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Macroecology of avian frugivore diversity

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“To do science is to search for repeated patterns, not simply to accumulate facts, and to do the science of geographical ecology is to search for patterns of plant and animal life that can be put on a map.”

Robert H. MacArthur (1972)

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CONTENTS

1 SUMMARY

The distribution of bird species can be influenced by a variety of factors (e.g., habitat structure, climate, food availability, biogeographic history) which can change in importance at different spatial scales. In this thesis, I examine geographic patterns of species richness of frugivorous birds – a guild of species specialized on fleshy–fruited plants as food resources. Using comprehensive databases on the distribution of all terrestrial bird species at regional, continental, and global spatial scales I test the potential of plant diversity, contemporary climate, habitat heterogeneity and biogeographic history to explain frugivore diversity at broad spatial scales. At a global scale, avian frugivore diversity is statistically best explained by climate, especially water-energy dynamics and productivity. There are significant differences in frugivore diversity between biogeographic regions which remained after differences in environment had been accounted for. Together with geographic diversification patterns of major clades and realm–specific richness–environment relationships these results indicate an important role of historical processes in shaping regional patterns of avian frugivore diversity. Analyses at regional and continental scales further show that influences of environmental variables on frugivore diversity are mainly indirect, via effects on plants, rather than only direct as often assumed. Spatial patterns of species richness of frugivorous birds and woody plants appear to be linked via functional relationships, either via trophic interactions with major food plants (e.g., Ficus) or vegetation structural complexity. Overall, the results of this thesis imply that biotic interactions, direct and indirect environmental effects as well as historical constraints need to be taken into account to fully understand patterns of species richness at broad spatial scales.

2 GENERAL INTRODUCTION

2.1 Background

Ecologists and naturalists have ever since been fascinated by the staggering contrast in biotic diversity between the tropics and the temperate regions (Darwin 1859; Wallace 1878). Although a large number of hypotheses about the origin and maintenance of species diversity have been proposed and debated for nearly two centuries (Willig et al. 2003), there still remains much debate about the precise mechanisms (Ricklefs 1987; Currie et al. 2004; Mittelbach et al. 2007). Consequently, the question "what determines species diversity" has been identified in the 125th Anniversary Issue of the journal *Science* as one of the 25 most important research themes in the near future (Pennisi 2005). Species diversity gradients are affected undoubtedly by a combination of biotic, environmental, historical and evolutionary factors but the major challenge is to disentangle the relative roles of each component (Ricklefs 1987; Brown 1995; Currie et al. 2004) and to generalize and synthesize patterns and processes across multiple spatial and temporal scales (Rahbek & Graves 2001; Wiens & Donoghue 2004; Mittelbach et al. 2007). At least two questions have to be unveiled to better explain and understand gradients in species diversity (Mittelbach et al. 2007). First, it remains largely unclear how biotic interactions and species coexistence influence the maintenance of species diversity. Second, the relative roles of environmental and historical processes in shaping patterns of species diversity need to be better understood. This thesis is an attempt examine these questions and to contribute to a better understanding of determinants of species diversity.

2.2 The macroecological approach

To study species diversity, ecologists usually go into the field or the laboratory and make observations or conduct experiments to understand how species and populations respond to environment or how they interact with each other. With this approach, much has been learned about the processes that regulate the abundance, distribution, and diversity of species in local habitats. But despite spectacular advances and progress in ecology, many of the fundamental questions have remained unanswered and many new ones have been raised (Brown 1995). Experimental field and laboratory studies are often costly and time-consuming and there are never enough time and resources to study all species or all populations. It is therefore impossible to know which results are specific to a particular system and which can be generalized to other systems. Moreover, it is often impractical, impossible, or immoral to perform replicated, controlled experiments on the spatial and temporal scales required to address many basic and applied questions in ecology. It was therefore necessary to find alternative ways to make inferences about the natural world (MacArthur 1972).

In response to the limitations of experimental studies, Brown & Maurer (1989) and Brown (1995) proposed to broaden the scope of ecology so that it can address questions on much larger spatial and temporal scales. Their ideas built upon work of early naturalists such as Charles Darwin, Alfred Russel Wallace and Alexander von Humboldt, and 20th century scientists like John Willis, Alfred Lotka, Robert MacArthur and Joseph Grinnell, who contributed with their writings to the description of broad-scale patterns and hypothesized mechanistic explanations (Brown 1995). To refer to this research program, Brown & Maurer (1989) and Brown (1995) used the term "macroecology" and defined it as a "nonexperimental, statistical investigation of the relationships between the dynamics and interactions of species populations that have typically been studied on small scales by ecologists and the processes of speciation, extinction, and expansion and contraction of ranges that have been investigated on much larger scales by biogeographers, paleontologists, and macroevolutionists" (Brown 1995, pp. 6-7). They advocated it as an effort to introduce simultaneously a geographic and a historical perspective to better understand the local abundance, distribution, and diversity of species, and to apply an ecological perspective to gain insights into the history and composition of regional and continental biotas.

Since Brown's seminal book in 1995, macroecology has developed and matured over the last decade (e.g. Blackburn & Gaston 2003). It's development has been facilitated by an increasing availability of high-quality data (Burgess et al. 1998; Rahbek & Graves 2001; Morawetz & Raedig 2007), advances in bio- and geoinformatics (R Development Core Team 2005; Rangel et al. 2006; Guralnick et al. 2007), and the pressing need to develop effective solutions to global change and its impact on biodiversity (Kerr et al. 2007). Recent macroecological efforts have gained important insights into global biodiversity hotspots (Myers et al. 2000; Orme et al. 2005; Lamoreux et al. 2006), continental and global centres of endemism (Jetz et al. 2004; Orme et al. 2005), broad-scale environmental and historical determinants of species richness (e.g. Rahbek & Graves 2001; Jetz & Rahbek 2002; Hawkins et al. 2003a; Kreft & Jetz 2007), and potential impacts of climate and land use change on global biodiversity (Van Vuuren et al. 2006; Jetz et al. 2007). Brown's (1995) book has obviously stimulated exciting new avenues and is likely to shape research in ecology and related disciplines for years to come.

