

Plant-frugivore interactions in a heterogeneous forest landscape of South Africa

Dissertation

In partial fulfilment of the requirements

for the award of a

Doctorate Degree in Natural Sciences (Dr. rer. nat)

The Faculty of Biology, Philipps-University of Marburg

Lackson Chama, MSc

Sinazongwe (Zambia)

June 2012, Marburg

From the Faculty of Biology, Philipps-University Marburg

als Dissertation am _____ angenommen.

Dekan: Prof. Dr. Paul Galland

Erstgutachterin: Prof. Dr. N. Farwig

Zweitgutachter: Prof. Dr. R. Brandl

Tag der Disputation: 25th June 2012

Dedicated to

my son, Mishila, who's first two years on earth I was hardly part of, due to my commitment towards this work.



Contents

CHAPTER 1: GENERAL INTRODUCTION	3
EFFECTS OF HUMAN ACTIVITIES ON FOREST BIODIVERSITY	4
PLANT-FRUGIVORE INTERACTIONS IN CHANGING LANDSCAPES	5
THE ROLE OF FUNCTIONAL DIVERSITY IN FRUGIVORE COMMUNITIES	5
EFFECTS OF SEED INGESTION BY FRUGIVOROUS BIRDS ON GERMINATION SUCCESS	6
AIMS OF THE THESIS	7
REFERENCES	9
CHAPTER 2: PLANT-FRUGIVORE NETWORKS IN MODIFIED LANDSCAPES.....	13
ABSTRACT	14
INTRODUCTION	15
MATERIAL AND METHODS	17
RESULTS	20
DISCUSSION	23
CONCLUSION	26
ACKNOWLEDGMENTS.....	27
REFERENCES	28
CHAPTER 3: FUNCTIONAL DIVERSITY OF FRUGIVORE COMMUNITIES IN MODIFIED LANDSCAPES	33
ABSTRACT	34
INTRODUCTION	35
MATERIAL AND METHODS	37
RESULTS	41
DISCUSSION	46
CONCLUSIONS.....	50
ACKNOWLEDGEMENTS	50
REFERENCES	51
CHAPTER 4: THE IMPORTANCE OF FRUGIVORES FOR GERMINATION SUCCESS OF PLANT SPECIES	57
ABSTRACT	58
INTRODUCTION	59
MATERIAL AND METHODS.....	60
RESULTS	63
DISCUSSION	66
CONCLUSIONS.....	67
ACKNOWLEDGMENTS.....	67
REFERENCES	69
CHAPTER 5: GENERAL CONCLUSIONS	72
SUMMARY OF METHODS AND KEY FINDINGS.....	73
IMPLICATIONS FOR CONSERVATION.....	74
FUTURE RESEARCH PROSPECTS.....	76
DEUTSCHE ZUSAMMENFASSUNG	77
APPENDICES	80

APPENDIX A	81
APPENDIX B	83
APPENDIX C.....	84
APPENDIX D	86
ACKNOWLEDGMENTS	87
CURRICULUM VITAE	90
ERKLÄRUNG	92

Chapter 1: General Introduction

Effects of human activities on forest biodiversity

Human-driven activities constitute the most serious threat linked with the loss of Earth's biological diversity (Forman & Collinge 1996, Bergman et al. 2004, Gibson et al. 2011). A recent global assessment of the impacts of human disturbance on biodiversity by Gibson et al. (2011) suggests that these threats are particularly high in tropical forest landscapes where both species diversity and human pressures on natural environments are high. The rapid increase in human land-use activities involving the conversion of tropical forests for agriculture and timber production (FAO 2006, Gibson et al. 2011) has not only considerably reduced the sizes of remaining forest, but also disproportionately increased the size of human dominated matrix surrounding these forest patches (Debinski & Holt 2000, Fahrig 2003). This leads to increased forest isolation and can undermine the quality of forest habitats (Saunders et al. 1991, Wunderle 1997, Fischer & Lindenmayer 2007). Moreover, these changes can alter the physical space where species grow and interact, and thus trigger biological responses that may lead to the disruption of species composition (Montoya 2008). With the global human population predicted to grow even further in the next three decades, it looks likely that these human driven threats on biodiversity will equally increase (Primack 2002) and could adversely impact on key ecological processes such as seed dispersal.

The process of seed dispersal plays a pivotal role in the regeneration and restoration of plant communities across forest ecosystems globally (Howe & Smallwood 1982). For instance, up to 50 and 90% of fleshy fruiting plant species in temperate and tropical forest ecosystems, respectively, depend on this process for the transportation of their propagules to suitable habitats (Aizen et al. 2002, Herrera 2003). Several studies showed that both forest patch quality and matrix habitat can modify single-pair seed dispersal interactions. However, these interactions have been shown to be linked in complex networks of mutually dependent plants and frugivores species (Fortuna & Bascompte 2006, Bascompte & Jordano 2007). Here, studies so far are scarce. With human activities increasingly likely to further isolate and reduce the sizes and quality of remaining forest patches (Rosenberg et al. 1999), it is vital to study plant-frugivore interactions in a community approach to better understand the effects of habitat modification on seed dispersal processes. Further, the functional roles in terms of species contribution and traits should be considered.

Plant-frugivore interactions in changing landscapes

Plant-frugivore mutualistic interactions form the physical template for seed dispersal and thus forest regeneration (Bascompte & Jordano 2007). Recent studies have shown that these interactions are often assembled in form of complex networks of interdependencies between species of both plants and frugivores (Bascompte & Jordano 2007, Reid & Armesto 2011, Menke et al. 2012). The pattern of interactions in the networks is highly heterogeneous, suggesting that a large proportion of species have less and weak interactions, while a few are much more connected than expected by chance (Fortuna & Bascompte 2006, Vázquez et al. 2009). This result in the formation of a nested plant-frugivore community, where less connected species interacts with a subset of the most connected species (Bascompte et al. 2003, Bascompte & Jordano 2007). These community structures can have important implications for the stability of plant-frugivore interactions especially in the face of human triggered habitat fragmentation (Fortuna & Bascompte 2006, Tylianakis et al. 2010a). However, not many studies have considered the effects of habitat fragmentation on seed dispersal networks.

So far it is known that species react differently to habitat modification due to different sensitivity to disturbances (Watson et al. 2005, Van Houtan et al. 2007). For instance, while some species may be able to take advantage of new ‘habitats’ provided by intervening matrix, such as farmland or scattered trees within farmland, others may not (Andren 1994). These changes in forest landscapes can lead to the decline and loss of key dispersers which may alter the interaction structure in mutualistic networks (Cordeiro & Howe 2003, Kirika et al. 2008). Thus, examining complex plant-frugivore mutualistic networks can help to better understand the long-term effects of anthropogenic impacts on the processes of seed dispersal (Bascompte & Jordano 2007). The functional diversity of frugivores within these communities should also be considered as this might serve as a suitable indicator of network stability to habitat modification, than the network structure per se.

The role of functional diversity in frugivore communities

Functional diversity defines the variety and significance of species traits that drives and sustains the functioning of an ecosystem (Naeem et al. 2000, Tilman 2001, Cadotte et al. 2011). In the case of frugivorous birds, functional diversity is determined by traits related to seed dispersal, such as

body mass, gape width and relative dietary dominance by fruit or feeding behavior (Fleming et al. 1993, Dennis & Westcott 2006). For example, larger frugivores may have the ability to consume large proportions of fruit, retain them for much longer in their digestive tracts and transport them over longer distances than smaller birds (Spiegel & Nathan 2007). Moreover, frugivores have generally also been shown to have different degrees of frugivory, whereby some species will almost entirely depend on fruit consumption for their nutritional supplements, while others may have alternative food resources besides fruits (Carnicer et al. 2009, Schleuning et al. 2011). These differing traits can influence the dynamics and stability of plant-frugivore interactions and thus the process of seed dispersal especially in the face of habitat fragmentation (Cramer et al. 2007, Spiegel & Nathan 2007).

Previous studies on the impacts of habitat fragmentation on ecological processes have focused more on measures of species diversity that only include information on the presence and abundance of species (e.g. Hector 1999, Gould & Walker 1999). However, a decrease or increase in species richness may not always mean there will be corresponding changes in functional diversity (Greenberg et al. 2000, Perfecto et al. 2004). Moreover, the influence of species richness on ecosystem function has been shown to largely depend on the traits and niches filled by species (Cadotte et al. 2011). In this case, the impact of habitat fragmentation and management practices on ecological processes is likely to be stronger if it changes the functional diversity rather than their species richness per se (Naeem et al. 2000, Cadotte et al. 2011). For example, while large dispersers have been shown to have the capacity to transport large proportions of seeds over long distances, their movements may be restricted by the magnitude of fragmentation (Peres 2000, Cramer et al. 2007). This may particularly disadvantage larger seeded plants that depend on larger dispersers for the transportation of their seeds (Moran et al. 2004, Cramer et al. 2007). Therefore, understanding the consequences of habitat fragmentation on the functional diversity of frugivores communities is paramount for the sustenance of seed dispersal processes (Cramer et al. 2007, Schleicher et al. 2011). In this context, it is also important to assess the impact of fruit or seed handling by various frugivorous species on germination

Effects of seed ingestion by frugivorous birds on germination success

The fruit handling behaviour of frugivorous birds plays a key role in determining their contribution to the seed dispersal process (Jordano & Schupp 2000). Frugivores that can swallow whole fruits,

transport and defecate intact seeds in suitable habitats are often regarded as legitimate dispersers (Jordano & Schupp 2000). Whether or not fruit consumption by birds translates into successful seed dispersal is still a subject of much debate. Successful seed dispersal involves not only the removal of fruit from a source plant and depositing the seed into suitable sites, but also the ability of the deposited seeds to germinate and establish seedlings after passage through digestive tracts of birds (Herrera & Jordano 1981, Schupp 1993). Evidence from previous studies show either neutral (Howe & Vande Kerckhove 1981, Barnea et al 1992), positive (e.g. Clergeau 1992, Murray et al 1994) or negative (e.g. Valido & Nogalas 1994, Crossland & Vander Kloet 1996) effects of gut treatment on the germination patterns of seeds from various plant species. The reasons for these differing results are still not universally clear, but a few studies suggest that this could be explained by differences in functional traits of various plants (e.g. fruit morphology) and frugivorous species (Treveset 1998, Miller 1995, Jordano 2000). Therefore, taking these traits of plants and frugivorous into account when studying germination patterns of ingested seed can help to predict which frugivorous species contribute to the seed dispersal of which plant species. One way of doing this can be to feed fruits from different plant species to different species of frugivores (Schleicher et al. 2011). Understanding the abilities of different frugivore species within seed dispersal communities to contribute to plant recruitment will help to predict the impacts of fragmentation on forest regeneration, particular if habitat fragmentation affects the structure and functional diversity of seed dispersal communities to which these frugivores belong.

Aims of the thesis

In this thesis I investigated plant-frugivore interactions in a highly modified landscape in and around Vernon Crookes Nature Reserve (VCNR), located within KwaZulu Natal province, South African. This region comprises clusters of remnant natural scarp forest patches surrounded by dissimilar matrix habitats, notably, natural forest, natural grassland and commercial sugarcane monocultures. Therefore, it was a suitable area for undertaking this study, as it allowed for comparison of ecological processes between clusters of forest patches of different matrix habitats. I compared (i) the structure of plant-frugivore interaction networks and (ii) functional diversity of frugivore communities within these networks. Moreover, I experimentally tested the impact of seed treatment in the digestive tracts of avian frugivorous to assess the importance of this specific trait (of seed treatment) on germination of dispersed seeds.

This thesis comprises three major chapters (2 - 4) which can be read independently. Each chapter is structured like a journal publication containing an abstract, introduction, followed by the methods, results, discussion and a conclusion. The thesis closes with the general conclusions (chapter 5) derived from three major chapters (2 - 4).

The first major chapter (2) examines the consequences of forest patch quality and matrix habitat on the structure and stability of plant-frugivore networks in the fragmented forest landscapes VCNR. To do this, I identified all fleshy fruiting plant species across forest patches surrounded by variable matrix habitats and assessed their interaction frequencies with avian frugivore species. These data were arranged in quantitative interaction matrices to construct plant-frugivore interaction networks. Different network parameters were used to compare the network structures among forest patches.

The second major chapter (3) tests the effects of forest patch quality and matrix habitat on functional diversity of frugivore communities. Using the same data set as in chapter 2, I recorded the functional diversity of frugivore species and compiled these data in a species-trait matrix. Then, I determined the effect of forest patch quality and matrix habitat on the species richness and functional diversity of these frugivorous communities.

The third chapter (4) examines the potential of different avian frugivore species to contribute to plant recruitment by testing the effects of their seed ingestion on germination. To do this, fruits collected from sixteen woody plant species were fed to a subset of generalist avian frugivores observed in seed dispersal networks and frugivore communities described in chapters 2 and 3. Defecated seeds were collected, planted and their germination responses in terms of (i) time to first seedling emergency and (ii) germination probability were compared with the germination responses of ripe manually depulped and whole fruits.

References

- AIZEN, M.A., ASHWORTH, L. & GALETTO, L. 2002. Reproductive success in fragmented habitats: do compatibility systems and pollination specialization matter? *Journal of Vegetation Science* 13: 885–892.
- ANDREN, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355 – 366.
- BARNEA, A., YOM-TOV Y. & FRIEDMAN J. 1992. Effect of frugivorous birds on seed dispersal and germination of multi seeded fruits. *Acta Oecologica* 13: 209–19.
- BASCOMPTE, J. & JORDANO, P. 2007. Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 38: 567-593.
- BASCOMPTE, J., JORDANO, P., MELIÁN, C.J. & OLESEN, J.M. 2003. The nested assembly of plant–animal mutualistic networks. *PNAS* 100: 9383–9387.
- BERGMAN, K.O., J. ASKLING, O. EKBERG, H. IGNELL, H. WAHLMAN & P. MILBERG, 2004. Landscape effects on butterfly assemblages in an agricultural region. *Ecography* 27: 619-628.
- CADOTTE, M.W., CARSCADDEN, K. & MIROTCHEV, N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* 48(5): 1079 – 1087.
- CARNICER, J., JORDANO, P. & MELIÁN, C. J. 2009. The temporal dynamics of resource use by frugivorous birds: a network approach. *Ecology* 90:1958-1970.
- CLERGEAU, P. 1992. The effect of birds on seed germination of fleshy-fruited plants in temperate farmland. *Acta Oecologica* 13: 679–686.
- CORDEIRO, N. J. & HOWE, H. F. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences of the United States of America* 100:14052-14056.
- CROSSLAND, D.R. & VANDER KLOET, S.P. 1996. Berry consumption by the American Robin, *Turdus migratorius*, and the subsequent effect on seed germination, plant vigour, and dispersal of the lowbush blueberry, *Vaccinium angustifolium*. *The Canadian Field Naturalist* 110: 303–309.
- Debinski, D.M. & Holt, R.D. 2000. A survey and overview of habitat fragmentation experiments. *Conservation biology* 14: 342-355.
- DENNIS, A. J. & WESTCOTT, D. A. 2006. Reducing complexity when studying seed dispersal at community scales: a functional classification of vertebrate seed dispersers in tropical forests. *Oecologia* 149:620-634.

- FAHRIG, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34:487-515.
- FAO. 2006. *World agriculture: towards 2030 – 2050. An FAO Perspective*. Rome, Italy: FAO.
- FISCHER, J., LINDENMAYER, D. B., BLOMBERG, S. P., MONTAGUE-DRAKE, R., FELTON, A. & STEIN, J. A. 2007. Functional richness and relative resilience of bird communities in regions with different land use intensities. *Ecosystems* 10:964-974.
- FLEMING, T., VENABLE, D. & HERRERA, L. 1993. Opportunism vs. specialization: the evolution of dispersal strategies in fleshy-fruited plants. *Vegetatio* 107(108):107-120.
- FORMAN, R.T.T. & COLLINGE, S.K. 1996. The ‘spatial solution’ to conserving biodiversity in landscapes and regions. Pp. 537–568 In DeGraaf, R.M., Miller, R.I. (Eds.), *Conservation of Faunal Diversity in Forested Landscapes*. Chapman and Hall, London, UK.
- FORTUNA, M.A. & BASCOMPTE, J. 2006. Habitat loss and the structure of plant-animal mutualistic networks. *Ecology letters* 9(3):278–283.
- GIBSON, L., LEE, T.M., KOH, L.P., BROOK, B.W., GARDNER, T.A., BARLOW, J., PERES, C.A., BRADSHAW, C.J.A., LAURANCE, W.F., LOVEJOY, T.E. & SOD, N.S. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478: 378–381.
- GOULD, W.A. & WALKER, M.D. 1999. Plant communities and landscape diversity along an arctic river. *Journal of Vegetation Science* 10: 537-548.
- GREENBERG, R., BICHIER, P., CRUZ ANGON, A., MACVEAN, C., PEREZ, R. & CANO, E. 2000. The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations. *Ecology* 81:1750-1755.
- HECTOR, A., SCHMID, B., BEIERKUHNLEIN, C., CALDEIRA, M.C., DIEMER, M., DIMITRAKOPOULOS, P.G., FINN, J.A., FREITAS, H., GILLER, P.S., GOOD, J., HARRIS, R., HÖGBERG, P., HUSS-DANEL, K., JOSHI, J., JUMPPONEN, A., KÖRNER, C., LEADLEY, P.W., LOREAU, M., MINNS, A., MULDER, C.P.H., DONOVAN, G.O., OTWAY, S.J., PEREIRA, J.S., PRINZ, A., READ, D.J., SCHERER-LORENZEN, M., SCHULZE, E.D., SIAMANTZIOURAS, A.S.D., SPEHN, E.M., TERRY, A.C., TROUMBIS, A.Y., WOODWARD, F.I., YACHI, S. & LAWTON, J.H. 1999. Plant Diversity and Productivity Experiments in European Grasslands. *Science* 286(5442): 1123-1127.
- HERRERA, C. M. & JORDANO, P. 1981. *Prunus mahaleb* and birds: the high efficiency seed dispersal system of a temperate fruiting tree. *Ecological Monographs* 51: 203-21.
- HERRERA, C.M. 2003. Seed dispersal by vertebrates. Pp. 185 - 208 In Herrera, C.M. and Pellmyr, O. (eds) *Plant–Animal Interactions: An evolutionary approach*. Blackwell, Oxford, UK.

- HOWE, H.F. & SMALLWOOD, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.
- HOWE, H.F. & VANDE KERCKHOVE, G.A. 1979. Fecundity and seed dispersal of a tropical tree. *Ecology* 60: 180–189.
- JORDANO, P. & SCHUPP, E.W. 2000. Determinants of seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* 70: 591-615.
- JORDANO, P. 2000. Fruits and frugivory. Pp 125-165 In M.Fenner (ed.) *Seeds: The Ecology of Regeneration in Plant Communities* CABI, Wallingford, UK.
- KIRIKA, J.M, FARWIG, N. & BÖHNING-GAESE, K. 2008. Effects of local disturbance of tropical forests on frugivores and seed removal of a small-seeded afrotropical tree. *Conservation Biology* 22(2): 318 – 328.
- MENKE, S., BÖHNING-GAESE, K. & SCHLEUNING, M. 2012. Plant–frugivore networks are less specialized and more robust at forest–farmland edges than in the interior of a tropical forest. *Oikos* 000: 001–014.
- MILLER, M. F. 1995. Acacia seed survival, seed germination and seedling growth following pod consumption by large herbivores and seed chewing by rodents. *Africa Journal of Ecology* 33: 194–210.
- MONTOYA, D., ZAVALA, M.A., RODRÍGUEZ, M.A. & PURVES, D.W. 2008. Animal versus wind dispersal and the robustness of tree species to deforestation. *Science* 320: 1502 – 1504.
- MORAN, C., CATTERALL, C. P., GREEN, R. J. & OLSEN, M. F. 2004. Functional variation among frugivorous birds: implications for rainforest seed dispersal in a fragmented subtropical landscape. *Oecologia* 141:584-95.
- MURRAY, K.G., RUSSELL, S., PICONE, C.M., WINNETT-MURRAY, K., SHERWOOD, W. & KUHLMANN, M.L. 1994. Fruit laxatives and seed passage rates in frugivores: consequences for plant reproductive success. *Ecology* 75: 989–994.
- NAEEM, S., KNOPS, J.M.H., TILMAN, D., HOWE, K.M., KENNEDY, T. & GALE, S. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91(1): 97 – 108.
- PERES, C.A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests, *Conservation Biology* 14(1): 240-253.
- PERFECTO, I., VANDERMEER, J. H., BAUTISTA, G. L., IBARRA, G., GREENBERG, R., BICHER, P. & LANGRIDGE, S. 2004. Greater predation in shaded coffee farms: the role of resident neotropical birds. *Ecology* 85:2677-2681.
- PRIMACK, R.B. 2002. *Essentials of conservation biology*. 3rd edition. Sinauer Associates,U.S.A.

- REID, S. & ARMESTO, J. J. 2011. Interaction dynamics of avian frugivores and plants in a Chilean Mediterranean shrubland. *Journal of Arid Environments* 75:221-230. Elsevier Ltd.
- ROSENBERG, K.V., LOWE, J.D. & DHONDT, A.A. 1999. Effects of forest fragmentation on breeding tanagers: A continental perspective. *Conservation Biology* 13(3): 568-583.
- SAUNDERS, D. A., HOBBS, R. J. & MARGULES, C. R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18-32.
- SCHLEICHER, A., PEPLER-LISBACH, C. & KLEYER, M. 2011. Functional traits during succession: is plant community assembly trait-driven? *Preslia* 83: 347–370.
- SCHLEUNING, M., BLÜTHGEN, N., FLÖRCHINGER, M., BRAUN, J., SCHAEFER, H. M. & BÖHNING-GAESE, K. 2011. Specialization and interaction strength in a tropical plant-frugivore network differ among forest strata. *Ecology* 92:26-36.
- SCHUPP, EW. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetation* 107(108): 15–29.
- SPIEGEL, O. & NATHAN, R. 2007. Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology letters* 10:718-28.
- TILMAN, D. 2001. Functional diversity. Pp 109-120 In Levin, S. A. (ed.), *Encyclopedia of biodiversity*. Academic Press.
- TRAVESET, A. 1998. Effect of seed passage through vertebrate frugivores' gut on germination: a review. *Perspective in Plant Ecology, Evolution and Systematics* 1(2): 151–90.
- TYLIANAKIS, J.M., LALIBERTÉ, E., NIELSEN, A. & BASCOMPTE, J. 2010. Conservation of species interaction networks. *Biological Conservation* 143(10): 2270-2279.
- VALIDO, A. & NOGALES, M. 1994. Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xerix habitat of the Canary Islands. *Oikos* 70: 403–411.
- VAN HOUTAN, K.S., PIMM S.L., HALLEY J.M., BIERREGAARD JR R.O. & LOVEJOY T.E. 2007. Dispersal of Amazonian birds in continuous and fragmented forest. *Ecology Letters* 10: 219–229.
- VÁZQUEZ, D. P., BLÜTHGEN, N., CAGNOLO, L. & CHACOFF, N. P. 2009. Uniting pattern and process in plant-animal mutualistic networks: a review. *Annals of Botany* 103:1445-1457.
- WATSON, J.E.M., WHITTAKER, R.J. & FREUDENBERGER, D. 2005. Bird community responses to habitat fragmentation: how consistent are they across landscapes? *Journal of Biogeography* 32: 1353–1370.
- WUNDERLE, J.M.JR. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest ecology and management* 99: 223 – 235.

