinschaften stark auf saisonale Schwankungen in der Nahrungsverfügbarkeit reagieren, wobei die Art der Reaktion sich zwischen Nahrungsgilden unterscheidet. Während Frugivore anscheinend flexibel auf saisonale Schwankungen reagieren können, z. B. indem sie ihren Fruchtressourcen über

Habitatgrenzen hinweg folgen, scheinen insektivore Vögel anfälliger für den erwarteten Anstieg saisonaler Schwankungen der Ressourcenverfügbarkeit zu sein.

1.5 Synthese

Die Umwandlung von tropischen Regenwäldern in Agrarland als Folge menschlichen Handelns wirkt sich grundlegend auf die biologische Diversität und die damit verbundenen Ökosystemfunktionen aus (Millennium Ecosystem Assessment 2005). Es wird weithin diskutiert, in welchem Ausmaß anthropogen modifizierte Landschaften die tropische Biodiversität und ihre Ökosystemfunktionalität aufrechterhalten können (z. B. Sekercioglu *et al.* 2007, Waltert *et al.* 2004). In meiner Arbeit habe ich einen zeitlich replizierten Datensatz verwendet, um den Wert von verschiedenen Habitaten unterschiedlicher Landnutzungsintensität für die Vogelgemeinschaften im tropischen Ost-Afrika zu ermitteln. Ich untersuchte Artenreichtum und Häufigkeiten von Vögeln entlang eines Wald-Agrarland-Gradienten und bestimmte die räumlichen und zeitlichen Schwankungen von Vogelgemeinschaften und deren Nahrungsressourcen.

Ich konnte in meiner Arbeit zeigen, dass Wald- und Agrarlandhabitate distinkte Vogelgemeinschaften beherbergen. Außerdem wurde deutlich, dass der Schutz von natürlichen Wäldern höchste Priorität genießen muss, um die hohe Diversität von Vogelarten, die speziell an Wälder gebunden sind, zu erhalten. Meine Arbeit zeigt aber auch, dass strukturreiche Agrarlandhabitate in der Nähe von natürlichen Wäldern eine hohe Vogeldiversität unterstützen können. Ausgehend von meinen Ergebnissen schlussfolgere ich, dass die Umwandlung von Wald zu Agrarland zu substantiellen Verlusten an Vogeldiversität führt, insbesondere bei spezialisierten Nahrungsgilden wie den

Insektivoren. Auch die Umwandlung der Agrarländer von strukturell heterogener Subsistenzwirtschaft in Zuckerrohrplantagen setzt die Vogeldiversität herab. Beide Ergebnisse sind entscheidend für die Planung von Schutzmaßnahmen in Zeiten, in denen tropische Regenwälder und Agrarökosysteme unter hohem Nutzungsdruck durch steigende Bevölkerungszahlen und steigender weltweiter Nachfrage nach Biotreibstoffen stehen (Gibbs *et al.* 2008).

Aus Sicht der Ökosystemfunktionen zeigt meine Arbeit, dass Agrarökosysteme über ein wichtiges Potential für die Aufrechterhaltung von wichtigen Ökosystemfunktionen wie Samenausbreitung durch frugivore Vögel und Schädlingsbekämpfung durch insektivore Vögel verfügen. Ich konnte zeigen, dass die Häufigkeiten von frugivoren als auch insektivoren Vögeln stark von ihren entsprechenden Nahrungsressourcen abhängen, was impliziert, dass saisonale Veränderungen in Frucht- und Insektenverfügbarkeit in Kakamega Forest und dem umgebenen Agrarland die Dynamik der Vogelgemeinschaften und das lokale Bewegungsmuster der Vögel beeinflussen. Besonders interessant ist, dass Nahrungsgilden unterschiedlich auf Schwankungen in der Nahrungsverfügbarkeit reagierten. Der Artenreichtum der Frugivoren schwankte asynchron in Wald- und Agrarlandhabitaten, was darauf hindeutet, dass die entsprechenden Vogelarten bei der Nahrungssuche auch Habitatgrenzen überschreiten. Im Gegensatz dazu fand ich für Insektivore, dass sie in beiden Habitattypen synchron ab- und zunahmen, was Flüge über Habitatgrenzen hinweg ausschließt. Insektivore Vogelgemeinschaften in dieser Wald-Agrarland-Landschaft erscheinen daher anfälliger gegenüber Klima- und Landnutzungsänderungen zu sein aufgrund ihrer engeren Habitatnische und der begrenzten Fähigkeit, ihre Bewegungsmuster den sich verändernden Nahrungsressourcen anzupassen.

Die Tatsache, dass sich in meinem Untersuchungsgebiet Vogelarten regelmäßig über Habitatgrenzen hinweg bewegten, impliziert, dass diese fähig sind Samenausbreitung über lange Distanzen und zwischen isolierten Habitaten aufrecht zu erhalten. Unter der Voraussetzung, dass Waldfragmente innerhalb einer Matrix aus Agrarhabitaten geschützt werden, können Vögel einen wichtigen Beitrag für die Waldregeneration in anthropogen modifizierten Landschaften leisten, wie sie in weiten Teilen des tropischen Afrikas vorherrschen. Meine Arbeit unterstreicht weiterhin die Bedeutung von Schutzstrategien, die über den reinen Waldschutz hinausgehen und explizit auch das Agrarland in Waldmanagementpläne einbeziehen. Diese Pläne sollten auf den Erhalt strukturreicher Agrarlandschaften fokussieren, um ein breites Spektrum an tropischer Artendiversität zu erhalten. Solche Managementempfehlungen sollten Farmern Anreize gegeben, ihre traditionelle Subsistenzwirtschaft beizubehalten, oder Gemeinschaftsprojekte zu initiieren, die eine Erhöhung der Habitatheterogenität und Konnektivität zwischen Habitaten zum Ziel haben.

2. INTRODUCTION

2.1 Background

The current decline of global forest cover is a major threat to biodiversity (Sala *et al.* 2000) and thus is of great concern to ecologists and conservationists alike (Tews *et al*. 2004, Butchart *et al*. 2010). In particular, human induced deforestation in many tropical regions has led to the transformation of native forests into impoverished forest fragments (Laurance and Bierregaard 1997), secondary forests, pastures, croplands and other human-dominated habitats (Myers 1992, Sala *et al.* 2000, Kammesheidt 2002). These land-use changes often have strong impacts on tropical biodiversity, because land-use intensity affects vegetation structure, which in turn affects diversity, abundance and distribution of animal populations (Hansen *et al.* 2001).

Although undisturbed tropical rain forests are arguably the most species-rich ecosystems on earth (Myers *et al.* 2000), tropical agroecosystems have been shown to hold high biodiversity as well (Peh *et al.* 2006, Ranganathan *et al.* 2010). However, there is still much debate about the potential value of agroecosystems for the maintenance of tropical biodiversity (Waltert *et al.* 2004). While most strategies for biodiversity conservation in tropical countries do not incorporate farmlands into their management plans (Millennium Ecosystem Assessment 2005), there is an increasing awareness that the vast extent of agroecosystems throughout the tropics should receive more attention in conservation planning (Ranganathan *et al.* 2010). It has been realized that restricting conservation efforts to set-aside conservation areas is not sufficient for slowing global biodiversity decline (Mora and Sale 2011). Birdlife International's Important Bird Areas (IBA) program takes this into account and includes farmlands as priority sites for conservation, although only if they hold globally threatened bird species (BirdLife International 2007).

Although many taxa have been affected by the ongoing land use changes, birds have received particular attention in terms of research and conservation activities (Ormerod and Watkinson 2000). This is largely due to their suitability as indicators of the effects of environmental change (Bibby *et al*. 1992). Being highly mobile, birds respond rapidly to fluctuations in habitat conditions (Whelan *et al.* 2008) and their diversity and distribution vary both in space and over time (White *et al.* 2010). Consequently, bird species richness and abundance may reflect responses of many other types of biodiversity (Bennun 1999, Gregory *et al.* 2003). Ecologically, birds play a key role in the functioning of ecosystems, notably pollination and seed dispersal services for plants, as well as controlling populations of invertebrate and vertebrate pests (Sekercioglu 2006). There is a growing consensus in ecosystem research that functional diversity rather than taxonomic diversity strongly determines ecosystem functioning (Diaz and Cabido 2001, Gamfeldt *et al.* 2008). Therefore, a broader understanding of the distribution of functional groups of birds at a landscape scale is useful in management and planning from a conservation and ecosystem-services perspective.

2.2 Study area

The study reported in this thesis was conducted in Kakamega forest, one of Kenya's biodiversity hotspots. Kakamega forest is a mid-altitude tropical rainforest (1520-1680 m, 0°10' - 0°21'N, 34°47' - 34°58'E). Annual precipitation in Kakamega averages about 2,000 mm with distinct bimodal peaks from March to May and from July to October (Farwig *et al.*

2008). Daily mean temperatures range between 10.6°C (rainy season) and 27.7°C (dry season) (Tsingalia 1990). Kakamega is one of the easternmost outliers of the Guineo-Congolian rainforests (Bennun and Njoroge 1999), thus the biodiversity occurring here has many affinities with that of Central and West African rainforests (Wagner *et al.* 2008). As such it is famous for its diverse avifauna, where over 410 bird species have been recorded within the forest and its surroundings (Shanni and de Bruinj 2006). It harbors two globally threatened bird species (Turner's Eremomela *Eremomela tuneri* and Chapin's Flycatcher *Muscicapa lendu*) (BirdLife International 2011) and 15 regionally threatened bird species (e.g. Crowned Eagle *Stephanoaetus coronatus,* Southern Hyliota *Hyliota australis*, Toro Oive Greenbul *Phyllastrephus hypochloris*) (Bennun and Njoroge 1999). Kakamega's altitudinal position gives it a rich assemblage of central African lowland species as well as Afrotropical highland species. This site has a higher number of forest-dependent bird species than any other Kenyan forest and almost 50 bird species are probably found nowhere else in Kenya (Bennun and Njoroge 1999). Based on its rich avifauna the forest is listed as one of Kenya's 60 Important Bird Areas (Bennun and Njoroge 1999).

Although the entire forest complex covers about 18,000 ha, only 10,000 ha are still continuous near-natural forest (Bennun and Njoroge 1999). Since 1986, about 4,000 ha of the northern portion of the forest, along with the adjacent 457 ha Kisere Forest, were gazetted as a National Reserve, managed by the Kenya Wildlife Service (KWS). The remaining forest is Forest Reserve, managed by Kenya Forest Service (KFS) and includes two small Nature Reserves, Yala and Isecheno (totaling about 700 ha). Whereas the National Reserve is strictly protected against logging or hunting activities, other forest areas within the forest complex are still faced with illegal logging and charcoal burning

(Bleher *et al.* 2006, Müller and Mburu 2009). Kakamega forest is surrounded by one of the most densely populated agricultural areas in Kenya with up to 643 persons per km^2 (Schaab *et al.* 2010). The agricultural landscape around the forest is characterized by large fields of sugarcane, a major cash crop in this region, and small scale subsistence farming of maize, beans and vegetables. The farmland is interspersed with patches of semi-natural vegetation of indigenous and exotic trees which occur in small woods or forest patches, scattered in between pastures or along streams, roads and field boundaries. Overall, the landscape in this study system is characterized by a mosaic of different types of land-use intensities, including near natural and secondary forests in the Kakamega National Reserve protected by the Kenya Wildlife Service as well as subsistence farmland and sugarcane plantations within the neighboring farmland areas. Due to its mosaic character, this landscape is perfectly suited for investigating spatial and temporal fluctuations of bird communities in different habitat types reflecting a gradient of anthropogenic land-use intensity.

2.3 Structure and objectives of the thesis

2.3.1 Thesis structure

After an extended German summary (Chapter 1) and a general introduction (Chapter 2), my thesis has two major research chapters (Chapter 3 and 4). Each of these chapters deals with specific questions addressing my overarching study topic and is structured in the form of a full journal publication. Chapter 5 provides a general synthesis of my study with overall conclusions and future perspectives for research and conservation actions. All references cited throughout this thesis are placed at the end of the thesis followed by appendices including supplementary information.

2.3.2 Thesis objectives

The objectives of my thesis are founded on the premise that land-use change is a key driver and threat of current and future global biodiversity. In my study I sought to contribute to the understanding of spatial and temporal relationships of bird communities to land-use intensity and resource availability across a mosaic of habitat types at a landscape scale. The thesis aims at contributing to conservation management in tropical Africa: If the diversity and composition of bird communities differ substantially among habitat types in this forest-farmland mosaic, then management plans for bird conservation in Kenya must have a stronger emphasis on land-use management in both forest and agricultural ecosystems.

Kakamega forest and its surroundings offered an ideal study system for my study objectives as it offers a comprehensive land-use gradient ranging from intact forest to highly modified agricultural farmland. To cover the entire land-use gradient, I investigated bird communities in two forest habitat types (near-natural forest and secondary forest) and two farmland types (mixed farmland and sugarcane plantation). I conducted bird surveys over a one year period covering different seasons, thus achieving an almost complete inventory of temporal variation in habitat occupancy, e.g. due to seasonal fluctuations in bird communities related to breeding activities and migration (Cox 2010). In addition, the one-year sampling period in all habitat types accounts for temporal habitat heterogeneity, which could lead to underestimation of bird abundance and diversity within a given habitat type (Brown 2006).

In chapter 3, I compared bird abundance and species richness along a forest-farmland habitat gradient under different land-use intensities. Furthermore, I assessed the effects of the structural diversity of the vegetation on bird abundance and species richness within forest and farmland habitats aiming at identifying landscape keystone elements that sustain high bird diversity in the respective habitat types. Finally, I examined the relative contributions of spatial and temporal species turnover to bird diversity and quantified bird community turnover for different functional groups of birds along the forest-farmland gradient. For this chapter, I collected the bird data in the field myself with the help of my field assistants, i.e. Patrick Luteshi and Jonathan Mukaisi. I analysed the data and wrote the manuscript. Matthias Schleuning and Katrin Böhning-Gaese contributed to the study design, data analysis and to writing the manuscript.

In chapter 4, I examined seasonal fluctuations in fruit and invertebrate resources and related fluctuating resource availabilities to abundance and richness of the corresponding avian feeding guilds (frugivorous and insectivorous birds) in Kakamega forest and neighboring farmlands. I investigated fluctuations of resources (fruits and invertebrates) and bird guilds (frugivores and insectivores) over an entire year and tested whether fluctuations in both resources and bird communities were habitat-specific. More specifically, I tested whether fluctuations in resource abundance predicted fluctuations in the corresponding feeding guilds. Since there have been more studies relating resources and birds about frugivorous than about insectivorous birds, I sought to establish whether the two feeding guilds responded differently to resource fluctuations, for instance by guild-specific foraging movements within or across habitat types. Such cross-habitat and community-wide relationships between birds and spatiotemporal variation in their food resources have hardly been addressed in previous studies and therefore this study is an important contribution to our knowledge on seasonal fluctuations among bird communities. This knowledge is increasingly important since seasonal climatic fluctuations have increased and are expected to intensify further in the near future (Fischlin *et al.* 2007). I collected the data on fruit and insect abundance in the field myself with the help of field assistants, i.e. Benson Chituyi and Colins Alusiola. The bird data are identical to the data in chapter 3. I analysed the data and wrote the manuscript. Matthias Schleuning, Eike Lena Neuschulz and Katrin Böhning-Gaese contributed to the design of the study, the analyses of the data and to writing the manuscript.

CHAPTER 3

HIGH BIRD SPECIES DIVERSITY IN STRUCTURALLY HETEROGENEOUS FARMLAND IN WESTERN KENYA

Submitted to an international ecology journal as:

Mulwa, R. K., Böhning-Gaese, K. & Schleuning, M. (submitted). High Bird Species Diversity in Structurally Heterogeneous Farmland in Western Kenya.

3.1 Abstract

Tropical ecosystems are globally important for bird diversity. In many tropical regions, land-use intensification has caused conversion of natural forests into human-modified habitats such as secondary forests and heterogeneous agricultural landscapes. Despite previous research, the distribution of bird communities in these forest-farmland mosaics is not well understood. To achieve a comprehensive understanding of bird diversity and community turnover in a human-modified Kenyan landscape, we recorded bird communities at 20 sites covering the complete habitat gradient from forest (near natural forest, secondary forest) to farmland (subsistence farmland, sugarcane plantation) using point counts and distance sampling. Bird density and species richness were on average higher in farmland than in forest habitats. Within forest and farmland, bird density and species richness increased with vegetation structural diversity, i.e. were higher in near natural than in secondary forest and in subsistence farmland than in sugarcane plantations. Bird communities in forest and farmland habitats were very distinct and very few forest specialists occurred in farmland habitats. Moreover, insectivorous bird species declined in farmland habitats whereas carnivores and herbivores increased. Our study confirms that tropical farmlands can hardly accommodate forest specialist species. Contrary to most previous studies, our findings show that structurally-rich tropical farmlands hold a surprisingly rich and distinct bird community that is threatened by conversion of subsistence farmland into sugarcane plantations. We conclude that conservation strategies in the tropics must go beyond rainforest protection and should integrate structurally heterogeneous agroecosystems into conservation plans that aim at maintaining the diverse bird communities of tropical forest-farmland mosaics.

3.2 Introduction

Human-induced deforestation is rampant in many tropical regions (Sala *et al.* 2000). As a result, tropical forests worldwide are being reduced to biologically impoverished remnants (Laurance and Bierregaard 1997) and regenerating secondary forests (Kammesheidt 2002) embedded in agroecosystems (Daily *et al.* 2001). Besides much debate about the value of these agroecosystems for the maintenance of tropical biodiversity (Waltert *et al.* 2004), their vast extent throughout the tropics means that they should receive more attention in conservation planning (Ranganathan *et al.* 2010). However, most strategies for biodiversity conservation in tropical countries do not incorporate farmlands into their management plans (Millennium Ecosystem Assessment 2005). One exception is Birdlife International's Important Bird Areas (IBA) program which includes farmlands as priority sites for conservation (BirdLife International 2007), though only if they hold globally threatened bird species.

Although undisturbed tropical rain forests are recognized as the most species-rich ecosystems on earth (Myers *et al.* 2000), tropical agroecosystems can also hold high biodiversity (Peh *et al.* 2006, Ranganathan *et al.* 2010). The occurrence of forest bird species in farmlands depend, among other factors, on the distance to remnant forest patches and on the local structural diversity in farmland habitats (Laube *et al.* 2008). In addition to spatial variation, the distribution of bird diversity can also vary temporally (White *et al.* 2010) because birds are highly mobile and respond rapidly to fluctuations in habitat conditions (Whelan *et al.* 2008). To understand how bird diversity is distributed in human-modified tropical forest-farmland mosaics, it is necessary to examine bird species richness (α-diversity) as well as spatial and temporal community turnover (β-diversity) at a landscape scale (Neuschulz *et al.* 2011). Such comprehensive approaches can help to guide strategies for maintaining biological diversity and ecosystem integrity in human-dominated landscapes (Sarr and Puettmann 2008).

There is a growing consensus that functional diversity rather than taxonomic diversity strongly determines ecosystems functioning (Gamfeldt *et al.* 2008). Given the pivotal ecological roles played by birds in both forest and farmland ecosystems, notably pollination, seed dispersal and pest control (Sekercioglu 2006, Whelan *et al.* 2008), it is necessary to understand the distribution patterns of different functional groups of birds across landscapes. A broader knowledge of the distribution of different functional groups of birds at a landscape scale will be helpful for conservation planning from an ecosystem-services perspective.