2.3 The frugivore guild

It has long been recognized that species fundamentally differ in their ecological attributes, for instance, in their requirements for resources (Lindeman 1942; Hutchinson 1959; MacArthur 1972). This has important implications as species with different resource requirements are likely to respond differently to environmental conditions. Ecologist therefore often classify species into ecological guilds to better understand the responses of species with similar ecological adaptations and the ecosystem services they provide (Sekercioglu 2006). One possibility is to define functional groups based on the primary diet of species. This grouping usually parallels the main ecological function that species have (Sekercioglu 2006). One such group is the guild of frugivores which is composed of species that are specialized on fleshy–fruited plants as food resources. Frugivores have been of great interest to ecologists because they play an important role for plant reproduction and ecosystem functioning via seed dispersal services (Howe & Smallwood 1982; Fleming et al. 1987; Bleher & Böhning-Gaese 2001; Herrera 2002; Sekercioglu 2006). Many frugivorous species are currently extinction prone which might have far reaching consequences for ecosystem functioning (Sekercioglu et al. 2004).

Despite decades of research on frugivores especially at local spatial scales (e.g., Herrera 1985; Levey 1988; Bleher et al. 2003; see also references in Shanahan et al. 2001a), little is known about the ecological and evolutionary processes that shape geographic patterns of frugivore diversity at broad spatial scales (Fleming et al. 1987; Primack and Corlett 2005). The first assessment of the biogeographic distribution of frugivores was compiled by Fleming et al. (1987) who compared differences in regional frugivore species richness, fruit availability, foraging locations, degree of dietary specialization, and frugivore movement behavior between major tropical regions (Neotropics, Africa, Southeast Asia) and Old World Islands (Madagascar, Borneo, New Guinea). Since this pioneering paper, however, research on frugivory and plant-animal interactions at broad spatial scales has been scarce (Burns 2004; Márquez et al. 2004). One recent, noteworthy exception is Fleming's (2005) paper which compares 27 field studies on plant–frugivore communities and finds that the relationship between food plant diversity and species richness of vertebrate frugivores is particularly strong in the Neotropics (Fleming 2005). The geographic distribution of frugivores has not been examined using continental or global high-quality databases and determinants of frugivore diversity at broad spatial scales remain unknown.

2.4 Aim of thesis

This thesis intends to complement the current field- and lab-based knowledge on frugivory with a macroecological perspective where frugivore diversity is examined at regional, continental, and global spatial scales. Recent advances in data availability, bio- and geoinformatics, and ecological modeling make this avenue possible and now allow the testing of hypotheses about determinants of frugivore diversity at broad spatial scales. Frugivores appear to be a good model system to study (1) broad-scale biotic interactions between food resources and consumer species and direct and indirect environmental effects on animal species richness, and (2) the relative roles of environmental and historical constraints in shaping global patterns of diversification and spatial distribution of species. The advantages of focusing on a specific dietary guild like frugivores are that (1) comprehensive knowledge on frugivore ecology is available from field and laboratory studies, (2) food resources (i.e., food plants) can be well defined and quantified even at regional and continental scales, and (3) species can be easily assigned to this dietary guild based on published knowledge on feeding ecology and dietary breadth. Moreover, previously published studies suggest that both environmental as well as historical factors have likely been important for the diversification of fruit-eating species (Fleming et al. 1987) which gives the opportunity to evaluate the relative importance of environmental and historical constraints and to refine our understanding of mechanisms behind the diversification of major clades.

My thesis consists of three major chapters (chapter 3-5) which have been organized so that they can be read independently. Each chapter is organized like a journal publication containing an abstract followed by an introduction, methods, results, and discussion section. The thesis ends with general conclusions and acknowledgements, and with a list of tables and a list of figures. To guarantee readability and compactness of the three major chapters, all additional and complementary material, which is not directly necessary for the main focus of each chapter, has been transferred into Appendices which are found at the very end of this thesis.

In the first major chapter (chapter 3) I examine species richness of avian frugivores at a global scale by scrutinizing a comprehensive database of all terrestrial bird species in the world established by Walter Jetz (University of California San Diego). I elucidate taxonomic patterns of major clades and use spatial and nonspatial modeling techniques to test the potential of contemporary climate (water–energy, productivity, seasonality), habitat heterogeneity and biogeographic history to explain geographic patterns in the species richness and proportion of frugivores. These analyses allow to examine the interplay between environment and biogeographic history in shaping patterns of frugivore distribution at the global scale.

The second major chapter (chapter 4) investigates avian frugivore diversity at the continental scale of sub-Saharan Africa by scrutinising a comprehensive distribution database of African breeding birds (compiled by the Zoological Museum, University of Copenhagen, and provided by Carsten Rahbek). The aim is to evaluate whether food plant diversity, contemporary climate and energy, or habitat heterogeneity determine species richness patterns of bird guilds with decreasing specialization on fruit eating. Path models are used to disentangle direct and indirect effects of predictor variables and spatial and nonspatial regression models are used to examine the effect of spatial autocorrelation in the dataset.

In the third major chapter (chapter 5) I establish a database on the distribution of all birds and woody plants in Kenya (woody plant data were contributed by Richard Field, University of Nottingham) and examine in more detail at a regional scale the relative roles of functional relationships (resource-consumer interactions, vegetation structural complexity) between birds and woody plants and direct and indirect environmental effects on broad-scale species richness of both groups. I use path models and spatial and nonspatial regression models to disentangle determinants of species richness of different avian frugivore guilds and fleshy-fruited and non-fleshy-fruited woody plants.

The thesis ends with a general conclusion section where the major findings are summarized and prospects of future research highlighted.