Chapter 2: Plant-frugivore networks in modified landscapes

With Dana G. Berens, Colleen Downs and Nina Farwig

Abstract

Plant-frugivore networks play a key role in the regeneration of sub-tropical forest ecosystems. However, information about the impact of human-induced forest modification on seed-dispersal networks is scarce. We investigated the importance of matrix habitat versus forest patch quality in affecting structure and robustness of plant-frugivore networks within forest patches. We compared networks across three forest types (natural forest, natural fragments and fragments in agricultural fields) in a human-dominated forest landscape of South Africa. In total, 54 avian species were involved in fruit removal on 31 fleshy-fruited plant species. Species and network-level specialisation did not vary with matrix habitat, but increased with increasing fruit abundance and decreased with increasing fruiting plant richness and canopy cover within patches. Linkage density and interaction diversity were unaffected by matrix habitat and fruit abundance, but increased with increasing fruiting plant richness and canopy cover. These findings suggest that habitat quality of forest patches is more important than the surrounding matrix in determining network robustness. The susceptibility of plant-frugivore networks to land-use may therefore largely be driven by changing forest patch quality. Conservation efforts should devise measures that promote the quality of forest patches to ensure the long-term functionality of seed dispersal processes.

Introduction

Increasing impact of human land-use changes the structure and composition of ecosystems across the globe (Foley et al. 2005, Tylianakis et al. 2008). Forests are among the most threatened ecosystems of the world with less than 50% still intact (FAO 2009). Large-scale destruction of natural forests leads to forest fragmentation and increase the amount of surrounding matrix habitat. Small-scale changes within remaining forest patches may alter the environmental conditions, e.g. availability of fruit resources or vegetation structure (Saunders et al. 1991, Fischer & Lindenmayer 2007). These changes may influence diversity, processes and the overall functioning of forest ecosystems (Myers et al. 2000, Foley et al. 2005).

The process of seed dispersal forms the template for recruitment of forests (Jordano & Godoy 2002). It is particularly important in tropical and sub-tropical ecosystems as up to 90% of fleshy-fruited plant species rely upon animal vectors to transport their propagules (Howe & Smallwood 1982). Dispersed seeds escape from the high density of competing siblings and from natural enemies in the vicinity of the parent trees (Howe & Smallwood 1982). Moreover, seed dispersal enables the colonization of vacant recruitment sites and directed dispersal to non-random habitats suitable for establishment (Howe & Smallwood 1982).

A number of studies have shown that forest destruction and degradation lead to changes in community composition and ecological processes like seed dispersal (Cordeiro & Howe 2003, Farwig et al. 2006). Most of these studies investigated the impact of human activities on one-to-one interactions with contrasting results (Cordeiro & Howe 2003, Farwig et al. 2006). For instance, (Cordeiro & Howe 2003) showed reduced frugivore numbers and seed dispersal of a tropical tree as a consequence of anthropogenic fragmentation of a rainforest in Tanzania. In contrast, frugivores and seed dispersal of the tree species *Prunus africana* were positively affected by human disturbance in a Kenyan forest (Farwig et al. 2006). The high variability in the results reveals the difficulty of using model systems for predicting consequences of human impact on ecological processes. Thus, community-wide studies can contribute to a better understanding of mutualistic plant-animal interactions in the face of land-use changes.

Recently, the analyses of complex mutualistic interaction networks have gained in importance (Rezende et al. 2007, Blüthgen 2010). These community-wide studies consider both occurrence and frequency of interactions between all species pairs within a community (Tylianakis et al. 2008, Bascompte 2009). The structure of interaction networks can be used to analyze the stability and thus response of mutualistic relationships to land-use change. For instance, seed

disperser networks are in general less specialised, and thus more functionally redundant, than pollinator networks (Blüthgen et al. 2007). High functional redundancy may contribute to the persistence of networks, even if some interactions disappear (Jordano 1987, Bascompte & Jordano 2007), and may thus lead to a higher robustness towards land-use changes. Moreover, parameters such as interaction diversity and linkage density can be used to describe the heterogeneity of interaction frequencies or relative quantitative abundances of different species in the network (Vázquez et al. 2005, Blüthgen et al. 2008). Thus, they can be used as yardsticks for highlighting the ecological complexity of associations within mutualistic networks and their response to land-use change (Blüthgen et al. 2007, 2008). However, until now, the impact of land-use changes on entire plant-frugivore networks has rarely been studied (Reid & Armesto 2011).

When analyzing the robustness of seed dispersal networks in modified forest ecosystems, both the environmental conditions and quality of the remaining natural habitat as well as the surrounding matrix need to be considered (Wethered & Lawes 2003, Franklin & Lindenmayer 2009). Resource availability may influence the frequency of interactions in networks if frugivores change their feeding behavior (Vázquez et al. 2009, Carnicer et al. 2009). Depending on structure and permeability, surrounding matrices may complement natural habitat, i.e. by facilitating animal movement among habitat remnants, or function as ecological barriers constraining plant-animal interactions (Tewksbury et al. 2002). If barrier effects are strong and habitat quality of remaining forest patches is low, seed dispersal in forest remnants may rely on a depleted community, leading to lower robustness of networks towards habitat modification.

Here, we present a study on the effects of surrounding matrix habitat and forest patch quality on plant-frugivore interaction networks in a human-dominated sub-tropical forest landscape of South Africa. We compared the structure and specialisation of plant-frugivore interaction networks in forest patches with three different matrix habitats: large natural forest, natural forest fragments surrounded by natural grassland and remnant forest fragments embedded in agricultural fields. We further assessed the influence of habitat quality within forest patches in terms of e.g. resource availability and vegetation structure on these networks. We hypothesized that (1) a decrease in matrix quality negatively affects the redundancy as well as the diversity and density of interactions of seed dispersal networks due to a loss of interacting species within forest patches. Further, we expected (2) local habitat quality of forest patches to positively influence plant-frugivore interactions, as enhanced habitat quality comprises favorable conditions, i.e. in

terms of resources availability, fruiting plant species diversity and vegetation structure (e.g. (Clough et al. 2009).

Material and Methods

Study site and design

We conducted this study over two successive years, 2009/10 and 2010/11 in a heterogeneous scarp forest landscape in and around Vernon Crookes Nature Reserve (VCNR) situated on the south coast of South Africa's KwaZulu Natal Province (150 – 610 m a.s.l., 30°16' S, 30°35' E). Monthly rainfall in the area ranges from 1–148 mm and annual temperature from 6–31°C (von Maltitz 2003). Covering an area of about 2,189 ha, VCNR is mainly a combination of hilly grasslands with wooded valleys. It is surrounded a matrix of commercial sugarcane monocultures and timber plantations, within which a series of remnant natural scarp forest patches exist. Fruiting by fleshy-fruited plants occurs almost all year round, although the main fruiting season ranged from November to April, during the main rainfall season (Boon 2010).

We worked in forest patches characterized by three different matrix habitats that are representative for the area: 1) large natural forest (NatFor), representing the largest protected natural scarp forest with 130 ha, predominantly surrounded by forest and partly by a matrix of natural grassland within VCNR; 2) natural forest fragments (NatFra; mean area = 5.82 ha ± 1.8 SD) within VCNR, occurring naturally due to microclimatic and terrain conditions and being completely surrounded by natural grassland; 3) remnant forest fragments (AgrFra; mean area = 4.85 ha ± 0.5 SD) embedded in a matrix of sugar cane fields at the border of VCNR. Despite the dissimilarities in matrices surrounding these three forest patches, they all harbour similar communities of plants and birds and occur within the same natural geographic range of scarp forests (Mucina & Rutherford 2006, Neuschulz et al. 2011).

We established nine (200 m × 200 m) study sites, i.e. three replicates per forest patch. The distance between study sites ranged from 0.53 to 1.06 km (mean = 0.80 ± 0.3 km SD). Given the likelihood of strong edge effects in forest patches compared to the large natural forest (Harrison & Bruna 1999), we situated all sites at forest gaps or edges.

Measuring local forest patch quality

We measured local forest patch quality by assessing three habitat characteristics, namely fruit abundance, fruiting plant species richness and canopy cover in each study site. We calculated fruit abundance (at the onset of fruit ripening) by estimating the number of fruits for each plant monitored and any other fleshy-fruited plants within a radius of 50 m. We then calculated the mean fruit abundance for each study site, which ranged from 11,000 to 66,000 (mean = 45,000 \pm 28,000 SD) over the two years. To determine fruiting plant species richness, we identified all fleshy fruited woody plants in each site to species level. Overall, fruiting plant species richness ranged from 9 to 15 (mean = 12 \pm 3 SD) across study sites. We estimated canopy cover standing in the centre of four (50 \times 50 m) quadrates in each site and calculated the mean per site. Canopy cover ranged from 64 to 92 % (mean = 84 \pm 14 % SD) across study sites.

Assessment of plant-frugivore interactions

We observed all fleshy fruited plant species in each study site to assess interactions with frugivorous birds. Observations were undertaken during the main fruiting seasons in 2009/10 and 2010/11. Due to low abundance of plant species, coupled with a lack of fruits on some individuals, only one individual of each plant species was monitored in each site. We observed each plant for a total of 18 h, ideally split into 9 h per year. In cases where we could not achieve 9 h in the first fruiting year, we increased the number of observation hours in the second fruiting year to attain the standard total of 18 h per plant. We split the observations into three monitoring sessions, namely early morning (06:00 am – 09:00 am), mid-morning (09:00 am to 12:00 am) and afternoon (2:00 pm – 5:00 pm), conducted at three different days during the main fruiting period of each plant species in each year. Observations of species were evenly spread across the three sessions. Using binoculars (Luger DA 10X42, Köln, Germany) observations were carried out from a camouflaged hide at ca. 20 m distance to the plant individual. All plant visiting birds and their fruit handling behaviour on the plant were recorded. If more than one feeding bird was present on the plant (<0.5 % of observations), one randomly chosen individual was selected for which fruit consumption was observed.

Network analysis

We compiled interaction frequencies of each plant species (p) with each frugivore species (f) in a quantitative interaction matrix, whereby interaction frequency was defined as the number of fruit-eating individuals per plant species (Vázquez et al. 2005). Thus, only species that fed on fruits (potential dispersers) were included in the analyses. Using the number of feeding visits to calculate the interaction frequencies between plants and frugivores allowed for comparison with other studies (Vázquez et al. 2005, Schleuning et al. 2011). We constructed interaction networks for each study site and calculated different network parameters at both the species and network level, which we used as response variables in our analyses. At the species level, we calculated specialisation as the standardized Kullback-Leibler distance (d') of each plant (d'_p) and each frugivore (d'_f) species and calculated a weighted mean of the index per site for both plants and frugivores (Blüthgen et al. 2006). At the network level, we calculated H_2' , as the standardized two-dimensional Shannon entropy (Blüthgen et al. 2006). Both d' and H_2' range between 0 and 1, for complete generalisation and complete specialisation, respectively (Blüthgen et al. 2006). A quantitative weighted version of linkage density, i.e. the mean number of interactions per species, was also calculated for each network following (Tylianakis et al. 2007). Finally, the diversity of all interactions in a network was computed with the help of the Shannon-diversity index. All network analyses were conducted with the bipartite package (version 1.13; (Dormann et al. 2008)) in R (version 2.12.0; R Development Core Team). To test if annual variations affected the structure of our plant-frugivore interaction networks, we constructed separate interaction networks per study site for each of the two years. As observation hours were unevenly distributed between the two years on some plant species, we used a subset of species for which we had at least 6 h of observation per year. For species where more than 6 h of observations were available for each year, we equally sampled a 6 h-subset of the dataset from the three observation sessions. With the help of this sub-dataset, we analysed the differences in the above-mentioned network parameters between the two years. As year did not have an effect in any of the analyses, we pooled the data set across the two years and used 18 h of frugivore observation for each plant species in each forest patch. Henceforth, all analyses were based on this pooled data set.

Statistical analysis

All measures of habitat quality, i.e. fruit abundance, fruiting plant species richness and canopy cover were uncorrelated (all p-values > 0.462). We used matrix habitat of the three forest patches

(NatFor, NatFra, AgrFra) as well as fruit abundance, fruiting plant species richness and canopy cover as explanatory variables to examine their effect on network parameters, i.e. the mean specialisation of plants (d'_p) and frugivores (d'_f), complementary specialisation (H_2'), linkage density and interaction diversity in separate analyses of covariance (ANCOVA). We used type III sums of squares as no specific order of independent variables in affecting dependent variables could be assumed and simplified our models by stepwisely deleting non-significant variables to construct minimum adequate models. Model selection was done with the help of Akaike's information criterion (AIC). We used Tukey's HSD to establish pair-wise differences between study sites. All statistical analyses were performed in R.

Results

Across the nine study sites, we monitored a total of 31 fruiting plant species. During 1,854 observation hours we recorded a total of 54 frugivorous bird species and 8,145 frugivore visitors involved in fruit removal activities on the focal plants. Plants that had most interactions with frugivores included the Common Wild Fig (*Ficus burkei*), Forest Knobwood (*Zanthoxylum davyi*) and Red-beech (*Protorhus longifolia*; Appendix a). Frugivores with most interactions on plants included the Dark-capped Bulbul (*Pycnonotus tricolor*), Cape White-eye (*Zosterops virens*) and Knysna Turaco (*Tauraco corythaix*; Appendix a). Plant species richness was 11 ± 1 (mean \pm 1 SD if not otherwise noted) in AgrFra, 12 ± 3 in NatFra, 12 ± 3 in NatFor and did not differ significantly between matrix habitats ($F_{2,6} = 0.13$; $p = 0.881$, $r^2 = 0.04$). Avian frugivore species visiting fruiting plants were 22 ± 4 in AgrFra, 23 ± 4 in NatFor, 28 ± 4 in NatFra and did also not differ significantly between matrix habitats ($F_{2,6} = 1.55$; $p = 0.286$, $r^2 = 0.34$).

Specialisation of plants and frugivores

The mean weighted specialisation of plants on frugivores (d'_p) was 0.35 ± 0.03 in AgrFra, 0.38 ± 0.04 in NatFor, 0.44 ± 0.07 in NatFra and did not differ between matrix habitats (Table 1; Fig. 1a). The specialisation of frugivores on plants (d'_f) was 0.33 ± 0.01 in AgrFra, 0.33 ± 0.02 in NatFor, 0.37 ± 0.04 in NatFra and did also not differ between matrix habitats (Table 1; Fig. 1a). Both plant and frugivore specialisation increased with increasing fruit abundance (Table 1; Fig. 2a), but decreased with increasing fruiting plant species richness (Table 1, Fig. 2b) and canopy cover (Table 1, Fig. 2c).

Table 1. ANCOVA models highlighting effects of fruit abundance, fruiting plant species richness, canopy cover (%) and matrix habitat on plant specialisation ($d'p$), frugivore specialisation ($d'f$), network specialisation (H_2'), linkage density and interaction diversity of plant-frugivore networks ($n = 9$). Models were simplified using type III sums of squares and single term deletion to construct the minimum adequate models. Given are df , R^2 , F and P values for the final models and for each parameter in the final model. Note: all significant P values are highlighted in bold.

	Plant specialization ($d'p$)				Frugivore specialization ($d'f$)				Network specialization (H_2')				Linkage density (LD)				Interaction diversity (ID)			
	df	R^2	F	P	df	R^2	F	P	df	R^2	F	P	df	R^2	F	P	df	R^2	F	P
Final model	3, 5	0.79	6.46	0.036	3, 5	0.92	20.32	0.003	3, 5	0.96	42.69	< 0.001	4, 4	0.87	6.55	0.048	4, 4	0.85	5.50	0.064
Fruit abundance	1	-	6.43	0.052	1	-	11.44	0.020	1	-	17.63	0.008	-	-	-	-	-	-	-	-
Fruiting plant species richness	1	-	5.19	0.072	1	-	13.98	0.013	1	-	88.68	< 0.001	1	-	13.71	0.021	1	-	7.13	0.056
Canopy cover	1	-	4.20	0.096	1	-	22.19	0.005	1	-	13.86	0.014	1	-	6.93	0.058	1	-	7.40	0.053
Matrix habitat	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1.70	0.292	2	-	3.68	0.124

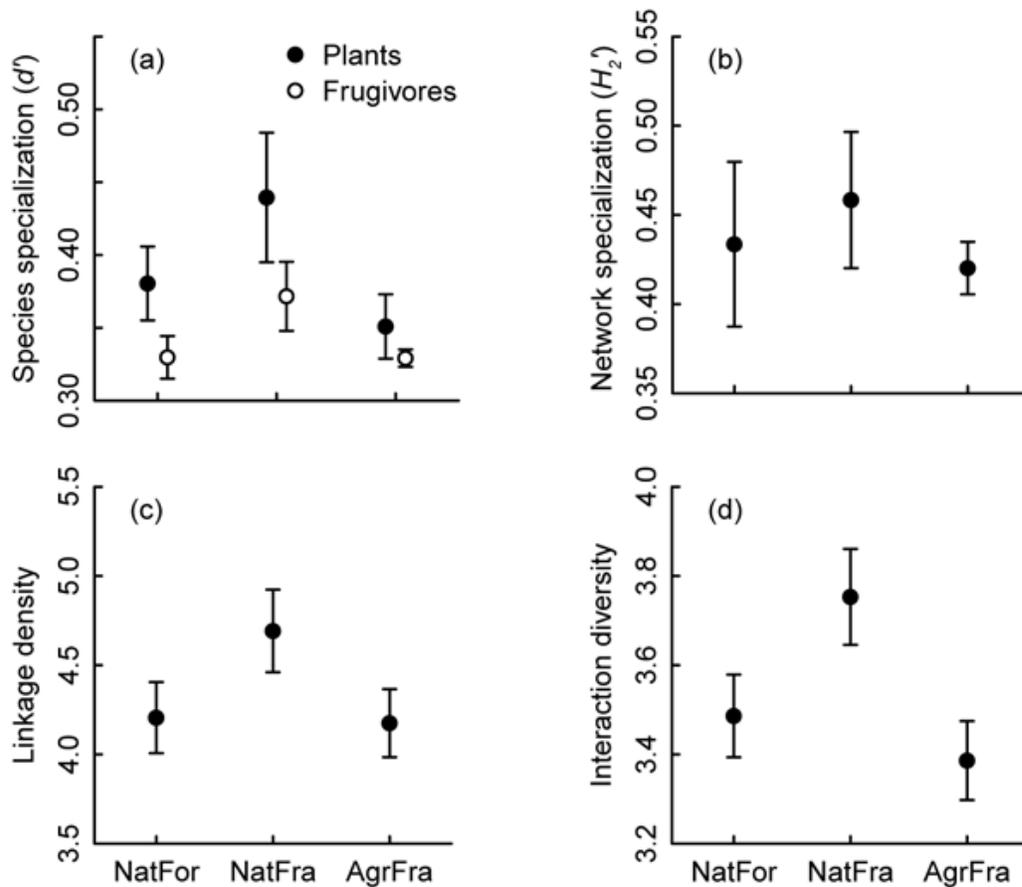


Fig.1. Least square means \pm standard errors (controlling for all other variables in the model, see table 1) of species and network parameters across matrix habitats; (a) specialisation of plants on frugivores ($d'p$) and of frugivores on plants ($d'f$), (b) network level specialisation (H_2'), (c) linkage density and (d) interaction diversity ($n = 9$). NatFor = large natural forest, NatFra = natural forest fragments, AgrFra = remnant forest fragments embedded within an agricultural matrix; for calculation of network parameters, see methods.

Network specialisation (H_2'), linkage density and interaction diversity

Overall, the mean network complementary specialisation (H_2') was 0.42 ± 0.02 in AgrFra, 0.43 ± 0.08 in NatFor, 0.46 ± 0.06 in NatFra and remained similar across matrix habitats (Table 1; Fig. 1b). The mean linkage density was 4.21 ± 0.15 in AgrFra, 4.40 ± 0.72 in NatFra, 4.46 ± 0.60 in NatFor and did not differ between matrix habitats (Table1; Fig. 1c). The mean interaction diversity was 3.42 ± 0.17 in AgrFra, 3.60 ± 0.24 in NatFor, 3.61 ± 0.27 in NatFra and did also not differ between matrix habitats (Table 1, Fig. 1d). Network specialisation (H_2') increased with increasing fruit abundance (Table 1; Fig. 2a), and decreased with increasing fruiting plant species richness (Table 1, Fig. 2b) and canopy cover (Table 1, Fig. 2c). Both linkage density and interaction

diversity were unaffected by fruit abundance (Table 1, Fig. 2d), but increased with increasing fruiting plant species richness and canopy cover (Table 1, Fig. 2e and f).