Here, we present a bird-community study from the Kakamega forest area in western Kenya that comprises 1,440 point counts from an entire year covering a habitat gradient from structurally rich to structurally poor habitats. The habitats include two forest (near natural forest and secondary forest) and two farmland habitat types (subsistence farmland and sugarcane plantation). The objectives of this study were to compare bird density and species richness between forest and farmland habitats and to assess the effects of vegetation structural diversity on bird communities within forest and farmland habitats. In addition, we examined the relative contributions of spatial and temporal species turnover to bird diversity and quantified bird community turnover for different habitat and feeding guilds along the forest-farmland gradient. We predicted that (1) overall bird density and species richness are higher in forest than in farmland habitats, that (2) birds are more abundant and diverse in habitats with high structural diversity and that (3) bird communities in forest and farmland habitats are distinct and are dominated by different habitat and feeding guilds. If the diversity and composition of bird communities differ substantially among habitat types in this forest-farmland mosaic, then this should have important implications for bird conservation and land-use management in tropical Africa.

3.3 Methods

3.3.1 Study area

The study was conducted within and around Kakamega forest in western Kenya, a mid-altitude tropical rainforest (1520-1680 m, 0°10' - 0°21'N, 34°47' - 34°58'E, Fig. 3.1). Kakamega forest is one of the easternmost outliers of the Guineo-Congolian rainforests (Kokwaro 1988). The forest is known for its diverse avifauna, being home to over 410 bird species (Shanni and de Bruinj 2006). It harbors two globally threatened (BirdLife International 2011) and 15 regionally threatened bird species, and is thus listed as one of Kenya's 60 Important Bird Areas (Bennun and Njoroge 1999). Annual precipitation in Kakamega averages 2,007 mm with distinct bimodal peaks from March to May and from July to October (Farwig *et al.* 2008). Daily mean temperatures range between 10.6°C (rainy season) and 27.7°C (dry season) (Tsingalia 1990). The forest is surrounded by one of the most densely populated agricultural areas in Kenya with up to 643 persons per km^2 (Schaab *et al.* 2010). The human settlements around the forest are characterized by large fields of sugarcane, a major cash crop in this region, and small scale subsistence farming of maize, beans and vegetables. The farmland is interspersed with patches of natural vegetation as well as indigenous and exotic trees. The current study covered near natural and secondary forests in the Kakamega National Reserve protected by the Kenya Wildlife

Service as well as subsistence farmland and sugarcane plantations within the neighboring farmland areas (Fig. 3.1). The National Reserve is strictly protected since the early 1980s and logging activities are prohibited. Outside the National Reserve, illegal logging and charcoal burning do occur more frequently (Bleher *et al.* 2006, Müller and Mburu 2009).

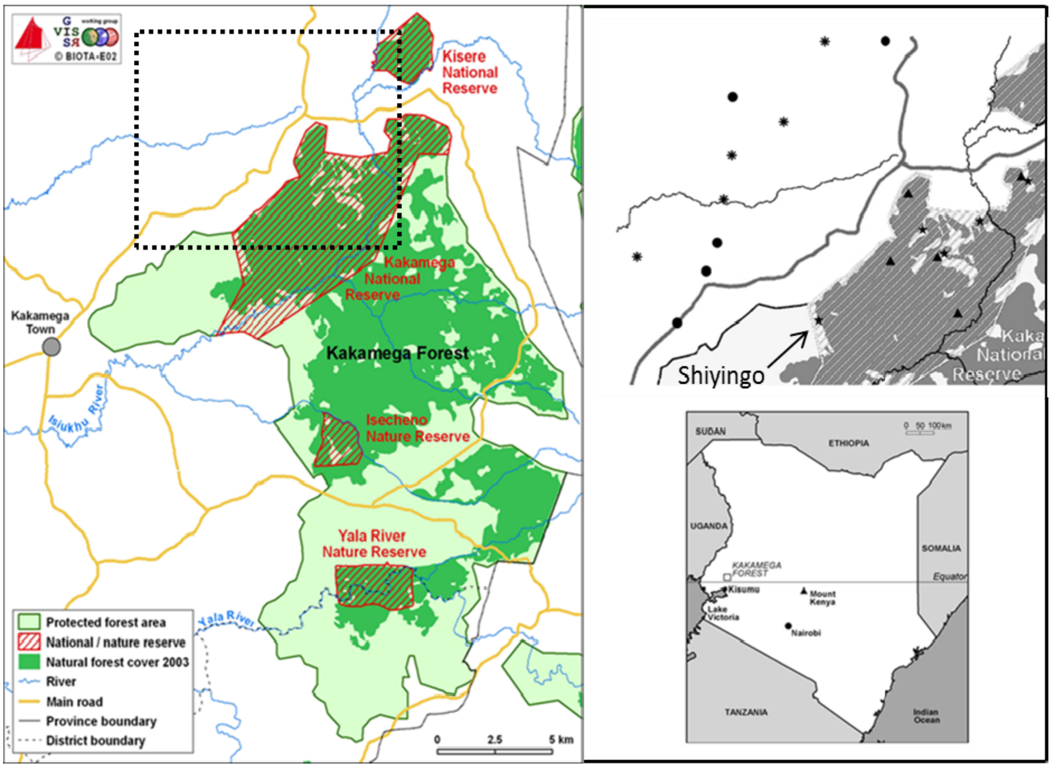

Figure 3.1: Location of the study area in Kakamega forest, Western Kenya. The dotted box indicates the location of the study area. Study sites are indicated by habitat type as triangles (near natural forests), stars (secondary forests), solid circles (subsistence farmlands), and asterisks (sugarcane plantations).

3.3.2 Study design

Between February 2009 and January 2010, we recorded birds and vegetation structure in four habitat types (two in forest and two in farmland) representing a gradient in land-use intensity and vegetation structural heterogeneity, i.e. (1) near natural forest, (2) secondary forest, (3) subsistence farmland and (4) sugarcane plantation. Near natural forest sites were located in undisturbed dense forest characterized by canopy tree species such as *Croton megalocarpus, Olea capensis* and *Funtumia africana*. Secondary forests constituted formerly disturbed, regenerating forests with low and open canopy dominated by secondary plant species such as *Polyscias fulva, Harungana madagascariensis* and *Psidium guajava*. Subsistence farmlands were small-scale mixed crop farms, with patches of fallow land, isolated trees, bushes, hedgerows and small gallery forests. Sugarcane plantations were large fields dominated by sugarcane with few isolated indigenous and exotic trees and little natural vegetation. Widespread woody plant species in farmland include *Croton macrostachyus, Harungana madagascariensis, Eucalyptus saligna, Psidium guajava* and *Lantana camara*.

Using a stratified sampling design, we selected five replicate study sites for each of the four habitat types from different parts of the study area (Fig. 3.1, Appendix 1). Within each of these 20 sites, we placed six point count locations where both birds and vegetation structure were sampled. Adjacent point count locations in each site were 100 m apart. All farmland sites were placed at least 2 km from the forest edge, while forest sites were at least 250 m away from the forest edge. Adjacent sites of the same habitat type were at least 1.25 km apart.

3.3.3 Vegetation structure

At all 120 sampling plots (4 habitat types x 5 study sites x 6 point count locations) in forest and farmland habitats, we surveyed vegetation structure within a 20 m radius from the centre of the plot. Two aspects of vegetation structure, i.e. vertical foliage diversity and tree basal area, were sampled once for all sites. To determine vertical foliage diversity, we estimated the percentage vegetation cover to the nearest 5 percent at vertical layers between 0 m and 32 m (i.e. at 0 m, 1 m, 2 m, 4 m, 8 m, 16 m and 32 m). Vertical foliage diversity in each plot was then obtained using the Shannon-Wiener diversity index (Bibby *et al.* 2000). In the forest sites, 5x5 m plots were placed 10 m from the center of each plot along the four compass directions. We measured the diameter at breast height (DBH) for all trees with a DBH >10 cm within these plots. At farmland sites, DBH of all trees with a DBH >10 cm was measured within the entire 20 m radius. We used DBH measurements to calculate tree basal area per hectare (TBA, m^2/ha) in both forest and farmland sites (Sagar and Singh 2006).

3.3.4 Bird surveys

We surveyed birds over a one year period by point counts using distance sampling. All 120 point count locations were surveyed once every month, adding up to a total of 1,440 point counts. All point counts were conducted between 0700 h and 0900 h when birds were most active. At each point, we recorded all birds seen or heard up to a 50 m radius within 15 minutes. We determined the radial distances between the observer at the point centre and the birds' location using a laser rangefinder. Birds in flight were not recorded.

3.3.5 Bird density and species richness

We estimated the overall density of the bird community across all species using DISTANCE Version 6 (Thomas *et al.* 2009). Density estimates based on distance sampling account for different detection probabilities in different habitats by fitting a detection function for the relationship between detection and distance from the observer (Thomas *et al.* 2010). Prior to fitting an appropriate detection function, we split the 50 m distances into ten 5 m-intervals because distance estimates from the field had an accuracy of about 5 m. Observations of conspecific bird flocks comprising more than a single individual were treated as clusters of individuals. In addition, we applied a 10 percent right truncation, i.e. we discarded observations beyond 45 m as recommended by Buckland *et al.* (2001). We then pooled bird counts from the same month from the six points within a study site and treated repeated counts in different months as sampling replications. To determine the best detection function, we tested functions and adjustments suggested by Thomas *et al.* (2010). We selected the best model according to AIC. In our analyses, uniform key with cosine adjustment was selected in 14 of the 20 sites as the best model, hazard-rate key with simple polynomial adjustments in five sites (two in near natural, one in secondary forest and two in subsistence farmland), and half-normal key with cosine adjustments in one site (sugarcane plantation) (Appendix 1).

Consistent with the community focus of our study, we obtained densities for the entire bird community (birds per ha) and not for individual species. Given our data set, it was not feasible to fit individual detection functions for every single species because species diversity was very high and many species were rare. Since DISTANCE has typically been used to assess the density of individual species (Buckland *et al.* 2001; but see Otieno *et* *al.* 2011), we tested whether the estimates of community-wide densities obtained from DISTANCE were consistent with the estimates of bird density without applying a detection function. We found that the differences in bird densities between habitats were qualitatively the same irrespective of the method, i.e. with fixed radii of 20 m, 50 m and with the respective detection function. Thus, potential differences in detectability among habitat types did not affect our findings.

To quantify bird species richness, we also accounted for potentially different detection probabilities among habitats by calculating an expected species richness per ha for each site and month. Using an individual-based rarefaction (function ‘rarefy’ in R package vegan; Oksanen *et al.* 2010), we determined the expected number of bird species for the DISTANCE-based densities of bird individuals based upon species-accumulation curves for each site and month. In further analyses, we compared the mean species richness per month between habitat types.

3.3.6 Partitioning of species diversity across time and space

We determined temporal and spatial species turnover using additive partitioning of species diversity (Crist *et al.* 2003). Alpha diversity (α) was defined as the mean number of species per site and month. The temporal turnover (β_T) in species richness between months was calculated for each site as the total number of species found within that site (over the entire year) minus the mean number of species per month for that site (α). Spatial turnover (β_S) was calculated as the total number of species found within a habitat type (over the entire year) minus the mean number of species per site for that habitat type (over the entire year). The overall diversity (γ) of a habitat type was thus described as $\gamma = \alpha + \beta_T + \beta_S$.

In addition, we partitioned diversity across all habitat types and determined means of the different diversity components across habitat types, i.e. calculated the proportions of α, $\beta_{T,}$ and β_S from the total number of species. The proportion of γ-diversity that was due to bird community turnover between habitats (i.e. turnover), was then defined as: Turnover = 1 – (mean α/n + mean β_T/n + mean β_S/n), where n is the total number of species recorded from all habitats (Hagen and Kraemer 2010).

3.3.7 Community composition

To compare bird community composition between different habitats, we compiled a site by species matrix summed over the six point locations per study site and over the 12 months. For this analysis, we assigned bird species to different habitat and feeding guilds. Habitat guilds followed Bennun *et al.* (1996): (1) forest specialists (species that breed in the interior of undisturbed forest), (2) forest generalists (species that breed in both near natural and secondary forest), (3) forest visitors (species that occur in forest habitats but are more common in non-forest habitats), (4) farmland birds (species that are not classified in any forest category). For the classification of feeding guilds, we used a database of major food items of birds from sub-Saharan Africa by Kissling *et al.* (2007), i.e. (1) carnivores (feeding on vertebrates), (2) insectivores (feeding on invertebrates), (3) omnivores (feeding on both plant and animal material), (4) herbivores (feeding mainly on plant parts, including seeds, leaves, shoots, roots, flowers, bulbs), (5) frugivores (feeding on fruits). In addition, we inferred the conservation status of each species from the IUCN (BirdLife International 2011) and regional (Bennun and Njoroge 1999) red lists.

3.3.8 Statistical analysis

We conducted all statistical analyses using R version 2.11.1 (R Development Core Team 2011). We compared vegetation structure (vertical foliage diversity and tree basal area), bird densities and species richness between different habitat types using ANOVA. According to our sampling design, we defined three orthogonal contrasts to compare forest vs. farmland habitats, near natural vs. secondary forest (within forest) and subsistence farmland vs. sugarcane plantations (within farmland). Significance of contrasts was assessed with t-tests. We used a MANOVA to test whether partitioning of bird diversity differed between habitat types by comparing the proportions of alpha diversity (α) and temporal beta diversity (β_T) between habitats. For ANOVA and MANOVA analyses, we confirmed the assumptions of normality and variance homogeneity.

To assess differences in bird community composition, we conducted a nonmetric multidimensional scaling (NMDS) analysis of the quantitative site by bird species matrix; a two-dimensional NMDS ($k = 2$ axes) performed very well (stress = 3.33). We tested whether habitat variables (i.e. habitat type, vertical foliage diversity and tree basal area) explained differences between sites in the NMDS plot; the significance of the habitat variables was tested with permutation tests. Furthermore, we applied a fourth-corner analysis to link community turn-over along the habitat gradient to changes in bird traits (i.e. in habitat and feeding guilds) (Dray and Legendre 2008, Leyequién *et al.* 2010) using the R package ‘ade4’ (function 'fourthcorner'). We carried out the analysis across the entire forest-farmland gradient and separately for forest and farmland habitats, respectively. To account for differences in overall bird densities and species richness, the bird community matrix was Hellinger transformed prior to the analysis (Legendre and Gallagher 2001). The significance of the relationship between species traits and habitat types was then tested with a χ^2-statistic and a permutation test (999 iterations). We chose permutation model 1 following Aubin *et al.* (2009), which is based on a permutation of abundances for each species independently and tests the null hypothesis that species are randomly distributed along the habitat gradient (Dray and Legendre 2008). To assess the significance of the relationships between habitat type and habitat and feeding guilds, we corrected the P-values with a Bonferroni correction.

3.4 Results

3.4.1 Vegetation structure

Vertical foliage diversity and tree basal area differed significantly between the four habitat types ($F_{(3,16)} = 11.38$, $P < 0.001$ and $F_{(3,16)} = 64.87$, $P = 0.001$, respectively). Vertical foliage diversity and tree basal area were higher in forest than in farmland sites ($t_{(18)} = 4.64$, $P < 0.001$ and $t_{(18)} = 12.27$, $P < 0.001$ respectively, Fig. 3.2). Moreover, vertical foliage diversity was higher in near natural than in secondary forest and in subsistence farmland than in sugarcane plantations ($t_{(8)} = 2.45$, $P = 0.028$ and $t_{(8)} = 2.57$, $P = 0.021$ respectively, Fig. 3.2). Tree basal area was higher in near natural than in secondary forests ($t_{(8)} = 6.39$, $P < 0.001$), but did not differ significantly between subsistence farmland and sugarcane plantations ($t_{(8)} = 1.79$, $P = 0.093$, Fig. 3.2).

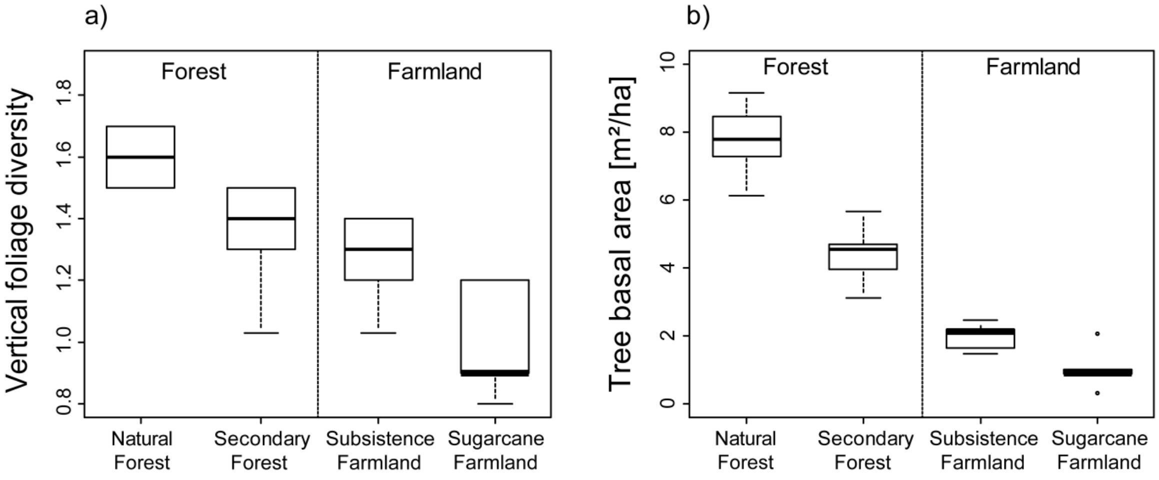

Figure 3.2: Differences in a**)** vertical foliage diversity and in b) tree basal area between four types of forest (near-natural and secondary) and farmland (subsistence and sugarcane) habitats in Kakamega forest and neighboring farmlands. Lines across boxes are medians, boxes indicate 25th and 75th percentiles, whiskers indicate 10th and 90th percentiles, and circles are outliers. Tree basal area was square-root transformed.

3.4.2 Bird density and species richness

A total of 19,073 individual birds belonging to 237 species and 50 families were recorded across all sites and months (Appendix 2). The species pool included two globally and eleven regionally threatened species as well as one regionally rare species. Habitat type significantly affected both bird density ($F_{(3,16)} = 17.42$, $P < 0.001$) and species richness ($F_{(3,16)} = 17.17$, $P < 0.001$). Overall, farmland sites had significantly higher bird density and species richness than forest sites ($t_{(18)} = 5.79$, $P < 0.001$ and $t_{(18)} = 4.87$, $P = 0.001$, respectively Fig. 3.3a, 3.3b). Bird density in near natural and secondary forest sites did not differ significantly ($t_{(8)} = 0.99$, $P = 0.333$), but was significantly higher in subsistence farmland than in sugarcane plantations ($t_{(8)}$ = 4.04, $P < 0.001$, Fig. 3.3a, Appendix 1). Furthermore, bird species richness was higher in near natural than in secondary forest ($t_{(8)}$ = 2.57, P = 0.021) and in subsistence farmland than in sugarcane plantations ($t_{(8)}$ = 4.60, $P <$ 0.001, Fig. 3.3b).