3 THE GLOBAL DIVERSITY OF AVIAN FRUGIVORES – ENVIRONMENTAL CONSTRAINTS OR HISTORICAL CONTINGENCIES?

3.1 Abstract

The relative roles of contemporary environment and historical constraints in shaping broad–scale patterns of species richness remain controversial. Here we examine both taxonomic and geographic patterns of the global diversity of avian frugivores – a guild of 1,230 species specialized on fleshy–fruited plants as food resources. We test the potential of contemporary climate (water–energy, productivity, seasonality), habitat heterogeneity and biogeographic history to explain species richness and proportion of frugivores. Actual evapotranspiration (AET) and other measures of productivity emerge as strongest predictors of global frugivore diversity possibly due to indirect effects of water–energy dynamics on food plants. There are significant differences in frugivore richness and proportion between most biogeographic regions which remained after differences in environment (i.e., AET) had been accounted for. Our results indicate that, in addition to geographic patterns of diversification of major clades and realm–specific richness–environment relationships, historical influences on global frugivore diversity cannot be neglected. We suggest that the diversification and distribution of frugivorous birds has mainly been influenced by the evolutionary history of fleshy–fruited plant taxa, niche conservatism, and past climate change. Overall our results support an important role of co-diversification and environmental constraints on regional assembly over macroevolutionary timescales.

Keywords: biodiversity, biogeography, birds, climate history, frugivory, plant-animal interactions.

3.2 Introduction

Broad–scale geographic patterns of species richness are central to ecology and have gained much attention in recent years (e.g., Brown 1995; Jetz & Rahbek 2002; Hawkins et al. 2003a; Currie et al. 2004). Although a number of studies have shown a remarkably strong association between species richness and contemporary climate or habitat heterogeneity (Rahbek & Graves 2001; Jetz & Rahbek 2002; Hawkins et al. 2003a) there remains much debate about the precise mechanisms (Ricklefs 1987, 2006a; Mittelbach et al. 2007). Ecologists recognize that ecological communities are not only constrained by contemporary environment but also by historical processes such as the evolutionary history of the lineages and the biogeographic history of the region (Ricklefs & Schluter 1993; Wiens & Donoghue 2004; Mittelbach et al. 2007). For instance, comparisons between different regions with similar environment can show substantial differences in species richness (Qian & Ricklefs 2000) suggesting important controls due to immigration, speciation and extinction dynamics, past climate history, or the geographical position of dispersal barriers (Ricklefs 1987, 2006a; Ericson et al. 2003; Barker et al. 2004; Wiens & Donoghue 2004; Mittelbach et al. 2007). However, studies that merge ecological and evolutionary approaches at broad spatial scales remain scarce (Harrison & Cornell 2007; Johnson & Stinchcombe 2007).

Global studies and cross–continental comparisons can help to elucidate the relative roles of environmental or historical constraints on broad–scale patterns of species richness (Hawkins et al. 2003b; Primack & Corlett 2005; Buckley & Jetz 2007; Kreft & Jetz 2007; Hawkins et al. 2007). However, the multitude of environmental factors, the contingency of historical events and the fundamental differences between taxa has made it difficult to generalize findings across phylogenetically unrelated or ecologically dissimilar species. For instance, the fundamental differences in the metabolic requirements of different taxa (e.g., plants vs. animals, ectotherms vs. endotherms) might provoke differences in the relative importance of environmental predictor variables (Allen et al. 2002; Whittaker et al. 2007; Kissling et al. 2008). Moreover, if historical factors are important in shaping geographic patterns of species richness, then the same contemporary environmental factors can differ in strength between regions or continents with different biogeographic histories (Ricklefs 1987; Ricklefs & Schluter 1993; Buckley & Jetz 2007; Davies et al. 2007; Kreft & Jetz 2007). Furthermore, the rapid speciation and evolutionary divergence of certain taxa might have been influenced by the synchronous diversification of other lineages including reciprocal or non-reciprocal interactions among species of two or more lineages over macroevolutionary time (Johnson &

Stinchcombe 2007). Overall, this suggests that guild–specific analyses help to refine our understanding of mechanisms behind the diversification of clades, and to evaluate the relative importance of environment and historical contingencies in shaping broad–scale species richness patterns (Brown 1995; Kissling et al. 2007, 2008; McPherson & Jetz 2007).

The unique knowledge about both the global distribution (Orme et al. 2005; Jetz et al. 2007) and ecology (e.g., Newton 2003; Sekercioglu et al. 2004; Davies et al. 2007) of all birds now allows a first evaluation of how an ecological adaptation, here dietary specialization on fleshy fruits, and geographic distributions interact and underpin richness gradients at the global scale for a whole clade. The guild of frugivores is composed of species that are specialised on fleshy–fruited plants as food resources. Frugivores are of great interest to ecologists because they play an important role for plant reproduction and ecosystem functioning via seed dispersal services (Karr 1976a; Fleming et al. 1987; Bleher & Böhning-Gaese 2001; Herrera 2002; Sekercioglu et al. 2004). Yet, despite decades of research on frugivores especially at local spatial scales (e.g., Herrera 1985; Levey 1988; Bleher et al. 2003; see also references in Shanahan et al. 2001a), little is known about the ecological and evolutionary processes that shape geographic patterns of frugivore diversity at continental and global scales (Fleming et al. 1987; Primack & Corlett 2005; Kissling et al. 2007).

Frugivorous birds may serve as an intriguing model system to study the relative roles of environmental and historical constraints on diversification and spatial distribution of species. On the one hand, the distribution and diversity of fleshy–fruited plants and fruit biomass production are largely determined by water–energy dynamics and seasonality of the climate (Karr 1976a; Fleming et al. 1987; Kreft & Jetz 2007; Kissling et al. 2007). This suggests an important role of contemporary climatic factors in determining frugivore diversity at broad spatial scales. On the other hand, the diversification of frugivores might have strongly been influenced by historical factors. These include the evolutionary history and diversification of fleshy–fruited plants (Snow 1981; Gentry 1982; Fleming et al. 1987; Harrison 2005), the presence or absence of mammalian competitors (Fleming et al. 1987; Primack & Corlett 2005), or past climate history and the geographical position of dispersal barriers (Karr 1976b; Fleming et al. 1987; Newton 2003). This implies a strong imprint of evolutionary history on geographic patterns of avian frugivore diversity at the global scale.