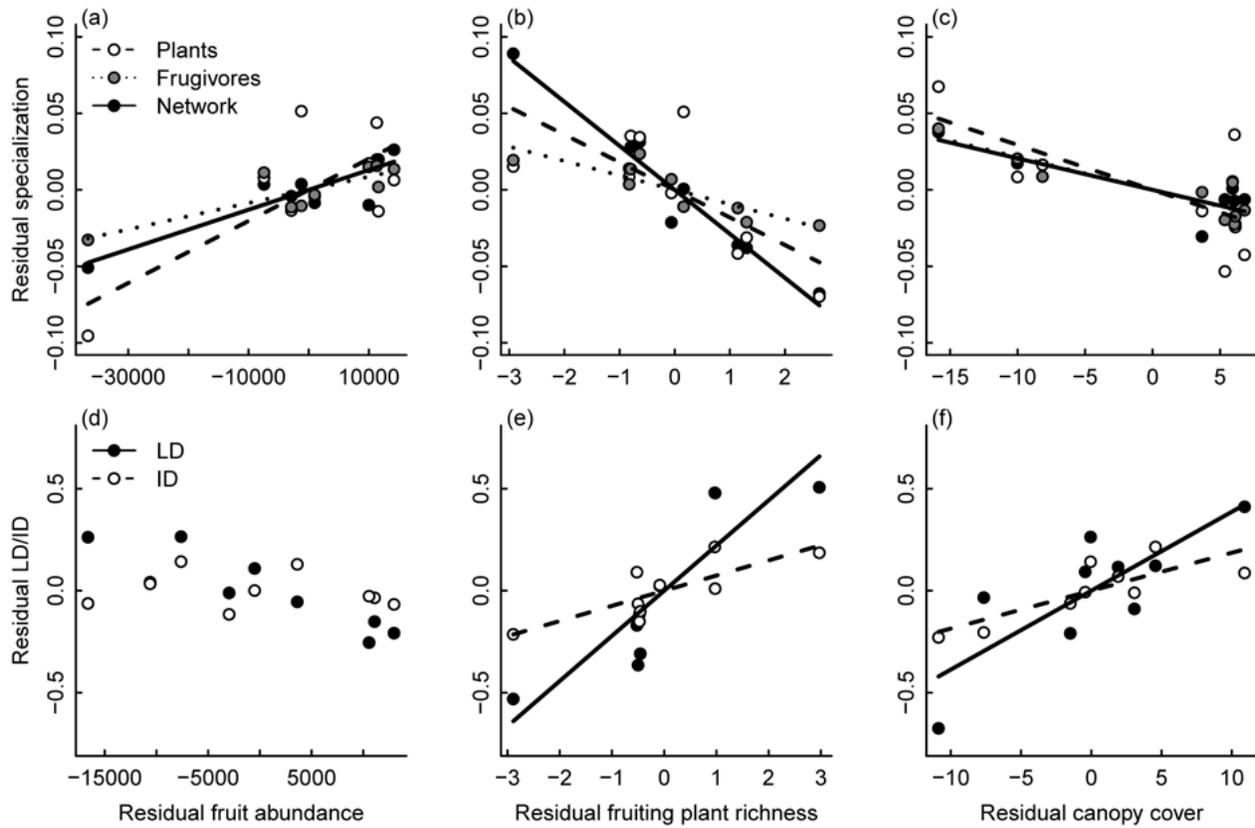


Fig.2. Species and network specialisation ($d'p$, $d'f$ and $H2'$) in relation to (a) fruit abundance, (b) fruiting plant species richness and (c) canopy cover (%), as well as linkage density (LD) and interaction diversity (ID) in relation to (d) fruit abundance, (e) fruiting plant species richness and (f) canopy cover (%), for plant-frugivore networks ($n = 9$; for calculation of network parameters, see methods). Shown are residual plots controlling for all other variables in the model (see Table 1).

Discussion

Our study shows that networks across all three forest types were similarly characterized by low specialisation in the plant-frugivore interactions. Generally, network structure was not influenced by matrix habitat, while forest patch quality strongly affected network structure. High fruit abundance led to higher specialisation, while increasing fruiting plant species richness and canopy cover reduced network specialisation, but increased linkage density and interaction diversity

across study sites. These findings suggest that the structure of plant-frugivore interaction networks is rather driven by local forest patch quality than by surrounding matrix habitat.

Comparison with other mutualistic networks

Overall, network specialisation was comparable, albeit slightly higher than in other plant-bird (Schleuning et al. 2011) and indeed many plant-bat (Mello et al. 2011) networks. Thus, our results are consistent with previous research suggesting low specialisation in plant-disperser networks as compared with pollination networks (Jordano 1987, Blüthgen et al. 2007). A lower specialisation in seed dispersal than in pollination networks may largely be explained by differences in phenotypic matching between interacting species (Blüthgen et al. 2007, 2008). Whereas fleshy fruits are largely exposed to attract a broad spectrum of dispersers, the morphological attributes of flowers may act as barriers to some pollinators (Vázquez et al. 2009). This implies that trait matching is rather absent, consequently leading to high generalisation in seed dispersal networks (Vázquez & Aizen 2006, Blüthgen et al. 2008).

Low specialisation in seed dispersal networks is generally expected in subtropical and tropical ecosystems (Schleuning et al. 2011). A recent study of plant-frugivore networks in a temperate region (Albrecht et al., unpublished data) found a slightly higher specialisation (0.6) than in subtropical/tropical regions (see also (Schleuning et al. 2011)). Frugivores in the temperates are less dependent on fruit consumption than tropical birds as fruits are available only during a limited time span (Jordano 2000). Thus, a higher specialisation of seed disperser networks in temperate regions might be caused by selective fruit foraging of birds to complete their diet. In contrast, year-round fruit availability and diversity and dependence of frugivores on these fruits are both high in tropical ecosystems (Jordano 2000). Thus frugivores forage in a more generalist way, leading to the lower network specialisation observed here.

Matrix habitat and plant-frugivore networks

In contrast to our hypothesis, network specialisation, linkage density and interaction diversity remained similar across forest patches, suggesting that the surrounding matrix has no major influence on the structure and robustness of complex plant-frugivore interactions. On the one hand, this agrees with previous research suggesting that frugivores are highly flexible and mobile species and can cross unsuitable matrix habitat when foraging (Berens et al. 2008, Neuschulz et al. 2011) to track fruits over long distances in response to spatiotemporal availability (Saracco et al.

2004). Hence, the matrix habitat may not necessarily limit the accessibility of forest remnants by frugivorous birds, resulting in comparable seed dispersal networks in different forest patches. On the other hand, the similarity in specialisation and interaction diversity across study sites is also consistent with previous studies suggesting that bird diversity of forest patches may be comparable with that of natural forests (Neuschulz et al. 2011). Forest patches within agricultural landscapes could act as “magnets” for attracting high densities of foraging frugivores primarily due to an unsuitable surrounding matrix (Farwig et al. 2006, Neuschulz et al. 2011). Consequently, this stresses the importance of these forest remnants in the agricultural landscape for biodiversity conservation. The absence of matrix effects *per se* in our study highlights that it is mostly the quality of these local forest patches that determines the plant-frugivore interactions, notably fruit availability, fruiting plant richness and canopy cover.

Fruit abundance and network structure

The increase in fruit abundance resulted in an increase in specialisation at both network and species level. This implies that higher availability of fruits within a forest patch leads to higher specialisation of frugivores on plants and vice versa, thus suggesting contrasting effects on the two trophic levels within the network. From the plants’ perspective, high specialisation may limit interactions with a broad spectrum of dispersers, thereby increasing their dependency on single or few dispersers that may either be effective or non-effective, e.g. based on their foraging capacity, efficiency (e.g. fruit handling behavior) and dispersal distances (Kankam & Oduro 2011). From the frugivore perspective, this may denote their highly flexible foraging behavioral changes in the event of high fruit availability across and within forest patches (Loiselle & Blake 1990, Saracco et al. 2004). High resource availability reduces both the average foraging time as well as the distance covered to move between fruiting plants (Khamcha et al. 2012). Moreover, this may also reduce competition for scarce resources (Blüthgen et al. 2007), allowing frugivores to access specific fruit types with less handling and search effort or energy loss (Blüthgen et al. 2007), thereby increasing specialisation. In contrast, lower resource availability increases generalisation due to high search effort, as confirmed by the negative effect of fruiting plant species richness on specialisation (see also (MacArthur & Pianka 1966)). Thus, a higher specialisation with increasing fruit abundance is likely to be less beneficial for plants than frugivores (Kessler-Rios & Kattan 2012) in the context of seed dispersal. Nonetheless, fruit abundance neither affected linkage density nor interaction diversity at the network level, suggesting that complexity and stability of networks are independent of overall resource availability.

Fruiting plant species richness, canopy cover and network structure

Specialisation at both species and network levels decreased, while linkage density and interaction diversity increased with increasing fruiting plant species richness and canopy cover. While our forest patches are surrounded by different matrix habitats, they were all characterized by comparable structural complexity, i.e. in terms of fruiting plant species richness and canopy cover. Thus, the two variables of habitat quality are largely responsible for explaining the similarly generalised network structures across the patches.

Specifically, the decrease in frugivore specialisation with increasing richness of fruiting plants underpins our idea that frugivores follow and optimize their foraging depending on fruit diversity (see above). Higher fruiting plant species richness allows for higher generalisation of frugivores. The increase in network complexity (i.e. linkage density, interaction diversity) particularly with increasing fruiting plant species richness denotes that high diversity of food resources promotes network stability. This is consistent with other studies showing that habitat quality is important for conservation of plant-disperser interactions (Estrada & Coates-Estrada 1996, Anzures-Dadda & Manson 2007). Under such conditions, plants would profit from a broad spectrum of seed dispersers and consequently reduce seed aggregation. This may potentially aid the recruitment of their offspring in diverse communities. Decreasing specialisation with increasing canopy cover is congruent with results from the study of (Schleuning et al. 2011) suggesting that canopy plants contribute more to overall fruit crop. A higher canopy cover thus provides higher fruit crop and consequently attracts a broad spectrum of frugivores that forage on different canopy tree species with fleshy fruits. Both fruiting plant species richness and canopy cover are among the key characteristics underpinning habitat structural complexity (Schmidt & Rypstra 2010). Thus, structurally complex habitats offer more niches for a more complex seed disperser community, resulting in highly stable and complex network structures, which are robust and thus less vulnerable to further habitat modification.

Conclusion

Our study shows that networks across local forest patches were all characterized by high redundancy in the associations between plants and frugivores, suggesting a stable coexistence of species in the plant-frugivore communities. Thus, secondary extinctions of mutualists, due to

resource losses are less likely in these networks (Estrada 2007, Blüthgen et al. 2008), as species have numerous reassembly pathways (Law & Blackford 1992). Such stability in networks was largely enhanced by habitat quality of local forest patches and remained unaffected by the surrounding matrix habitat. This suggests that complex networks may be resilient to matrix effects in heterogeneous fragmented forest landscapes if their mutualistic interactions involve highly flexible and mobile partners and if a sufficient quality of remaining forest patches is given. These results highlight that remnant forest patches embedded in a heterogeneous agricultural matrix are important in safeguarding and sustaining key ecological processes, as they provide alternative habitats outside protected sites and may connect nature reserves. Thus, we encourage conservation efforts to promote management strategies that will maintain habitat quality, especially structural complexity and abundance of fruit resources, in remaining forest patches. Moreover, future studies should also endeavor to establish how such complex interactions between plants and frugivores translate into effective seed dispersal and forest regeneration.

Acknowledgments

We thank the Ezemvelo KZN Wildlife for the permission to undertake this study in Vernon Crooks Nature Reserve and G. Archibald for granting us access to the forest patches at his farm. Our utmost gratitude goes to T. Ngidi for assisting with field observations as well as to F. Voigt and P. Pillay for their joint administrative support. The identification and selection of study sites was facilitated by E. Neuschulz and I. Grass at the onset of the study. We thank J. Albrecht for help with figures and D. Hodgson for his contribution to the statistical analysis. The conservation ecology group (Marburg University) gave valuable comments on the earlier version of this manuscript. The study was funded by the Robert Bosch Stiftung.

References

- ANZURES-DADDA, A. & MANSON, R. H. 2007. Patch- and landscape-scale effects on Howler Monkey distribution and abundance in rainforest fragments. *Animal Conservation* 10:69-76.
- BASCOMPTE, J. 2009. Disentangling the web of life. *Science* 325:416-419.
- BASCOMPTE, J. & JORDANO, P. 2007. Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 38:567-593.
- BERENS, D. G., FARWIG, N. & SCHAAB, G. 2008. Exotic guavas are foci of forest regeneration in Kenyan farmland. *Biotropica* 40:104-112.
- BLÜTHGEN, N. 2010. Why network analysis is often disconnected from community ecology: A critique and an ecologist's guide. *Basic and Applied Ecology* 11:185-195.
- BLÜTHGEN, N., FRÜND, J., VÁZQUEZ, D. P. & MENZEL, F. 2008. What do interaction network metrics tell us about specialization and biological traits? *Ecology* 89:3387-99.
- BLÜTHGEN, N., MENZEL, F. & BLÜTHGEN, N. 2006. Measuring specialization in species interaction networks. *BMC Ecology* 6:9.
- BLÜTHGEN, N., MENZEL, F., HOVESTADT, T., FIALA, B. & BLÜTHGEN, N. 2007. Specialization, constraints, and conflicting interests in mutualistic networks. *Current Biology* 17:341-346.
- BOON, R. 2010. Pooley's trees of Eastern South Africa: a complete guide. Flora and Fauna Publications Trust, Durban.
- CARNICER, J., JORDANO, P. & MELIÁN, C. J. 2009. The temporal dynamics of resource use by frugivorous birds: a network approach. *Ecology* 90:1958-1970.
- CHITTENDEN, H. 2007. Roberts bird guide: A comprehensive field guide to over 950 birds species in Southern Africa. John Voelcker Bird Book Fund, Cape Town.
- CLOUGH, Y., DWI PUTRA, D., PITOPANG, R. & TSCHARNTKE, T. 2009. Local and landscape factors determine functional bird diversity in Indonesian cacao agroforestry. *Biological Conservation* 142:1032-1041. Elsevier Ltd.
- CORDEIRO, N. J. & HOWE, H. F. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences of the United States of America* 100:14052-14056.

- DORMANN, C. F., GRUBER, B. & FRÜND, J. 2008. Introducing the bipartite package: analysing ecological networks. *R News* 8:8-11.
- ESTRADA, A. & COATES-ESTRADA, R. 1996. Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. *International Journal of Primatology* 17:759-783.
- ESTRADA, E. 2007. Topological structural classes of complex networks. *Physical Review E* 75:016103-1-016103-12.
- FAO. 2009. FAOSTAT online statistical service. Food and Agriculture Organization of the United Nations (FAO), Rome.
- FARWIG, N., BÖHNING-GAESE, K. & BLEHER, B. 2006. Enhanced seed dispersal of *Prunus africana* in fragmented and disturbed forests? *Oecologia* 147:238-52.
- FISCHER, J. & LINDENMAYER, D. B. 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* 16:265-280.
- FOLEY, J. A., DEFRIES, R., ASNER, G. P., BARFORD, C., BONAN, G., CARPENTER, S. R., CHAPIN, F. S., COE, M. T., DAILY, G. C., GIBBS, H. K., HELKOWSKI, J. H., HOLLOWAY, T., HOWARD, E. A., KUCHARIK, C. J., MONFREDA, C., PATZ, J. A., PRENTICE, I. C., RAMANKUTTY, N. & SNYDER, P. K. 2005. Global consequences of land use. *Science* 309:570-574.
- FRANKLIN, J. F. & LINDENMAYER, D. B. 2009. Importance of matrix habitats in maintaining biological diversity. *Proceedings of the National Academy of Sciences of the United States of America* 106:349-350.
- HARRISON, S. & BRUNA, E. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22:225-232.
- HOWE, H. F. & SMALLWOOD, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201-228.
- JORDANO, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *The American Naturalist* 129:657-677.
- JORDANO, P. 2000. Fruits and frugivory. Pg. 125-166 in Fenner, M. (ed.). *Seeds: the ecology of regeneration in plant communities* (2nd edition). CABI Publishers, Wallingford, UK.

- JORDANO, P. & GODOY, J. A. 2002. Frugivore-generated seed shadows: a landscape view of demographic and genetic effects. Pg. 305-321 in Levey, D. J., Silva, W. R. & Galetti, M. (eds.). Seed dispersal and frugivory: ecology, evolution and conservation. CAB International, Wallingford, UK.
- KANKAM, B. O. & ODURO, W. 2011. The effect of frugivory on postdispersal seed removal and germination in the pantropical forest tree *Antiaris toxicaria* Leschenault. *African Journal of Ecology* 50:21-28.
- KESSLER-RIOS, M. M. & KATTAN, G. H. 2012. Fruits of Melastomataceae: phenology in Andean forest and role as a food resource for birds. *Journal of Tropical Ecology* 28:11-21.
- KHAMCHA, D., SAVINI, T., BROCKLEMAN, W. Y., CHIMCHOME, V. & GALE, G. A. 2012. Influence of food availability and distribution on the movement patterns of a forest avian frugivore, the puff-throated bulbul (*Alophoixus pallidus*). *Journal of Tropical Ecology* 28:1-9.
- LAW, R. & BLACKFORD, J. C. 1992. Self-assembling food webs: a global viewpoint of coexistence of species in Lotka-Volterra communities. *Ecology* 73:567-578.
- LOISELLE, B. A. & BLAKE, J. G. 1990. Diets of understory birds in Costa Rica: seasonality and resource abundance. *Studies in Avian Biology*:91-103.
- MACARTHUR, R. H. & PIANKA, E. R. 1966. On optimal use of a patchy environment. *The American Naturalist* 100:603-609.
- MELLO, M. A. R., MARQUITTI, F. M. D., GUIMARÃES, P. R., KALKO, E. K. V., JORDANO, P. & DE AGUIAR, M. A. M. 2011. The missing part of seed dispersal networks: structure and robustness of bat-fruit interactions. *PloS one* 6:e17395.
- MUCINA, L. & RUTHERFORD, M. C. 2006. The vegetation of South Africa, Lesotho and Swaziland. South African National Botanical Institute, Pretoria.
- MYERS, N., MITTERMEIER, R. A., MITTERMEIER, C. G., DA FONSECA, G. A. & KENT, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.
- 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.
- REID, S. & ARMESTO, J. J. 2011. Interaction dynamics of avian frugivores and plants in a Chilean Mediterranean shrubland. *Journal of Arid Environments* 75:221-230. Elsevier Ltd.

- REZENDE, E. L., JORDANO, P. & BASCOMPTE, J. 2007. Effects of phenotypic complementarity and phylogeny on the nested structure of mutualistic networks. *Oikos* 116:1919-1929.
- SARACCO, J. F., COLLAZO, J. A & GROOM, M. J. 2004. How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. *Oecologia* 139:235-245.
- SAUNDERS, D. A., HOBBS, R. J. & MARGULES, C. R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18-32.
- SCHLEUNING, M., BLÜTHGEN, N., FLÖRCHINGER, M., BRAUN, J., SCHAEFER, H. M. & BÖHNING-GAESE, K. 2011. Specialization and interaction strength in a tropical plant-frugivore network differ among forest strata. *Ecology* 92:26-36.
- SCHMIDT, J. M. & RYPSTRA, A. L. 2010. Opportunistic predator prefers habitat complexity that exposes prey while reducing cannibalism and intraguild encounters. *Oecologia* 164:899-910.
- TEWKSBURY, J. J., BLACK, E., NUR, N., SAAB, V. A., LOGAN, B. D. & DOBKIN, D. S. 2002. Effects of anthropogenic fragmentation and livestock grazing on western riparian bird communities. *Studies in Avian Biology* 25:158-202.
- THE R DEVELOPMENT CORE TEAM. 2006. R: A language and environment for statistical computing. Vienna, Austria. (<http://www.R-project.org>).
- TYLIANAKIS, J. M., DIDHAM, R. K., BASCOMPTE, J. & WARDLE, D. A. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351-1363.
- TYLIANAKIS, J. M., TSCHARNTKE, T. & LEWIS, O. T. 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* 445:202-205.
- VÁZQUEZ, D. P. & AIZEN, M. A. 2006. Community-wide patterns of specialization in plant–pollinator interactions revealed by null models. Pp. 200–219 in Waser, N. M. & Ollerton, J. (eds.). *Plant–pollinator interactions: from specialization to generalization*. University of Chicago Press, Chicago, Illinois, USA.
- VÁZQUEZ, D. P., BLÜTHGEN, N., CAGNOLO, L. & CHACOFF, N. P. 2009. Uniting pattern and process in plant-animal mutualistic networks: a review. *Annals of Botany* 103:1445-1457.
- VÁZQUEZ, D. P., MORRIS, W. F. & JORDANO, P. 2005. Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecology Letters* 8:1088-1094.

VON MALTITZ, G. 2003. Classification system for South African indigenous forests: an objective classification for the Department of Water Affairs and Forestry. Environmentek report ENV-P-C 2003-017, CSIR.

WETHERED, R. & LAWES, M. J. 2003. Matrix effects on bird assemblages in fragmented Afromontane forests in South Africa. *Biological Conservation* 114:327-340.

Chapter 3: Functional diversity of frugivore communities in modified landscapes

With Dana G. Berens, Jörg Albrecht and Nina Farwig

Abstract

The potential impact of forest modification on the ecosystem function of seed dispersal largely depends on associated changes in functional diversity of frugivore communities. However, knowledge on the functional composition of seed disperser communities in differently modified forest types is still scarce. In a heterogeneous forest landscape in South Africa, we investigated the impact of forest modification and habitat quality on species richness and on different measures of functional diversity of a frugivore community within plant-seed disperser networks. Our results showed that shifts in the functional composition of frugivore communities were rather determined by habitat quality than by modification of forest patches. The mean body mass of frugivore communities increased with increasing canopy cover. Gape width was negatively affected by fruit abundance and varied among forest types. Moreover, functional dispersion, i.e. niche differentiation, increased with increasing fruiting plant species richness and was highest in modified forest patches. Overall, canopy cover seems to be the most important determinant of functional diversity, as it positively influenced species richness, functional richness and functional dispersion, thereby increasing both the functional richness and the specialization of frugivores in sites with high canopy cover. To conclude, the strong influence of habitat quality on functional diversity of frugivore communities suggests that managing habitat quality of remaining forest patches may be a promising approach for the conservation of seed dispersal, regeneration processes and ecosystem functionality in the long-term.

Introduction

Forest modification and fragmentation are the main threats to forests in tropical and subtropical ecosystems (Laurance et al. 2001, Morris 2010). Matrices surrounding forest fragments pose barriers for a large number of species (Martensen et al. 2008). Moreover, remaining forest patches may show an altered habitat structure with poor quality in terms of vegetation structure or resource abundance (Saunders et al. 1991, Fischer & Lindenmayer 2007). This may lead to a loss of biodiversity, which may in turn imperil the functioning of these ecosystems.