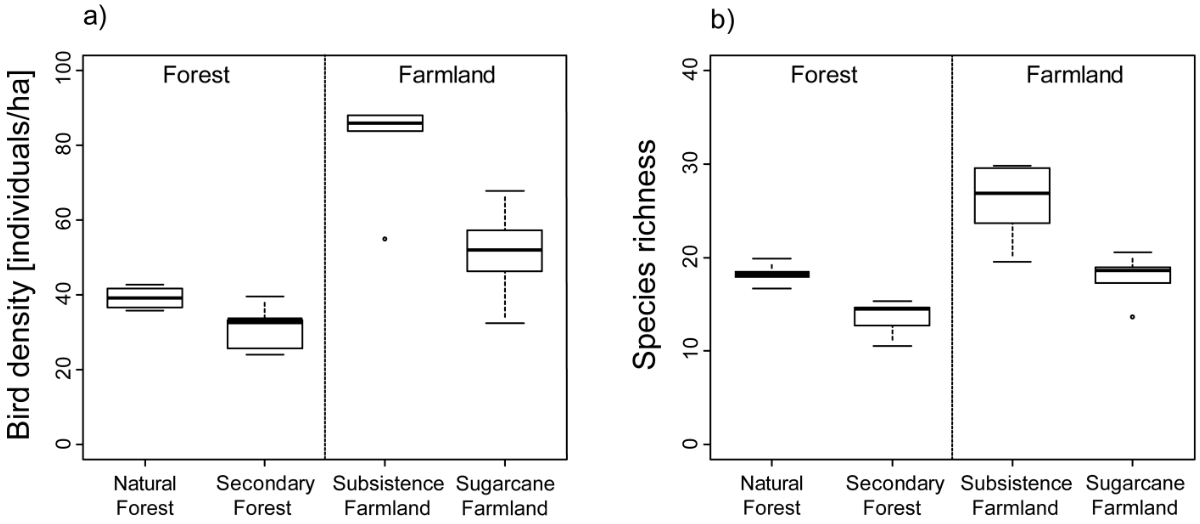

Figure 3.3: Differences in a) bird densities and b) expected bird species richness between four types of forest (near-natural and secondary) and farmland (subsistence and sugarcane) habitats in Kakamega forest and neighboring farmlands. Lines across boxes are medians, boxes indicate 25th and 75th percentiles, whiskers indicate 10th and 90th percentiles, and circles are outliers.

Across all sites, there were no significant correlations between bird abundance (density and species richness) and vegetation structure (vertical foliage diversity and tree basal area) (Table 3.1). However, in separate analyses for forest and farmland sites, both bird density and species richness were positively correlated to vertical foliage diversity in the two habitat types. In addition, tree basal area was positively correlated to both bird density and species richness within farmland sites and to species richness within the forest sites (Table 3.1).

Table 3.1: Correlation analyses between bird density and species richness and vertical foliage diversity and tree basal area in Kakamega forest and neighboring farmlands. Analyses were conducted across all 20 study sites and separately for 10 forest sites and 10 farmland sites. Significant effects ($P < 0.05$) are printed in bold.

Study sites	**Bird variables**	**Vertical foliage diversity**		**Tree basal area**	
		r	***P***	***r***	***P***
All sites	Density	-0.091	0.703	-0.427	0.060
	Species richness	0.067	0.780	-0.248	0.292
Forest sites	Density	0.668	**0.035**	0.508	0.134
	Species richness	0.823	**0.003**	0.645	**0.044**
Farmland sites	Density	0.800	**0.005**	0.878	**0.001**
	Species richness	0.751	**0.012**	0.830	**0.003**

3.4.3 Partitioning of species diversity across time and space

Overall, alpha diversity comprised 10.5 percent of the total diversity of the study region (237 species). Temporal and spatial turnover comprised 21.5 percent and 22.4 percent, respectively. A high proportion of 45.6 percent of overall species diversity represented species turnover between the different habitat types (Fig. 3.4a). The four habitat types differed in the relative partitioning of diversity in time and space. In comparison to the other habitat types, near natural forest had significantly higher proportions of alpha diversity, but a lower proportion of spatial species turnover (β_S) (MANOVA, $F_{(6,30)} = 15.46$, $P < 0.001$; Fig. 3.4b). Therefore, alpha diversity was significantly higher in forest than in farmland sites ($t_{(16)} = 3.03$, $P = 0.008$) and in near natural than in secondary forest ($t_{(16)} = 5.48$, $P < 0.0001$); spatial species turn-over showed the opposite pattern. Secondary forest, subsistence farmland and sugarcane plantations had similar proportions of alpha diversity (α), temporal (β_T) and spatial (β_S) species turnover (Fig. 3.4b).

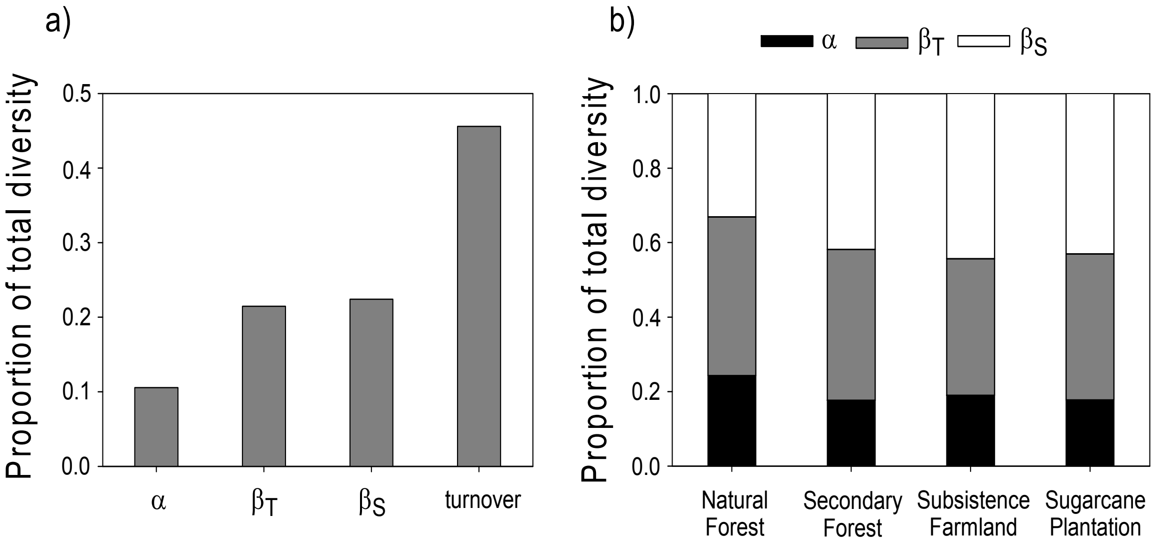

Figure 3.4: Partitioning of total diversity (γ) into alpha (α) diversity and temporal (β_T) and spatial (β_S) turnover. a) Diversity partitioning across all habitat types and b) partitioning of species diversity for the respective habitat types. Alpha diversity represents the mean number of species per site per month, temporal turnover (β_T) is the total number of species found within a site (over the entire year) minus the mean number of species per month for that site (α), spatial turnover (β_S) is the total number of species found within a habitat type over the entire year minus the mean number of species per site in that habitat type (over the entire year) and turnover is the proportion of γ-diversity that is due to species turn-over among habitat types.

3.3.4 Community composition

Bird communities were very distinct between forest and farmland habitats (Fig. 3.5a). A single secondary forest site (Shiyingo) had a bird community that was intermediate between forest and farmland, though much closer to forest sites. Differences in vertical foliage diversity ($R^2 = 0.60$, $P < 0.001$), tree basal area ($R^2 = 0.85$, $P < 0.001$) and habitat type

($R^2 = 0.95$, $P < 0.001$) were closely related to differences in bird community composition along the forest-farmland gradient (Fig. 3.5a). Accordingly, a rather small proportion of bird species occurred in both forest and farmland habitats (Fig. 3.5b). More bird species occurred in farmland habitats (148 species) compared to forest habitats (89 species, Fig. 3.5b). The distribution of bird species along the forest-farmland gradient was largely consistent with the forest dependence classification of Kenyan birds by Bennun *et al.* (1996). Forest specialists were largely restricted to forest sites (except the Red-chested Owlet *Glaucidium tephronotum,* only recorded in a riverine thicket in the farmland), whereas forest generalists and visitors occurred in both forest and farmland habitats (Fig. 3.5b, Appendix 2).

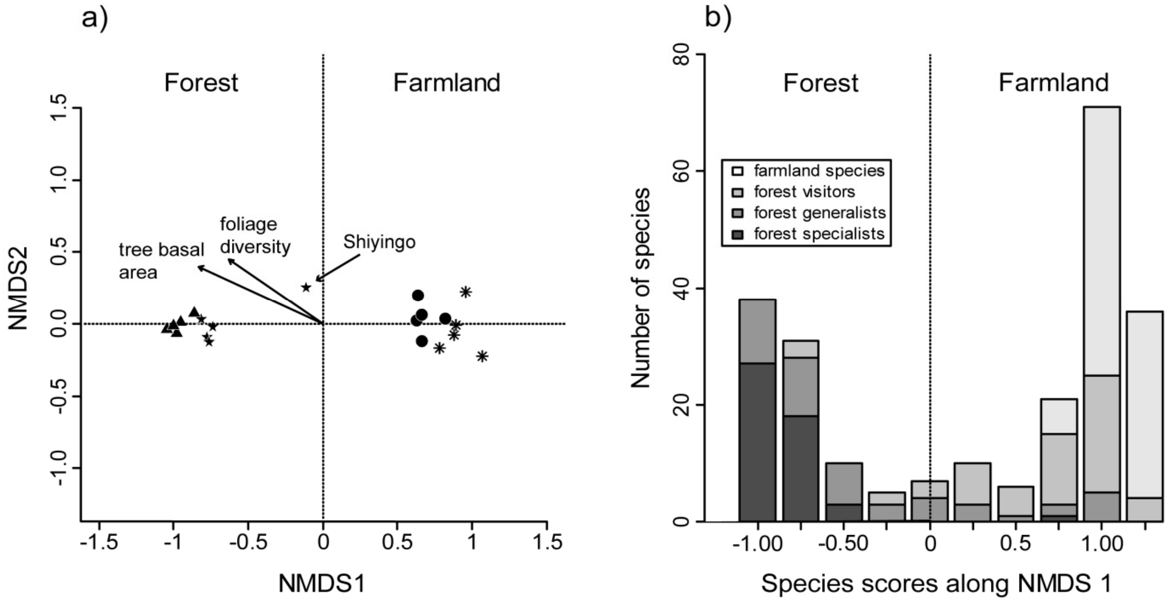

Figure 3.5: Results from non-metric multidimensional scaling (NMDS) analysis of differences in bird community composition between four habitat types in forest and farmland in Kakamega forest and its surroundings. a) Ordination plot of the 20 study sites situated in four different habitat types. Habitat types are indicated as triangles (near natural forests), stars (secondary forests), solid circles (subsistence farmlands) and asterisks (sugarcane plantations), and b) distribution of 237 bird species of different degree of forest dependence along the first axis of the ordination plot. The 1st NMDS axis shows a gradient of bird community composition with negative scores representing true forest communities and positive scores representing farmland communities.

Fourth-corner analysis confirmed a high turnover of habitat guilds from forest to farmland. Forest specialists and generalists were more frequent in forest than in farmland habitats, whereas forest visitors and farmland species were much more abundant in farmland habitats (Table 3.2). Within forest habitats, forest specialists were more frequent in near natural than in secondary forest, whereas forest visitors and farmland species showed the opposite trend (Table 3.2). Within farmland habitats, forest generalists and visitors were more frequent in subsistence farmland than in sugarcane plantations, while farmland species increased in abundance in sugarcane. Similarly, feeding guild composition also changed from forest to farmland (Table 3.2). Insectivores decreased in relative abundance in the farmland, whereas carnivores and herbivores increased. The relative abundances of frugivores and omnivores were not related to the forest-farmland gradient (Table 3.2). Within forest and farmland habitats, feeding guild composition was not significantly different between near natural and secondary forest and between subsistence farmland and sugarcane plantations, respectively (Table 3.2).

Table 3.2: Results of a fourth-corner analysis of the relationship between bird guilds and habitat types in Kakamega forest and neighboring farmlands. Bird guild composition was compared between (a) forest and farmland sites, between (b) near natural and secondary forest, and between (c) subsistence farmland and sugarcane plantations. χ^2 statistics were tested in a permutation model that tests whether bird species are randomly distributed across habitat types (Dray and Legendre 2008). For significant relationships at the 5% significance level after Bonferroni correction, the sign indicates if the statistic is above (+) or below (–) the expected value; blanks indicate non-significant relationships.

Bird guilds	**a) Forest vs. Farmland**			**b) Near natural vs. Secondary**			**c) Subsistence vs. Sugarcane**		
	χ^2	***P***	**Effect**	χ^2	***P***	**Effect**	χ^2	***P***	**Effect**
Habitat guilds									
Forest specialists	39.93	**0.001**	+	1.46	**0.001**	+	0.10	0.097	
Forest generalists	11.10	**0.001**	+	0.06	0.164		1.00	**0.001**	+
Forest visitors	12.71	**0.001**	–	2.60	**0.001**	–	0.41	**0.001**	+
Farmland species	32.43	**0.001**	–	0.70	**0.002**	–	1.89	**0.001**	–
Feeding guilds									
Carnivores	1.07	**0.001**	–	<0.01	0.932		<0.01	0.796	
Insectivores	2.05	**0.001**	+	0.12	0.049		0.03	0.236	
Omnivores	<0.01	0.921		<0.01	0.783		0.02	0.404	
Herbivores	2.06	**0.001**	–	0.13	0.046		0.04	0.210	
Frugivores	<0.01	0.804		0.02	0.357		0.15	0.021	

3.5 Discussion

Contrary to our expectation and despite a substantial drop in vegetation structural diversity from forest to farmland, bird density and species richness in western Kenya were on average higher in farmland than in forest habitats. Most previous studies in the tropics have reported higher bird species richness in forested areas than in nearby agroecosystems (Thiollay 1995, Daily *et al.* 2001, Naidoo 2004, Waltert *et al.* 2004, Seavy 2009; but see Marsden *et al.* 2006, Gove *et al.* 2008). This trend of decreasing bird species richness with increasing land-use intensity in the tropics is consistent with studies from temperate regions where the decline in bird species richness in structurally simple farmlands is particularly strong (Heikkinen *et al.* 2004, Breitbach *et al.* 2010). Our findings contradict the long-standing paradigm of decreasing bird species richness from forest to farmland habitats (MacArthur and MacArthur 1961) and rather suggest that the distribution of bird diversity in tropical forest-farmland mosaics is highly context-dependent. The general trend of lower bird species richness in tropical farmland than in forest habitats could be due to the fact that most previous studies investigated intensively utilized agroecosystems (e.g. Waltert *et al.* 2004, Seavy 2009). A factor that may account for the exceptionally high diversity of farmland birds in this Kenyan locality is the occurrence of a large species pool of widespread open-country birds that have always occupied the vast savannah woodland and grassland areas in Eastern Africa (Zimmerman *et al.* 1996).

Previous studies have pointed out that land-use intensity and thus the structural diversity in tropical farmlands strongly influence bird diversity (Harvey *et al.* 2006, Sekercioglu *et al.* 2007, Laube *et al.* 2008). The high bird species richness in the farmlands around Kakamega forest may partly be attributable to its high structural diversity, particularly in the subsistence farmland, which comprises forest galleries, hedgerows, marshy streams and different crops. These heterogeneous structural elements may constitute different micro-habitats and niches for a wide variety of bird species (Tews *et al.* 2004). The high spatial turnover of bird diversity in farmland habitats found in this study is consistent with this explanation and indicates that the complex mosaic structure of the farmland strongly contributed to the exceptionally high bird diversity in this Kenyan farmland. We did not test the effects of landscape-level variables on bird communities which could affect bird communities differently than local-scale conditions (Leyequién *et al.* 2010). In our study area, however, locally high species richness as well as high spatial species turn-over indicate high bird diversity at both local and landscape scale in this subsistence farmland. We stress that bird diversity could be differently distributed in other parts of rural Africa where current and historical land tenure systems could be different from those around Kakamega Forest. Future studies comparing bird diversity between different subsistence systems will be crucial for testing the generality of our findings.

For the Kakamega system, our findings imply that the conversion of structurally heterogeneous subsistence farmlands to large scale monocultures would result in a substantial reduction of bird diversity. Bird diversity and abundance were reduced by more than 30 percent in sugarcane habitats compared to subsistence farmland. We therefore emphasize the importance of retaining keystone habitat elements such as indigenous trees, forest galleries, hedgerows and other native vegetation in tropical farmland landscapes. Similar recommendations have recently been put forward for other tropical farmland landscapes (see Haslem and Bennett 2011, MacGregor-Fors and Schondube 2011).

Our study has demonstrated that bird density and diversity in forest and farmland sites can be predicted by the vegetation structural diversity within each habitat type. This pattern is consistent with the 'habitat heterogeneity hypothesis' (MacArthur and MacArthur 1961) which predicts that areas with high vegetation cover provide more niches and thus support a higher species diversity (Tews *et al.* 2004). Since a high structural diversity of the vegetation seems to be crucial for maintaining high bird species richness in and around Kakamega forest, landscape scale monitoring schemes for bird conservation should consider vegetation complexity as an adequate measure of habitat quality for birds across different habitat types.

Bird species community composition in forest and farmland habitats was very distinct. This difference was mostly driven by a high turnover of habitat guilds along the landscape gradient. Forest specialists were largely restricted to forest habitats, in particular near natural forests, whereas forest visitors and farmland species were mainly encountered in farmlands. During our study, forest specialist species were rarely recorded in the farmland, i.e. only 12 (25%) of the 49 species were recorded in low numbers. Possibly, these species use farmland habitats only for occasional feeding but not as breeding grounds. This suggests that movements of forest specialists between forest and farmland in Kakamega are rare. Therefore, our findings highlight that farmland habitats do not provide suitable habitat conditions for most forest specialists indicating that such species would go extinct with forest conversion to farmland. This is consistent with studies from Nigeria (Elgood and Sibley 1964), Liberia (Kofron and Chapman 1995), Ivory Coast (Waltert 2000) and Costa Rica (Daily *et al.* 2001) which suggest a regional species loss of 66-71 percent if tropical forests were converted to agroecosystems.

The high turnover in community composition also resulted in significant shifts in functional diversity along the forest-farmland gradient. We found that the relative abundance of insectivorous birds was much lower in the farmland than in the forest.

This is consistent with the decrease in forest specialist species in the farmland because a high proportion of about 75 percent of forest specialist species is insectivorous. Previous studies have postulated that insectivorous forest birds are particularly sensitive to forest degradation and land-use change and therefore strongly decline in human-dominated landscapes (Sekercioglu *et al.* 2002, Tscharntke *et al.* 2008). In contrast to insectivores, frugivorous and omnivorous species are less habitat-specific and thus are more tolerant to habitat alteration (Waltert *et al.* 2005, Gomes *et al.* 2008). Therefore, retaining high tree cover within agricultural landscapes could help to maintain a high functional bird diversity (Harvey *et al.* 2006) and essential ecosystem services such as pest control (Van Bael *et al.* 2008).