Here I present a first global–scale analysis on geographic and taxonomic patterns of species richness of frugivorous birds and their potential environmental and historical determinants. Analysing a comprehensive database covering the distribution of all terrestrial bird species (*n* = 8,918) I elucidate the taxonomic distribution of frugivore richness within orders and families. Using both nonspatial and spatial (controlling for spatial autocorrelation) modeling techniques, I test the potential of contemporary environment (water–energy, productivity, seasonality, habitat heterogeneity) and biogeographic history to explain avian frugivore richness and the proportion of frugivores in bird assemblages. I am particularly interested in the interplay between environment and biogeographic context in shaping patterns of frugivore distribution at the global scale.

3.3 Methods

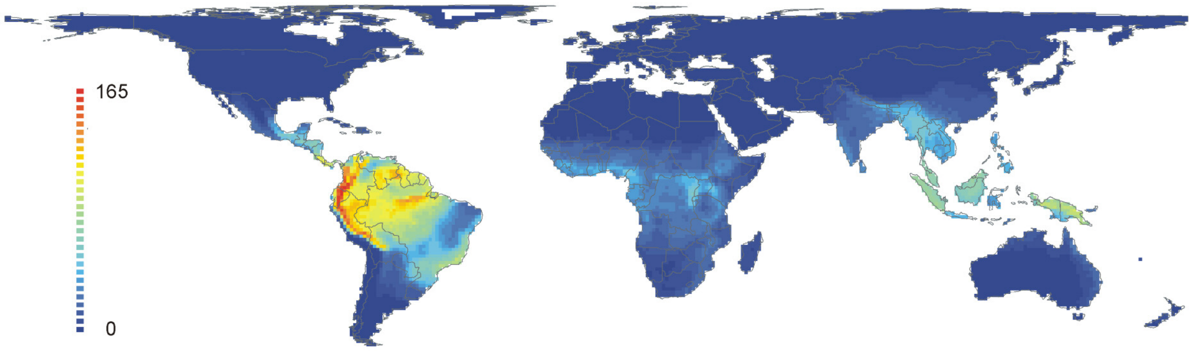
3.3.1 Species richness data

This study is based on a comprehensive database of the breeding distributions of all bird species in the world (Jetz et al. 2007). I included all 8,918 terrestrial bird species (out of 9,753 total) in my analysis, excluding birds that predominantly feed in freshwater or marine habitats ($n = 835$). The maps represent extent of occurrence during breeding season and were compiled from the most accurate sources for a given broad geographic region or taxonomic group (see Figure S4 of Jetz et al. 2007 and references therein). Originally in polygon format, the maps of all species were overlaid onto a grid in cylindrical equal area projection with either 110 × 110 or 220 × 220 km resolution (equivalent to ca. 1° × 1° or 2° × 2° near the equator, respectively). A recent validation analysis confirmed satisfactory range map accuracy for this same dataset at roughly 150 km to 200 km grid cell resolution across North America, Southern Africa and Australia (Hurlbert & Jetz 2007). The classification of species follows Sibley & Ahlquist (1990) for nonpasserines and Barker et al. (2004) for passerines and was updated for newly described species and recent splits and lumps.

3.3.2 Frugivore classification

The diets of all species in the database were determined from a comprehensive literature survey (see Appendix 1) and the classification procedure follows Sekercioglu et al. (2004). For all species, the dietary components mentioned in the literature were assigned to nine categories (fish, fleshy fruits, invertebrates, nectar, aquatic invertebrates, plant material, carrion, seeds, vertebrates) and each category was ranked in importance for each individual species. Both the ranks and the diet breadth (i.e., number of diet categories a species has) were used to assign the relative importance of each diet category for each individual species. From this assignment I classified frugivores as those species that have fleshy fruits as their main diet. This included only species where fleshy fruits were identified as the most important diet category (i.e., rank = 1) and that simultaneously had no more than three diet categories (i.e., diet breadth up to 3). Note that this definition of frugivory is conservative but corresponds to other authors who define a frugivore as an animal whose diet is composed of >50% fleshy fruits (e.g., Fleming et al. 1987). From the 8,918 terrestrial bird species a total of 1,230 species (14%) were thus classified as frugivores (see Appendix 1).

(A) Frugivore richness



(B) Proportion of frugivores

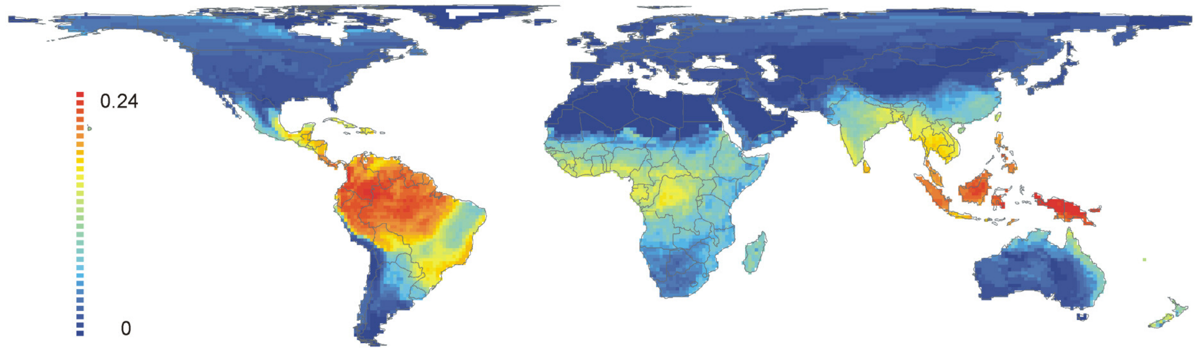


Figure 3.1: Geographical patterns of avian frugivore distribution across the world. (A) species richness, and (B) proportion of frugivores in total bird species assemblages. Equal interval classification is shown across an equal area grid (12,364 km², ~1° latitude × 1° longitude near the equator) with colors varying from dark blue (lowest values) to dark red (highest values).