Studies on the consequences of biodiversity loss for the functioning of degraded ecosystems have gained importance over the last years (Loreau et al. 2001, Sekercioglu et al. 2004, 2006, 2007). Thereby, the relationship between biodiversity and ecosystem function rather depends on the spectrum of functional roles of species than on species identity (Diaz & Cabido 2001, Petchey & Gaston 2006). As different species may provide the same function, studying species loss alone does not allow for drawing conclusions about ecosystem function (Cumming & Child 2009). Thus, reduced or increased species richness does not necessarily mean there will be parallel changes in functional diversity (Greenberg et al. 2000, Perfecto et al. 2004). On the other hand, non-existent effects of habitat degradation on species richness may mask existing changes in the functional diversity of communities. This may be the case when functional redundancy within a community is low, i.e. when species are complementary in their functional roles. Thus, to assure the long-term conservation of ecosystems exposed to degradation, it is not only important to understand effects on species richness, but also on functional diversity within these habitats.

Several studies could show that forest fragmentation and degradation lead to changes in species richness and the community composition of bird species (e.g. Moran, Catterall, & Kanowski 2009, Neuschulz, Botzat, & Farwig 2011). The functional composition of bird communities may be altered in modified forests as both land-use intensity in the surrounding and habitat quality of remaining forest patches may act as environmental filters (Tscharntke et al. 2008, Guerrero et al. 2011). Matrix habitats surrounding forests influence the movement of individuals among these patches (Kennedy et al. 2010). Large-bodied species, for example, are able to cross open areas more easily than less mobile species (Luck & Daily 2003, Spiegel & Nathan 2007). Further, high within-patch habitat quality, e.g. in terms of a high abundance of resources and high structural diversity, may facilitate the persistence of diverse bird communities even within small forest fragments (e.g. Anzures-Dadda & Manson, 2007, Garcia, Zamora, & Amico, 2010).

Seed dispersing birds play an important functional role in tropical and subtropical forests, as they lay the template for regeneration for > 90 % of plant species in these ecosystems (Howe & Smallwood 1982, Willson et al. 1989, Farwig & Berens 2012). Bird species differ in their disperser effectiveness depending on certain functional traits that determine their resource use, e.g. body size or degree of frugivory (Fleming et al. 1993, Dennis & Westcott 2006). Highly mobile large-bodied birds have a longer gut retention time and can transport seeds over longer distances than small birds (Spiegel & Nathan 2007). Further, obligate frugivores are more generalized than opportunistic frugivores and hence are expected to be more central in plant frugivore-networks (Whelan et al. 1998, Carnicer et al. 2009, Schleuning et al. 2011). Overall, plants are expected to profit from a broad functional diversity of seed dispersers as it reduces seed aggregation and may potentially aid the recruitment of their offspring in a diverse range of habitats.

To our knowledge, only two studies assessed the effect of forest modification on the functional composition of frugivore communities (Moran et al. 2004, 2009). Moran et al. (2004, 2009) have shown that, even though the abundance of several frugivorous species was reduced in fragmented forests, functional overlap in bird species could sustain the potential for seed dispersal for many plant species. In these studies, the authors applied a functional classification of frugivore species according to morphometric and dietary traits. Even though it is a valid approach, functional classification may be problematic as forming groups is mostly subjective and information is discarded (Mason et al. 2005). Thus, it is inferior to the continuous measurement of functional diversity (Fonseca & Ganade 2001, Mason et al. 2005). Newly developed metrics to calculate the functional diversity within communities (Mason et al. 2005, 2008, Villéger et al. 2008) directly measure the distribution of species in functional niche space on a continuous scale (Mason et al. 2005). They can further reveal the importance of mechanisms driving the assembly of frugivore communities in degraded forests, i.e. the impact of environmental filtering, neutral assembly or competition filtering (limiting similarity; Mouchet, Villéger, Mason, & Mouillot, 2010). Environmental filtering assumes that environmental conditions act as a filter allowing only a narrow spectrum of species to coexist, which are then more similar to each other than expected by chance (Zobel 1997, Mouchet et al. 2010). In contrast, competitive exclusion (or limiting similarity) assumes that only dissimilar species can coexist in a community (Hardin 1960, MacArthur & Levins 1967). Functional diversity can be split in different components, e.g. functional richness, evenness and dispersion. Functional richness (FRic) measures the amount of niche space filled by species in the community; functional evenness (FEve) measures the evenness of abundance distribution in filled niche space (Mason et al. 2005, Villéger et al. 2008) and

functional dispersion (FDis) assesses the spread of species in niche space, or the degree of niche differentiation (Laliberté & Legendre 2010). Assessing effects on these different components of functional diversity allows for a detailed examination of the linkage between functional diversity and ecosystem functionality in degraded forests (Mason et al. 2005).

Here, we investigated the species richness and functional diversity of a frugivore community within plant-seed disperser networks in a human-dominated sub-tropical forest landscape of South Africa. We compared different components of functional diversity in forest types along a gradient of forest modification: large natural forest, natural forest fragments surrounded by grassland and remnant forest fragments embedded in agricultural fields. We further assessed the influence of habitat quality within forest patches in terms of e.g. resource availability and vegetation structure on the functional diversity of frugivore communities. We hypothesized that (1) both the degree of forest modification and habitat quality of forest fragments lead to shifts in the functional composition of frugivore communities, (2) an increase in forest modification negatively affects the species richness as well as the functional diversity of the frugivore community due to their filtering effect for a set of species, (3) local habitat quality of forest patches positively influences species and functional diversity, as enhanced habitat quality comprises more niches due to higher resources availability, fruiting plant species diversity and vegetation structure (e.g. Clough et al. 2009)

Material and Methods

Study site and design

We conducted this study over two successive years, 2009/10 and 2010/11 in a heterogeneous scarp forest landscape in and around Vernon Crookes Nature Reserve (VCNR) situated on the south coast of South Africa's KwaZulu Natal Province (150 – 610 m a.s.l., 30°16' S, 30°35' E). Monthly rainfall in the area ranges from 1–148 mm and annual temperature from 6–31°C (von Maltitz 2003). Covering an area of about 2,189 ha, VCNR is mainly a combination of hilly grasslands with wooded valleys. It is surrounded by a matrix of commercial sugarcane monocultures and timber plantations, within which a series of remnant natural scarp forest patches, exist. Fruiting by fleshy-fruited plants occurs almost all year round, although the main fruiting season ranged from November to April, during the main rainfall season (Boon 2010).

We worked in forest types characterized by decreasing degree of forest modification that are representative for the area: 1) large natural forest (NatFor), representing the largest protected natural scarp forest with 130 ha, predominantly surrounded by forest and partly by a matrix of natural grassland within VCNR; 2) natural forest fragments (NatFra; mean area = 5.82 ha \pm 1.8 SD) within VCNR, occurring naturally due to microclimatic and terrain conditions and being completely surrounded by natural grassland; 3) remnant forest fragments (AgrFra; mean area = 4.85 ha \pm 0.5 SD) embedded in a matrix of sugar cane fields at the border of VCNR. Despite the dissimilarities in matrices surrounding these three forest types, they all harbour similar communities of plants and birds and occur within the same natural geographic range of scarp forests (Mucina & Rutherford 2006, Neuschulz et al. 2011).

We established nine (200 m \times 200 m) study sites, i.e. three replicates per forest patch. The distance between study sites ranged from 0.53 to 1.06 km (mean = 0.80 \pm 0.3 km SD). Given the likelihood of strong edge effects in forest patches compared to the large natural forest (Harrison & Bruna 1999), we situated all study sites in close vicinity to forest gaps or edges.

Measuring local forest patch quality

We measured local forest patch quality by assessing three habitat characteristics, namely fruit abundance, fruiting plant species richness and canopy cover in each study site. We calculated fruit abundance (at the onset of fruit ripening) by estimating the number of fruits for each plant monitored and any other fleshy-fruited plants within a radius of 50 m. We then calculated the mean fruit abundance for each study site, which ranged from 11,000 to 66,000 (mean = 45,000 \pm 28,000 SD) over the two years. To determine fruiting plant species richness, we identified all fleshy fruited woody plants in each site to species level. Fruiting plant species richness ranged from 9 to 15 (mean = 12 \pm 3 SD) across study sites. We estimated canopy cover standing in the centre of four (50 \times 50 m) quadrates in each site and calculated the mean per site. Canopy cover ranged from 64 to 92 % (mean = 84 \pm 14 % SD) across study sites.

Assessment of plant-frugivore interactions

We observed all fleshy fruited plant species in each study site to assess interactions with frugivorous birds. Observations were undertaken during the main fruiting seasons in 2009/10 and 2010/11. The overall abundance of fruiting plant species in our study plots was low. Thus, one individual of each plant species was monitored in each site. We observed each plant for a total of

18 h, ideally split into 9 h per year. In cases where we could not achieve 9 h in the first fruiting year, we increased the number of observation hours in the second fruiting year to attain the standard total of 18 h per plant. We split the observations into three monitoring sessions, namely early morning (06:00 am – 09:00 am), mid-morning (09:00 am to 12:00 am) and afternoon (2:00 pm – 5:00 pm), conducted at three different days during the main fruiting period of each plant species in each year. Observations of species were evenly spread across the three sessions. Using binoculars (Luger DA 10X42, Köln, Germany) observations were carried out from a camouflaged hide at ca. 20 m distance to the plant individual. All plant visiting birds and their fruit handling behaviour on the plant were recorded. If more than one feeding bird was present on the plant (<0.5 % of observations), one randomly chosen individual was selected for which fruit consumption was observed.

For each plot, we constructed interaction matrices giving the abundance of each bird species on each plant species, whereby abundance was defined as the number of fruit-eating individuals of a given frugivore species. From these matrices, we calculated frugivore species richness per plot as the mean frugivore species richness across all plant species within a plot. Further, we constructed a plot-abundance-matrix giving the abundance of each frugivore species in each plot.

Functional traits

For each bird species feeding on fleshy-fruited plants during observations, we compiled data on three functional traits that are closely related to resource use and fruit consumption, i.e. body mass, gape width and the degree of frugivory. Data on these functional traits were compiled in a species-trait matrix. Data on body mass was taken from literature (Hockey et al. 2005). If body mass for both sexes was given, mass of male and female birds was averaged. In cases where a range was given, a mean value was used. Body mass was log-transformed. Gape width of bird species was measured during mist-netting in the same study area (Neuschulz et al. in prep). As body mass and gape width were highly correlated ($r = 0.83$), a linear regression between the two variables (both log-transformed) was calculated. The residuals of this regression were used as a trait in the species-trait matrix, expressing the remaining variance in gape width of bird species not explained by body mass (residual gape width in the following). Data on gape width was available for 40 out of 54 bird species only, so that all further analyses are based on these 40 species. To obtain the degree of frugivory, bird species were classified as “obligate”, “partial” and “opportunistic”

following Kissling, Rahbek & Böhning-Gaese (2007). Species that were not enlisted in Kissling et al. (2007) were classified following Hockey et al. (2005). The same criteria were used as in Kissling et al. (2007), with obligate frugivores depending almost entirely on fruit, partial frugivores feeding on different major food items (e.g. both fruits and insects) and opportunistic frugivores having fruits only as a minor food item. The nominal trait degree of frugivory was then transformed into two dummy variables, one for obligate frugivory and one for partial frugivory (0 = false, 1 = true), which at the same time determined opportunistic frugivores (false for both variables).

Functional diversity measures

All functional analyses were done in R (version 2.11.1, R development core team). We assessed the functional composition for each plot using the community-level weighted mean of the functional traits body mass and residual gape width (Lavorel et al. 2008) as implemented in the package FD (Laliberté & Shipley 2011). Accordingly, the proportion of obligate frugivores, partial frugivores and opportunistic frugivores were calculated for the nominal trait “degree of frugivory”. Observed functional diversity measures, i.e. FRic, FEve and FDis, were calculated from the observed plot-abundance matrix using the package FD. To determine the effect of environmental filtering, neutral assembly or competitive filtering on frugivore communities, we compared observed measures of functional diversity to expected measures. Expected functional diversity measures were calculated by randomization of the observed plot-abundance matrix. Using the Patefield algorithm implemented in the package bipartite (Dormann et al. 2008), we constructed 1000 randomized plot-abundance matrices, thereby keeping the marginal totals for plots and bird species constant. FRic, FEve and FDis were calculated for each randomized matrix and expected means of the measures were computed across the randomizations. We calculated the ratio of observed to expected measures of species richness and functional diversity using the index of variance (IV) developed by Mason et al. (2008):

$$IV = 2 \left[\frac{Obs}{Obs + Exp} \right] - 1$$

where Obs is the observed functional diversity and Exp the mean expected functional diversity obtained from randomizations (Mason et al. 2008). The index of variance calculated from observed and expected functional diversity measures ranges from -1 to 1. Significant negative

departures from expectations, i.e. values below zero, indicate environmental filtering, and significant positive values indicate competitive filtering. Non-significant departure, i.e. values close to zero, indicate neutral assembly (Mouchet et al. 2010). Significant deviation of observed from expected values was calculated from the randomizations using a two-tailed p-value of 0.025. In the following, we refer to FRic, FEve and FDis for simplicity reasons, even though all analyses were done on the IV of each measure.

Statistical analyses

All measures of habitat quality, i.e. fruit abundance, fruiting plant species richness and canopy cover were uncorrelated (all p-values > 0.462). In a first analysis, we determined the effect of forest type and habitat quality on the functional composition of frugivore communities. To do so, we tested the effect of forest type, fruit abundance, fruiting plant species richness and canopy cover (arcsine-square root-transformed) on the community-level weighted means of body mass (log-transformed), on residual gape width as well as on the proportion of obligate, partial and opportunistic frugivores within the communities. As no specific order of independent variables in affecting dependent variables could be assumed, we used type III sums of squares. Model selection was done with the help of Akaike's information criterion (AIC). We further tested for an effect of forest type, fruit abundance, fruiting plant species richness and canopy cover (arcsine-square-root transformed) on frugivore species richness, FRic, FEve and FDis, respectively, in a comparable way.

Results

In total, we monitored 31 plant species and a total number of 8,075 bird individuals. Body mass of the frugivore bird species ranged from 8.0 to 642.5 g and gape width from 4.7 to 35.6 mm. A number of eight species were categorized as obligate frugivores, 19 as partial and 13 as opportunistic frugivores. The three most common frugivorous bird species were the Cape White-Eye (*Zosterops capensis*, body mass: 13.50 g, gape width: 6.76 mm, partial frugivore), Dark-capped Bulbul (*Pycnonotus tricolor*, 37.50 g, 12.15 mm, obligate frugivore) and Black-bellied Starling (*Lamprotornis corruscus*, 50.00 g, 13.06 mm, partial frugivore).

The community-level weighted mean of body mass was $40.29 + 4.19/-3.79$ g (henceforth mean \pm SE if not otherwise stated; back-transformed mean). Mean body mass did not differ among forest types, but significantly increased with increasing canopy cover (Fig.1, Table 1). Residual gape width differed significantly among forest types, and was highest in NatFra, intermediate in NatFor and lowest in AgrFra. It further decreased significantly with increasing fruit abundance (Table 1, Fig.1). The mean proportion of obligate frugivores was 0.39 ± 0.03 across study plots, the mean proportion of partial frugivores 0.56 ± 0.04 and of opportunistic frugivores 0.05 ± 0.02 . Proportions of all frugivore categories neither differed among forest types nor were influenced by any of the habitat quality measures (Table 1).

Table 1. Anova results (type III sums of squares) giving effects of forest type, fruit abundance, fruiting plant species richness and canopy cover (arcsine-square-root transformed) on the community weighted means of body mass (log10 transformed), the residuals of gape width (obtained from regression between body mass and gape width, see methods for details), the proportion of obligate, partial and opportunistic frugivores. Marginally significant and significant p-values are highlighted in bold.

	Body mass			Resid(gape width)			Proportion obligate frugivores			Proportion partial frugivores			Proportion opportunistic frugivores		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
Forest type	2,5	2.70	0.160	2,3	14.61	0.028	-	-	-	-	-	-	2,5	1.98	0.233
Fruit abundance	-	-	-	1,3	6.83	0.079	-	-	-	-	-	-	-	-	-
Fruiting plant species richness	-	-	-	-	2.46	0.213	1,7	3.17	0.118	-	-	-	1,5	1.76	0.241
Canopy cover	1,5	8.48	0.033	1,3	0.79	0.438	-	-	-	-	-	-	-	-	-

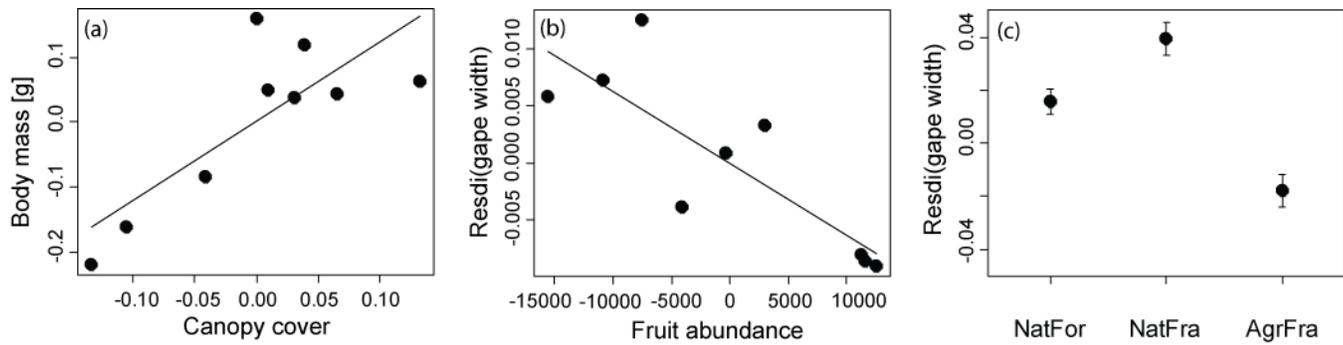


Fig.1. Partial regression plots (A, B) and least square means depicting the relationship between habitat variables and community-weighted means of different traits: A) canopy cover (arcsine-square-root-transformed) and body mass (log10-transformed), B) fruit abundance and residual gape width (obtained from regression between body mass and gape width, see methods for details), and C) forest types and residual gape width.

Mean species richness of frugivores was 5.77 ± 0.39 across plot. Frugivore species richness did neither differ among forest types nor was affected by fruit abundance or fruiting plant species richness. Canopy cover, however, had a marginally significantly positive effect on frugivore species richness (Table 2, Fig. 2).

Table 2. Anova results (type III sums of squares) giving effects of forest type, fruit abundance, fruiting plant species richness and canopy cover (arcsine-square-root transformed) on frugivore species richness, functional richness (FRic), functional evenness (FEve) and functional dispersion (FDis). Marginally significant and significant p-values are highlighted in bold.

	Species richness			FRic			FEve			FDis		
	df	F	P	df	F	P	df	F	P	df	F	P
Forest type	2,3	3.61	0.159	-	-	-	2,6	2.61	0.153	2,4	9.01	0.033
Fruit abundance	1,3	2.96	0.184	-	-	-	-	-	-	-	-	-
Fruiting plant species richness	1,3	2.67	0.200	-	-	-	-	-	-	1,4	13.85	0.020
Canopy cover	1,3	8.34	0.063	1,7	18.68	0.003	-	-	-	1,4	7.66	0.050

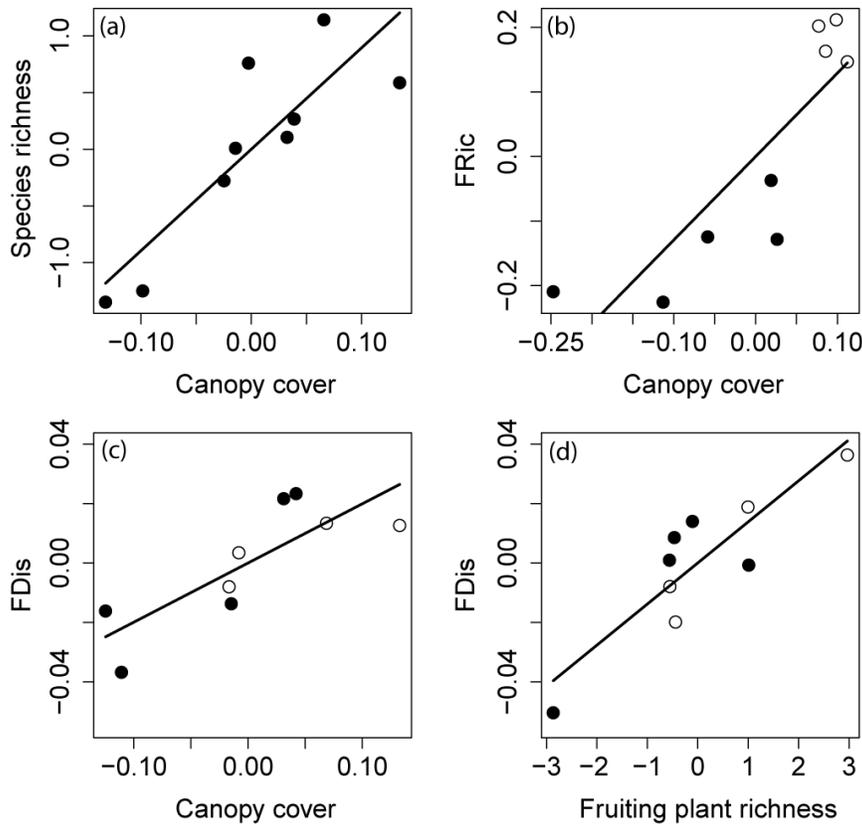


Fig.2. Partial regression plot depicting the relationship between canopy cover (arcsine-square-root-transformed) and A) species richness, B) functional richness (FRic) and C) functional dispersion (FDis), as well as D) between fruiting plant species richness and FDis.). Significant deviation of observed from expected measures of functional diversity is indicated in black, while white points indicate neutral assembly.