An interesting finding of our study was that bird communities in a recently regenerating secondary forest (Shiyingo, adjacent to a near natural forest) already comprised many species typical of near natural forest, notably White-spotted Flufftail (*Sarothrura pulchra*), Yellow-spotted Barbet (*Buccanodon duchaillui*), Red-tailed Bristlebill (*Bleda syndactyla*) and Uganda Woodland Warbler (*Phylloscopus budongoensis*). This site was a subsistence farmland until 13 years ago when it was incorporated into the Kakamega forest reserve. Thus, after barely one decade of forest regeneration, the bird community already comprised many forest species. It is a promising sign that in the proximity of natural forest, bird communities in fallow farmlands may rapidly shift towards a forest bird community. Other studies in India (Raman *et al.* 1998), Uganda (Naidoo 2004) and Ethiopia (Aerts *et al.* 2008) have demonstrated similarly rapid recoveries of forest bird communities in restoration sites in the proximity of natural forests. Forest restoration on abandoned farmlands therefore seems to be a valuable tool for the maintenance of forest biodiversity in tropical Africa, especially if larger forests that can act as sources for dispersal still occur in the vicinity.

3.6 Conclusion

Our findings demonstrate that bird communities and their feeding guild composition are very distinct between tropical forest and farmland habitats. Therefore, the maintenance of the diverse and unique forest bird communities can only be achieved by effective protection of near natural forests. The few larger remnants of tropical forests in East Africa, such as Kakamega forest, must therefore be efficiently protected against further logging and habitat modification. Nevertheless, we also demonstrate that structurally rich farmlands in western Kenya support a surprisingly high diversity of birds and therefore contribute substantially to the overall biodiversity of this landscape. To conserve this important component of tropical biodiversity, more conservation action for the widespread tropical agroecosystems is urgently required. This is a very timely obligation for tropical conservation because small-scale subsistence farmlands are being converted at alarming rates into high-intensity farmlands owing to increasing international demands for biofuel crops, such as sugarcane, and increasing human population densities in tropical countries (Gibbs *et al.* 2008). Our findings thus advocate for conservation strategies that go beyond forest protection and integrate agroecosystems into conservation planning, for instance through incentives to farmers to retain the traditional subsistence land-use practices in tropical agroecosystems. Ultimately, the conservation of biodiversity in tropical forest-farmland mosaics can only be successful if structurally-rich habitats are preserved through integrated policy and management approaches that consider both forest and farmland ecosystems from a landscape-scale perspective.

CHAPTER 4

SEASONAL FLUCTUATIONS OF RESOURCE ABUNDANCE AND AVIAN FEEDING GUILDS ACROSS HABITAT BOUNDARIES IN WESTERN KENYA

Submitted for publication in an international ecology journal as:

Mulwa, R. K., Neuschulz, E. L., Böhning-Gaese, K. & Schleuning, M. (submitted). Seasonal fluctuations of resource abundance and avian feeding guilds across habitat boundaries in Western Kenya.

4.1 Abstract

Seasonal fluctuations in climatic factors are expected to increase in future decades. However, we know very little about the response of tropical species communities to seasonal fluctuations in climate and resource availability, in particular across different habitat types. We examined the relationship between spatio-temporal fluctuations in the abundance of fruits and invertebrates and the two respective avian feeding guilds, i.e. frugivores and insectivores, in forest and farmland habitats in Western Kenya. Fruits and invertebrates fluctuated substantially throughout the year, but seasonal fluctuations were asynchronous between the two habitat types. Species richness and total abundance of frugivores and insectivores also fluctuated strongly and were closely related to the abundance of their respective resources. Frugivore species richness fluctuated anti-cyclical in forest and farmland habitats, suggesting that frugivorous species tracked fruit resources across habitat borders. In contrast, insectivorous bird richness fluctuated synchronously in the two habitat types, suggesting a lack of local-scale movements across habitat borders. We conclude that bird communities strongly respond to seasonal fluctuations in resource availability, but responses differ between feeding guilds. While frugivores seem to respond flexibly to seasonal fluctuations, for instance by tracking fruit resources across habitat borders, insectivorous birds appear to be more susceptible to the expected increase in seasonal fluctuations in resource availability.

4.2 Introduction

Seasonal fluctuations in climatic conditions have been globally increasing and are expected to intensify further in the coming decades (Fischlin *et al.* 2007). In particular in tropical climates with seasonal rainfall, seasonal anomalies severely affect ecosystems (Parmesan and Yohe 2003, Root *et al*. 2003) as well as rural human populations (Magadza 2000, Ojwang' *et al.* 2010). The effects of climatic fluctuations on tropical ecosystems are likely to be particularly severe in human-modified landscapes where tropical forests have been converted into agro-ecosystems (Morris *et al.* 2010). Despite reports of strong seasonal changes in the structure of tropical species communities (Brown 2006, Ahumada *et al.* 2011), we still know very little about the response of tropical ecosystems to seasonal fluctuations in climatic conditions, especially in landscapes with high human land-use intensities.

In most tropical bird communities, temporal fluctuations in species richness and abundance are a widespread phenomenon (Loiselle and Blake 1991, Cueto and de Casenave 2000, Malizia 2001). Such fluctuations are caused by local movements within and among habitats in response to food availability (Symes *et al.* 2002, Githiru *et al.* 2005, Herrera and García 2009) or could emerge from long-distance migrants being present for short seasonal time periods (Cox 2010). A number of studies that have addressed seasonal fluctuations in avian feeding guilds in relation to their food resources report synchronous patterns (Loiselle and Blake 1991, Poulin *et al*. 1993, Borghesio and Laiolo 2004, Monkkonen *et al*. 2006). However, most of these studies have focused on frugivores (Loiselle and Blake 1991, Githiru *et al.* 2005, Lehouck *et al.* 2009) and only rarely on insectivorous bird species (Poulin *et al.* 1993, Murakami 2002, Borghesio and Laiolo 2004). Furthermore, most studies have focused on few species of frugivores and plants (Bleher *et al.* 2003, Githiru *et al.* 2005, Lehouck *et al.* 2009). In contrast, community-wide studies of temporal fluctuations in avian feeding guilds and their corresponding resources are lacking. Similarly, there are few landscape-scale studies that follow fluctuations in resources and bird guilds not only in a single habitat type but across habitat borders in mosaic landscapes (but see Levey 1988, Loiselle and Blake 1991).

In the tropics, fruit and invertebrate resources are subject to substantial seasonal fluctuations (Poulin *et al.* 1992). Fruit abundance often peaks in dry seasons while invertebrates are most active in wet seasons (Poulin *et al.* 1992, Borghesio and Laiolo 2004). Fruits tend to be more unevenly distributed in time and space than other avian food resources (Blake and Loiselle 1991, Herrera and García 2009). Frugivorous birds respond to these strong spatio-temporal fluctuations by tracking fruit resources over large distances (Malizia 2001, Guitián and Bermejo 2006, García *et al.* 2011), even crossing habitat borders (García and Ortiz-Pulido 2004). Apart from long-distance migrations of insectivorous birds (Cox 2010), it is hardly known whether tropical insectivorous birds track their insect resources especially at smaller spatial scales, for instance among adjacent habitat types.

From studies along spatial gradients with different human land-use intensity, we know that forest understory insectivores are disproportionately sensitive to habitat modification (Sekercioglu *et al.* 2002, Tscharntke *et al.* 2008), although more generalized insectivores may be less affected (Lindell *et al.* 2004). In contrast, frugivorous species seem to be less sensitive to land-use change (O'Dea and Whittaker 2007). One explanation for this difference is that frugivores are able to access food resources outside their preferred habitat type (Eshiamwata *et al.* 2006, Berens *et al.* 2008). It remains to be investigated whether guild-specific responses to spatial land-use gradients also hold for responses to temporal fluctuations in resource abundance. This knowledge is crucial for predicting responses of different functional guilds to global change (Williams and Middleton 2008).

This study examines seasonal fluctuations in fruit and invertebrate resources and the corresponding avian feeding guilds in Kakamega Forest and neighboring farmlands in western Kenya. We tested (1) to what extent resources (fruits and invertebrates) and bird guilds (frugivores and insectivores) fluctuate over the course of a year, (2) whether these fluctuations differ between adjacent habitat types with different human land-use intensity, and (3) whether fluctuations in resource abundance predict fluctuations in the corresponding feeding guilds. We particularly sought to establish whether the two feeding guilds responded differently to resource fluctuations.

4.3 Methods

4.3.1 Study area and design

The study was conducted within and around Kakamega Forest, a mid-altitude tropical rainforest in western Kenya (1520-1680 m, 0°10' – 0°21'N, 34°47' – 34°58'E). Climatic conditions are characterized by constantly high temperatures, ranging from 19.0°C (September) to 24.4°C (March) (data from the study year). Seasonal fluctuations in precipitation are strong. During the study year, annual precipitation was 1857 mm with three distinct peaks in April, September and December (data from Kakamega Weather Station).

Kakamega forest is one of the easternmost outliers of the Guineo-Congolian rainforests and a biodiversity hotspot, in particular for birds (Bennun and Njoroge 1999). The agricultural landscape bordering Kakamega forest is characterized by large fields of sugarcane as well as small-scale subsistence farming of maize, beans and vegetables and holds a notably high bird diversity (Laube *et al.* 2008). Between February 2009 and January 2010, we surveyed fruits, invertebrates and birds at ten forest and ten farmland sites every month (Fig. 4.1). Forest sites covered both near-natural and secondary forest, and farmland sites represented both sugarcane and subsistence farmland. At each site, we placed six sampling points located 100 m apart. All farmland sites were placed at least 2 km from the forest edge, while forest sites were at least 250 m away from the forest edge. Adjacent sites of the same habitat type were at least 1.25 km apart.

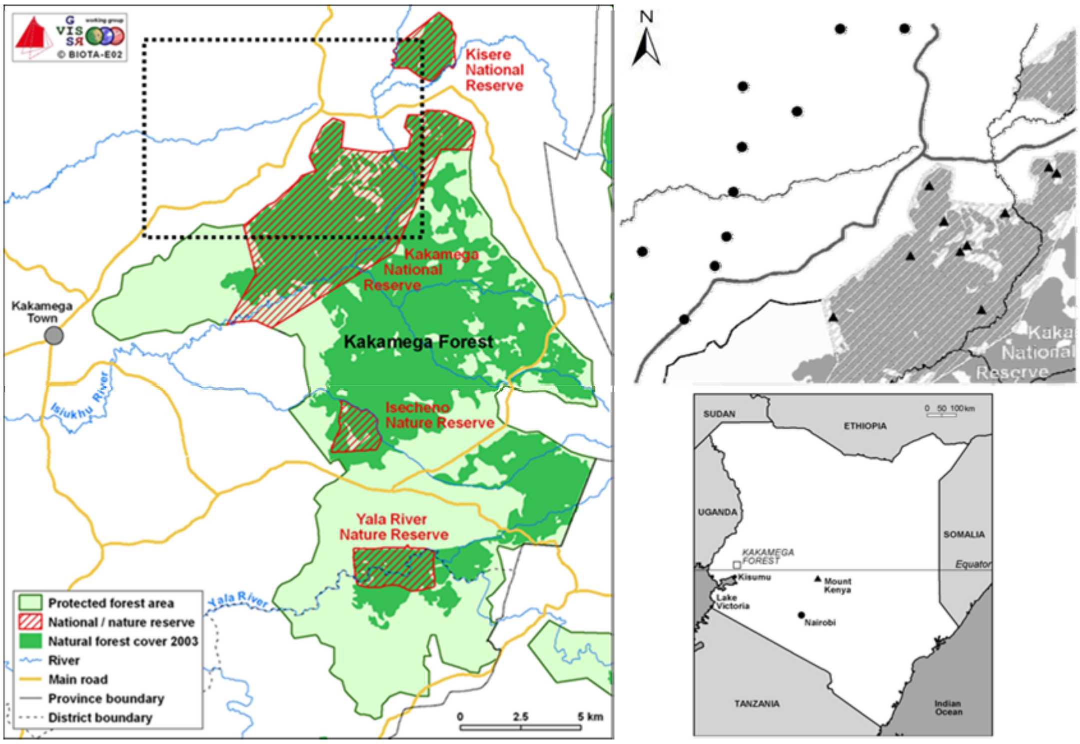

Figure 4.1: Location of the study area in Kakamega Forest in western Kenya. Dotted box indicates location of study area. Study sites in forest and farmlands are indicated by solid triangles and solid circles, respectively.

4.3.1.1 Fruit abundance

To estimate fruit abundance in each month, we recorded and identified all plants with fleshy fruits (according to Beentje 1994) within a radius of 20 m around each sampling point. For each fruiting plant, we estimated its crop size by counting fruits of two randomly-picked branches and subsequently extrapolated the total fruit number (e.g. Githiru *et al*. 2005). We summed crop sizes and the number of fruiting plant species across sampling points to obtain an estimate of fruit abundance (log-transformed) and the number of fruiting plant species (square-root transformed) for each site and month.

4.3.1.2 Invertebrate abundance

To assess the abundance of invertebrates in each month, we used a standardized sweep-netting design (Poulin and Lefebvre 1997). At each sampling point, we made a total of 20 sweeps, i.e. ten sweeps each along two perpendicular transects of 40 m cutting through each sampling site. All invertebrates were classified to order level, counted, sun-dried on tissue paper and weighed separately for each plot. We determined invertebrate abundance (log-transformed) and invertebrate dry biomass (log-transformed) for each sampling point and added these values to obtain a total estimate of both measures for each site and month. We are aware that sweep-netting only records understory invertebrates and not canopy invertebrates. However, we aimed at comparing seasonal fluctuations within each habitat type (forest versus farmland) which we assume to be similar in lower and higher habitat strata.

4.3.1.3 Bird surveys

We conducted point counts of birds between 0700 and 0900 hours once per month. At each sampling point, we recorded all birds seen or heard within a radius of 50 m for 15 minutes. We classified frugivorous and insectivorous species according to Kissling *et al.* (2007): all bird species consuming fruits as major part of their diet were considered as 'frugivores', and those having invertebrates as major food item as 'insectivores'. Species that have both fruit and invertebrates as major food items, e.g. birds that switch between fruit and invertebrate diet over the year, were included in both the 'frugivore' and 'insectivore' category (25 omnivore species in our data set; Appendix 2). Excluding those 25 omnivore species from the analyses resulted in qualitatively identical results.

In total, we recorded 202 species (17,620 individuals) of which 57 species were frugivorous (8,081 individuals) and 170 species were insectivorous (12,464 individuals). Among the species, 25 were Palearctic or Afrotropical migrants (582 individuals) including four frugivores (152 individuals) and 24 insectivores (440 individuals). For further analyses, we pooled bird abundance (square-root transformed) and species numbers across the six sampling points per site providing an estimate of total bird abundance and species richness for each feeding guild per site and month. We did not correct our estimates of bird abundance and richness for potentially different detectabilities among sites because we were primarily interested in seasonal fluctuations within sites, not in differences in bird diversity among sites.

4.3.2 Statistical analysis

We used linear mixed effect models to investigate seasonal fluctuations in food resources (fruits and invertebrates) and avian feeding guilds (frugivores and insectivores). Seasonal changes were depicted by fluctuations among different months. We explicitly tested whether seasonal changes in food resources or avian feeding guilds differed between habitat types (forest versus farmland) by including the interaction term between month and habitat type in all models. To account for the spatial sampling structure, we included study site as a random factor in all models. To link resource and bird data, we tested whether fruit and invertebrate abundance predicted seasonal fluctuations in species richness and abundance of the corresponding feeding guilds by fitting a mixed effect model with the respective resource data as predictor variable and site as random factor. To test whether birds in a given guild fluctuated synchronously between forest and farmland sites, we calculated mean bird richness and abundance across all forest and farmland sites, respectively, and correlated monthly forest and farmland estimates for each feeding guild. We used R 2.11.1 (R Development Core Team 2011) for all statistical analyses.

4.4 Results

4.4.1 Fluctuations in fruit and invertebrate abundances

Fruit abundance fluctuated significantly among months (Table 4.1). The monthly fluctuations were more pronounced in forest than in farmland habitats (Fig. 4.2a) as corroborated by a significant interaction between month and habitat (Table 4.1). While fruit abundance was high from September to March in forest sites, farmland fruit abundance was relatively constant during the year. Similar patterns were found for fruiting plant species richness (Table 4.2).

Invertebrate abundance was higher in farmland than in forest sites and fluctuated strongly among months reaching highest abundances around August and lowest abundances in May and November. Again, monthly fluctuations differed between the two habitat types (Figure 4.2b, significant interaction term in Table 4.1). Invertebrate biomass depicted a very similar pattern (Table 4.1).

Table 4.1: Linear mixed-effect models testing the effects of spatio-temporal fluctuations on two avian feeding guilds (frugivores, insectivores) and their respective resources at 20 sites in forest and farmland habitat in western Kenya. Each site was studied monthly over the course of an entire year. Site identity was included as random factor in all models. Note that asynchronous fluctuations in the two habitat types are corroborated by a significant interaction term between habitat and month. Significant effects ($P \leq 0.05$) are printed in bold.

Bird guild/Resources	**Habitat/Month**	**df**	***F***	***P***
Fruit abundance	Habitat	1,18	2.28	0.148
	Month	11,198	6.79	**<0.001**
	Habitat×Month	11,198	3.06	**0.001**
Frugivore species richness	Habitat	1,18	3.62	0.073
	Month	11,198	0.94	0.499
	Habitat×Month	11,198	3.62	**<0.001**
Frugivore abundance	Habitat	1,18	5.92	**0.026**
	Month	11,198	3.12	**0.001**
	Habitat×Month	11,198	3.60	**<0.001**
Invertebrate abundance	Habitat	1,18	8.42	**0.010**
	Month	11,198	15.51	**<0.001**
	Habitat×Month	11,198	3.32	**<0.001**
Insectivore species richness	Habitat	1,18	0.05	0.820
	Month	11,198	3.52	**<0.001**
	Habitat×Month	11,198	1.70	0.075
Insectivore abundance	Habitat	1,18	0.15	0.701
	Month	11,198	4.65	**<0.001**
	Habitat×Month	11,198	1.13	0.338

4.4.2 Fluctuations in bird abundance

Across the two habitat types, the number of frugivorous species did not fluctuate significantly among months (Table 4.1). However, there was a significant interaction between month and habitat type, indicating asynchronous seasonal fluctuations of frugivorous birds in forest and farmland habitats (Table 4.1, Fig. 4.2b). While there was an increase of frugivorous species from October to January in forest sites, we found low abundances of farmland frugivores during these months. Frugivore abundance differed significantly among months, and consistent with frugivore richness these fluctuations were habitat-specific (Table 4.1).

In contrast to frugivores, seasonal fluctuations in insectivore richness were not habitat-specific (Fig. 4.2e, no significant interaction term in Table 4.1), although seasonal fluctuations across the two habitat types were strong. Insectivore richness peaked from February to April for both forest and farmland sites but was low in June and January. Insectivore abundance showed a very similar pattern (Table 4.1, Fig. 4.2f).