3.3.3 Taxonomic and geographic patterns of avian frugivore diversity

I first examined taxonomic patterns of frugivore richness by subdividing total avian frugivore richness into species richness within orders and families. Simple goodness–of–fit tests (χ^2–statistics; Quinn & Keough 2002) were used to test whether the observed frequency of frugivorous species in each order significantly departed from the expected frequency of frugivorous species across all bird species (*n* = 1,230 frugivorous species within a total of 8,918 terrestrial bird species). Here, significance levels were adjusted to control Type I error rates using the sequential Bonferroni procedure (Quinn & Keough 2002).

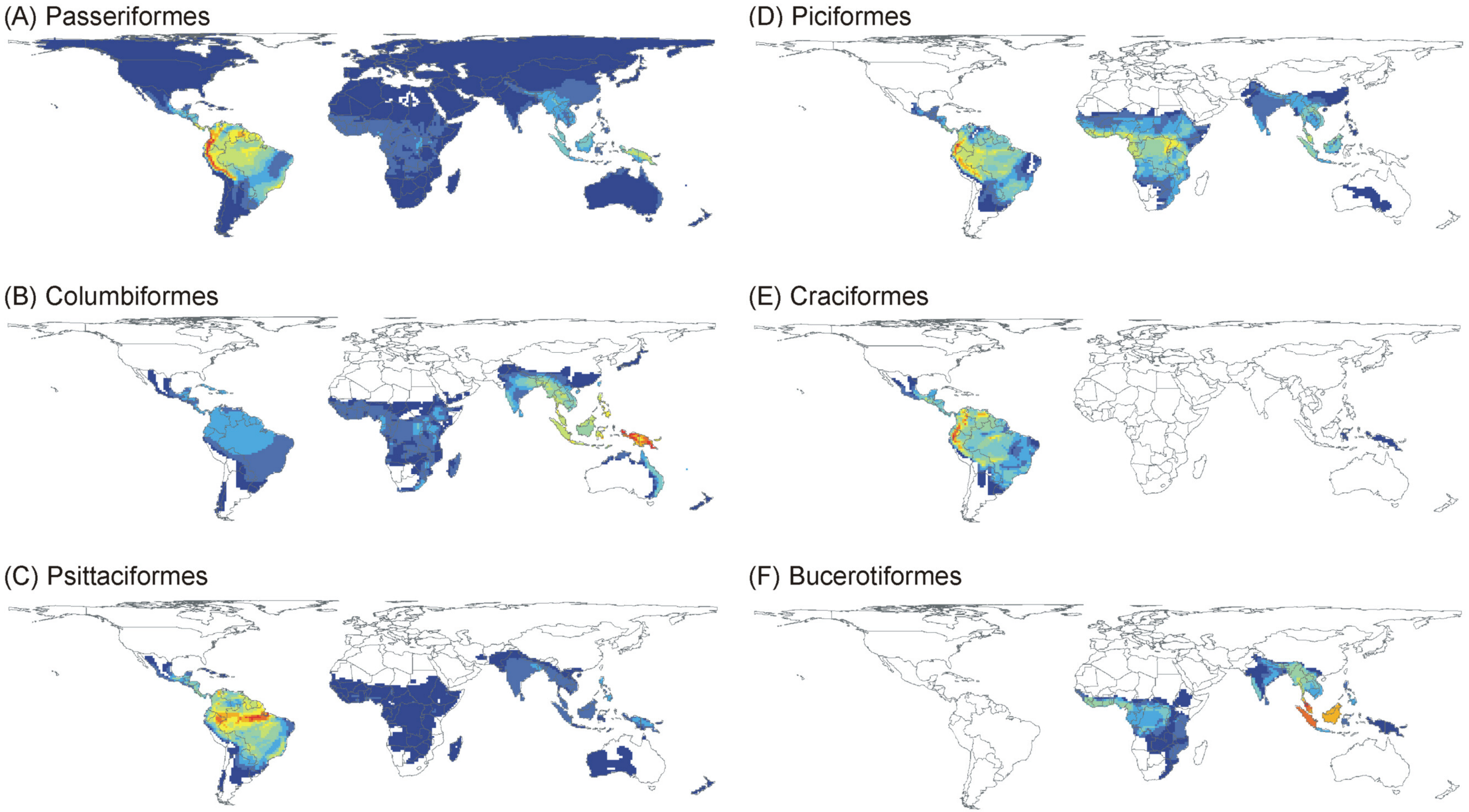


Figure 3.2: Global patterns of frugivorous species richness within the six orders with the highest absolute numbers of frugivorous species. (A) Passeriformes (*n* = 618), (B) Columbiformes (*n* = 179), (C) Psittaciformes (*n* = 141), (D) Piciformes (*n* = 112), (E) Craciformes (*n* = 50), and (F) Bucerotiformes (*n* = 38). Equal interval classification is shown across an equal area grid (12,364 km^2, ~1° latitude × 1° longitude near the equator) with colors varying from dark blue (lowest values) to dark red (highest values).

I then analyzed the overall geographic pattern of avian frugivore distribution across the world by calculating two variables for each grid cell: (i) the species richness of avian frugivores (i.e., the number of all frugivorous bird species present in each cell based on the extent of occurrence maps), and (ii) the proportion of frugivores in the total bird assemblage (i.e., the species richness of frugivores divided by overall bird species richness in each cell). The first measure gives the absolute number of frugivorous species across the world whereas the second provides a measure of the degree of frugivory in a bird community correcting for overall bird species richness. For both variables I identified hotspots as the richest 2.5% of grid cells with respect to species richness or frugivore proportion, respectively. Geographic patterns of frugivorous species richness for the most species–rich orders were also mapped to explore diversification patterns of major clades.