Mean FRic across plots was -0.229 ± 0.060 . Observed FRic was significantly lower than expected in one plot in NatFor, three plots in NatFra and one plot in AgrFra (Fig. 3). FRic neither differed among forest types nor was affected by fruit abundance and fruiting plant species richness. However, it significantly increased with increasing canopy cover, whereby plots with lower canopy cover showed significant negative deviation from neutral assembly, i.e. environmental filtering, and plots with higher canopy cover showed neutral assembly (Table 2, Fig. 2). Mean FEve was -0.001 ± 0.021 across plots. Observed FEve significantly differed from expected only in one plot in NatFor and one in AgrFra, which showed significant negative and positive deviation from neutral assembly, respectively (Fig. 3). FEve neither differed among forest types (Table 2), nor was influenced by fruit abundance, fruiting plant species richness or canopy cover. FDis had a mean value of -0.018 ± 0.012 across plots. Observed FDis was significantly lower than expected in two plots in NatFor, one plot in NatFra and one plot in AgrFra. One

AgrFra plot showed a significantly positive deviation from neutral assembly. FDis significantly differed among forest types (Table2), with AgrFra having the highest FDis (0.002 ± 0.013), followed by NatFra (-0.018 ± 0.016) and NatFor (-0.039 ± 0.031). Further, FDis significantly increased with increasing fruiting plant species richness and increased with increasing canopy cover (Table 2, Fig. 2).

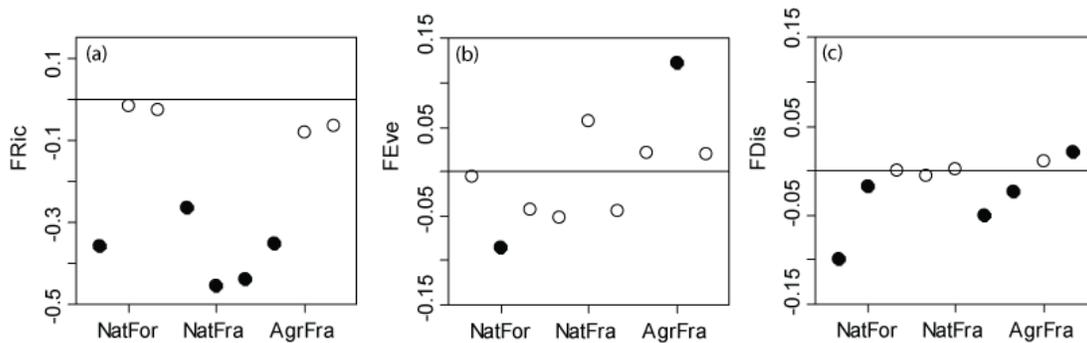


Fig.3. Index of variance of functional richness (FRic), functional evenness (FEve) and functional dispersion (FDis) in nine study plots across three differently modified forest types (NatFor = natural forest, NatFra = natural fragments, AgrFra = fragments surrounded by agricultural land). Significant deviation of observed from expected measures of functional diversity is indicated in black, while white points indicate neutral assembly. Black points below the neutral line indicate environmental filtering, those above the line competitive filtering.

Discussion

Our results showed that shifts in the functional composition of frugivore communities were rather determined by habitat quality than by modification of forest patches. The mean body mass of frugivore communities increased with increasing canopy cover. Residual gap width decreased with increasing fruit abundance and was lowest in heavily modified fragments. Moreover, FDis, i.e. niche differentiation, increased with increasing fruiting plant species richness and was higher in AgrFra than in NatFra and NatFor. Canopy cover seems to be the most important determinant of functional diversity, as it positively influenced species richness, FRic and FDis, thereby increasing both the functional richness and the specialization of frugivores in sites with high canopy cover.

Shifts in the functional composition of frugivore communities

Overall, the functional composition of frugivore communities was rather weakly influenced by forest modification. Only mean gap width in the communities differed among forest types, and

was smaller in modified forests than in NatFra or NatFor. This shows that the frugivore communities in modified forests are characterized by bird species differing in gape width from those in less modified fragments, which could potentially affect the spectrum of seeds dispersed within the communities. Comparably, Moran et al. (2004) found a higher abundance of small-gaped birds in heavily modified forest fragments, which they explained by a higher abundance of small-seeded plant species, e.g. shrubs and smaller trees, in modified fragments (Moran et al. 2004). In contrast to gape width, neither body mass nor the composition of the community in terms of degree of frugivory showed effects of forest modification. Thus, in general, the forest patches in our study area seem to be well-connected, and even severe matrix habitat like sugarcane fields surrounding them may be traversable by bird species. Comparably small distances among forest fragments in our study area allow for among-patch movement even of less mobile species and might explain these results (Neuschulz et al. in prep). Further, scarp forests have a history of isolation and fragmentation during the last glacial maximum (Eeley et al. 1999), which might have led to the adaptation of local bird communities to patchy environments (Neuschulz et al. in prep.). Moreover, the quality of the remaining forest patches might be a more important determinant of the functional composition of bird communities than forest modification per se (Garcia et al. 2010). In fact, community-level body mass and gape width were closely linked to canopy cover and fruit abundance, respectively. Thus, patches with higher vegetation complexity and resource abundance may be more attractive, especially for large birds moving across heterogeneous landscapes and tracking resources (Lloyd & Marsden 2011). Further, they provide more habitat niches and food resources. Thus, in line with other studies (Stouffer & Bierregaard 1995, Lees & Peres 2008, 2009), our results indicate that fragmented forests in a heterogeneous landscape can harbour a high diversity of frugivore communities.

We did not find shifts in community composition related to the degree of frugivory. Actually, also other studies have shown that frugivorous birds are less susceptible to degradation and fragmentation than other guilds (e.g. Tschardt et al. 2008, Neuschulz et al. in prep). The absence of a community shift might be due to low levels of fruit specialization of frugivores in our communities. Especially obligate and partial frugivores are dependent on fruit resources to meet their nutritional needs (Whelan et al. 1998) and are less specialized in fruit choice than e.g. opportunistic frugivores (Schleuning et al. 2011). In fact, across forest patches, partial and obligate frugivores accounted for the largest proportion of birds encountered. Thus, high quality forest fragments may sustain a broad functional diversity within the frugivore community, thereby potentially facilitating regeneration processes within these forest patches.

Effects of forest modification and habitat quality on species and functional diversity

In general, frugivore species richness per se was little influenced by any of the factors investigated in our study. It was comparable among forest types, which is in line with the findings of other studies showing that the species richness of frugivore communities can be maintained or even enhanced in modified forests (Estrada et al. 1993, Farwig et al. 2008, Ranganathan et al. 2008). Thus, potentially due to high movement capacity of birds among patches (Neuschulz et al. in prep), even strongly modified forest types may harbour a high taxonomic richness within frugivore communities in our study area. Especially frugivores depend on tracking fruit resources across the landscape and easily pass habitat boundaries (Graham 2001, Lenz et al. 2011). In congruence with species richness, also FRic did not differ among forest types. Considering entire bird communities, other studies found a decreasing functional diversity in agricultural as compared to natural areas (e.g. Fischer et al. 2007, Flynn et al. 2009). Thus, our results again indicate that frugivore communities may be less susceptible to habitat modification than other functional bird groups (Tschardt et al. 2008). Further, besides a high taxonomic richness, the forest fragments studied here also sustain a high functional richness of frugivorous birds even in an intensively used agricultural area.

Despite the overall suitability of forest fragments for frugivore communities found in our study, environmental filtering seems to be an important determinant of functional richness, as in several plots across habitats, observed FRic was significantly lower than expected FRic. This indicates that environmental filtering at least partly shapes the functional richness of bird communities in our study area. Due to the non-random distribution of resources, some species may be excluded from persisting in a local community, while species that do occur may be particularly adapted to that environment (Petchey et al. 2007, Mayfield et al. 2010). This in turn means that communities in fragments do not encompass the full functional spectrum of frugivores. Relating FRic to habitat quality revealed that canopy cover seems to be the main factor driving this effect, as both species richness and FRic increased with increasing canopy cover. Further, the effect of environmental filtering diminished in plots with high canopy cover. Canopy plants may contribute to large proportions of the overall fruit crop within forests (Shanahan & Compton 2001, Schleuning et al. 2011), thereby attracting a broad spectrum of frugivores foraging in canopy trees. This seems to be particularly true for large-bodied frugivores, as the community-level mean body-mass increased with increasing canopy cover as well (see above). While mere fruit abundance may only be a snapshot of the resources available in a limited time span, canopy cover might actually

represent the long-term level of resource availability within a fragment. High resource availability will, in turn, allow for an increasing functional richness within frugivore communities.

The degree of FEve measures how functional space is occupied within a community. Even though this measure is sensitive to environmental filtering (Mouchet et al. 2010), we detected only minor environmental effects on FEve in our study. All but two communities showed neutral assembly concerning FEve, which means that species abundances are evenly spread along the functional trait gradient (Pakeman 2011). In other words, communities are not dominated by species with certain functional traits, and the full range of functional trait space is evenly represented. In accordance, FEve neither varied with forest modification nor with any of the investigated measures of habitat quality.

We found a contrasting pattern for FDis, with higher levels of FDis in AgrFra than in NatFor and NatFra. Obviously, species show higher levels of niche differentiation in modified forest types, which might indicate that frugivores have a higher specialization on fruit resources in these habitats. Lower environmental filtering and potentially even higher competition among frugivores in highly modified habitats may result in a lower functional similarity, and thus a higher niche differentiation, within frugivore communities (Petchey et al. 2007). Besides varying across forest types, we found that FDis was strongly influenced by habitat quality of the forest patches. Both increasing fruiting plant species richness and increasing canopy cover led to higher levels of FDis. Thus, increasing canopy cover within forest patches enhances species richness, FRic and FDis. It thus leads to a higher amount of niche-space filled while at the same time functional trait space is more widely used, allowing functionally “extreme” or specialized frugivores to persist in the communities. In other words, decreasing canopy cover goes along with a loss of specialized frugivores, such as large-bodied species, from the communities. The same could be true for the positive effect of fruiting plant species richness. A higher variability of fruit resources may allow a higher specialization in frugivores (e.g. Fleming, 2005; Chama et al. in prep.). In fact, also other studies have shown that high habitat quality can lead to higher functional diversity within bird communities (Guerrero et al. 2011). Thus, high habitat quality within forest fragments may weaken the effects of environmental filtering due to impermeable matrices and sustain a broad functional spectrum of frugivores.

Conclusions

To conclude, functional diversity of frugivore communities in the heterogeneous forest landscape studied in South Africa seems to be influenced mainly by habitat conditions, which exclude for example large-bodied species from persisting within communities. Still, all forest types sustain a comparably high functional diversity within seed disperser communities. Further, the influence of environmental filtering on functional diversity seems to be weakened by increasing habitat quality, especially by increasing canopy cover. Thus, high-quality forest patches can sustain functional diversity of frugivore communities even in fragmented landscapes. A high functional diversity within frugivore communities may in turn result in a high quantity and quality of seed dispersal, and thus high seed dispersal functionality, even in heavily modified forest types in our study area. Thereby, managing habitat quality of remaining forest patches may be a promising approach for the conservation of seed dispersal, regeneration processes and ecosystem functionality in the long-term.

Acknowledgements

We thank EKZN-Wildlife for permission to work within the Nature Reserves as well as George Archibald who allowed the use of his land for this study. We thank Eike Lena Neuschulz for providing the frugivore gap width data. We extend our gratitude to Thulani Ngidi for assisting with field work and to Colleen Downs, Pravin Pillay, Friederike Voigt and Sandy-Lynn Steenhuisen for manifold support. The research was funded by the Robert Bosch Stiftung.

References

- ANZURES-DADDA, A. & MANSON, R. H. 2007. Patch- and landscape-scale effects on Howler Monkey distribution and abundance in rainforest fragments. *Animal Conservation* 10:69-76.
- BOON, R. 2010. Pooley's trees of Eastern South Africa: a complete guide. Flora and Fauna Publications Trust, Durban.
- CARNICER, J., JORDANO, P. & MELIÁN, C. J. 2009. The temporal dynamics of resource use by frugivorous birds: a network approach. *Ecology* 90:1958-1970.
- CLOUGH, Y., DWI PUTRA, D., PITOPANG, R. & TSCHARNTKE, T. 2009. Local and landscape factors determine functional bird diversity in Indonesian cacao agroforestry. *Biological Conservation* 142:1032-1041. Elsevier Ltd.
- CUMMING, G. S. & CHILD, M. F. 2009. Contrasting spatial patterns of taxonomic and functional richness offer insights into potential loss of ecosystem services. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364:1683-1692.
- DENNIS, A. J. & WESTCOTT, D. A. 2006. Reducing complexity when studying seed dispersal at community scales: a functional classification of vertebrate seed dispersers in tropical forests. *Oecologia* 149:620-634.
- DORMANN, C. F., GRUBER, B. & FRÜND, J. 2008. Introducing the bipartite package: analysing ecological networks. *R News* 8:8-11.
- EELEY, H. A. C., LAWES, M. J. & PIPER, S. E. 1999. The influence of climate change on the distribution of indigenous forest in South Africa. *Journal of Biogeography* 26:595-617.
- ESTRADA, A., COATES-ESTRADA, R., MERRIT JR., D., MONTIEL, S. & CURIEL, D. 1993. Patterns of frugivore species richness and abundance in forest islands and in agricultural habitats at Los Tuxtlas, Mexico. *Vegetatio* 107/108:245-257.
- FARWIG, N. & BERENS, D. G. 2012. Imagine a world without seed dispersers: A review of threats, consequences and future directions. *Basic and Applied Ecology*. Elsevier GmbH.
- FARWIG, N., SAJITA, N. & BÖHNING-GAESE, K. 2008. Conservation value of forest plantations for bird communities in western Kenya. *Forest Ecology and Management* 255:3885-3892.
- FISCHER, J. & LINDENMAYER, D. B. 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* 16:265-280.
- FISCHER, J., LINDENMAYER, D. B., BLOMBERG, S. P., MONTAGUE-DRAKE, R., FELTON, A. & STEIN, J. A. 2007. Functional richness and relative resilience of bird communities in regions with different land use intensities. *Ecosystems* 10:964-974.

- FLEMING, T., VENABLE, D. & HERRERA, L. 1993. Opportunism vs. specialization: the evolution of dispersal strategies in fleshy-fruited plants. *Vegetatio* 107/108:107-120.
- FLYNN, D. F. B., GOGOL-PROKURAT, M., NOGEIRE, T., MOLINARI, N., RICHERS, B. T., LIN, B. B., SIMPSON, N., MAYFIELD, M. M. & DECLERCK, F. 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology letters* 12:22-33.
- FONSECA, C. R. & GANADE, G. 2001. Species functional redundancy , random extinctions and the stability of ecosystems. *Society*:118-125.
- GARCIA, D., ZAMORA, R. & AMICO, G. C. 2010. Birds as suppliers of seed dispersal in temperate ecosystems: conservation guidelines from real-world landscapes. *Conservation biology: the journal of the Society for Conservation Biology* 24:1070-1079.
- GRAHAM, C. H. 2001. Factors influencing movement patterns of Keel-billed Toucans in a fragmented tropical landscape in Southern Mexico. *Conservation Biology* 15:1789-1798.
- GREENBERG, R., BICHER, P., CRUZ ANGON, A., MACVEAN, C., PEREZ, R. & CANO, E. 2000. The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations. *Ecology* 81:1750-1755.
- GUERRERO, I., MORALES, M. B., OÑATE, J. J., AAVIK, T., BENGTSSON, J., BERENDSE, F., CLEMENT, L. W., DENNIS, C., EGGERS, S., EMMERSON, M., FISCHER, C., FLOHRE, A., GEIGER, F., HAWRO, V., INCHAUSTI, P., KALAMEES, A., KINKS, R., LIIRA, J., MELÉNDEZ, L., PÄRT, T., THIES, C., TSCHARNTKE, T., OLSZEWSKI, A. & WEISSER, W. W. 2011. Taxonomic and functional diversity of farmland bird communities across Europe: effects of biogeography and agricultural intensification. *Biodiversity and Conservation* 20:3663-3681.
- FLEMING, H. T. 2005. The relationship between species richness of vertebrate mutualists and their food plants in tropical and subtropical communities differs among hemispheres. *Oikos* 111:556-562.
- HARDIN, G. 1960. The competitive exclusion principle. *Science* 131:1292-1297.
- HARRISON, S. & BRUNA, E. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22:225-232.
- HOCKEY, P., DEAN, W. & RYAN, P. (Eds.). 2005. *Roberts - Birds of Southern Africa (VIIth)*. The Trustees of the John Voelcker Bird Book Fund, Cape Town.
- HOOPER, D., CHAPIN, F., EWEL, J., HECTOR, A., INCHAUSTI, P., LAVOREL, S., LAWTON, J., LODGE, D. M., LOREAU, M., NAEEM, S., SCHMID, B., SETÄLÄ, H., SYMSTAD, A. J., VANDERMEER, J. & WARDLE, D. A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3-35.

- HOWE, H. F. & SMALLWOOD, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201-228.
- KENNEDY, C., MARRA, P., FAGAN, W. & NEEL, M. 2010. Landscape matrix and species traits mediate responses of neotropical resident birds to forest fragmentation in Jamaica. *Ecological Monographs* 80:651-669.
- KISSLING, W. D., RAHBEK, C. & BÖHNING-GAESE, K. 2007. Food plant diversity as broad-scale determinant of avian frugivore richness. *Proceedings. Biological sciences / The Royal Society* 274:799-808.
- LALIBERTÉ, A. E. & SHIPLEY, B. 2011. Package “FD.”
- LALIBERTÉ, E. & LEGENDRE, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299-305.
- LAURANCE, W. F., LOVEJOY, T. E., VASCONCELOS, H. L., BRUNA, E. M., DIDHAM, R. K., STOUFFER, P. C., GASCON, C., BIERREGAARD, R. O., LAURANCE, S. G. & SAMPAIO, E. 2001. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16:605-618.
- LAVOREL, S., GRIGULIS, K., MCINTYRE, S., WILLIAMS, N. S. G., GARDEN, D., DORROUGH, J., BERMAN, S., QUÉTIER, F., THÉBAULT, A. & BONIS, A. 2008. Assessing functional diversity in the field – methodology matters! *Functional Ecology* 22:134-147.
- LEES, A. C. & PERES, C. A. 2008. Avian life-history determinants of local extinction risk in a hyper-fragmented neotropical forest landscape. *Animal Conservation* 11:128-137.
- LEES, A. C. & PERES, C. A. 2009. Gap-crossing movements predict species occupancy in Amazonian forest fragments. *Oikos* 118:280-290.
- LENZ, J., FIEDLER, W., CAPRANO, T., FRIEDRICHS, W., GAESE, B. H., WIKELSKI, M. & BÖHNING-GAESE, K. 2011. Seed-dispersal distributions by trumpeter hornbills in fragmented landscapes. *Proceedings of the Royal Society B, Biological Sciences*.
- LLOYD, H. & MARSDEN, S. J. 2011. Between-patch bird movements within a high-Andean *Polylepis* woodland/matrix landscape: implications for habitat restoration. *Restoration Ecology* 19:74-82.
- LOREAU, M., NAEEM, S., INCHAUSTI, P., BENGTSSON, J., GRIME, J. P., HECTOR, A., HOOPER, D. U., HUSTON, M. A., RAFFAELLI, D., SCHMID, B., TILMAN, D. & WARDLE, D. A. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804-8.
- LUCK, G. & DAILY, G. C. 2003. Tropical countryside bird assemblages: richness, composition, and foraging differ by landscape context. *Ecological Applications* 13:235-247.

- MACARTHUR, R. & LEVINS, R. 1967. The limiting similarity, convergence and divergence of coexisting species. *The American Naturalist* 101:377-385.
- MARTENSEN, A. C., PIMENTEL, R. G. & METZGER, J. P. 2008. Relative effects of fragment size and connectivity on bird community in the Atlantic Rain Forest: Implications for conservation. *Biological Conservation* 141:2184-2192.
- MASON, N. W. H., IRZ, P., LANOISELÉE, C., MOUILLOT, D. & ARGILLIER, C. 2008. Evidence that niche specialization explains species-energy relationships in lake fish communities. *The Journal of animal ecology* 77:285-96.
- MASON, N. W. H., MOUILLOT, D., LEE, W. G., WILSON, J. B. & FUNCTIONAL, J. B. 2005. Functional richness , functional evenness and functional divergence : the primary components of functional diversity. *Oikos* 1:112-118.
- MAYFIELD, M. M., BONSER, S. P., MORGAN, J. W., AUBIN, I., MCNAMARA, S. & VESK, P. A. 2010. What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography*:423-431.
- MORAN, C., CATTERALL, C. & KANOWSKI, J. 2009. Reduced dispersal of native plant species as a consequence of the reduced abundance of frugivore species in fragmented rainforest. *Biological Conservation* 142:541-552. Elsevier Ltd.
- MORAN, C., CATTERALL, C. P., GREEN, R. J. & OLSEN, M. F. 2004. Functional variation among frugivorous birds: implications for rainforest seed dispersal in a fragmented subtropical landscape. *Oecologia* 141:584-95.
- 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, Biological sciences* 365:3709-18.
- MOUCHET, M. A., VILLÉGER, S., MASON, N. W. H. & MOUILLOT, D. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* 24:867-876.
- MUCINA, L. & RUTHERFORD, M. C. 2006. The vegetation of South Africa, Lesotho and Swaziland. South African National Botanical Institute, Pretoria.
- 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.