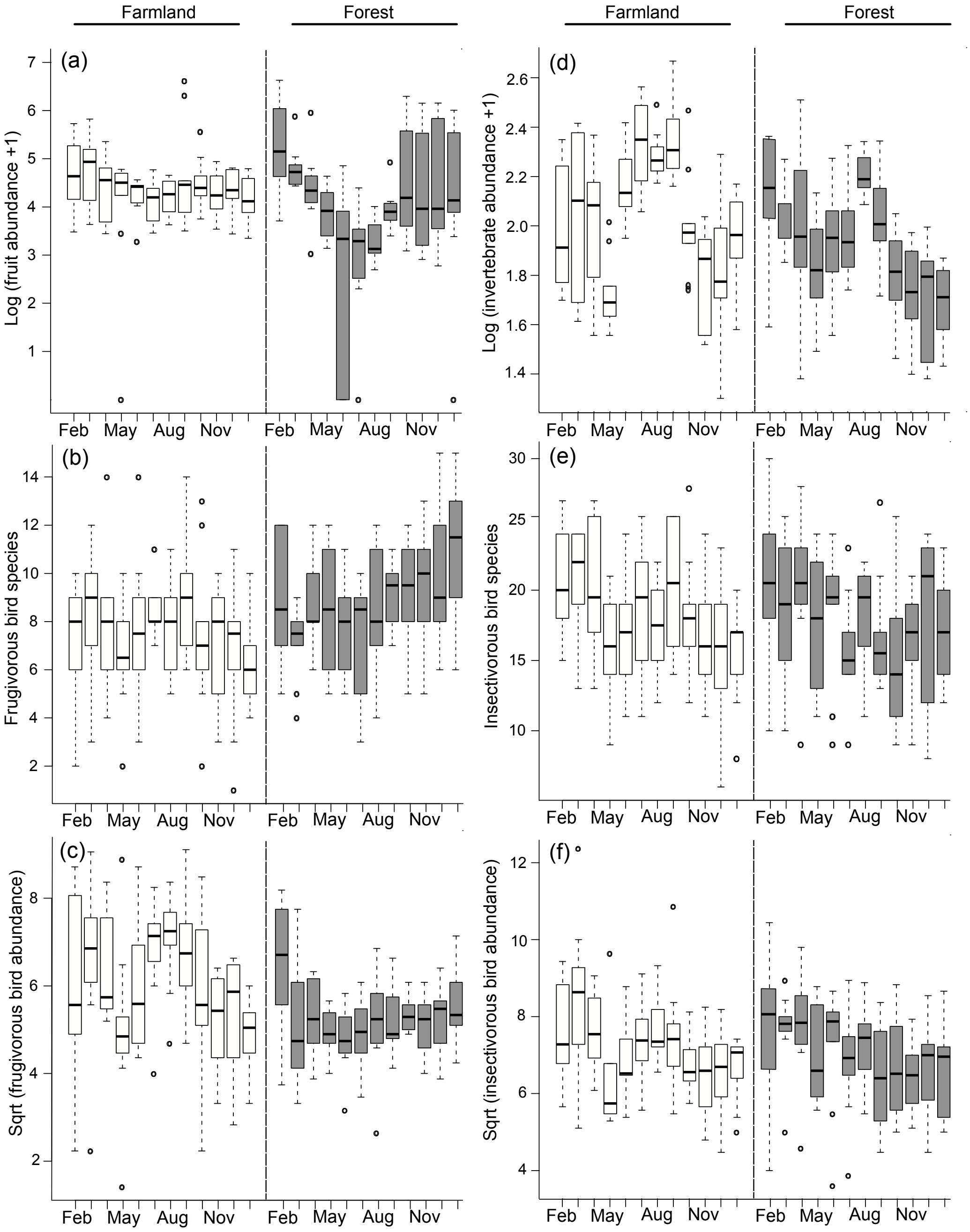

Figure 4.2: Spatio-temporal fluctuations of two bird feeding guilds and their resources over 12 months and at 20 sites in forest and farmland habitat in western Kenya. Shown are (a) fruit abundance, (b) frugivore species richness, and (c) frugivore abundance, as well as (d) invertebrate abundance, e) insectivore species richness, and (f) insectivore abundance for each month and habitat type. The one-year study period started in February 2009. Lines across boxes are medians, boxes indicate 25th and 75th percentiles, whiskers indicate 10th and 90th percentiles, and circles are outliers.

Table 4.2: Linear mixed-effect models testing the effects of spatio-temporal fluctuations of fruiting plant species and invertebrate biomass at 20 sites in forest and farmland habitat in western Kenya. Each site was studied monthly over the course of an entire year. Site identity was included as random factor in all models. Note that asynchronous fluctuations in the two habitat types are corroborated by a significant interaction term between habitat and month. Significant effects ($P \leq 0.05$) are printed in bold.

Bird guild/Resources	**Habitat/Month**	**df**	***F***	***P***
Fruiting plant species	Habitat	1,18	23.10	**<0.001**
	Month	11,198	6.66	**<0.001**
	Habitat×Month	11,198	2.26	**0.013**
Invertebrate biomass	Habitat	1,18	8.42	**0.010**
	Month	11,198	15.51	**<0.001**
	Habitat×Month	11,198	3.32	**<0.001**

Resource fluctuations predicted seasonal fluctuations in both feeding guilds. Fruit abundance was closely related to both frugivore species richness and abundance ($\beta = 0.18$, $t_{(219)} = 3.01$, $P = 0.003$, and $\beta = 0.28$, $t_{(219)} = 4.71$, $P < 0.001$ respectively). Similarly, insectivore species richness and abundance strongly increased with invertebrate abundance ($\beta = 0.25$, $t_{(219)} = 4.49$, $P < 0.001$, and $\beta = 0.34$, $t_{(219)} = 5.96$, $P < 0.001$).

Frugivore species richness was negatively correlated between forest and farmland sites ($r = -0.595 \pm 0.254$ SE) and tended to be so for frugivore abundance ($r = -0.081 \pm 0.129$ SE). In contrast, insectivorous species richness and insectivore abundance were positively correlated between forest and farmland sites ($r = 0.354 \pm 0.296$ SE and $r = 0.626 \pm 0.247$ SE, respectively). Differences in seasonal fluctuations between frugivores and insectivores across the two habitat types are corroborated by nonoverlapping standard errors of correlation coefficients between feeding guilds for bird species richness and abundance, respectively. These differences suggest that frugivorous birds fluctuated anti-cyclically between forest and farmland habitats, whereas insectivores show synchronous seasonal fluctuations across habitat borders.

4.5 Discussion

Species richness and abundance in both frugivorous and insectivorous birds fluctuated considerably over seasons. The strong seasonal fluctuations in both fruit and invertebrate resources predicted fluctuations in the respective feeding guilds. The strong relationships between resource availability and richness and total abundance of the corresponding feeding guild suggest a causal link between resource and bird abundance. Previous studies have reported similar results showing that spatio-temporal variation in resource abundance indeed influences the dynamics of bird communities (see also Poulin and Lefebvre 2002, Borghesio and Laiolo 2004, Monkkonen *et al*. 2006, Lehouck *et al.* 2009).

The most interesting finding of our study was that the two feeding guilds differed substantially in their response to seasonal resource fluctuations. We provide evidence that frugivores responded to seasonal resource fluctuations by tracking fruits across habitat borders by showing (1) a negative correlation of frugivore species richness between forest and farmland sites among months, and by (2) a strong habitat by month interaction in both frugivore richness and abundance. In contrast, insectivores appeared to respond less flexibly to seasonal fluctuations and exhibited a synchronous increase and decrease of species richness and abundance in forest and farmland.

On the basis of our results, we propose that frugivore feeding guilds are adapted to spatio-temporal fluctuations in food resources. Many tropical forests are characterized by irregular fruit production and occasional periods of low fruit availability (Wirminghaus *et al.* 2001). Consequently, frugivores often have to cope with unpredictable and limited food resources and have been shown to enhance their foraging efficiency by tracking their fruit resources over large areas (Symes *et al.* 2002, García and Ortiz-Pudilo 2004, Guitián and Bermejo 2006). Consistent with our observations, previous studies in this area report forest-dependent frugivorous species, such as Black-and-white Casqued Hornbill (*Bycanistes subcylindricus*), Tambourine Dove (*Turtur tympanistria*) and Yellow-rumped Tinkerbird (*Pogoniulus bilineatus*) not only in forest but also in the farmland (Eshiamwata *et al.* 2006, Kirika *et al.* 2007, Berens *et al.* 2008, Laube *et al.* 2008).

Some frugivorous species may also switch to other food resources to overcome periods of low resource availability (Carnicer *et al.* 2008, Lehouck *et al.* 2009). This is a likely response of forest specialist frugivores, e.g. Yellow-billed Barbet (*Trachylaemus purpuratus*), Yellow-whiskered Greenbul (*Andropadus latirostris)* and Shelley's Greenbul (*Andropadus masakuensis*) that seldom leave forests (Bennun *et al.* 1996). In our study system, months with the lowest fruit availability (June-August) were not those with the lowest invertebrate abundance, suggesting that asynchronous fluctuations in different resources can buffer food shortages for such species. Despite species-specific differences in responses to seasonal fruit shortage, our study provides evidence that fruit availability predicted frugivore richness and abundance and that fruit tracking was important at a community level, even across habitat borders. At the landscape level, this flexible response to resource fluctuations resulted in an almost constant number of about 35 frugivore species (mean = 35, SD = 3.69) in the study system across the entire year.

Our study is one of the first to show that insectivore richness and abundance are strongly related to fluctuations in invertebrate abundance. Previous studies have failed to show such a relationship, maybe because of the difficulties in obtaining reliable estimates of invertebrate abundance (e.g. Poulin and Lefebvre 1997). Our finding is important because it shows that seasonal fluctuations in invertebrate abundance can have cascading effects and translate into fluctuations in insectivorous bird species richness and abundance. Such seasonal fluctuations in insectivorous birds are likely to increase in the future because seasonal fluctuations in climate are bound to increase (Fischlin *et al.* 2007) and strongly determine seasonal fluctuations in invertebrate abundances (William and Middleton 2008).

In contrast to frugivores, we found synchronous fluctuations in insectivore species richness and abundance in the two habitat types. Seasonal fluctuations in invertebrate abundance, however, were asynchronous between forest and farmland habitats providing potential for a cross-habitat rescue effect in times of food shortages. Nevertheless, insectivorous bird communities fluctuated synchronously in forest and farmland habitats and are therefore unlikely to undergo seasonal movements crossing habitat borders. This is in line with previous studies showing that insectivores, in particular those in the forest understory, hardly cross habitat borders (Lens *et al.* 2002, Laurance *et al.* 2004). Instead, it is likely that insectivores are capable of switching between invertebrate and other food sources in times of low invertebrate abundance (see also Borghesio and Laiolo 2004, Carnicer *et al.* 2008, Lehouck *et al.* 2009), enabling the species to stay within the same habitat type, e.g. Brown-capped Weaver (*Ploceus insignis*), Least Honeyguide (*Indicator exilis*), and Olive Sunbird (*Cyanomitra olivacea*). Nevertheless, we found that both insectivore richness and abundance were strongly affected by fluctuations in invertebrate abundances; a pattern we would not expect if all species were capable of flexibly shifting between different resource types.

A possible explanation for these fluctuations can be fluctuations in bird population sizes in response to resource availability (Williams and Middleton 2008), e.g. by synchronizing breeding periods with peaks in invertebrate abundance (Poulin *et al.* 1992). However, breeding seasonality of Afrotropical birds and its relationship to resource fluctuations is not well understood. Another reason for seasonal fluctuations could be the increasing numbers of Afrotropical and Palearctic migrants in months of high invertebrate abundance. The relationship between invertebrate abundance and total abundance of migratory bird species, however, was not significant ($\beta = 0.07$, $t_{(219)} = 1.09$, $P = 0.276$). The strong seasonal fluctuations in the insectivorous bird community at the landscape level (mean = 93 species, SD = 11.00) suggests that some non-migratory insectivorous bird species temporarily left the study area in periods of food shortage. One explanation could be that the forest insectivores move to other forest patches that have persisted in the surroundings of Kakamega Forest, while farmland birds could move to other farmland areas in the surroundings. Considering our findings, partial migration of tropical birds is likely to occur (Boyle 2011) highlighting the importance of forest remnants in human-modified landscapes (Schleuning *et al.* 2011).

4.6 Conclusion

Overall, our results show that bird communities strongly responded to seasonal fluctuations in resource availability. This is an important finding in times when seasonal climatic fluctuations are intensifying and highlights that cascading effects of fruit and invertebrate abundance on higher trophic levels are likely to occur in tropical species communities. However, such cascading effects differed between bird foraging guilds in relation to different habitat types. Frugivorous birds seemed to respond flexibly to such changes, for instance by tracking fruit resources across habitat borders, while their species richness hardly varied at the landscape scale over the course of a year. In contrast, insectivorous birds rarely crossed habitat borders and probably depended on short-distance movements to similar habitats in the surroundings at times when invertebrate abundance was low. Their strong seasonal fluctuations and potential dependence on rescue habitats in the proximity make insectivorous birds more susceptible to the increasing seasonal fluctuations in resource availability than it is the case for frugivorous birds.

5. CONCLUSIONS

5.1 Synthesis

The impacts of human activities, notably the conversion of tropical forests into farmland habitat, has profound impacts on biological diversity and ecosystem functions (Millennium Ecosystem Assessment 2005). It is widely debated to what extent human-modified landscapes can maintain tropical biodiversity and their ecosystem functionality (e.g. Waltert *et al.* 2004, Sekercioglu *et al.* 2007). In this thesis, I have used a huge and temporarily replicated dataset to assess the value of different habitat types differing in land-use intensities for bird communities in tropical East Africa. I investigated bird abundance and species richness along a forest-farmland habitat gradient and assessed spatial and temporal fluctuations of bird assemblages and their food resources.

I could show that forest and farmland habitats harbor distinct bird communities. Moreover, the protection of natural forests merits the highest priority for conserving the high diversity of forest-dependent bird species. My study, however, also shows that farmland habitats in the proximity of natural forest can support a high bird diversity. High bird diversity in tropical farmlands depends on a high structural complexity, such as in small-scale subsistence farmlands. From my findings, I conclude that the conversion of forest to farmland leads to substantial losses in bird diversity, in particular in specialized feeding guilds such as insectivores, while the conversion of structurally heterogeneous subsistence farmlands to sugarcane plantation causes erosion of bird diversity in agricultural ecosystems. Both findings are important for conservation planning in times when tropical forests and agroecosystems are under constantly high pressure due to increasing human population numbers and global demands for biofuel crops (Gibbs *et al.* 2008).

From an ecosystem function perspective, my study demonstrates the potential of agroecosystems in supporting important ecosystem functions, such as seed dispersal by frugivorous birds and pest control by insectivorous birds. I could show that bird abundances in both frugivorous and insectivorous guilds were strongly predicted by their respective food resources, implying that seasonal shifts in fruit and invertebrate abundance at Kakamega forest and surrounding farmlands affect community dynamics and appear to influence local movement patterns of birds. The most interesting finding of this study was that feeding guilds responded idiosyncratically to resource fluctuations. Frugivore richness fluctuated asynchronously in forest and farmland habitats, suggesting foraging movements and fruit tracking across habitat borders. In contrast, I found that insectivores fluctuated synchronously in the two habitat types, suggesting a lack of inter-habitat movements. I therefore predict that insectivorous bird communities in this forest-farmland landscape may be more susceptible to the combined effects of land-use and climate change, due to their narrow habitat niche and limited capacity to track their resources.

The fact that a number of bird species regularly moved across the landscape mosaic in my study system implies that birds are able to provide long-distance seed dispersal across habitat borders. Thus, birds may enhance forest regeneration in human-modified landscapes, such as those in most parts of tropical Africa, given that forest remnants are protected within an agricultural habitat matrix. In order to effectively conserve tropical biodiversity within forest-farmland mosaics, this study advocates for conservation strategies that go beyond forest protection and explicitly integrate farmlands into forest management plans and policies. This should emphasize the retention of keystone habitat elements within tropical farmland landscapes, such as indigenous trees, forest galleries and hedgerows, whose presence enhance species diversity. Such grassroot-level approaches can be operationalized for instance through providing incentives to farmers to maintain their traditional subsistence land-use practices and through community-based livelihood projects aiming at enhancing local habitat heterogeneity and inter-habitat connectivity.

5.2 Future perspectives

This study identifies future challenges and opportunities for conservation research and monitoring. Since deforestation and land use-changes are ongoing and even accelerating in the tropics, long-term biodiversity monitoring in human-modified tropical landscape mosaics is strongly needed. To this end, my study provides reliable baseline data for the study area in question and provides a methodological framework on how bird diversity across forest-farmland landscape mosaics can be monitored in the future.

Furthermore, since my data suggested synchronous temporal fluctuations in insectivorous birds in forest and farmland habitats, it remains to be investigated where birds actually move to in periods of food shortage. To this end, I recommend long-term studies that address movement patterns of birds at small spatial scales in more detail. For instance, radio-tracking studies of short distance or partial migrants could be of great interest.

I could show that fruit and invertebrate abundance may fluctuate differentially between habitats, seasons and even years. Therefore, long-term multi-habitat studies could help to document the effect of seasonality on resource-bird guild interactions more comprehensively. Here, it might be of particular interest to examine if time lags exist between changes in resource abundance and response by birds of different guilds.

Furthermore, a worthwhile follow-up study in the future could address intra-guild preferences for particular fruit and invertebrate resources as different guild species could respond differently to the seasonal fluctuations of their resources.

My thesis provides an in-depth understanding of how bird communities respond to human-induced changes and to temporal fluctuations along a forest-farmland gradient in western Kenya. The generality of my findings across other tropical regions and among other taxa remain to be investigated, for instance in areas with different land tenure systems and in areas with different patterns of climatic seasonality. Such studies seem particularly important as the distribution of bird diversity in dynamic tropical forest-farmland mosaics could be context-dependent (Vallecillo *et al.* 2009). Nevertheless, my study represents a widely adoptable model for biodiversity assessment in similar forest-farmland landscapes that are widespread throughout the tropics. Such comprehensive monitoring studies of tropical biodiversity are highly valuable for the definition of country-wide conservation priorities as well as for local applications such as nature reserve establishment or environmental impact assessment for infrastructural development projects.

6. REFERENCES

Aerts, R., Lerouge, F., November, E., Lens, L., Hermy, M. & Muys, B. (2008) Land rehabilitation and the conservation of birds in a degraded Afromontane landscape in northern Ethiopia. *Biodiversity and Conservation,* **17**: 53–69.

Ahumada, J. A., Silva, C. E. F., Gajapersad, K., Hallam, C., Hurtado, J., Martin, E., McWilliam, A., Mugerwa, B., O'Brien, T., Rovero, F., Sheil, D., Spironello, W. R., Winarni, N. & Andelman, S. J. (2011) Community structure and diversity of tropical forest mammals: data from a global camera trap network. *Philosophical Transactions of the Royal Society of London Series B,* **366**: 2703–2711.

Aubin, I., Ouellette, M., Legendre, P., Messier, C. & Bouchard, A. (2009) Comparison of two plant functional approaches to evaluate natural restoration along an old-field, deciduous forest chronosequence. *Journal of Vegetation Science,* **20**: 185–198.

Beentje, H. (1994) *Kenya trees, shrubs and lianas*. National Museums of Kenya, Nairobi.

Bennun, L. A., Dranzoa, C., & Pomeroy, D. (1996) The forest birds of Kenya and Uganda. *Journal of East African Natural History,* **85**: 23–48.

Bennun, L. A. (1999) Threatened birds and rural communities: Balancing the equation. In: Adams, N. J. & Slotow, R. H. (eds) *Proc. 22 Int. Ornithol. Congr., Durban:* 1546-1555. Johannesburg: BirdLife South Africa.