3.3.4 Putative determinants

I tested a total of 14 environmental predictor variables as potential determinants of the richness pattern of frugivorous birds. The variables belonged to three categories, i.e., water–energy and productivity (nine variables), seasonality (three variables), and habitat heterogeneity (two variables). One additional variable, realm, was used to capture historical factors related to the biogeographic history of a region. All variables have previously been shown to be strongly correlated with species richness of vertebrates and/or woody plants at continental and global scales (e.g., Rahbek & Graves 2001; Jetz & Rahbek 2002; Hawkins et al. 2003a, 2003b; Buckley & Jetz 2007; Davies et al. 2007; Kreft & Jetz 2007; Kissling et al. 2007).

Environmental and geographic data were assembled and extracted in ArcGIS (version 9.1, ESRI, Redlands, CA, USA) and resampled to the same resolution as the bird data. Among the variables related to water–energy and productivity, I used potential evapotranspiration (PET), mean annual temperature (TEMP), and number of frost days (FROST) to assess the effect of temperature and energy availability on species richness. I included annual precipitation (PREC) and number of wet days (WET) to indicate water availability, and used actual evapotranspiration (AET) as an integrated measure of the water–energy balance. Additionally, I used net primary productivity (NPP), which is often thought to be a good proxy for food availability in terrestrial ecosystems (Wright 1983; Jetz & Rahbek 2002; Hawkins et al. 2003b; Kissling et al. 2007). I considered total annual aboveground productivity (NPPann) and total productivity of the least and most productive three–month period (NPPmin, NPPmax) as estimates of energy availability. All climate variables were extracted from the mean monthly climatic database for the period 1961–1990 with 10’ resolution provided by New et al. (2002), except PET and AET which originated from the Ahn & Tateishi (1994) dataset at 30’ resolution, and mean monthly NPP values which were provided by Bondeau et al. (2007) for the time period 1961–90 at 0.5° resolution.

Seasonality in climate and productivity has been shown to strongly affect avian species richness (Hurlbert & Haskell 2003), and this might be especially true for avian frugivores because seasonality in climate directly influences the availability of fruit resources (e.g., Karr 1976a). I used the ratio of total productivity of the least productive three months and total productivity of the most productive three months (NPPratio = NPPmin / NPPmax), the seasonal pulse of production in relation to productivity of the most productive three months (NPPpulse = (NPPmax - NPPmin) / NPPmax), and the coefficient of variation of monthly NPP values (NPPcv) as estimates of seasonality. Habitat heterogeneity quantified either as topographic relief or as number of habitat types has also been shown to determine broad–scale patterns of bird species richness (Rahbek & Graves 2001; Jetz & Rahbek 2002; Davies et al. 2007). I used altitudinal range from the GTOPO–30 digital elevation model (TOPO, i.e., the difference between maximum and minimum elevation) and the number of vegetation classes (HABDIV) according to the Olson global land cover classification to indicate habitat heterogeneity (both variables were derived from the Global Land Cover Characteristics Data Base available at http://edcsns17.cr.usgs.gov/glcc/).

Finally, I investigated the potential effects of historical contingencies by partitioning the data into six biogeographic realms (REALM, including Afrotropics, Australasia, Indo–Malaya, Nearctic, Neotropics, and Palearctic; see Udvardy 1975). While the representation of evolutionary and biogeographic history as realms is relatively crude, it does capture major differences in frugivore diversification rates, such as those between the Old and New World tropics (Fleming et al. 1987). Grid cells falling within Oceania or Antarctica were omitted for statistical modeling since environmental data were lacking for these realms (see below). Differences between realms in mean frugivore richness and mean frugivore proportion were tested with multiple pair wise comparisons using Tukey’s HSD test which controls the group–wise Type I error rate (Quinn & Keough 2002). To test the interplay of environmental and historical factors on shaping global patterns of avian frugivore richness I examined whether the influence of environmental factors on avian frugivore richness varied by realm (see below).

3.3.5 Statistical analysis

To analyse the potential of predictor variables in explaining global patterns of species richness and frugivore proportion I performed both nonspatial and spatial linear regression models. To improve normality and homogeneity of variance I log transformed frugivore richness and arcsine square root transformed proportion of frugivores. I first tested all single predictor variables with nonspatial generalized linear models (GLMs with Gaussian error distribution and identity link). I then used the best single environmental predictors from each category (i.e., water–energy and productivity, seasonality, and habitat heterogeneity, respectively) and the historical predictor variable REALM to test combined multi–predictor models. To account for potential hump–shaped relationships, I included squared terms in the single and multiple predictor regression models in case the model's AIC value improved by at least 1%. I choose the 1% AIC threshold because most squared terms improved the model fits (AIC) due to the large sample size and, consequently, the large AIC values (>10,000 for the full dataset).

In a further step, I repeated these analyses but calculated spatial linear models (SLM), which can account for the spatial autocorrelation structure in model residuals that affects Type I error rates of non–spatial analyses (Legendre & Legendre 1998). SLMs were calculated as 'spatial simultaneous autoregressive error models, which have been shown to perform best in terms of parameter estimation and Type I error control (Kissling & Carl 2008). The degree of spatial autocorrelation in GLM and SLM residuals was quantified with Moran's I values (Legendre & Legendre 1998) which indicate high spatial autocorrelation with values close to 1/-1, and no autocorrelation with values close to 0. Final model selection was based on the reduction of spatial autocorrelation in model residuals (evaluated with Moran's I values), the increase in R^2–values, and the minimization of AIC values (Kissling & Carl 2008). For SLMs, two R^2–values are provided which indicate the non–spatial smooth (R^2_{trend}) and the total fit between predicted and observed values (R^2_{fit}: composed of non–spatial and spatial smooth).

To illustrate the interaction between environment and biogeographic history in more detail I analyzed the relationship between proportion of frugivores and AET for each realm separately. For this analysis, I used non–spatial single predictor GLMs with proportion of frugivores (arcsine square root transformed) as response variable and AET as predictor variable. To account for spatial autocorrelation, I here corrected significance levels and F–statistics of each regression model using Duttileul's method (Dutilleul 1993). Duttileul's method determines the effective geographic degrees of freedom for each regression or correlation and thus allows testing the overall statistical significance by taking into account the non–independence of observations (Dutilleul 1993; Rangel et al. 2006). This analysis was done with the SAM software (Rangel et al. 2006; available at www.ecoevol.ufg.br/sam/).