- PAKEMAN, R. J. 2011. Functional diversity indices reveal the impacts of land use intensification on plant community assembly. *Journal of Ecology* 99:1143-1151.
- PERFECTO, I., VANDERMEER, J. H., BAUTISTA, G. L., IBARRA, G., GREENBERG, R., BICHIER, P. & LANGRIDGE, S. 2004. Greater predation in shaded coffee farms: the role of resident neotropical birds. *Ecology* 85:2677-2681.
- PETCHEY, O. L., EVANS, K. L., FISHBURN, I. S. & GASTON, K. J. 2007. Low functional diversity and no redundancy in British avian assemblages. *The Journal of animal ecology* 76:977-85.
- RANGANATHAN, J., DANIELS, R. J. R., CHANDRAN, M. D. S., EHRLICH, P. R. & DAILY, G. C. 2008. Sustaining biodiversity in ancient tropical countryside. *Proceedings of the National Academy of Sciences of the United States of America* 105:17852-17854.
- SAUNDERS, D. A., HOBBS, R. J. & MARGULES, C. R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18-32.
- SCHLEUNING, M., BLÜTHGEN, N., FLÖRCHINGER, M., BRAUN, J., SCHAEFER, H. M. & BÖHNING-GAESE, K. 2011. Specialization and interaction strength in a tropical plant-frugivore network differ among forest strata. *Ecology* 92:26-36.
- SHANAHAN, M. & COMPTON, S. G. 2001. Vertical stratification of figs and fig-eaters in a Bornean lowland rain forest: how is the canopy different? *Plant Ecology* 153:121-132.
- SPIEGEL, O. & NATHAN, R. 2007. Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology letters* 10:718-28.
- STOUFFER, P. C. & BIERREGAARD, R. O. 1995. Use of Amazonian forest fragments by understory insectivorous birds. *Ecology* 76:2429-2445.
- THE R DEVELOPMENT CORE TEAM. 2006. R: A language and environment for statistical computing. Vienna, Austria. (<http://www.R-project.org>).
- TSCHARNTKE, T., SEKERCIOGLU, C. H., DIETSCH, T. V., SODHI, N. S., TYLIANAKIS, J. M., JASON, M. & DIETSCH, V. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology* 89:944-951.
- VILLÉGER, S., MASON, N. W. H. & MOUILLOT, D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290-301.
- VON MALTITZ, G. 2003. Classification system for South African indigenous forests: an objective classification for the Department of Water Affairs and Forestry. Environmentek report ENV-P-C 2003-017, CSIR.

- WHELAN, C. J., SCHMIDT, K. A., STEELE, B. B., QUINN, W. J. & DILGER, S. 1998. Are bird-consumed fruits complementary resources? *Oikos* 83:195-205.
- WILLSON, M. F., IRVINE, A. K. & WALSH, N. G. 1989. Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica* 21:133-147.
- ZOBEL, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology & Evolution* 12:266-269.

Chapter 4: The importance of frugivores for germination success of plant species

With Dana G. Berens and Nina Farwig

Abstract

Frugivorous birds are the most important consumers of wild fruits particularly in sub-tropical and tropical forest ecosystems. Whether or not such plant-frugivore interactions contribute to germination enhancement is still a subject of much debate. We tested the effect of gut treatment by four captive species of avian frugivores in comparison to manually depulped and whole fruit on seedling emergence and germination probability of seeds from sixteen plant species in South Africa. Moreover, we determined whether fruit weight of each plant species affected germination patterns. Across plant species, a total of 2, 796 seeds were planted, of which 50.01% germinated. Both seedling emergence and germination probability neither differed among the bird species nor in comparison to manually depulped seeds. The bird species and manually depulped did also not differ with whole fruit. Further, seedling emergence and germination probability were both unaffected by fruit weight. However, the germination probability of all treatments increased similarly with increasing number of weeks after planting. Overall, these results suggest that seed depulping, neither by gut treatment nor manually improved germination of seeds, irrespective of their fruit weights. Thus, the major contribution of frugivores to forest regeneration may be more confined in transporting seeds away from the mother plant than in germination enhancement *per se*.

Introduction

Frugivorous vertebrates play a key role in the dispersal of seeds for many fleshy fruiting plants across global forest ecosystems (Jansen 1981, Stiles 2000, Farwig & Berens 2012). Approximately 90% of tropical and up to 50% of temperate plant species largely depend on frugivorous vertebrates for dispersing their propagules (Howe & Smallwood 1982). Avian frugivores in particular, have been shown to be among the most important of these dispersers, capable of transporting seed far away from the vicinity of mother plants (Howe & Smallwood 1982). This enables seeds and seedlings to escape disproportionate mortality (Howe 1986) and allows plants to colonize new and degraded habitats (Howe & Smallwood 1982). In this case, seed dispersal plays a pivotal role in shaping the ecology, evolution and dynamics of global forest ecosystems (Traveset 1998).

When studying plant-frugivore interactions, one has to consider not only the quantitative, but also the qualitative aspects in these mutualisms. This implies widening the scope from merely assessing the number of dispersed seeds, to establishing the probability that dispersed seeds will germinate after passage through the guts of different frugivorous animals (Howe & Smallwood 1982, Schupp 1993). Whether or not the treatment of seeds in the digestive tracts of animals affects germination has been a subject of much research. For example, studies that found no effect of gut treatment on germination probability (Howe & Vande Kerckhove 1981, Barnea et al 1992, Clout & Tilley 1992) are almost as frequent as those in which a significantly positive (e.g. Barnea et al. 1990, 1991, Clergeau 1992, Murray et al. 1994) or negative (e.g. Valido & Nogalas 1994, Nogales et al. 1995, Crossland & Kloet 1996) effect was found. The positive effects of gut treatment on germination arise from the assumption that pulp removal in the digestive tracts of frugivores eliminates germination inhibitors present in the pulp (Traveset 1998). Pulp removal can also reduce the susceptibility of seeds to microbial and fungal infections (Jackson et al. 1988). Moreover, some studies have suggested that frugivores can increase the permeability of seeds to both water and gases by modifying their seed coats (Izhaki & Safriel 1990, Barnea et al. 1991, Clergeau 1992), consequently enhancing germination (Traveset 1998). However, frugivores can also inhibit germination (e.g. Valido & Nogalas 1994, Nogales et al. 1995, Crossland & Kloet 1996), by the chemical and mechanical abrading of seed coats in their digestive tracts or by traces of faeces on the excreted seeds. This may consequently attract microbial and fungal infections on the seeds, hence the negative effects of gut treatment on germination (Crossland & Kloet 1996, Traveset 1998).

In addition, the survival of seeds passing through the gut has been shown to vary with fruit or seed size (Traveset & Verdú 2002). Fruit or seed size can affect the time that seeds are retained in the digestive tracts of animals, with the larger and heavier seeds reported to have quicker retention time than the smaller and lighter seeds (Garber 1986, Gardener et al. 1993). These variations in gut retention time (Clergeau 1992, Izhaki et al. 1995) and in the overall effects of gut treatment on germination patterns suggest that the digestive systems of frugivorous animal species differs greatly, both morphologically and physiologically (Schupp 1993, Traveset 1998). Therefore, examining different species of frugivores might reveal the traits that affect germination. In particular, it remains important to establish whether variations occur among different species of animals consuming the same fruits and if such variations could be attributed to the differences in animal species or plant traits such as fruit weight.

For this reason, we studied the germination pattern of sixteen woody plant species after passage through the digestive tracts of four generalist avian frugivore species in KwaZulu Natal, South Africa. Woody plant species mirrored the range of available fruit weights while birds varied in mean body mass, ranging from 55 to 310 grams. Taking into account the mean weights of the fruits, we examined (i) seedling emergence and (ii) germination probability of each plant species following gut treatment by each of the four frugivores species. We expected (a) different species of frugivores to affect both the seedling emergence and germination probability differently based on the assumption that their gut treatment effects differ, (b) gut treatment to generally enhance germination due to both fruit pulp removal and the abrasive effect within their digestive tracts (c) fruit or seed weight to have a positive effect on both seedling emergence and germination probability given that larger seeds have quicker retention times and thereby less susceptible to abrading than smaller seeds.

Material and methods

Woody fruiting plant species

Between 2010 and 2011, fruits from different native and non-native woody fruiting plant species (n = 16) that interacted with native avian frugivores (Jordaan et al. 2011, Chama et al. in prep) were collected in the field. Fruits from the native plant species (n = 14) were collected from Vernon Crookes Nature Reserve (VNCR) while those from non-native (n = 2) were collected in Pietermaritzburg. Fruits were collected during the fruiting season of plant species (Appendix d). After collection, fruits were stored in clean plastic jars in a refrigerator and used within 48hrs of

collection. The fruit weight of each plant species was recorded prior to the onset of the experiment, i.e. as the mean weight of 20 fruits or seeds per plant species.

Frugivore species

Four of the five captive and predominantly generalist species of native frugivorous birds at the University of KwaZulu Natal (UKZN) in Pietermaritzburg, South Africa, were used in this experiment. These included (i) Spectacled Mousebird (*Colius striatus*; 55g; n = 5) (ii) Red-winged Starling (*Onychognathus morio*; 140g; n = 4), (iii) Purple-crested Turaco (*Tauraco porphyreolophus*; 285g; n = 2) and (iv) Knysna Turaco (*Tauraco corythiix*; 310g; n = 4). The frugivores are housed in outside flight aviaries (1 x 2.12 x 2.66 m) either in pairs or groups depending on their body masses. Here, they are fed a maintenance diet comprising mixtures of (i) fruit (apples, bananas, carrots, oranges, papaya, and pears) and (ii) Aviplus Softbill/ Mynah crumble and pellets on a daily basis. Water is also provided *ad libitum*.

Feeding experiment

Birds were relocated from the outside aviaries into a separate room. They were each placed in separate cages for an adaptation period of two days, during which they were fed a maintenance diet similar to what they were fed in the outside aviaries. The temperature in the room was constantly maintained at $25 \pm 1^{\circ}\text{C}$. On the day of the experiment, birds were provided only with whole fruit collected from the sixteen plant species (Appendix d). At least 30 fruits were fed to each individual bird. Feeding experiments started at 06:00am. The length of the experiment for each bird species varied between three and 48 hrs, largely depending on their capacity to consume and defecate the minimum total of at least 20 seeds per plant species. As it was not always possible for some individuals from each of the four bird species to consume and defecate 20 seeds, we pooled the seeds defecated by all individuals of the same species in order to reach this minimum sample size. If it was not possible to collect this number of seeds on the first day, the experiment was repeated on the following day until the seeds defecated by all individuals of one bird species reached at least 20. Defecated seeds (hence forth referred to as gut treated seeds) were collected from the trays placed under each cage every three to six hrs and in the morning after the last experimental day.

Germination experiment

Gut-treated seeds were stored at ambient temperature until sown within one to three days after collection. Seeds for each plant species were sown in six different treatments, i.e. –one treatment for each bird species (gut treatment), manually depulped and whole fruit. Manually depulped consisted of seed whose pulp was manually or hand stripped and washed with water prior to the experiment to reduce or eliminate potential inhibition effects on the germination of the seeds (Cipollini and Levey 1997), while whole fruit (i.e. with intact pulp) served as control. For each treatment and each species, similar quantities of seeds ($n \geq 20$) were planted together in one tray. Seeds were sown at regular intervals and covered in trays (265 x 180 x 75mm) containing sterilized potting soil at a depth of 0.5 cm. Seeds of all treatments for each plant species were sown simultaneously and under the same conditions to allow for comparison of seedling emergence and survivorship. The trays were placed in the greenhouse at UKZN where they were watered with the aid of automated over-head sprinklers on a daily basis. The positions of these trays were randomly interchanged between the treatments once every week. When monitoring germination, we firstly recorded the seedling emergence (i.e. when the cotyledon or embryonic-first-leaf shoot was first seen emerging from the soil) and then the germination probability at the end of the experiment (i.e. when no further germination could take place after the twelfth month). Two of the sixteen plant species (*Croton sylvaticus* and *Sapium ellipticum*) had between two and three seeds per fruit and/or fruit endocarp. Under such circumstances, the fruit and /or endocarp was considered a seed and only one germination event from each fruit and/ or endocarp was recorded (Bradford 2010). Germination was recorded once every week in the first three months, after which it was recorded only once every four weeks up to the twelfth month. The total number of weeks, i.e. time from planting to final or maximum possible germination probability, was recorded and used as a covariate when analysing the effects of seed treatment on germination probability.

Statistical analysis

We tested whether seed treatment had an effect on (i) seedling emergence and (ii) germination probability (data arcsine-square-root transformed) with linear mixed effects models. Planned contrasts were incorporated in each analysis to compare the effects of different treatments on germination. In the first analysis, we tested if gut treatment affected seedling emergence and the proportion of germination differently from manual depulping. To do so, we used planned contrasts

between each of the four bird species versus manually depulped seeds. These contrasts also allowed us to indirectly test if the four bird species affected germination differently from each other. In the next step, we tested whether seedling emergence and germination probability differed significantly between depulped vs. whole fruit using mixed effect models with cf-tests. To do so, we aggregated the germination records for both gut treatment and manually depulped seed (henceforth collectively referred to as “depulped” seeds) and calculated the mean seedling emergence and germination probability. We then used seedling emergence as a response against fruit weight and treatment (i.e. depulped vs. whole fruit) as fixed effects, while treatment was nested within plant species. Germination probability as a response variable was tested against fruit weight, treatment and week as fixed effects. In this analysis, week was nested within treatment, and treatment nested within plant species. All statistical analyses were performed in R (version 2.12.0; R Development Core Team 2006).

Results

Of 7,385 fruits fed to the birds, 57.21% were consumed, of which 80.28% were defecated and used in the germination experiments. Across treatments, a total of 2,796 seeds were planted, i.e. 466 per treatment. The weights of fruits used in the experiment ranged from 0.013 (*Trema orientalis*) to 5.35g (*Harpephyllum caffrum*; Appendix d).

Seedling emergence

Overall, seedling emergence ranged from 14 to 331 days (129 ± 119 ; i.e. mean \pm SD if not otherwise noted) and did not differ between the naturally and manually depulped seeds ($p > 0.05$), indirectly also suggesting that there was no difference among bird species. Seedling emergence did also not differ significantly between depulped seeds and whole fruits (Table 1, Fig. 1a), albeit depulped seeds emerged slightly earlier (101 ± 112 days) than whole fruit (108 ± 121 days). Moreover, seedling emergence remained unaffected by fruit weight (Table 1, Fig.1b).

Germination probability

Of the 2,795 seeds planted, the total germination probability was 50.01%, split into $18.32 \pm 1.24\%$ for naturally depulped, 17.91% for manually depulped and 11.82% for whole fruit. Germination probability did not differ between the naturally and manually depulped seeds ($p > 0.05$), indirectly

also suggesting that there was no difference among bird species. There was also no significant difference between the mean germination probability for depulped seed (i.e. naturally and manually depulped; $34 \pm 40\%$) and whole fruit ($23 \pm 33\%$; Table 1, Fig1c). Overall, germination probability remained unaffected by fruit weight (Table 1, Fig. 1d), but increased with increasing number of weeks after planting (Table 1, Fig.2).

Table 1. Results of mixed effects models showing estimated parameters, standard errors (SE), z and p values of fixed effects. Significant p-values are highlighted in bold. Note: depulped = collective mean of both gut treatment and manually depulped seeds.

Fixed effects	Seedling emergence				Germination probability			
	Estimate	SE	Z value	P	Estimate	SE	Z value	P
Treatment (depulped vs. whole fruit)	-3.37	9.20	-0.37	0.714	0.02	0.14	0.18	0.858
Fruit weight	-13.14	28.22	-0.47	0.642	-0.13	0.25	-0.50	0.620
Week	-	-	-	-	0.01	0.00	3.47	<0.01
Fruit weight: Treatment	-3.63	16.47	-0.22	0.825	0.11	0.24	0.46	0.646
Fruit weight: Treatment	-	-	-	-	-0.00	0.00	-0.61	0.545
Treatment: week	-	-	-	-	0.00	0.00	0.20	0.844

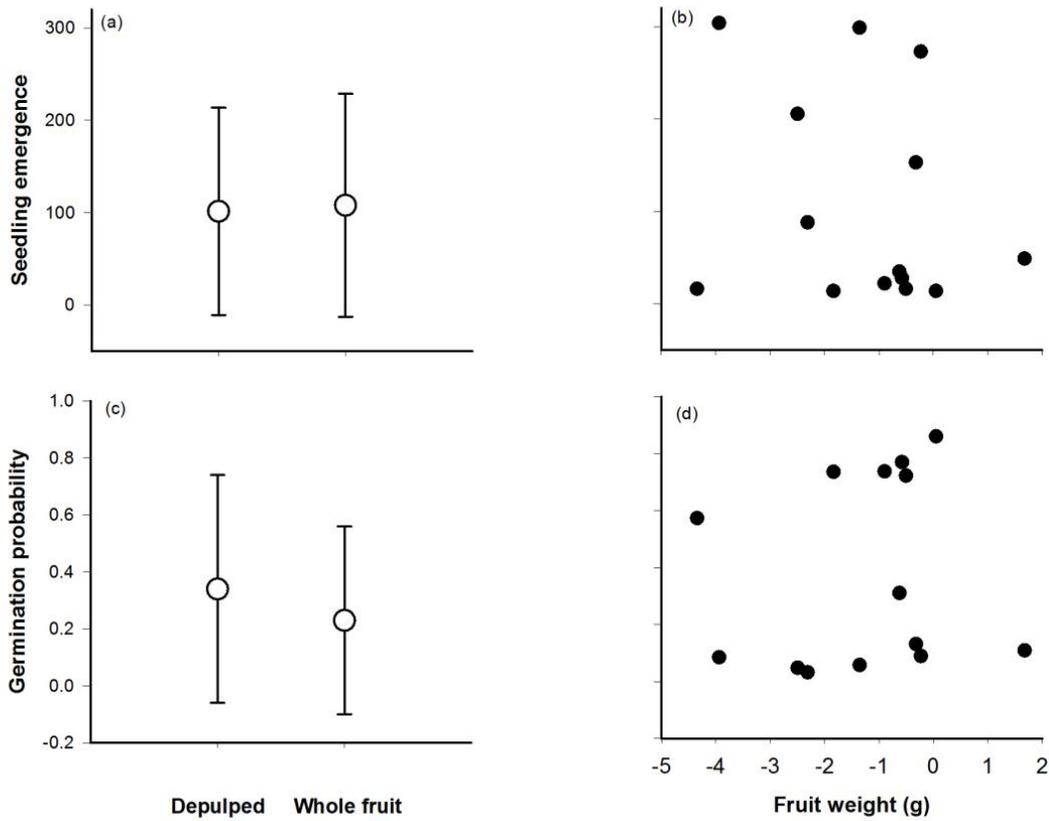


Fig.1. Shown are the means of (i) seedling emergence in relation to (a) treatment and (b) fruit weight and (ii) germination probability in relation to (c) treatment and (d) fruit weight. Note: treatment = means \pm standard deviations of depulped seeds and whole fruit

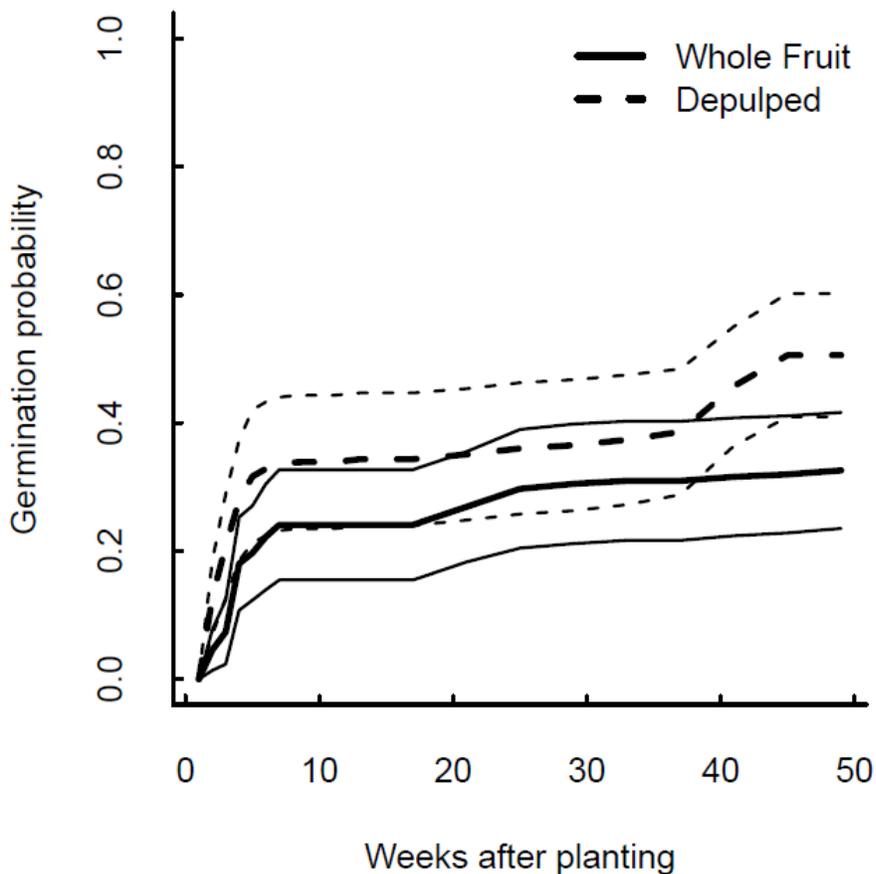


Fig 2. Least square means \pm standard errors of germination probability for depulped seeds and whole fruits in relation to the number of weeks after planting

Discussion

Our study showed that gut treatment by any of the four frugivore species did not affect germination as both mean seedling emergence and germination probability remained similar across all treatments. Both seedling emergence and germination probability were unaffected by fruit weight. However, germination probability increased similarly across all treatments with increasing number of weeks after planting, suggesting that seed depulping, neither by gut treatment nor manually enhanced germination.

Effects of gut treatment on seedling emergence and germination probability

While gut treatment has been shown to enhance germination by numerous previous studies (e.g. Barnea et al. 1990, 1991, Murray et al. 1994, Traveset & Verdú 2002), the frugivores in our study did not affect germination, neither in terms of seedling emergence nor in terms of germination probability. Moreover, the mean germination probability of depulped seeds increased similarly with that of whole fruits over the weeks (Fig. 2). Our results are consistent with previous studies that found no significant effect of seed ingestion by avian frugivores on germination (e.g. Traveset & Willson 1997, Wilson & Downs 2011). On the one hand, these findings suggest that gut treatment does not necessarily improve germination irrespective of the species of the dispersers involved. On the other hand, this could suggest that the avian frugivores used in the study are generally not effective enough to eliminate germination inhibitors and dormancy mechanisms enshrined in these particular seeds. Alternatively, seeds from these plant species may not necessarily depend on gut treatment to enhance their germination. These assumptions are supported by evidence from a recent study by Wilson and Downs (2011) who found no effect of gut treatment by the Knysna Turaco (*Tauraco corythiix*) on the germination of seeds from several plant species, four of which were also tested in this study. In this case, the germination patterns of the studied seeds may probably be improved if ingested by dispersers that are different from these frugivores (Traveset 1998). These findings may also support previous reports suggesting that the effects of gut treatment on germination are not universal largely due to several uncontrolled factors or traits (e.g. seed texture, coat thickness, sculpture, etc.) intrinsic to the plant and its fruit consumers (Barnea et al. 1991, Traveset & Wilson 1997, Jordano 2000). Overall our results suggest that the positive effect of frugivorous birds is more on transportation, than improving the germination of seeds *per se*. Thus, frugivores help to promote plant colonisation of new habitats

and escape from disproportional post-dispersal mortality in the vicinity of parent plants (Howe 1986).