Bennun, L. A. & Njoroge, P. (1999) *Important Bird Areas of Kenya.* East Africa Natural History Society. Nairobi.

Berens, D. G., Farwig, N., Schaab, G. & Böhning-Gaese, K. (2008) Exotic guavas are foci of forest regeneration in Kenyan farmland. *Biotropica,* **40**: 104–112.

Bibby, C. J., Burgess, N. D. & Hill, D. A. (1992) *Bird Census Techniques.* Academic Press Limited, London.

Bibby, C. J., Burgess, N. D., Hill, D. A. & Mustoe, S. H. (2000) *Bird census techniques*. Academic Press, London.

Birdlife International (2007) *Preliminary report: BirdLife Partners use of IBA Directories as tools in Advocacy.* Cambridge, U.K.

Birdlife International (2011) Species fact sheets. http://www.birdlife.org.

Blake, J. G. & Loiselle, B. A. (1991) Variation in resource abundance affects capture rates of birds in three lowland habitats in Costa Rica. *Auk,* **108**: 114–130.

Bleher, B., Potgieter, C. J., Johnson, D. N. & Böhning-Gaese, K. (2003) The importance of figs for frugivores in a South African coastal forest. *Journal of Tropical Ecology,* **19**: 375–386.

Bleher, B., Uster, D. & Bergsdorf, T. (2006) Assessment of threat status and management effectiveness in Kakamega Forest, Kenya. *Biodiversity and Conservation,* **15**: 1159–1177.

Borghesio, L. & Laiolo, P. (2004) Seasonal foraging ecology in a forest avifauna of northern Kenya. *Journal of Tropical Ecology,* **20**: 145–155.

Boyle, W. A. (2011) Short-distance partial migration of Neotropical birds: a community-level test of the foraging limitation hypothesis. *Oikos* **120**: 1803–1816.

Breitbach, N., Laube, I., Steffan-Dewenter, I. & Böhning-Gaese, K. (2010) Bird diversity and seed dispersal along a human land-use gradient: high seed removal in structurally simple farmland. *Oecologia,* **162**: 965–976.

Brown, M. (2006) Annual and seasonal trends in avifaunal species richness in a coastal lowlands forest reserve in South Africa. *Ostrich,* **77**: 58–66.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. & Thomas, L. (2001) *Introduction to Distance Sampling.* Oxford University Press, Oxford.

Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., Galloway, J. N., Genovesi, P., Gregory, R. D., Hockings, M., Kapos, V., Lamarque, J., Leverington, F., Loh, J., McGeoch, M. A., McRae, L., Minasyan, A., Morcillo, M. H., Oldfield, T. E. E., Pauly, D., Quader, S., Revenga, C., Sauer, J. R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S. N., Symes, A., Tierney, M., Tyrrell, T. D., Vié, J. & Watson, R. (2010) Global Biodiversity: Indicators of Recent Declines. *Science,* **328**: 1164–1168.

Carnicer, J., Abrams, P. A. & Jordano, P. (2008) Switching behavior, coexistence and diversification: comparing empirical community-wide evidence with theoretical predictions. *Ecology Letters,* **11**: 802–808.

Cox, G. W. (2010) *Bird migration and global change*. Island Press, Washington DC.

Crist, T. O., Veech, J. A., Gering, J. C. & Summerville, K. S. (2003) Partitioning species diversity across landscapes and regions: a hierarchical analysis of α, β and γ diversity. *American Naturalist,* **162**: 734–743.

Cueto, V. R. & de Casenave, J. L. (2000) Seasonal changes in bird assemblages of coastal woodland in east-central Argentina. *Studies on Neotropical Fauna and Environment,* **35**: 173–177.

Daily, G. C., Ehrlich, P. R. & Sanchez-Azofeifa, G. A. (2001) Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecological Applications,* **11**: 1–13.

Díaz, S. & Cabido, M. (2001) Plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution,* **16**: 646–655.

Dray, S. & Legendre, P. (2008) Testing the species traits–environment relationships: the fourth-corner problem revisited. *Ecology,* **89**: 3400–3412.

Elgood, J. H. & Sibley, E. C. (1964) The tropical forest edge avifauna of Ibadan, Nigeria. *Ibis,* **106**: 221–248.

Eshiamwata, G. W., Berens, D. G., Bleher, B., Dean, W. R. J. & Böhning-Gaese, K. (2006) Bird assemblages in isolated ficus trees in Kenyan farmland. *Journal of Tropical Ecology,* **22**: 723–726.

Farwig, N., Braun, C. & Böhning-Gaese, K. (2008) Human disturbance reduces genetic diversity of an endangered tropical tree, *Prunus africana* (Rosaceae). *Conservation Genetics,* **9**: 317–326.

Fischlin, A., Midgley, G. F., Price, J. T., Leemans, R., Gopal, B., Turley, C., Rounsevell, M. D. A., Dube, O. P., Tarazona, J., & Velichko, A. A. (2007) Ecosystems, their properties, goods and services. In: Parry, M. L., Canziani, O. F., Palutikof, J. P., van der Linden, P. J. & Hanson, C. E. (eds) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, pp. 211–272.

Gamfeldt, L., Hillebrand, H. & Johnson, P. R. (2008) Multiple functions increase the importance of biodiversity for ecosystem functioning. *Ecology,* **89**: 1223–1231.

García, D. & Ortiz-Pulido, R. (2004) Patterns of resource tracking by avian frugivores at multiple spatial scales: two case studies on discordance among scales. *Ecography,* **27**: 187–196.

García, D., Zamora, R. & Amico, G. C. (2011) The spatial scale of plant-animal interactions: effects of resource availability and habitat structure. *Ecological Monographs,* **81**: 103–121.

Gibbs, H. K., Johnston, M., Foley, J. A., Holloway, T., Monfreda, C., Ramankutty, N. & Zaks, D. (2008) Carbon payback times for crop-based biofuel expansion in the tropics: the effects of changing yield and technology. *Environmental Research Letters* **3**: doi:10.1088/1748-9326/3/3/034001.

Githiru, M., Bennun, L. A., Lens, L. & Ogol, C. P. K. O. (2005). Spatial and temporal variation in fruit and fruit-eating birds in the Taita Hills, south-east Kenya. *Ostrich,* **76**: 37–44.

Gomes, L. G. L., Oostra, V., Nijman, V., Cleef, A. M. & Kappelle, M. (2008) Tolerance of frugivorous birds to habitat disturbance in a tropical cloud forest. *Biological Conservation,* **141**: 860–871.

Gove, A. D., Hylander, K., Nemomisa, S. & Shimelis, A. (2008) Ethiopian coffee cultivation - implications for bird conservation and environmental certification. *Conservation Letters,* **1**: 208–216.

Gregory, R. D., Noble, D., Field, R., Marchant, J., Raven M. & Gibbons D. W. (2003). Using birds as indicators of biodiversity. *Ornis Hungarica,* **12-13**: 11–24.

Guitián, J. M. & Bermejo, T. (2006) Dynamics of plant-frugivore interactions: a long-term perspective on holly-redwing relationships in northern Spain. *Acta Oecologica,* **30**: 151–160.

Hagen, M. & Kraemer, M. (2010) Agricultural surroundings support flower–visitor networks in an Afrotropical rain forest. *Biological Conservation,* **143**: 1654–1663.

Hansen, A. J., Neilson, R. P., Dale, V. H., Flather, C. H., Iverson, L. R., Currie, D. J., Shafer, S., Cook, R. & Bartlein, P. J. (2001) Global change in forests: responses of species, communities, and biomes. *BioScience,* **51**: 765–779.

Harvey, C. A., Medina, A., Sánchez, D. M., Vílchez, S., Hernández, B., Saenz, J. C., Maes, J. M., Casanoves, F. & Sinclair, F. L. (2006) Patterns of animal diversity in different forms of tree cover in agricultural landscapes. *Ecological Applications,* **16**: 1986–1999.

Haslem, A. & Bennett, A. F. (2011) Countryside vegetation provides supplementary habitat at the landscape scale for woodland birds in farm mosaics. *Biodiversity and Conservation,* **20**: 2225–2242.

Heikkinen, R. K., Luoto, M., Virkkala, R. & Rainio, K. (2004) Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. *Journal of Applied Ecology,* **41**: 824–835.

Herrera, J. M. & García, D. (2009) The role of remnant trees in seed dispersal through the matrix: being alone is not always so sad. *Biological Conservation,* **142**: 149–158.

Kammesheidt, L. (2002) Perspectives on secondary forest management in tropical humid lowland America. *Ambio,* **31**: 243–250.

Kirika, J. M., Farwig, N. & Böhning-Gaese, K. (2007) Effects of local disturbance of tropical forests on frugivores and seed removal of a small-seeded Afrotropical tree. *Conservation Biology,* **22**: 318–328.

Kissling, W. D., Rahbek, C. & Böhning-Gaese, K. (2007) Food plant diversity as broad-scale determinant of avian frugivore richness. *Proceedings of the Royal Society of London B,* **274**: 799–808.

Kofron, C. P. & Chapman, A. (1995) Deforestation and bird species composition in Liberia, West Africa. *Tropical Zoology,* **8**: 239–256.

Kokwaro, J. O. (1988) Conservation status of the Kakamega forest in Kenya. The Eastern most relic of the equatorial rainforest of Africa. *Monographs in Systematic Botany from the Missouri Botanical Garden*, **25**: 471–489.

Laube, I., Breitbach, N. & Böhning-Gaese, K. (2008) Avian diversity in a Kenyan agroecosystem: effects of habitat structure and proximity to forest. *Journal of Ornithology,* **149**: 181–191.

Laurance, W. F. & Bierregaard, R. O. (1997) *Tropical forest remnants: ecology, management and conservation of fragmented communities.* University of Chicago Press, Chicago.

Laurance, S. G. W., Stouffer, P. C. & Laurance, W. F. (2004) Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. *Conservation Biology,* **18**: 1099–1109.

Legendre, P. & Gallagher, E. D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**: 271–280.

Lehouck, V., Spanhove, T., Vangestel, C., Cordeiro, N. J. & Lens, L. (2009) Does landscape structure affect resource tracking by avian frugivores in a fragmented Afrotropical forest? *Ecography,* **32**: 789–799.

Lens, L., Van Dongen, S., Norris, K., Githiru, M. & Matthysen, E. (2002) Avian persistence in fragmented rainforest. *Science,* **298**: 1236–1238.

Levey, D. J. (1988) Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs,* **58**: 251–269.

Leyequién, E., de Boer, W. F. & Toledo, V. M. (2010) Bird community composition in a shaded coffee agro-ecological matrix in Puebla, Mexico: the effects of landscape heterogeneity at multiple spatial scales. *Biotropica,* **42**: 236–245.

Lindell, C. A., Chomentowski, W. H. & Zook, J. R. (2004) Characteristics of bird species using forest and agricultural land covers in southern Costa Rica. *Biodiversity Conservation,* **13**: 2419–2441.

Loiselle, B. A. & Blake, J. G. (1991) Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology,* **72**: 180–193.

MacArthur, R. H. & MacArthur, J. W. (1961) On bird species diversity. *Ecology,* **42**: 594–598.

MacGregor-Fors, I. & Schondube, J. E. (2011) Use of tropical dry forests and agricultural areas by neotropical bird communities. *Biotropica,* **43**: 365–370.

Magadza, C. H. D. (2000) Climate change impacts and human settlements in Africa: prospects for adaptation. *Environmental Monitoring and Assessment,* **61**: 193–205.

Malizia, L. R. (2001) Seasonal fluctuations of birds, fruits, and flowers in a subtropical forest of Argentina. *Condor,* **103**: 45–61.

Marsden, S. T., Symes, C. T. & Mack, A. L. (2006) The response of a New Guinean avifauna to conversion of forest to small-scale agriculture. *Ibis,* **148**: 629–640.

Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-being: Biodiversity Synthesis.* World Resources Institute, Washington DC.

Monkkonen, M., Forsman, J. T. & Bokma, F. (2006) Energy availability, abundance, energy-use and species richness in forest bird communities: a test of the species-energy theory. *Global Ecology and Biogeography Letters,* **15**: 290–302.

Mora, C. & Sale, P. F. (2011) Ongoing global biodiversity loss and the need to move beyond protected areas: a review of the technical and practical shortcomings of protected areas on land and sea. *Marine Ecology Progress Series*, **434**: 251–266.

Morris, R. J. (2010) Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. *Philosophical Transactions of the Royal Society of London Series B*, **365**: 3709–3718.

Müller, D. & Mburu, J. (2009) Forecasting hotspots of forest clearing in Kakamega Forest, Western Kenya. *Forest Ecology and Management,* **257**: 968–977.

Murakami, M. (2002) Foraging mode shifts of four insectivorous bird species under temporally varying resource distribution in a Japanese deciduous forest. *Ornithological Science*, **1**: 63–69.

Myers, N. (1992) *The primary source: tropical forests and our future*. W. W. Norton & Company, New York.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature,* **403**: 853–858.

Naidoo, R. (2004) Species richness and community composition of songbirds in a tropical forest-agricultural landscape. *Animal Conservation,* **7**: 93–105.

Neuschulz, E. L., Botzat, A. & Farwig, N. (2011) Effects of forest modification on bird community composition and seed removal in a heterogeneous landscape in South Africa. *Oikos,* **120**: 1371–1379.

O'Dea, N. & Whittaker, R. J. (2007) How resilient are Andean montane forest bird communities to habitat degradation? *Biodiversity Conservation,* **16**: 1131–1159.

Ojwang, G. O., Agatsiva, J. & Situma, C. (2010) *Analysis of climate change and variability risks in the smallholder sector. Case studies of the Laikipia and Narok districts representing major agro-ecological zones in Kenya. In: Environment and natural resources.* Management Working Paper 41, FAO, Rome.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., O'hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H. & Wagner, H. (2010) *vegan: Community Ecology Package.*

Ormerod, S. J. & Watkinson, A. R. (2000) Birds and agriculture. *Journal of Applied Ecology,* **37**: 699–705.

Otieno, N. E., Gichuki, N., Farwig, N. & Kiboi, S. (2011) The role of farm structure on bird assemblages around a Kenyan tropical rainforest. *African Journal of Ecology,* **49**: 410–417.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature,* **421**: 37–42.

Peh, K. S. H., Sodhi, N. S., De Jong, J., Sekercioglu, C. H., Yap, C. A. M. & Lim, S. L. H. (2006) Conservation value of degraded habitats for forest birds in southern Peninsular Malaysia. *Diversity and Distributions,* **12**: 572–581.

Poulin, B. & Lefebvre, G. (1997) Estimation of arthropod availability to birds: effects of trapping techniques, prey distribution, and bird diet. *Journal of Field Ornithology,* **68**: 426–442.

Poulin, B. & Lefebvre, G. (2002) Effect of winter cutting on the passerine breeding assemblage in French Mediterranean reedbeds. *Biodiversity Conservation,* **11**: 1567–1581.

Poulin, B., Lefebvre, G. & McNeil, R. (1992) Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology,* **73**: 2295–2309.

Poulin, B., Lefebvre, G. & McNeil, R. (1993) Variations in bird abundance in tropical arid and semi-arid habitats. *Ibis,* **135**: 432–441.

R Development Core Team (2011) *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna.

Raman, T. R. S., Rawat, G. S. & Johnsingh, A. J. T. (1998) Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, north-east India. *Journal of Applied Ecology,* **35**: 214–231.

Ranganathan, J., Krishnaswamy, J. & Anand, M. O. (2010) Landscape-level effects on avifauna within tropical agriculture in the Western Ghats: insights for management and conservation. *Biology Conservation,* **143**: 2909–2917.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. & Pounds, J. A. (2003) Fingerprints of global warming on wild animals and plants. *Nature,* **421**: 57–60.

Sagar, R. & Singh, J. S. (2006) Tree density, basal area and species diversity in a disturbed dry tropical forest of northern India: implications for conservation. *Environment Conservation,* **33**: 256–262.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M. & Wall, D. H. (2000) Global biodiversity scenarios for the year 2100. *Science,* **287**: 1770–1774.

Sarr, D. A. & Puettmann, K. J. (2008) Forest management, restoration, and designer ecosystems: integrating strategies for a crowded planet. *Ecoscience,* **15**: 17–26.

Schaab, G., Khayota, B., Eilu, G. & Wägele, W. (eds) (2010) *The Biota East Africa atlas. Rainforest change over time*. Karlsruhe University of Applied Sciences, Karlsruhe.

Schleuning, M., Farwig, N., Peters, M. K., Bergsdorf, T., Bleher, B., Brandl, R., Dalitz, H., Fischer, G., Freund, W., Gikungu, M. W., Hagen, M., Garcia, F. H., Kagezi, G. H., Kaib, M., Kraemer, M., Lung, T., Naumann, C. M., Schaab, G., Templin, M., Uster, D., Wägele, J. W., Böhning-Gaese, K. (2011) Forest fragmentation and selective logging have inconsistent effects on multiple animal-mediated ecosystem processes in a tropical forest. *PLoS One*, **6**: e27785.

Seavy, N. E. (2009) Bird use of banana plantations adjacent to Kibale national park, Uganda: evaluating the conservation value of a matrix habitat. *Journal of East African Natural History,* **98**: 211–222.

Sekercioglu, C. H., Ehrlich, P. R., Daily, G. C., Aygen, D., Goehring, D. & Sandi, R. F. (2002) Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the National Academy of Sciences of the United States of America,* **99**: 263–267.

Sekercioglu, C. H. (2006) Increasing awareness of avian ecological function. *Trends in Ecology and Evolution,* **21**: 464–471.

Sekercioglu, C. H., Loarie, S. R., Brenes, F. O., Ehrlich, P. R. & Daily G. C. (2007) Persistence of forest birds in the Costa Rican agricultural countryside. *Conservation Biology,* **21**: 482–494.

Shanni, I. & De Bruijn, B. (2006) *A checklist of the birds of Kakamega forest.* East Africa Natural History Society. Nairobi.

Symes, G. T., Wirminghaus, J. O. & Downs, C. T. (2002) Species richness and seasonality of forest avifauna in three South African Afromontane forests. *Ostrich,* **73**: 106–113.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography,* **31**: 79–92.

Thiollay, J. M. (1995) The role of traditional agroforests in the conservation of rain forest bird diversity in Sumatra. *Conservation Biology,* **9**: 335–353.

Thomas, L., Laake, J. L., Rexstad, E., Strindberg, S., Marques, F. F. C., Buckland, S. T., Borchers, D. L., Anderson, D. R., Burnham, K. P., Burt, M. L., Hedley, S. L., Pollard, J. H., Bishop, J. R. B. & Marques, T. A. (2009) *Distance 6.0. Release 2.* Research Unit for Wildlife Population Assessment, University of St. Andrews, UK.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marques, T. A. & Burnham, K. P. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology,* **47**: 5–14.

Tscharntke, T., Sekercioglu, C. H., Dietsch, T. V., Sodhi, N. S., Hoehn, P. & Tylianakis, J. M. (2008) Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology,* **89**: 944–951.

Tsingalia, M. H. (1990) Habitat disturbance, severity and patterns of abundance in Kakamega forest, Western Kenya. *African Journal of Ecology,* **28**: 213–226.

Vallecillo, S., Brotons, L. & Thuiller, W. (2009) Dangers of predicting bird species distributions in response to land-cover changes. *Ecological Applications,* **19**: 538–549.