For statistical modeling, I excluded cells for which environmental data were missing (i.e., Oceania, Antarctica, plus remaining island cells; see Appendix 2 for details of frugivorous species that exclusively occur on islands). Excluding cells with more than 50% water did not change the results of my analyses, so I included them. From these cells, I only included cells with frugivore presence in my statistical models (n = 8,563 at resolution equivalent to 1°; n = 2,221 at resolution equivalent to 2°). Due to memory limitations on the calculation of SLMs with global datasets I developed a bootstrapping approach where I randomly sub–sampled (10%, i.e., n = 857 cells at a resolution equivalent to 1°; 40%, i.e., n = 888 cells at a resolution equivalent to 2°) the whole global dataset 100 times. For each of the 100 random sub–samples I calculated (single and multiple predictor) GLMs and SLMs and extracted the relevant model and test statistics (i.e., AIC, R^2, and Moran's I values). I then calculated mean values of all model and test statistics across the 100 random sub–samples. In all cases, standard errors of mean values were much smaller than 10% of the mean values and are not reported. Unless otherwise stated, statistical analyses were done with R (R Development Core Team 2005) and spatial analyses were conducted using the R library 'spdep', v. 0.4–2 (2007, R. Bivand, available at http://cran.r-project.org/src/contrib/Descriptions/spdep.html). The spatial neighborhood of the SLMs was calculated by including the four (resolution equivalent to 1°) and two (resolution equivalent to 2°) nearest neighboring cells, respectively, within each sub–sample of the data and by using a row–standardized coding scheme to calculate the spatial weights matrix (see Kissling & Carl 2008).

3.4 Results

3.4.1 Taxonomic patterns of avian frugivory

Out of a total number of 1,230 frugivorous bird species, most (50%) are found among the Passeriformes (perching birds, n = 618 species), with the family of the finches (Fringillidae) as the most species rich (Table 3.1). Orders that contribute a significant number of frugivorous species (>100 species) include the Columbiformes (pigeons), Psittaciformes (parrots), and Piciformes (woodpeckers and relatives). The remaining eleven orders contribute much fewer frugivorous species (n < 50 species, i.e., less than 4% of all frugivores; Table 3.1).

Table 3.1: Taxonomic distribution of frugivorous bird species (*n* = 1,230) within orders and families. The expected proportion of frugivorous species within an order would be 14% based on the frequency of frugivorous species across all species.

Order	Frugivore Richness	Total species richness	Proportion of frugivores in order[1] (%)	Percentage of all frugivores (*n* = 1,230)	Families (Number of frugivorous species, total number of species)
Passeriformes	618	5841	11***	50	Bombycillidae (8, 8), Corvidae (82, 645), Eurylaimidae (4, 15), Fringillidae (180, 1029), Hypocoliidae (1, 1), Irenidae (1, 10), Melanocharitidae (6, 10), Meliphagidae (7, 177), Muscicapidae (37, 443), Nectariniidae (6, 172), Paramythiidae (2, 2), Passeridae (1, 387), Ptilonorhynchidae (20, 20), Pycnonotidae (58, 129), Sturnidae (68, 144), Sylviidae (12, 560), Tyrannidae (124, 574), Zosteropidae (1, 97)
Columbiformes	179	308	58***	15	Columbidae (179, 308)
Psittaciformes	141	351	40***	11	Cacatuidae (2, 21), Psittacidae (139, 330)
Piciformes	112	349	32***	9	Lybiidae (35, 41), Megalaimidae (26, 26), Picidae (3, 216), Ramphastidae (48, 49)
Craciformes	50	69	72***	4	Cracidae (48, 50), Megapodiidae (2, 19)
Bucerotiformes	38	54	70***	3	Bucerotidae (38, 52)
Musophagiformes	23	23	100***	2	Musophagidae (23, 23)
Tinamiformes	22	47	47***	2	Tinamidae (22, 47)
Trogoniformes	15	39	38***	1	Trogonidae (15, 39)
Galliformes	13	211	6***	1	Odontophoridae (2, 32), Phasianidae (11, 173)
Coliiformes	6	6	100***	<1	Coliidae (6, 6)
Cuculiformes	5	136	4***	<1	Cuculidae (5, 75)
Gruiformes	4	95	4***	<1	Psophiidae (3, 3), Rallidae (1, 59)
Struthioniformes	3	10	30	<1	Casuariidae (3, 4)
Strigiformes	1	314	<1***	<1	Steatornithidae (1, 1)

[1] Significance levels (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$) indicate whether the observed frequency of frugivorous species in each order significantly departs from the expected frequency of frugivorous species across all species (using simple goodness–of–fit tests with chi–square statistics). All significant results were also significant after sequential Bonferroni correction.

I present a simple overview to qualitatively illustrate the strong taxonomic and phylogenetic signal of the cross-clade variation in the occurrence of frugivory. In almost all orders, the observed proportion of frugivorous species departed significantly from an expectation of equal frequency across all clades given the global count (1,230 / 8,918 = 0.14) (Table 3.1). Some orders such as the African Turacos (Musophagiformes) or the African Mousebirds (Coliiformes) consisted exclusively of frugivores (100%), and the pigeons (Columbiformes), the chachalacas, guans, and curassows (Craciformes), and the hornbills (Bucerotiformes) had more than 50% frugivorous species (Table 3.1). Orders such as the Galliformes, Cuculiformes, Gruiformes and Strigiformes showed very low proportions of frugivorous species (<10%; Table 3.1).