Effect of fruit weight on seedling emergence and germination probability

In contrast to our hypothesis, both seedling emergence and germination probability remained unaffected by fruit weight. Our results are consistent with Traveset (1998) who found that seeds of different sizes have similar germination response to gut treatment. However, these results contrast those of Traveset & Verdú (2002) who found a positive effect of seed size on the germination of gut treated seed, with larger seeds reported to have high germination probabilities than smaller seeds. Larger seeds have shorter gut retention times than larger seeds (Garber 1986, Gardener et al. 1993). Thus, the seed coats of larger seeds are less likely to be abraded than the smaller seeds, thereby the positive effect of seed size on germination probability of gut treated seeds (Garber 1986, Gardener et al. 1993, Traveset & Verdú 2002). Nonetheless, our results suggest that seeds of different fruit weights are similarly affected in the digestive tracts of frugivores, irrespective of the reported variations in their gut retention times (Garber 1986, Gardener et al. 1993).

Conclusions

Our study showed no difference in germination patterns across all treatments, suggesting that gut treatment by the four frugivore species did not improve germination of the studied seeds, irrespective of their fruit weights. In this case, the overall contribution of frugivores to forest regeneration is more on transportation than in improving germination of seeds. The advantages of transporting seeds away from the mother plant are well documented (e.g. Howe & Smallwood 1982, Howe 1986), thereby stretching the importance of conserving the frugivorous communities for the sustenance of plant diversity in tropical and sub-tropical forest landscapes. As we only used a subset of frugivore species in this study, increasing the number of species and experiment time could highlight more general effects of gut treatment on natural forest regeneration.

Acknowledgments

We thank the Ezemvelo KZN Wildlife for the permission to collect fruits from various plants species in Vernon Crooks Nature Reserve. Special thanks are also due to C. Downs, M. Brown

and A. Young of the University of KwaZulu Natal (UKZN) for the administrative and technical support, particularly the permission to use the birds and facilities at UKZN for undertaking our experiments. Additional administrative support was provided by F. Voigt, P. Pillay and C. Zachariades. We deeply extend our gratitude to T. Ngidi for assisting with fruit collection in the field and to Moses Zungu for his assistance in monitoring the germination experiments in the greenhouse at UKZN. We thank J. Albrecht for his contribution to the statistical analysis. The study was funded by the Robert Bosch Stiftung.

References

- ABUL-FATIH, H. A. & BAZZAZ, F. A. 1979. The biology of *Ambrosia trifida* L. I. The influence of species removal on the organization of the plant community. *New Phytologist* 83: 813.
- BARNEA A., YOM-TOV Y. & FRIEDMAN J. 1992. Effect of frugivorous birds on seed dispersal and germination of multi seeded fruits. *Acta Oecologica* 13: 209–19.
- BARNEA, A., YOM-TOV, Y. & FRIEDMAN, J. 1990. Differential germination of two closely related species of *Solanum* in response to bird ingestion. *Oikos* 57: 222–228.
- BARNEA, A., YOM-TOV, Y. & FRIEDMAN, J. 1991. Does ingestion by birds affect seed germination? *Functional Ecology* 5: 394–402.
- FARWIG, N. & BERENS, D. G. 2012. Imagine a world without seed dispersers: A review of threats, consequences and future directions. *Basic and Applied Ecology* 13 (2): 109–115.
- BOON, R. 2010 *Pooley's trees of Eastern South Africa: a complete guide*. Durban: Flora and Fauna Publications Trust.
- BRADFORD, M.G. & WESTCOTT, D.A. 2010. Consequences of southern cassowary (*Casuarius casuarius*, L.) gut passage and deposition pattern on the germination of rainforest seeds. *Austral Ecology* 35: 325–333.
- BUSTAMANTE, R.O., GREZ, A.A., SIMONETTI, J.A., VÁSQUEZ, R.A. & WALKOWIAK, A.M. 1993. Antagonistic effects of frugivores on seeds of *Cryptocarya alba* (Mol.) Looser (Lauraceae): consequences on seedling recruitment. *Acta Oecologica* 14: 739–745.
- CIPOLLINI, M.L. & LEVEY, D.J. 1997. Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *American Naturalist* 150: 346–372.
- CLERGEAU, P. 1992. The effect of birds on seed germination of fleshy-fruited plants in temperate farmland. *Acta Oecologica* 13: 679–686.
- CLOUT, M.N. & TILLEY, J.A.V. 1992. Germination of miro (*Prumnopitys ferruginea*) seeds after consumption by New Zealand pigeons (*Hemiphaga novaeseelandiae*). *New Zealand Journal of Botany* 30: 25–28.
- CROSSLAND, D.R. & VANDER KLOET, S.P. 1996. Berry consumption by the American Robin, *Turdus migratorius*, and the subsequent effect on seed germination, plant vigour, and dispersal of the lowbush blueberry, *Vaccinium angustifolium*. *The Canadian Field Naturalist* 110: 303–309.
- GARBER, P.A. 1986. The ecology of seed dispersal in two species of callitrichid primates (*Saguinus mystax* and *Saguinus fuscicollis*). *American Journal of Primatology* 10: 155–170.

- GARDENER, C.J., MCIVOR, J.G. & JANZEN, A. 1993. Passage of legume and grass seeds through the digestive tract of cattle and their survival in faeces. *Journal of Applied Ecology* 30: 63–74.
- HOWE, H.F. & SMALLWOOD, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.
- HOWE, H.F. & VANDE KERCKHOVE, G.A. 1979. Fecundity and seed dispersal of a tropical tree. *Ecology* 60: 180–189.
- HOWE, H.F. 1986. Seed dispersal by fruit-eating birds and mammals. *Seed Dispersal* (ed. D.R. Murray), Academic Press, New York: 123–190.
- IZHAKI, I. & SAFRIEL, U.N. 1990. The effect of some Mediterranean scrubland frugivores upon germination patterns. *Journal of Ecology* 78: 56–65.
- IZHAKI, I., KORINE, C. & ARAD, Z. 1995. The effect of bat (*Rousettus aegyptiacus*) dispersal on seed germination in eastern Mediterranean habitats. *Oecologia* 101, 335–342.
- JACKSON, P.S.W., CRONK, Q.C.B. & PARNELL, J.A.N. 1988. Notes on the regeneration of two rare Mauritian endemic trees. *Tropical Ecology* 78: 56–65.
- JANSEN, D. H. 1981. *Enterolobium cyclocarpum* seed passage rates in cows and horses, Costa Rican Pleistocene seed dispersal agents. *Ecology* 62: 593–601.
- JORDANO, P. (2000) Fruits and frugivory. *Seeds: The Ecology of Regeneration in Plant Communities* (ed. M.Fenner), 125–165. CABI, Wallingford, UK.
- LISCI, M. & PACINI, E. 1994. Germination ecology of drupelets of the fig (*Ficus carica*). *Botanical Journal of the Linnean Society* 114: 133–146.
- MILLER, M. F. 1995. Acacia seed survival, seed germination and seedling growth following pod consumption by large herbivores and seed chewing by rodents. *Africa Journal of Ecology* 33: 194–210.
- MURRAY, K.G., RUSSELL, S., PICONE, C.M., WINNETT-MURRAY, K., SHERWOOD, W. & KUHLMANN, M.L. 1994. Fruit laxatives and seed passage rates in frugivores: consequences for plant reproductive success. *Ecology* 75: 989–994.
- NOGALES, M., VALIDO, A. & MEDINA, F.M. 1995. Frugivory by *Plocama pendula* (Rubiaceae) by the rabbit (*Oryctolagus cuniculus*) in xerophytic zones of Tenerife (Canary Islands). *Acta Oecologica* 16: 585–591.
- ROSS, M.A., HARPER, J.L. 1972. Occupation of biological space during seedling establishment. *Journal of Ecology* 60:77 – 88 .

- SCHUPP, E.W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetation* 107/108: 15–29.
- STILES, E.W. 2000. Animals as seed dispersers. *Seeds: The Ecology of Regeneration in Plant Communities* (ed. M.Fenner), 111–124. CAB International, Wallingford, UK.
- THE R DEVELOPMENT CORE TEAM. 2006. R: A language and environment for statistical computing. Vienna, Austria. (<http://www.R-project.org>).
- TRAVESET, A. 1998. Effect of seed passage through vertebrate frugivores' gut on germination: a review. *Perspective in Plant Ecology, Evolution and Systematics* 1/2: 151–90.
- TRAVESET, A. & VERDÚ, M. 2002. A meta-analysis of the effect of gut treatment on seed germination. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D.J.Levey, W.R.Silva & M.Galetti), 339–350. CABI Publishing, Wallingford, UK/New York, USA.
- TRAVESET, A. & WILLSON, M.F. 1997. Effects of birds and bears on seed germination in the temperate rainforests of Southeast Alaska. *Oikos* 80: 89–95.
- VALIDO, A. & NOGALES, M. 1994. Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xerix habitat of the Canary Islands. *Oikos* 70: 403–411.
- VAN DER PIJL, L. 1982. *Principles of Dispersal in Higher Plants*. Springer Verlag, Berlin.
- WILSON, A.L. & DOWNS, C.T. 2011. Knysna Turacos (*Tauraco corythaix*) do not improve seed germination of ingested fruit of some indigenous South African tree species. *South African Journal of Botany* 78: 55 – 62.
- WUNDERLE, J.M.JR. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest ecology and management* 99: 223 – 235.

Chapter 5: General conclusions

Summary of methods and key findings

In this thesis, I studied the consequences of forest patch quality and matrix habitats for plant-frugivore mutualistic network structures and functional diversity of frugivore communities within these networks, in a human dominated sub-tropical landscapes of eastern South Africa. In addition, I also studied if the passage of seeds through the digestive tracts of frugivores enhances germination.

In the first approach (chapter 2) I focused on plant-frugivore networks across forest patches surrounded by dissimilar matrix habitats in and around Vernon Crookes Nature Reserve in South Africa. I addressed the question whether changes in the quality of forest patches or surrounding matrix habitat affect the structure and stability of plant-frugivore mutualistic networks. I compared the network structures in a large scarp forest (NatFor) surrounded by a natural forest matrix with those in two small natural forest patches, one surrounded by natural grassland (NatFra) and the other by sugarcane agriculture (AgrFra). Forest patch quality was measured by assessing the fruit abundance, fruiting plant richness and canopy cover in each forest patch. I then recorded the interaction frequencies of all fleshy fruiting plant species with avian frugivore species in each forest patch. Using these data, I compiled quantitative interaction matrices and constructed plant-frugivore interaction networks. Network structures were compared among forest patches in relation to both forest patch quality and matrix habitat. The results show that networks across forest patches were all similarly characterized by a high degree of redundancy in the plant-frugivore interactions. Overall, none of the network parameters varied with matrix habitat, but were strongly influenced by forest patch quality. These findings suggest that the structure and stability of plant-frugivore interaction networks is rather determined by local forest patch quality than by surrounding matrix habitat.

In the second approach (chapter 3), I used the same data as in chapter 2 and investigated the consequences of forest patch quality and matrix habitat on different measures of functional diversity of the frugivore communities within the plant-frugivore networks. I recorded data on three functional traits related to seed dispersal, namely body mass, gape width and degree of frugivory for each frugivore species observed in the networks. From these data, I calculated three indices of functional diversity, i.e. functional richness, functional evenness and functional dispersion. I then tested the effect of forest patch quality and matrix habitat on these measures of functional diversity as well as on species richness of frugivore communities. Results showed that functional diversity was rather weakly affected by matrix habitat, but by forest patch quality. The

mean body mass increased with increasing canopy cover. Further, functional dispersion increased with increasing fruiting plant species richness and was higher in AgrFra than in NatFra and NatFor. Canopy cover had a positive effect on species richness, functional richness and functional dispersion. These results suggest that canopy cover is the most important determinant of functional diversity, as both the functional richness and the specialization of frugivores increased in sites with high canopy cover.

In the third approach (chapter 4), I tested the effects of seed ingestion by frugivores on germination. I addressed the question whether the passage of seeds through the digestive tracts of frugivores during transportation affects the seedling emergence and germination probability. Moreover, I also determined whether the effect of gut passage on germination was influenced by the weight of the fruits consumed. To do this, I collected fruits from sixteen woody plant species, mostly from Vernon Crookes Nature Reserve. I weighed and fed the fruits to four different captive avian frugivore species at the University Of KwaZulu Natal in South Africa. Seeds defecated by each species were collected and planted. Their seedling emergence and germination probabilities were recorded and compared with those of manually depulped and whole fruits planted at the same time under similar conditions. Results show that neither seedling emergence nor germination probability differed among the birds. Further, seedling emergence and germination probability of gut treated seeds were also similar to both manually depulped and whole fruits, suggesting that seed depulping, neither by gut treatment nor manually, did not affect germination. Fruit weight had no effect on germination either. Broadly, these results suggest that the effect of frugivorous birds on natural forest regeneration is more on seed transportation, than improving the germination.

Implications for conservation

The results obtained in this thesis have important implications for conservation of biodiversity, especially in tropical and sub-tropical forest landscapes. Firstly, the structure of seed dispersal networks in my study area seemed to be very robust because of high forest patch quality and a heterogeneous landscape. In this case, these networks are less likely to be disrupted by fragmentation, as their species might have various reassembly pathways. The high levels of redundancy observed in the plant-frugivore interactions suggest that plants in the networks profit from a broad spectrum of seed dispersers, thereby maximizing the opportunities for recruitment of

their offspring in diverse habitats. Secondly, the functional diversity of frugivores in the studied networks also turned out to be similarly high due to forest patch quality. Canopy cover was particularly of major importance as it enhanced both richness and dispersion of functional roles among frugivores. A high functional diversity within frugivore communities may impact positively on the functionality of seed dispersal processes, as it enhances both the quality and quantity of dispersed seeds. Finally, the passage of seeds through the digestive tracts of frugivores did neither improve nor reduce the germination of seeds from sixteen plant species. Therefore, the major contribution of frugivores to plant recruitment seems to be more in transportation of seeds away from the mother plant, than in improving germination per se.

Overall these findings, particularly from the first two studies suggest that forest patch quality was an important driver of network stability and functional diversity among frugivorous communities. This was largely due to a highly heterogeneous landscape, suggesting that matrix habitats are also of conservation importance. These findings could be partly explained by the fact that frugivorous birds have a highly flexible and mobile foraging behaviour and can track food resources over long distances in response to spatiotemporal availability. In this case, their movements may not be limited by intervening matrix habitats, resulting in similar characteristics of seed dispersal communities across different forest patches. This is particularly also supported by the relatively shorter distances separating the forest patches in our study area, thereby allowing for inter-patch movement by frugivores species of various functional abilities (Neuschulz et al. in prep). This is consistent with recent findings by Neuschulz et al (in prep) suggesting a high cross-matrix movement activity by diverse avian frugivorous species within our study area.

In sum, these findings suggests that seed dispersal processes may be resilient to the matrix effects in heterogeneous fragmented forest landscapes if their mutualistic interactions involve highly flexible and mobile partners and if a sufficient size and quality of remaining forest patch is attractive. Further, these findings suggest that remnant forest patches embedded in agricultural matrix can also provide avenues for sustaining key ecological processes. In this case, they provide alternative habitats outside protected areas and may also serve as natural corridors linking protected areas. Thus, conservation efforts should shift from the traditional strategies centred only on large forest areas, to also include the protection of biodiversity in small forest fragments. This thesis has also experimentally demonstrated that avian frugivores are legitimate dispersers. However, their survival and indeed that of seed dispersal processes in particular, will largely depend on maintaining habitats of sound quality. A further reduction in the sizes of these forest patches due

to an expansion in matrix habitats could have negative implications on patch quality and thus seed dispersal processes. Conservation planners should therefore strive to promote management strategies that will not only maintain patch quality, but also protect these forest patches from further fragmentation.

Future research prospects

As scarp forests have a history of isolation and fragmentation during the last glacial maximum (Eeley et al. 1999, cited in chapter 3), it is likely that the avian frugivore communities in this region have potentially become adaptive to patchy environments (Neuschulz et al., in prep.), thus shielding the potential effects of matrix habitats. Therefore, future research could benefit from undertaking similar studies also in other landscapes to get a better understanding of how matrix habitats and forest modification in general affects plant-frugivore interactions. Moreover, it would also be enriching to highlight whether the observed seed dispersal network structures and functional diversity of disperser communities would remain similar if the distances between the study sites were to increase. Further, given the current threats of increased human activities in subtropical forest landscapes (references in the general introduction), it would be enlightening to also study other disperser groups and their traits and effects on germination. Such studies will benefit from looking in more detail from the plant side, especially taking various traits (e.g. seed texture, coat thickness, nutrients, chemical content, etc.) into consideration to really evaluate the role of frugivores for plant regeneration. Monitoring the seedling growth and survival beyond the mere recording of seedling emergence and germination probability will be even more important in the context of evaluating natural forest regeneration processes.

Deutsche Zusammenfassung

Zusammenfassung

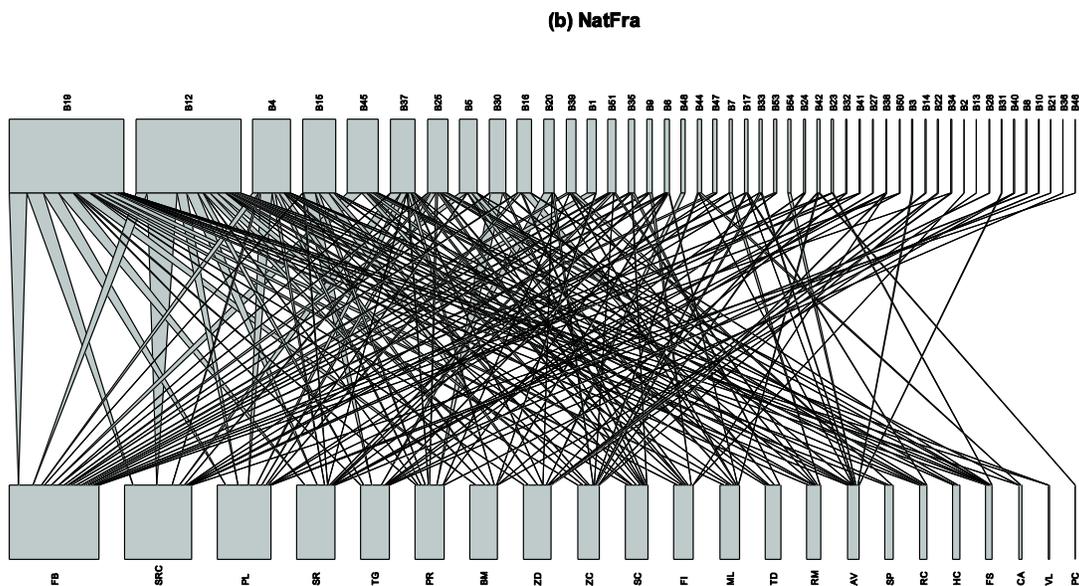
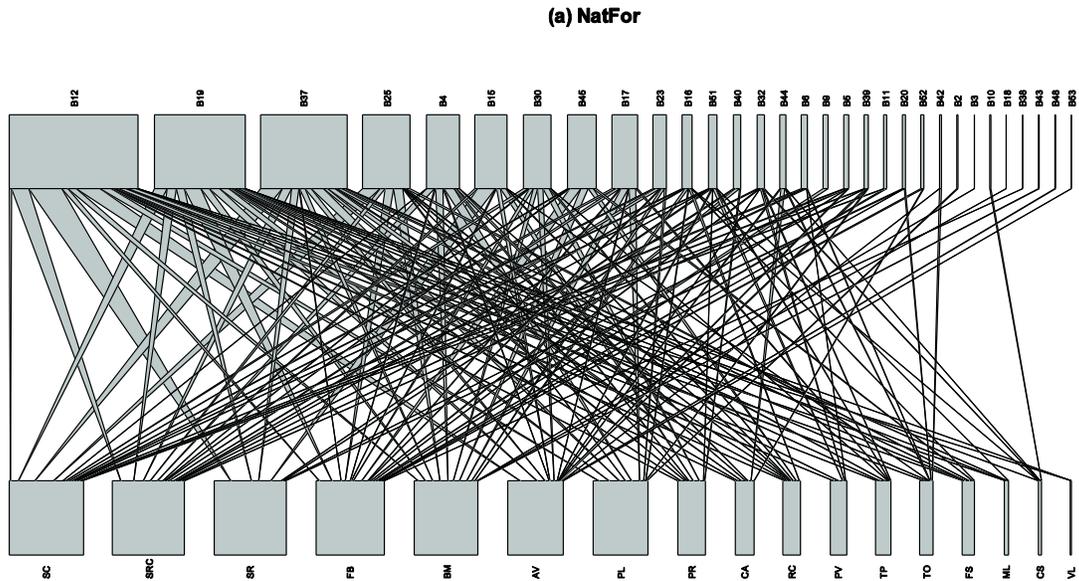
Die Samenausbreitung durch Tiere ist ein bedeutsamer ökologischer Prozess. Dies ist besonders in den Tropen und Subtropen der Fall, wo bis zu 90 % der Pflanzenarten fleischige Früchte haben und auf den Transport ihrer Samen in geeignete Habitate angewiesen sind. Frugivore Vögel gehören zu den wichtigsten samenausbreitenden Vertebraten und tragen damit entscheidend zur natürlichen Waldregeneration bei. Veränderungen in der Habitatqualität von Waldfragmenten sowie der Struktur der sie umgebenden Matrix haben Konsequenzen für Samenausbreitungsinteraktionen. Des Weiteren können Veränderungen in Waldhabitaten die funktionelle Diversität von Samenausbreitergemeinschaften beeinflussen und somit weit reichende Konsequenzen für die natürlichen Regenerationsprozesse vieler Pflanzenarten nach sich ziehen. Um die Effekte von Habitatqualität und umgebender Matrix von Waldfragmenten auf den Prozess und die Funktion von Samenausbreitung zu untersuchen, habe ich (i) die Struktur von Pflanze-Frugivoren-Netzwerken und (ii) die funktionelle Diversität der Frugivorengemeinschaften innerhalb dieser Netzwerke zwischen Waldfragmenten verglichen, die von unterschiedlichen Matrixhabitaten umgeben waren. Die Studien fanden in der Umgebung und innerhalb des Vernon Crookes Nature Reserves in Südafrika statt. Zusätzlich prüfte ich in einem experimentellen Ansatz die Legitimität frugivorer Vögel als Samenausbreiter, indem ich den Einfluss der Aufnahme und Verdauung von Samen durch frugivore Vögel auf die Keimung verschiedener Pflanzenarten untersuchte. In der Pflanze-Frugivoren Netzwerkstudie verglich ich die Netzwerkstruktur in einem großen, von Waldmatrix umgebenen Schluchtwaldgebiet mit der von zwei kleinen natürlichen Waldtypen, der eine umgeben von natürlichem Grasland, der andere umgeben von Zuckerrohrfeldern. Dabei setzte ich die Netzwerkstruktur in Beziehung zur Habitatqualität der Waldfragmente sowie zum umgebenden Matrixhabitat. Insgesamt beobachtete ich 54 fruchtfressende Vogelarten an 31 Pflanzenarten mit fleischigen Früchten. Die Netzwerkstruktur unterschied sich nicht zwischen den Waldtypen mit unterschiedlichen Matrixhabitaten. Die Netzwerke waren in ihrer Robustheit vergleichbar und stark durch die Habitatqualität der Waldfragmente beeinflusst. Diese Ergebnisse deuteten darauf hin, dass die Struktur und Stabilität von Pflanze-Frugivoren Interaktionsnetzwerken stärker durch die lokale Habitatqualität beeinflusst wurde als durch die umgebende Matrix der Waldfragmente. In der Studie zur funktionellen Diversität der Frugivorengemeinschaften innerhalb der Netzwerke stellte ich Daten zu drei funktionellen Eigenschaften der Vögel zusammen, die in Zusammenhang mit Samenausbreitung stehen, und zwar zur Körpergröße, Schnabelbreite und dem Grad der Abhängigkeit von Früchten