Van Bael, S. A., Philpott, S. M., Greenberg, R., Bichier, P., Barber, N. A., Mooney, K. A. & Gruner, D. S. (2008) Birds as predators in tropical agroforestry systems. *Ecology,* **89**: 928–934.

Wagner, P., Kohler, J., Schmitz, A. & Bohme, W. (2008) The biogeographical assignment of a west Kenyan rain forest remnant: further evidence from analysis of its reptile fauna. *Journal of Biogeography,* **35**: 1349–1361.

Waltert, M. (2000) *Diversity and structure of a bird community in a logged forest in south-east Cote d'Ivoire*. PhD Dissertation. Georg-August-University, Göttingen, Germany.

Waltert, M., Mardiastuti, A. & Mühlenberg, M. (2004) Effects of land use on bird species richness in Sulawesi, Indonesia. *Conservation Biology,* **5**: 1339–1346.

Waltert M., Bobo, K. S., Sainge, N. M., Fermon, H. & Mühlenberg, M. (2005) From forest to farmland: habitat effects on Afrotropical forest bird diversity. *Ecological Applications,* **15**: 1351–1366.

Whelan, C. J., Wenny, D. G. & Marquis, R. J. (2008) Ecosystem services provided by birds. *Annals of the New York Academy of Sciences,* **1134**: 25–60.

White, E. P., Ernest, S. K. M., Adler, P. B., Hurlbert, A. H. & Lyons, S. K. (2010) Integrating spatial and temporal approaches to understanding species richness. *Philosophical Transactions of the Royal Society of London Series B*, **365**: 3633–3643.

Williams, S. E. & Middleton, J. (2008) Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: implications for global climate change: *Diversity and Distribution*, **14**: 69–77.

Wirminghaus, J. O., Downs, C. T., Symes, C. T. & Perrin, M. R. (2001) Fruiting in two Afromontane forests in KwaZulu-Natal, South Africa: the habitat type of the endangered Cape Parrot *Poicephalus robustus*. *South African Journal of Botany,* **67**: 329–336.

Zimmerman, D. A., Turner, D. A. & Pearson, D. J. (1996) *Birds of Kenya and Northern Tanzania.* Russel Friedman Books, Halfway House.

7. ACKNOWLEDGEMENTS

I owe many thanks to numerous people and institutions whose generous support made this study possible. In particular, I am grateful to **Prof. Dr. Katrin Böhning-Gaese** for offering me this PhD scholarship opportunity and for guiding me throughout the study as my principal supervisor. In addition I wish to express my sincere thanks to **Prof. Dr. Rüdiger Wittig,** my second supervisor and expert assessor for my thesis.

I gratefully acknowledge the valuable guidance provided by **Dr. Matthias Schleuning, Prof. Dr. Katrin Böhning-Gaese** and **Dr. Eike-Lena Neuschulz** in study design, data analyses and manuscript writing. By working closely with **Dr. Matthias Schleuning**, I learned many things; especially proficiency in the statistical package 'R' besides greatly improving my manuscript writing skills. Special thanks are due to **Mathias Templin** (Matze) for his kind and tireless assistance with a wide range of logistical support and especially for translating my thesis summary from English to German. The numerous data used in this thesis were collected in the field with the resourceful assistance of **Benson Bwibo Chituyi** (BBC), **Patrick Luteshi, Jonathan Mukaisi and Collins Alusiola.**

I owe many thanks to the **Kenya Wildlife Service** (KWS) and the **land owners** around Kakamega Forest Reserve for kindly granting me the permission to access the study sites. I am very grateful to my host institution the **National Museums of Kenya** (NMK) for according me a study leave to undertake this PhD training as well as unlimited logistical support throughout the study period. **Nature Kenya** offered additional logistical support and contributed viable ideas towards my study.

Financial support was provided by the German Federal Ministry of Education and Research within the BIOTA East Africa framework, through (and with additional support from) the Catholic Academic Exchange Service (KAAD). My study program was further facilitated within the Biodiversity and Climate Research Centre (BiK-F) by the research funding program “Landes-Offensive zur Entwicklung wissenschaftlich ökonomischer Exzellenz (LOEWE)” of Hesse’s Ministry of Higher Education, Research, and the Arts.
Within KAAD I am especially indebted to **Frau Simone Saure** and **Dr. Marko Kuhn** for their kind support throughout my scholarship period. As a KAAD scholar I received many benefits; notably, the opportunity to attend numerous seminars that were not only exposing and educative but also useful for integration within the German culture and other international settings. In addition the German language course made my life in Germany much easier.

During my studies and stay in Germany, I received immense support from members of our working groups in Johannes Gutenberg University, Mainz and later in the Biodiversity and Climate Research Centre and Goethe University, Frankfurt. In particular, **Matze, Tanja, Tonka, Matthias, Irina, Dana, Sven, Eike, Nils, Johanna, Claudia, Monika, Marc, Birgit, Susanne, Christian, Conny, Marcia, Baptiste, Stefan, Thomas, Imran, Jaroslav and many more** offered not only assistance in diverse ways, but were part of a friendly working environment.

Finally, the successful completion of this study drew a lot from the moral support from my wife **Mercy**, my daughters (**Sarah, Lorna and Sonnie**) my mother **Monica,** my brothers, sisters, nephews and nieces.

To all these and many more not listed here I say ‘*Asante Sana’* (**Thank you very much**).

8. APPENDICES

Appendix 1: Geographical locations of sampling sites. GPS coordinates and elevation represent point count locations at the center of each site. Estimates of bird densities for each site and the respective detection functions are as indicated.

Site	Land use type	GPS Coordinates of center point (UTM)		Bird density estimates from DISTANCE	
		Latitude	Longitude	Individual birds per ha	Detection function model (Key function/adjustment term)
Colobus	Near natural forest	0040099 N	0706432 E	41.629	Uniform/Cosine
Bukhaywa	Near natural forest	0037809 N	0705818 E	39.12	Hazard-rate/Simple Polynomial
Buyangu Hill	Near natural forest	0037947 N	0707433 E	35.845	Uniform/Cosine
Ivakale	Near natural forest	0040686 N	0710314 E	36.57	Uniform/Cosine
Salazar	Near natural forest	0036053 N	0708129 E	42.873	Hazard-rate/Simple Polynomial
Buyangu Hill	Secondary forest	0038065 N	0707678 E	43.332	Uniform/Cosine
Guest house	Secondary forest	0038888 N	0706938 E	25.756	Hazard-rate/Simple Polynomial
Isiukhu falls	Secondary forest	0039177 N	0708906 E	33.246	Uniform/Cosine
Ivakale	Secondary forest	0040521 N	0710561 E	33.085	Uniform/Cosine
Shiyingo	Secondary forest	0035812 N	0703323 E	24.009	Uniform/Cosine
Angatia	Subsistence farmland	0043324 N	0700370 E	83.75	Uniform/Cosine
Mondoli	Subsistence farmland	0038418 N	0699838 E	113.38	Uniform/Cosine

Shikutsi	Subsistence farmland	0037468 N	0699457 E	88.011	Hazard-rate/Simple Polynomial
Stage-mboga	Subsistence farmland	0035719 N	0698461 E	55.022	Hazard-rate/Simple Polynomial
Tumaini	Subsistence farmland	0045207 N	0705631 E	85.879	Uniform/Cosine
Emukava	Sugarcane plantation	0037941 N	0697084 E	52.086	Uniform/Cosine
Magale	Sugarcane plantation	0042506 N	0702119 E	32.352	Half-normal/Cosine
Muting'ong'o	Sugarcane plantation	0045196 N	0703534 E	67.781	Uniform/Cosine
Okumu	Sugarcane plantation	0039881 N	0700056 E	57.285	Uniform/Cosine
Shianda	Subsistence farmland	0041357 N	0700333 E	46.358	Uniform/Cosine

Appendix 2: List of 237 bird species observed during surveys at each habitat type in Kakamega forest and neighboring farmlands; nomenclature and taxonomic sequence follow Zimmerman *et al*. (1996). Key to abbreviations: NMDS – nmds ordination scores for each species, Hab – habitat guild, Guild – feeding guild, Status – conservation and migration status, NN – near natural forest, SEC – secondary forest, SF – Subsistence farmland, SP – sugarcane plantation, FF – forest specialist, F – forest generalist, f – forest visitor, s – farmland species, Carn – carnivore, ins – insectivore, omn – omnivore, herb – herbivore (including seeds, leaves, shoots, roots, flowers, bulbs), frug – frugivore, E – endangered, V – globally vulnerable, v (lower case) – regionally vulnerable, AM – afro-tropical migrant, PM – Palearctic migrant (lowercase am and pm – part of the population is resident), R – rare species. The number of individuals of each species observed in each habitat type during the entire year is also indicated.

Family and Common Name	Scientific name	NMDS	Habitat	Guild	Status	NN	SEC	SF	SP	Total
Numididae: guineafowl										
Crested Guineafowl	*Guttera pucherani*	1.11	F	herb		12	0	0	0	**12**
Helmeted Guineafowl	*Numida meleagris*	-1.10	s	herb		0	0	0	64	**64**
Phasianidae: quails, francolins, spurfowl and allies										
Crested Francolin	*Francolinus sephaena*	-1.11	s	omn		0	0	0	2	**2**
Ciconiidae: storks										
Abdim's Stork	*Ciconia abdimii*	-1.09	s	ins	AM	0	0	1	61	**62**
Threskiornithidae: ibises and spoonbills										
Hadada Ibis	*Bostrychia hagedash*	-0.68	s	ins		1	2	36	15	**54**
Sacred Ibis	*Threskiornis aethiopicus*	-0.75	s	ins		0	0	4	0	**4**
Ardeidae: herons, egrets and bitterns										
Great White Egret	*Ardea alba*	-0.75	s	carn		0	0	6	0	**6**
Black-headed Heron	*Ardea melanocephala*	-1.00	s	carn		0	0	1	5	**6**
Scopidae: Hamerkop										
Hamerkop	*Scopus umbretta*	-1.06	s	carn		0	0	1	2	**3**
Accipitridae: diurnal birds of prey other than falcons										
Great Sparrowhawk	*Accipiter melanoleucus*	0.09	F	carn		10	5	21	3	**39**

Little Sparrowhawk	*Accipiter minullus*	0.89	f	carn		0	2	0	0	**2**
Augur Buzzard	*Buteo augur*	-0.97	s	carn		0	0	3	7	**10**
Brown Snake Eagle	*Circaetus cinereus*	-0.92	s	carn		0	0	0	2	**2**
Booted Eagle	*Hieraaetus pennatus*	-0.75	s	carn	PM	0	0	1	0	**1**
Lizzard Buzzard	*Kaupifalco monogrammicus*	-0.76	f	carn		0	0	4	0	**4**
Long-crested Eagle	*Lophaetus occipitalis*	-0.98	f	carn		0	0	3	8	**11**
Black Kite	*Milvus migrans*	-0.78	s	carn	am, pm	0	0	11	1	**12**
African Harrier Hawk	*Polyboroides typus*	-0.41	f	omn		2	0	8	1	**11**
Crowned Eagle	*Stephanoaetus coronatus*	1.05	FF	carn	v	3	0	0	0	**3**
Rallidae: rails and relatives										
White-spotted Flufftail	*Sarothrura pulchra*	0.69	FF	ins		9	8	0	0	**17**
Gruidae: cranes										
Grey Crowned Crane	*Balearica regulorum*	-1.00	s	omn	V	0	0	4	6	**10**
Columbidae: pigeons and doves										
Eastern Bronze-naped Pigeon	*Columba delegorguei*	1.14	FF	frug		2	0	0	0	**2**
Ring-necked Dove	*Streptopelia capicola*	-0.75	f	herb		0	0	5	0	**5**
African Mourning Dove	*Streptopelia decipiens*	-1.03	s	herb		0	0	19	22	**41**
Red-eyed Dove	*Streptopelia semitorquata*	-0.71	f	herb		8	3	114	71	**196**
African Green Pigeon	*Treron calvus*	-0.89	F	frug		0	1	66	81	**148**
Blue-spotted Wood Dove	*Turtur afer*	-0.48	f	herb		0	11	73	22	**106**
Tambourine Dove	*Turtur tympanistria*	0.16	F	herb		96	85	142	37	**360**
Psittacidae: lovebirds and parrots										
Red-headed Lovebird	*Agapornis pullarius*	-0.78	s	herb		0	0	1	0	**1**
Meyer's Parrot	*Poicephalus meyeri*	-1.04	s	herb		0	0	2	12	**14**
Musophagidae: turacos										
Great Blue Turaco	*Corythaeola cristata*	0.57	F	frug		3	7	0	0	**10**
Eastern Grey Plantain-eater	*Crinifer zonurus*	-0.90	s	frug		0	0	20	12	**32**
Ross's Turaco	*Musophaga rossae*	-0.11	F	frug		1	15	34	1	**51**

White-crested Turaco	*Tauraco leucolophus*	-0.75	f	frug		0	0	1	0	**1**
Black-billed Turaco	*Tauraco schuetti*	1.21	FF	frug		2	0	0	0	**2**
Cuculidae: cuckoos and coucals										
Blue-headed Coucal	*Centropus monachus*	-0.83	s	ins		0	0	4	2	**6**
Senegal Coucal	*Centropus senegalensis*	-1.01	f	carn		0	0	17	40	**57**
Yellowbill	*Ceuthmochares aereus*	1.13	F	ins	am	4	0	0	0	**4**
Diederik Cuckoo	*Chrysococcyx caprius*	-0.89	s	ins	am	0	0	2	1	**3**
African Emerald Cuckoo	*Chrysococcyx cupreus*	0.71	F	ins		4	8	1	0	**13**
Klaas's Cuckoo	*Chrysococcyx klaas*	-0.09	f	ins		0	18	16	4	**38**
Common Cuckoo	*Cuculus canorus*	-0.78	s	ins	PM	0	0	1	0	**1**
Red-chested Cuckoo	*Cuculus solitarius*	0.35	F	ins	am	14	29	21	4	**68**
Strigidae: typical owls										
Verreaux's Eagle-Owl	*Bubo lacteus*	-0.09	f	carn		2	0	7	0	**9**
Red-chested Owlet	*Glaucidium tephronotum*	-0.75	FF	carn	v	0	0	4	0	**4**
Coliidae: mousebirds										
Speckled Mousebird	*Colius striatus*	-0.81	s	frug		0	23	390	447	**860**
Trogonidae: trogons										
Narina Trogon	*Apaloderma narina*	0.89	F	ins		0	11	0	0	**11**
Bar-tailed Trogon	*Apaloderma vittatum*	1.03	FF	ins		4	3	0	0	**7**
Alcedinidae: kingfishers										
African Pygmy Kingfisher	*Ceyx pictus*	-0.74	f	ins	am	0	1	14	9	**24**
Grey-headed Kingfisher	*Halcyon leucocephala*	-1.11	f	ins	am	0	0	0	2	**2**
Woodland Kingfisher	*Halcyon senegalensis*	-1.11	s	ins	am	0	0	0	3	**3**
Meropidae: bee-eaters										
White-throated Bee-eater	*Merops albicollis*	-0.32	f	ins	AM	1	0	5	0	**6**
Eurasian Bee-eater	*Merops apiaster*	-0.99	f	ins	PM	0	0	26	12	**38**
Blue-headed Bee-eater	*Merops muelleri*	1.17	FF	ins		14	0	0	0	**14**
Cinamon-chested Bee-eater	*Merops oreobates*	-0.78	F	ins		0	0	2	0	**2**

Little Bee-eater	*Merops pusillus*	-0.94	s	ins		0	0	3	15	**18**
Upupidae: Hoopoe										
Hoopoe	*Upupa epops*	-0.78	s	ins	am, pm	0	0	2	0	**2**
Phoeniculidae: wood-hoopoes										
White-headed Wood-Hoopoe	*Phoeniculus bollei*	1.08	FF	ins		52	9	0	0	**61**
Bucerotidae: hornbills										
Black-and-white Casqued Hornbill	*Bycanistes subcylindricus*	0.40	F	frug		82	47	42	10	**181**
Capitonidae: barbets and tinkerbirds										
Yellow-spotted Barbet	*Buccanodon duchaillui*	0.95	FF	frug		84	53	0	0	**137**
Grey-throated Barbet	*Gymnobucco bonapartei*	0.82	F	omn		59	50	0	0	**109**
Double-toothed Barbet	*Lybius bidentatus*	-0.72	f	omn		1	0	24	6	**31**
Yellow-rumped Tinkerbird	*Pogoniulus bilineatus*	0.44	F	frug		202	221	101	21	**545**
Yellow-billed Barbet	*Trachylaemus purpuratus*	0.97	F	omn		90	22	0	0	**112**
Hairy-breasted Barbet	*Tricholaema hirsuta*	1.03	F	frug		19	8	0	0	**27**
Spot-flanked Barbet	*Tricholaema lacrymosa*	-0.78	s	frug		0	0	1	0	**1**
Indicatoridae: honeyguides										
Thick-billed Honeyguide	*Indicator conirostris*	1.21	FF	omn	v	1	0	0	0	**1**
Least Honeyguide	*Indicator exilis*	0.77	FF	omn	v	3	1	1	0	**5**
Lesser Honeyguide	*Indicator minor*	0.90	f	omn		0	2	0	0	**2**
Cassin's Honeybird	*Prodotiscus insignis*	0.86	FF	ins	v	0	1	0	0	**1**
Picidae: wrynecks and woodpeckers										
Brown-eared Woodpecker	*Campethera caroli*	0.98	F	ins		7	24	0	0	**31**
Buff-spotted Woodpecker	*Campethera nivosa*	0.30	f	ins		0	11	6	2	**19**
Cardinal Woodpecker	*Dendropicos fuscescens*	0.23	f	ins		4	10	5	6	**25**
African Grey Woodpecker	*Dendropicos goertae*	-0.89	f	ins		0	0	11	9	**20**
Yellow-crested Woodpecker	*Dendropicos xantholophus*	1.05	F	ins		7	6	0	0	**13**
Red-throated Wryneck	*Jynx ruficollis*	-0.75	f	ins		0	0	1	0	**1**
Eurylaimidae: broadbills										

African Broadbill	*Smithornis capensis*	1.15	FF	ins		17	1	0	0	**18**
Platysteiridae: batises, wattle-eyes and relatives										
Chestnut Wattle-eye	*Dyaphorophyia castanea*	1.00	FF	ins		11	17	0	0	**28**
Yellow-bellied Wattle-eye	*Dyaphorophyia concreta*	1.14	FF	ins	v	3	0	0	0	**3**
Jameson's Wattle-eye	*Dyaphorophyia jamesoni*	1.02	FF	ins		77	74	0	0	**151**
Shrike Flycatcher	*Megabyas flammulatus*	1.17	FF	ins		4	0	0	0	**4**
Brown-throated Wattle-eye	*Platysteira cyanea*	0.11	f	ins		11	100	68	6	**185**
Malaconotidae: helmetshrikes, bushshrikes, tchagras and puffbacks										
Bocage's Bushshrike	*Chlorophoneus bocagei*	0.69	F	ins		8	28	0	1	**37**
Pink-footed Puffback	*Dryoscopus angolensis*	1.11	FF	ins		14	1	0	0	**15**
Northern Puffback	*Dryoscopus gambensis*	-0.88	F	ins		0	0	3	2	**5**
Tropical Boubou	*Laniarius aethiopicus*	-0.59	f	ins		3	17	136	65	**221**
Black-headed Gonolek	*Laniarius erythrogaster*	-0.92	s	omn		0	0	4	7	**11**
Luhder's Bushshrike	*Laniarius luehderi*	0.58	F	ins		16	10	1	2	**29**
Brown-crowned Tchagra	*Tchagra australis*	-0.96	s	ins		0	0	5	10	**15**
Marsh Tchagra	*Tchagra minutus*	-1.11	s	ins		0	0	0	2	**2**
Black-crowned Tchagra	*Tchagra senegalus*	-1.03	s	ins		0	0	3	11	**14**
Campephagidae: cuckooshrikes										
Black Cuckooshrike	*Campephaga flava*	-0.92	f	ins	am	0	0	0	1	**1**
Petit's Cuckooshrike	*Campephaga petiti*	0.74	FF	ins		5	10	0	0	**15**
Red-shouldered Cuckooshrike	*Campephaga phoenicea*	0.86	f	ins		0	2	0	0	**2**
Laniidae: shrikes										
Common Fiscal	*Lanius collaris*	-0.96	s	ins		0	0	63	118	**181**
Grey-backed Fiscal	*Lanius excubitoroides*	-0.92	s	carn		0	0	0	3	**3**
Mackinnon's Fiscal	*Lanius mackinnoni*	-0.83	f	carn		0	0	2	2	**4**
Oriolidae: orioles										
African Golden Oriole	*Oriolus auratus*	-0.77	f	omn	AM	0	0	2	0	**2**
Western Oriole	*Oriolus brachyrhynchus*	1.10	F	ins		77	3	0	0	**80**

Dicruridae: drongos										
Square-tailed Drongo	*Dicrurus ludwigii*	1.08	F	ins		231	14	0	0	**245**
Monarchidae: monarch flycatchers										
African Blue Flycatcher	*Elminia longicauda*	-0.27	f	ins		28	12	149	47	**236**
Dusky Crested Flycatcher	*Elminia nigromitrata*	1.06	F	ins		26	3	0	0	**29**
African Paradise Flycatcher	*Terpsiphone viridis*	0.37	f	ins	am	36	31	35	5	**107**
Corvidae: crows and allies										
Pied Crow	*Corvus albus*	-0.75	s	omn		0	0	9	0	**9**
Paridae: tits										
Dusky Tit	*Parus funereus*	1.00	FF	ins		50	2	0	0	**52**
Hirundinidae: saw-wings, swallows and martins										
Lesser Striped Swallow	*Cecropis abyssinica*	-1.03	s	ins		0	0	23	24	**47**
Mosque Swallow	*Cecropis senegalensis*	-1.14	s	ins		0	0	1	2	**3**
Common House Martin	*Delichon urbica*	-1.08	s	ins	PM	0	0	3	19	**22**
Barn Swallow	*Hirundo rustica*	-1.04	s	ins	PM	0	0	10	21	**31**
White-headed Saw-wing	*Psalidoprocne albiceps*	-0.69	f	ins		0	2	49	16	**67**
Black Saw-wing	*Psalidoprocne pristoptera*	-0.59	f	ins		0	10	62	40	**112**
Cisticolidae: cisticolas and allies										
Yellow-breasted Apalis	*Apalis flavida*	-0.92	f	ins		0	0	2	2	**4**
Black-throated Apalis	*Apalis jacksoni*	0.52	FF	ins		4	4	2	2	**12**
Chestnut-throated Apalis	*Apalis porphyrolaema*	0.90	F	ins		0	2	0	0	**2**
Black-collared Apalis	*Apalis pulchra*	0.16	F	ins		6	11	39	1	**57**
Buff-throated Apalis	*Apalis rufogularis*	0.97	FF	ins		29	22	1	0	**52**
Grey-backed Camaroptera	*Camaroptera brachyura*	0.08	f	ins		23	227	171	56	**477**
Olive-green Camaroptera	*Camaroptera chloronota*	1.00	FF	ins		273	68	0	2	**343**
Siffling Cisticola	*Cisticola brachypterus*	-1.05	s	ins		0	0	1	16	**17**
Singing Cisticola	*Cisticola cantans*	-0.97	s	ins		0	0	97	126	**223**
Rattling Cisticola	*Cisticola chiniana*	-1.03	s	ins		0	0	5	23	**28**

Chubb's Cisticola	*Cisticola chubbi*	-0.95	F	ins		0	0	130	207	**337**
Hunter's Cisticola	*Cisticola hunteri*	-1.18	s	ins		0	0	0	4	**4**
Grey-capped Warbler	*Eminia lepida*	-0.90	f	ins		0	0	31	27	**58**
Banded Prinia	*Prinia bairdii*	1.09	F	ins		2	1	0	0	**3**
Tawny-flanked Prinia	*Prinia subflava*	-0.83	f	ins		0	7	54	68	**129**
White-chinned Prinia	*Schistolais leucopogon*	0.14	F	ins		3	15	17	1	**36**
Pycnonotidae: bulbuls										
Ansorge's Greenbul	*Andropadus ansorgei*	0.97	FF	herb		3	13	0	0	**16**
Plain Greenbul	*Andropadus curvirostris*	0.96	FF	herb		27	21	0	0	**48**
Slender-billed Greenbul	*Andropadus gracilirostris*	1.01	FF	frug		14	12	0	0	**26**
Little Grey Greenbul	*Andropadus gracilis*	1.06	FF	herb		25	6	0	0	**31**
Yellow-whiskered Greenbul	*Andropadus latirostris*	0.91	F	omn		435	428	3	0	**866**
Shelley's Greenbul	*Andropadus masukuensis*	0.95	FF	omn		18	7	0	1	**26**
Little Greenbul	*Andropadus virens*	1.04	F	omn		20	7	0	0	**27**
Honeyguide Greenbul	*Baeopogon indicator*	0.98	FF	frug		35	13	1	0	**49**
Red-tailed Bristlebill	*Bleda syndactyla*	1.01	FF	ins		168	74	0	0	**242**
Yellow-throated Leaflove	*Chlorocichla flavicollis*	-0.79	f	frug		3	2	350	220	**575**
Joyful Greenbul	*Chlorocichla laetissima*	0.86	F	herb		60	28	2	0	**90**
Cabanis's Greenbul	*Phyllastrephus cabanisi*	1.04	FF	ins		250	127	0	0	**377**
Toro Olive Greenbul	*Phyllastrephus hypochloris*	0.94	FF	ins	v	5	55	0	0	**60**
Common Bulbul	*Pycnonotus barbatus*	-0.21	f	herb		129	282	637	547	**1595**
Sylviidae: Old World warblers										
Black-faced Rufous Warbler	*Bathmocercus rufus*	1.02	FF	ins		180	65	1	0	**246**
Dark-capped Yellow Warbler	*Chloropeta natalensis*	-0.86	s	ins		0	3	40	59	**102**
Turner's Eremomela	*Eremomela turneri*	1.13	FF	ins	E	60	0	0	0	**60**
Icterine Warbler	*Hippolais icterina*	-0.92	s	ins	PM	0	0	0	2	**2**
Olive-tree Warbler	*Hippolais olivetorum*	-1.04	s	ins	PM	0	0	0	1	**1**
Eastern Olivaceous Warbler	*Hippolais pallida*	-0.55	s	ins	PM	0	1	1	4	**6**

Green Hylia	*Hylia prasina*	0.95	F	ins		0	1	0	0	**1**
Southern Hyliota	*Hyliota australis*	1.17	F	ins	v	2	0	0	0	**2**
Moustached Grass Warbler	*Melocichla mentalis*	-0.89	s	ins		0	0	3	1	**4**
Uganda Woodland Warbler	*Phylloscopus budongoensis*	1.02	FF	ins		236	91	0	0	**327**
Willow Warbler	*Phylloscopus trochilus*	-0.03	f	ins	PM	4	2	14	1	**21**
Blackcap	*Sylvia atricapilla*	0.58	F	omn	PM	1	2	1	0	**4**
Timaliidae: illadopses, babblers and chatterers										
Scaly-breasted Illadopsis	*Illadopsis albipectus*	1.02	FF	ins		130	91	0	0	**221**
Brown Illadopsis	*Illadopsis fulvescens*	0.94	FF	ins		63	41	3	0	**107**
Mountain Illadopsis	*Illadopsis pyrrhoptera*	0.98	FF	ins		1	2	0	0	**3**
Pale-breasted Illadopsis	*Illadopsis rufipennis*	0.99	FF	ins		108	78	0	0	**186**
Grey-chested Babbler	*Kakamega poliothorax*	1.06	FF	ins	v	9	3	0	0	**12**
Arrow-marked Babbler	*Turdoides jardineii*	-0.77	s	ins		0	0	3	0	**3**
Brown Babbler	*Turdoides plebejus*	-0.99	s	ins		0	0	20	41	**61**
Zosteropidae: white-eyes										
African Yellow White-eye	*Zosterops senegalensis*	-0.23	f	ins		13	79	201	83	**376**
Sturnidae: starlings and oxpeckers										
Violet-backed Starling	*Cynniricinclus leucogaster*	-0.08	f	frug	AM	21	21	64	36	**142**
Lesser Blue-eared Starling	*Lamprotornis chloropterus*	-0.87	s	omn		0	0	15	0	**15**
Superb Starling	*Lamprotornis superbus*	-1.02	s	ins		0	0	0	2	**2**
Stuhlmann's Strarling	*Poeoptera stuhlmanni*	0.82	FF	frug		4	22	1	0	**27**
Turdidae: thrushes										
Brown-chested Alethe	*Alethe poliocephala*	1.04	FF	ins		48	16	0	0	**64**
White-tailed Ant Thrush	*Neocossyphus poensis*	1.01	FF	ins		57	64	0	0	**121**
Olive Thrush	*Turdus olivaceus*	-0.66	F	omn		1	1	30	6	**38**
African Thrush	*Turdus pelios*	-0.37	f	omn		9	30	141	77	**257**
Muscicapidae: chats, wheatears and Old World flycatchers										
African Grey Flycatcher	*Bradornis microrhynchus*	-0.77	s	ins		0	0	1	0	**1**

Pale Flycatcher	*Bradornis pallidus*	-0.76	s	ins		0	1	16	15	**32**
Brown-backed Scrub Robin	*Cercotrichas hartlaubi*	-0.65	f	ins		0	7	26	37	**70**
White-browed Scrub Robin	*Cercotrichas leucophrys*	-0.86	s	ins		0	4	34	66	**104**
Blue-shouldered Robin-Chat	*Cossypha cyanocampter*	0.97	F	ins		97	50	0	0	**147**
White-browed Robin-Chat	*Cossypha heuglini*	-0.67	f	ins		0	20	188	91	**299**
Red-capped Robin-Chat	*Cossypha natalensis*	0.92	FF	omn	am	0	4	0	0	**4**
Snowy-headed Robin-Chat	*Cossypha niveicapilla*	0.53	F	omn		3	4	2	0	**9**
Northern Black Flycatcher	*Melaenornis edolioides*	-0.68	s	ins		2	4	160	46	**212**
White-eyed Slaty Flycatcher	*Melaenornis fischeri*	-0.76	s	ins		0	0	4	0	**4**
African Dusky Flycatcher	*Muscicapa adusta*	-0.71	F	ins		1	0	21	7	**29**
Whinchat	*Saxicola rubetra*	-1.11	s	ins	PM	0	0	1	9	**10**
Common Stonechat	*Saxicola torquata*	-1.06	s	ins		0	0	11	50	**61**
Equatorial Akalat	*Sheppardia aequatorialis*	1.05	FF	ins		90	24	0	0	**114**
Grey-winged Robin	*Sheppardia polioptera*	0.85	FF	ins	v	3	7	1	0	**11**
Nectariniidae: sunbirds										
Western Violet-backed Sunbird	*Anthreptes longuemarei*	-0.77	f	omn		0	0	4	0	**4**
Green-throated Sunbird	*Chalcomitra rubescens*	-0.90	F	omn		0	0	11	3	**14**
Scarlet-chested Sunbird	*Chalcomitra senegalensis*	-0.88	s	omn		0	0	20	5	**25**
Olive-bellied Sunbird	*Cinnyris chloropygius*	0.34	F	omn		2	1	4	0	**7**
Copper Sunbird	*Cinnyris cupreus*	-0.78	f	ins		0	0	1	0	**1**
Northern Double-collared Sunbird	*Cinnyris reichenowi*	-0.24	F	omn		1	7	33	1	**42**
Variable Sunbird	*Cinnyris venustus*	-0.53	f	omn		0	16	41	58	**115**
Olive Sunbird	*Cyanomitra olivacea*	0.94	FF	omn		70	42	1	0	**113**
Green-headed Sunbird	*Cyanomitra verticalis*	-0.39	F	omn		1	2	12	3	**18**
Collared Sunbird	*Hedydipna collaris*	1.00	F	herb		20	29	0	0	**49**
Bronze Sunbird	*Nectarinia kilimensis*	-0.71	f	omn		3	16	305	312	**636**
Passeridae: sparrow weavers, Old World sparrows and petronias										
Grey-headed Sparrow	*Passer griseus*	-0.92	s	herb		0	0	42	44	**86**

Ploceidae: weavers, bishops and widowbirds									
Grosbeak Weaver	*Amblyospiza albifrons*	-0.99	f	omn		0	0	4	6	**10**
Fan-tailed Widowbird	*Euplectes axillaris*	-1.10	s	herb		0	0	3	6	**9**
Yellow Bishop	*Euplectes capensis*	-1.05	s	omn		0	0	12	31	**43**
Black Bishop	*Euplectes gierowii*	-1.03	s	herb		0	0	1	10	**11**
Marsh Widowbird	*Euplectes hartlaubi*	-0.78	s	omn	v	0	0	6	0	**6**
Yellow-mantled Widowbird	*Euplectes macrourus*	-1.01	s	omn		0	0	43	133	**176**
Red-headed Malimbe	*Malimbus rubricollis*	1.11	FF	ins		22	1	0	0	**23**
Baglafecht Weaver	*Ploceus baglafecht*	-0.97	f	ins		0	0	111	183	**294**
Dark-backed Weaver	*Ploceus bicolor*	1.03	F	omn		224	118	1	0	**343**
Village Weaver	*Ploceus cucullatus*	-0.95	s	omn		0	0	328	351	**679**
Brown-capped Weaver	*Ploceus insignis*	0.81	FF	omn		7	3	0	0	**10**
Black-necked Weaver	*Ploceus nigricollis*	-0.04	f	ins		0	4	4	1	**9**
Spectacled Weaver	*Ploceus ocularis*	-1.04	f	ins		0	0	0	5	**5**
Speke's Weaver	*Ploceus spekei*	-0.89	s	omn		0	0	2	3	**5**
Holub's Golden Weaver	*Ploceus xanthops*	-0.96	s	omn		0	0	1	4	**5**
Estrildidae: waxbills										
Brown Twinspot	*Clytospiza monteiri*	-0.92	f	omn		0	0	0	11	**11**
Common Waxbill	*Estrilda astrild*	-1.25	s	omn		0	0	0	8	**8**
Black-crowned Waxbill	*Estrilda nonnula*	-1.11	f	herb		0	0	1	8	**9**
Fawn-breasted Waxbill	*Estrilda paludicola*	-0.95	s	herb		0	0	3	20	**23**
Black-rumped Waxbill	*Estrilda troglodytes*	-1.04	s	omn		0	0	0	4	**4**
Black-bellied Firefinch	*Lagonosticta rara*	-1.01	s	herb		0	0	10	11	**21**
African Firefinch	*Lagonosticta rubricata*	-0.94	s	herb		0	0	13	10	**23**
Bar-breasted Firefinch	*Lagonosticta rufopicta*	-0.87	f	herb		0	0	3	2	**5**
Red-billed Firefinch	*Lagonosticta senegala*	-1.04	s	herb		0	0	3	23	**26**
Grey-headed Negrofinch	*Nigrita canicapilla*	-0.09	F	omn		0	5	3	3	**11**
Black-and-white Mannikin	*Spermestes bicolor*	-0.92	f	herb		0	0	191	89	**280**

Bronze Mannikin	*Spermestes cucculatus*	-0.82	s	herb		0	6	95	92	**193**
Red-headed Bluebill	*Spermophaga ruficapilla*	0.56	F	omn		7	1	5	0	**13**
Red-cheeked Cordon-bleu	*Uraeginthus bengalus*	-0.95	s	herb		0	0	17	9	**26**
Viduidae: Parasitic Weaver, indigobirds and whydahs										
Pin-tailed Whydah	*Vidua macroura*	-0.92	s	herb		0	1	22	22	**45**
Vieillot's Black Weaver	*Ploceus nigerrimus*	-0.88	f	ins		0	0	16	8	**24**
Motacillidae: wagtails, longclaws and pipits										
Grassland Pipit	*Anthus cinnamomeus*	-0.86	s	ins		0	1	0	14	**15**
Plain-backed Pipit	*Anthus leucophrys*	-1.25	s	ins		0	0	0	3	**3**
Yellow-throated Longclaw	*Macronyx croceus*	-1.07	s	ins		0	0	11	23	**34**
African Pied Wagtail	*Motacilla aguimp*	-0.97	s	ins		0	0	56	87	**143**
Yellow Wagtail	*Motacilla flava*	-1.04	s	ins	PM	0	0	3	13	**16**
Fringillidae: canaries, citrils, seedeaters and relatives										
Black-throated Seedeater	*Crithagra atrogularis*	-0.78	s	herb	R	0	0	1	0	**1**
African Citril	*Crithagra citrinelloides*	-0.91	f	omn		0	0	27	18	**45**
Yellow-fronted Canary	*Crithagra mozambica*	-0.81	s	herb		0	17	73	126	**216**
Streaky Seedeater	*Crithagra striolata*	-1.03	f	omn		0	0	3	3	**6**
Brimstone Canary	*Crithagra sulphurata*	-0.98	s	herb		0	0	1	3	**4**

9. CURRICULUM VITAE

Ronald K. Mulwa

Place and Date of Birth: Kitui, Kenya - 12 July 1970

Nationality: Kenyan

Biodiversität und Klima Forschungszentrum (BiK-F)
Senckenberganlage 25
60325 Frankfurt am Main
Germany

e-mail: Ronald.Mulwa@senckenberg.de; rmulwa@museums.co.ke; ronmulwa@yahoo.com

Phone: c/o Mathias Templin 0049 69 7542 1893

09/10 – Present PhD at the Institute for Ecology, Evolution and Diversity; Goethe-University Frankfurt, Germany in cooperation with the Biodiversity and Climate Research Centre (BiK-F), Frankfurt, Germany.
Supervisor: Prof. Dr. Katrin Bohning-Gaese

1998-2001: **MSc.** Animal Ecology, Kenyatta University, Kenya.

1990-1994: **BSc.** Wildlife Management, Moi University, Kenya.

Employment: 2001 – present. Research Scientist - National Museums of Kenya, Ornithology Section, Department of Zoology.

Research grants

- **International Foundation for Science (IFS)** (2008) – Samburu Oxpeckers
- **Rufford Small Grant** (RSG 2005-2006). Bird Surveys in dryland hill tops in Kitui/Mwingi.
- **British Ecological Society** (BES) 2004-2005. Samburu Oxpeckers
- **WWF - EFN** Professional Development Grant (2004). Conference travel grant - Tunisia