als Nahrungsquelle. Daraufhin testete ich den Effekt der Habitatqualität der Waldfragmente und des umgebenden Matrixhabitats auf drei verschiedene Maße funktioneller Diversität sowie auf den Artenreichtum der Frugivorengemeinschaften. Die Ergebnisse ließen darauf schließen, dass alle Waldtypen eine vergleichbar hohe funktionelle Diversität der Samenausbreitergemeinschaften aufwiesen. Insgesamt waren die funktionelle Zusammensetzung und die funktionelle Diversität stärker durch die Habitatqualität der Waldfragmente beeinflusst als durch die umgebende Matrix. Zur Durchführung des Keimungsexperiments sammelte ich Früchte von sechzehn Pflanzenarten und verfütterte sie an vier frugivore Vogelarten. Ausgeschiedene Samen wurden eingepflanzt und der Zeitpunkt ihrer Keimung sowie ihre Keimungswahrscheinlichkeit zum Einen mit der Keimung ganzer Früchte und zum Anderen mit Samen verglichen, die manuell von Fruchtfleisch befreit worden waren. Die Ergebnisse zeigten weder Unterschiede im Zeitpunkt der Keimung sowie in der Keimungswahrscheinlichkeit zwischen den Vogelarten noch zwischen den unterschiedlichen Behandlungsmethoden. Diese Resultate ließen darauf schließen, dass ein positiver Effekt der Frugivoren auf die natürliche Waldregeneration eher in Bezug auf die Ausbreitung der Samen als in Bezug auf die Verbesserung der Keimung gegeben schien. Insgesamt zeigten die Ergebnisse der ersten beiden Studien, dass die Habitatqualität von Waldfragmenten ein wichtiger Treiber für die Stabilität von Pflanze-Frugivoren Netzwerken und die funktionelle Diversität von Frugivorengemeinschaften zu sein scheint. Bei gegebener hoher Habitatqualität können demnach Waldfragmente, die von unterschiedlichen Matrices umgeben sind, einen hohen Wert für den Naturschutz in heterogenen Waldlandschaften haben. Der Erhalt der im Experiment als legitime Samenausbreiter identifizierten Vogelarten hängt dabei vom Fortbestehen von Waldfragmenten ab, die durch eine hohe Habitatqualität und eine wenig einschränkende Matrix gekennzeichnet sind.

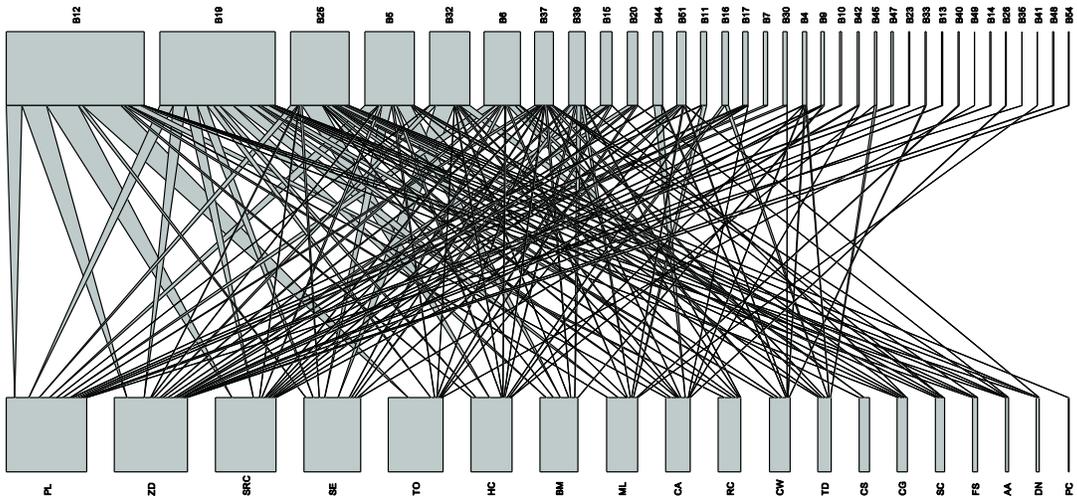
Appendices

Appendix a

Quantitative plant-frugivore networks in (a) large natural forest (NatFor), (b) natural forest fragments (NatFra) and (c) remnant fragments embedded in an agricultural matrix (AgrFra). For each network, the lower trophic level bars represent fruiting plant species while the upper trophic level bars represent frugivorous bird species. Each interaction between species is represented by a grey arrow; arrow width represents the frequency of interactions. See Appendices b and c for full names of species codes.



(c) AgrFra



Appendix b

Species codes, common and scientific names of fleshy-fruited plants in the networks across matrix habitats; nomenclature follows (Boon 2010).

Species code	Common name	Scientific name
AA	African False-currant	<i>Allophylus africanus</i>
AV	Tassel-berry	<i>Antidesma venosum</i>
BM	Mitzeeri Sweetberry	<i>Bridelia micrantha</i>
CA	White-stinkwood	<i>Celtis africana</i>
CG	Tinderwood	<i>Clerodendrum glabrum</i>
CS	Forest Croton	<i>Croton sylvaticus</i>
CW	Forest Corkwood	<i>Commiphora woodii</i>
DN	Acorn Jackal-berry	<i>Diospyros natalensis</i>
FB	Common Wild Fig	<i>Ficus burkei</i>
FI	Red-leaf Fig	<i>Ficus ingens</i>
FS	Brown-cluster Fig	<i>Ficus sur</i>
HC	Wild-plum	<i>Harpephyllum caffrum</i>
ML	False-assegai	<i>Measa lanceolata</i>
PC	Black Bird-berry	<i>Psychotria capensis</i>
PL	Red-beech	<i>Protorhus longifolia</i>
PR	Wild Date Plum	<i>Phoenix reclinata</i>
PV	Cheesewood	<i>Pittosporum viridiflorum</i>
RC	Quinine-tree	<i>Rauvolfia caffra</i>
RM	Cape-beech	<i>Rapanea melanophloeos</i>
SC	Waterberry	<i>Syzygium cordatum</i>
SE	Jumping-seed Tree	<i>Shirakiopsis elliptica</i>
SP	Common Wild Currant	<i>Searsia pyroides</i>
SR	Blunt-leaf Crow-berry	<i>Searsia rehmanniana</i>
SRC	Red Currant	<i>Searsia chirindensis</i>
TD	Forest Natal Mahogany	<i>Trichilia dregeana</i>
TG	Wild-mulberry	<i>Trimeria grandifolia</i>
TO	Pigeonwood	<i>Trema orientalis</i>
TP	Brides-bush	<i>Tarrenna pavettoides</i>
VL	White-ironwood	<i>Vepris lanceolata</i>
ZC	Small Knobwood	<i>Zanthoxylum capense</i>
ZD	Forest Knobwood	<i>Zanthoxylum davyi</i>

Appendix c

Species codes, common and scientific names of frugivores (birds) in the networks across all matrix habitats; nomenclature follows (Chittenden 2007).

Species code	Common name	Scientific name
B1	African Green-pigeon	<i>Treron calvus</i>
B2	African Olive-pigeon	<i>Columba arquatrix</i>
B3	Barratt's Warbler	<i>Bradypterus barratti</i>
B4	Black-bellied Starling	<i>Lamprotornis corruscus</i>
B5	Black-collard Barbet	<i>Lybius torquatus</i>
B6	Black-headed Oriole	<i>Oriolus larvatus</i>
B7	Brimstone Canary	<i>Crithagra sulphuratus</i>
B8	Bush Blackcap	<i>Lioptilus nigricapillus</i>
B9	Cape Glossy Starling	<i>Lamprotornis nitens</i>
B10	Cape Turtle-dove	<i>Streptopelia capicola</i>
B11	Cape Weaver	<i>Ploceus capensis</i>
B12	Cape White-eye	<i>Zosterops virens</i>
B13	Cape Robin-chat	<i>Cossypha caffra</i>
B14	Chorister Robin-chat	<i>Cossypha dichroa</i>
B15	Collared Sunbird	<i>Hedydipna collaris</i>
B16	Crowned Hornbill	<i>Tockus alboterminatus</i>
B17	Dark-backed Weaver	<i>Ploceus bicolor</i>
B18	Dark-capped Yellow Warbler	<i>Chloropeta natalensis</i>
B19	Dark-capped Bulbul	<i>Pycnonotus tricolor</i>
B20	Olive Sunbird	<i>Cyanomitra olivacea</i>
B21	Forest Canary	<i>Crithagra scotops</i>
B22	Garden Warbler	<i>Sylvia borin</i>
B23	Green Wood-hoopoe	<i>Phoeniculus purpureus</i>
B24	Grey Sunbird	<i>Cyanomitra veroxii</i>
B25	Knysna Turaco	<i>Tauraco corythaix</i>
B26	Lemon Dove	<i>Aplopelia larvata</i>
B27	Southern Double-collared Sunbird	<i>Cinnyris chalybeus</i>
B28	Malachite Sunbird	<i>Nectarinia famosa</i>
B29	Marsh Warbler	<i>Acrocephalus palustris</i>
B30	Olive Thrush	<i>Turdus olivaceus</i>
B31	Orange Ground-thrush	<i>Zoothera gurneyi</i>
B32	Red-eyed Dove	<i>Streptopelia semitorquata</i>
B33	Red-fronted Tinkerbird	<i>Pogoniulus pusillus</i>
B34	Red-capped Robin-chat	<i>Cossypha natalensis</i>
B35	Red-winged Starling	<i>Onychognathus morio</i>
B36	Scarlet-chested Sunbird	<i>Chalcomitra senegalensis</i>

B37	Sombre Greenbul	<i>Andropadus importunus</i>
B38	Southern Black Tit	<i>Parus niger</i>
B39	Speckled Mousebird	<i>Colius striatus</i>
B40	Spectacled Weaver	<i>Ploceus ocularis</i>
B41	Streaky-headed Seedeater	<i>Crithagra gularis</i>
B42	Tambourine Dove	<i>Turtur tympanistria</i>
B43	Terrestrial Brownbul	<i>Phyllastrephus terrestris</i>
B44	Thick-billed Weaver	<i>Amblyospiza albifrons</i>
B45	Trumpeter Hornbill	<i>Bycanistes bucinator</i>
B46	Village Weaver	<i>Ploceus cucullatus</i>
B47	Violet-backed Starling	<i>Cinnyricinclus leucogaster</i>
B48	White-starred Robin	<i>Pogonocichla stellata</i>
B49	Willow Warbler	<i>Phylloscopus trochilus</i>
B50	Yellow Canary	<i>Crithagra flaviventris</i>
B51	Yellow-rumped Tinkerbird	<i>Pogoniulus bilineatus</i>
B52	Yellow Weaver	<i>Ploceus subaureus</i>
B53	Yellow-fronted Canary	<i>Crithagra mozambica</i>
B54	Yellow-streaked Greenbul	<i>Phyllastrephus flavostriatus</i>

Appendix d

List of woody plants used in this study. Given are their scientific and family names, fruit weights and fruiting period for each plant species. Nomenclature follows Boon (2010).

Plant species	Family	Mean fruit weight	Fruiting period
<i>Protorhus longifolia</i>	Anacardiaceae	0.605	Sep - Dec
<i>Searsia chirindensis</i>	Anacardiaceae	0.099	Dec - Apr
<i>Bridelia micrantha</i>	Euphorbiaceae	0.408	Nov - Apr
<i>Trema orientalis</i>	Celtidaceae	0.013	Feb - Nov
<i>Celtis africana</i>	Celtidaceae	0.160	Oct - Apr
<i>Clerodendrum glabrum</i>	Lamiaceae	0.535	Feb - Jul
<i>Phoenix reclinata</i>	Arecaceae	0.726	Jan - Aug
<i>Antidesma venosum</i>	Euphorbiaceae	0.083	Jan - May
<i>Syzygium cordatum</i>	Myrtaceae	1.050	Oct - Jan
<i>Harpephyllum caffrum</i>	Anacardiaceae	5.350	Jan - Sep
<i>Croton sylvaticus</i>	Euphorbiaceae	NA	Dec - May
<i>Shirakiopsis elliptica</i>	Euphorbiaceae	NA	Nov - Mar
<i>Rapanea melanophloeos</i>	Myrsinaceae	0.258	Aug - May
<i>Searsia rehmanniana</i>	Anacardiaceae	0.020	Mar - Jul
<i>Schinus terebinthifolius</i>	Anacardiaceae	0.301	Sep - Apr
<i>Syzygium paniculata</i>	Myrtaceae	0.432	Jan - May

Acknowledgments

Acknowledgments

The road to writing this thesis has been enormously long, emotionally consuming and mentally challenging. Without the help of many people, friends, relatives and institutions, reaching this destination would have been impossible. Therefore, I would like to express my utmost gratitude to the following:

Prof. Dr. Nina Farwig for not only having accorded me this PhD studentship, but also, for entrusting me with the sole responsibility of undertaking such an exceptionally high level research project in South Africa. Opportunities that are as rewarding as this one are particularly rare for Africans. Dr. Dana Berens co-supervised my work with Prof. Dr. Farwig. Together, their supervision was impartially inspirational and strengthened both my analytical and scientific writing skills. These skills will certainly go a long way in benefiting the conservation training and movement in my country Zambia and the African continent at large. I will ever remain humbled and grateful to you both for your trust and support in various ways.

Prof. Dr. Roland Brandl for taking the responsibility of being the second reviewer of my thesis as well as Prof. Dr. Birgit Ziegenhagen and Prof. Dr. Lothar Beck for accepting to be part of the team examining my work, even though we hardly knew each other before. Thank you very much indeed.

Prof. Dr. Colleen Downs and Dr. Mark Brown for the administrative support, particularly for according me an opportunity to use the library as well as the captive birds and green house facilities when undertaking my germination experiments at the University of KwaZulu Natal in South Africa. I am grateful to Dr. Friederike Voigt and her husband Pravin Pillay for the logistical and emotional support that they rendered to me during my research work in South Africa. Dr. Voigt and Mr. Pillay assisted not only with my South African Visa application, but also in organizing my research permit to work in Vernon Crooks Nature Reserve, as well as in taking care of project resources including the field vehicle. Having to work with such a helpful and hospitable family made me feel at home and gave me sufficient motivation to carry on with my work.

Ezemvelo KZN Wildlife for the permission to undertake this study in Vernon Crooks Nature Reserve and Mr. George Archibald for granting me access to the forest patches at his farm. Undertaking both field observation in Vernon Crookes Nature Reserve and Green House experiments at the University of KwaZulu Natal in Pietermaritzburg could not have been possible without the distinguished help I received from my two research assistants, Thulan Ngidi and Moses Zungu respectively. Given the high infestation of ticks in and around Vernon Crookes, not

many local people were willing to work with me during my field observations. I therefore pay special tribute to Thulan Ngidi for his unquestionably remarkable commitment in helping me to successfully undertake my work in this nature reserve. His knowledge of local species of birds and plants was particular helpful in this case. Thank you very much Mr. Ngidi!

All my colleagues (namely, Alex, Eike, Ingo, Julia, Lena and Simon) in the Conservation group (Marburg University), not only for warmly well-coming me in their country (Germany), but also for having accepted to share project facilities with me during our work in South Africa. I extend my gratitude also to Jörg, Franzi, and Pedro. My stay in Germany would have been unfruitful without the overwhelming brotherly solidarity I received from you guys. Jörg's statistical skills were especially helpful during the analysis of my data. Sascha Rösner also helped me in various ways during my stay in Germany, including rushing me to the emergency clinic when I was ill. Thank you very much.

Prof. Dr. Brendan J. Godley, Dr. Dave Hodgson (both from the University of Exeter) and Dr. Michael Kennedy (from the University of Aberdeen) for having supported my application for this PhD studentship. During the last three years, both Dr. Hodgson and Dr. Kennedy have been regularly in touch, encouraging me not to give up. I am very grateful for their support.

My parents, Uncle (Ben Chanda), brothers (Frank, Patrick and Chama Jr.) and sisters (Maureen, Beatrice, Belita and Idah) for their love, overwhelming support and understanding during the course of undertaking this work. I am certainly indebted to my dear wife, Chitambo Chola, for having rallied behind me during the past three years that I was committed to working on this thesis. I particularly salute her for having accepted the responsibility to take care of our under-two yrs old son, Mishila, during my absence. From my side, it was emotional, but she always spoke positively about my work and encouraged me to never give up. Thank you very much Chitambo for having been a symbol of true love and loyalty. I also thank Chitambo's parents and relatives and everyone who helped her to take care of our son. I am very hopeful that Mishila will one day grow to appreciate the benefits of my commitment towards undertaking the work highlighted in this thesis.

My close friends in Zambia, notably, Mr. Basil Mweempwa, Fair Mufwafwi, Ricky Mapulanga, Donald Chungu and Tundu Kaonga for the plentiful support they gave both to me and my family during the last three years when was largely out of the country.

All those who helped me in one way or the other, but their names have unfortunately not been acknowledged here.

Curriculum Vitae



PERSONAL DETAILS

First name	Lackson
Last name	Chama
Date of Birth:	9th January 1977
Place and country of birth	Sinazongwe, Zambia
Nationality	Zambian
Marital status	Married
Contact details:	P.O. Box 91, Sinazongwe, Southern Province, Zambia. Email: chama@staff.uni-marburg.de or l.c.chama@gmail.com Web: www.lacksonchama.net Mobile: +26097 605688; +26097874459

TRAINING

Aug 2009 – Aug 2012	Philipps University of Marburg, PhD Research student with Jun.-Prof. Dr. Nina Farwig, Conservation Ecology group
Sept 2008 – Sept 2009	University of Exeter (UK), MSc Conservation and Biodiversity (Full-time)
Jan 2000 – Dec 2003	Zambia Forestry College, Diploma in Forest sciences (full-time)

EMPLOYMENT PROFILE

Jan. 2006 – Feb. 2008	Kasanka National Park, Research Assistant , Project title: Conservation of Wetlands and Associated Biodiversity in Northern Zambia. Funding: by UK Darwin initiative and Holly Hill trust, and administered through the University of Aberdeen
Aug. 2004 – Dec. 2005	Support to Decentralized Rural Development (SDRD) Programme, Junior Planning Officer ; Funding: A bilateral development cooperation project between the Germany and Zambian governments
Jan – Jul. 2004	The Danish International Development Aid Agency (DANIDA): Natural Resources Management Component Project, Project Technical Officer

OTHER ENGAGEMENTS

1st Feb – 28th Feb. 2005	Germany Technical Cooperation (GTZ); Consultant ; Assessing & Evaluating the Impact of the Food Security Programme Implemented by Germany Government in the Southern Province of Zambia in the year 2004
1st Feb. - 31st Mar. 2004	Centre for the Improvement of Maize & Wheat Production (CIMMITY - Zimbabwe); Conducting a survey on maize Seed Varieties prioritised by subsistence farmers in Zambia

REFEREES

Prof. Dr. Nina Farwig	Department of Ecology - Conservation Ecology, Faculty of Biology, Philipps-Universität Marburg, Karl-von-Frisch-Str. 8, 35032 Marburg, Germany. Fax: +49 6421 28 23387, Email: farwig@staff.uni-marburg.de
Prof. Dr. Brendan J. Godley	Centre for Ecology & Conservation, University of Exeter, Cornwall Campus, TR10 9EZ, UK, Tel: +44 (0)1326 371861, Fax: +44 (0)1326 253638, Email: B.J.Godley@exeter.ac.uk
Dr. Michael. P. Kennedy	University of Aberdeen, School of Biological Sciences, Zoology Building, Tillydrone Avenue, AB24 2TZ, UK; Tel: +44 (0) 1224273638, Email: m.p.kennedy@abdn.ac.uk
Dr Kevin J. Murphy	The University of Glasgow, Institute of Biomedical & Life Sciences, Division of Environmental & Evolutionary Biology Graham Kerr Building, Glasgow, G12 8QQ,; Tel: +44 (0)141 3306632, Fax: +44 (0) 141 3305971; Email: k.Murphy@bio.gla.ac.uk or Mearnskevin@aol.com

Erklärung

Ich versichere, daß ich meine Dissertation

Plant-frugivore interactions in a heterogeneous forest landscape of South Africa

selbständig, ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe.

Die Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Marburg, 4th June 2012



(Ort/Datum)

(Lackson Chama)