3.4.2 Geographic patterns of avian frugivory

Across all orders, species richness of frugivorous birds was highest in the Neotropics (Figure 3.1A). Neotropical hotspots of avian frugivore richness were found in the Andes, the Guiana–Venezuela highlands, and along the Amazon River basin in Brazil (Figure 3.1A). Once accounting for overall bird species richness, the proportion of frugivores in bird assemblages was similarly high at equatorial latitudes in the Neotropics and in Southeast Asia (Figure 3.1B). The Afrotropics showed the lowest overall species numbers of frugivorous birds and the lowest proportions of frugivores of all tropical regions (Figure 3.1). On all continents, species richness and proportion of frugivores was highest in the tropics and decreased towards the poles (Figure 3.1).

Geographic patterns of frugivore richness of the six orders with the highest absolute numbers of frugivorous birds showed distinct differences across the globe (Figure 3.2). Some orders such as the Passeriformes (Figure 3.2A), Piciformes (Figure 3.2D), and Craciformes (Figure 3.2E) had their highest species richness along the Andes in South America whereas other orders showed highest frugivore richness in the lowland tropical rainforests of the Amazon basin (Psittaciformes; Figure 3.2C), in Indonesia (Bucerotiformes; Figure 3.2F), or in New Guinea (Columbiformes; Figure 3.2B). Mainland Australia generally showed low numbers of frugivorous species (Figures 3.1 and 3.2).

3.4.3 Environmental determinants and biogeographic variation

Among individual climatic variables, actual evapotranspiration (AET) emerged as the strongest single climatic predictor variable explaining a remarkable 71–73% of variation in global frugivore richness and proportion of frugivores (see Table 3.2 for 1° and Appendix 3 for 2° equivalent models).

Table 3.2: Results of single predictor models examined at resolution equivalent to 1° to explain global avian frugivore richness and the proportion of frugivores in avian assemblages. Within each category the best single predictor variable is highlighted in bold.

		Frugivore richness							Proportion of frugivores						
		GLM			SLM				GLM			SLM			
Variables	+/-	R^2	AIC	Moran	R^2_{trend}	R^2_{fit}	AIC	Moran	R^2	AIC	Moran	R^2_{trend}	R^2_{fit}	AIC	Moran
NULL		–	1685	0.91***	–	0.93	-173	0.02	–	-1340	0.92***	–	0.94	-3362	0.02
Water–energy and productivity															
PET	+	0.52	1062	0.81***	0.52	0.93	-241	0.03	0.48	-1896	0.85***	0.48	0.94	-3400	0.03
PET^2		0.56	992	0.76***	0.48	0.93	-243	0.03	0.57	-2061	0.75***	0.49	0.94	-3400	0.03
TEMP	+	0.43	1212	0.83***	0.43	0.93	-215	0.03	0.38	-1751	0.88***	0.38	0.94	-3414	0.03
TEMP^2		0.48	1127	0.79***	0.32	0.93	-222	0.03	0.50	-1936	0.81***	0.39	0.94	-3414	0.03
FROST	-	0.52	1053	0.75***	0.52	0.93	-187	0.02	0.50	-1928	0.81***	0.50	0.94	-3387	0.02
PREC	+	0.55	1009	0.73***	0.55	0.93	-264	0.02	0.62	-2165	0.69***	0.62	0.95	-3471	0.01
PREC^2		0.58	951	0.76***	0.56	0.94	-331	0.02	–	–	–	–	–	–	–
WET	+	0.05	1641	0.92***	0.05	0.93	-272	0.01	0.06	-1388	0.92***	0.06	0.94	-3410	0.02
AET	**+**	**0.73**	**579**	**0.74*****	**0.73**	**0.94**	**-459**	**0.02**	**0.71**	**-2412**	**0.75*****	**0.71**	**0.95**	**-3587**	**0.01**
NPPann	+	0.51	1071	0.83***	0.51	0.94	-392	0.01	0.48	-1902	0.83***	0.48	0.95	-3523	0.01
NPPann^2		0.56	976	0.75***	0.45	0.94	-408	0.01	0.59	-2098	0.71***	0.49	0.95	-3523	0.01
NPPmin	+	0.54	1017	0.73***	0.54	0.93	-248	0.02	0.62	-2159	0.70***	0.62	0.95	-3458	0.02
NPPmin^2		0.60	904	0.70***	0.60	0.93	-270	0.03	0.64	-2206	0.70***	0.63	0.95	-3474	0.02
NPPmax	+	0.04	1655	0.92***	0.04	0.93	-275	0.01	0.03	-1360	0.92***	0.03	0.94	-3410	0.02
NPPmax^2		0.20	1493	0.85***	0.12	0.94	-321	0.01	0.17	-1491	0.86***	0.08	0.94	-3423	0.02

Table 3.2 continued

Seasonality															
NPPratio	+	0.52	1064	0.73***	0.52	0.93	-233	0.02	0.59	-2099	0.71***	0.59	0.94	-3441	0.02
NPPratio²		0.55	1001	0.72***	0.55	0.93	-244	0.03	–	–	–	–	–	–	–
NPPpulse	+	0.52	1056	0.73***	0.52	0.93	-233	0.02	0.59	-2105	0.71***	0.59	0.94	-3442	0.02
NPPpulse²		0.57	991	0.72***	0.55	0.93	-245	0.03	–	–	–	–	–	–	–
NPPcv	-	0.55	1002	0.79***	0.55	0.93	-293	0.02	0.51	-1941	0.82***	0.51	0.95	-3470	0.02
NPPcv²		**0.60**	**911**	**0.75*****	**0.58**	**0.93**	**-300**	**0.02**	**0.63**	**-2182**	**0.74*****	**0.60**	**0.95**	**-3493**	**0.02**
Heterogeneity															
TOPO	-	0.00	1689	0.91***	0.00	0.93	-198	0.03	0.00	-1341	0.92***	0.00	0.94	-3362	0.02
HABDIV	**-**	**0.01**	**1681**	**0.90*****	**0.01**	**0.93**	**-225**	**0.02**	**0.03**	**-1364**	**0.90*****	**0.03**	**0.94**	**-3372**	**0.03**
History															
REALM		**0.68**	**712**	**0.69*****	**0.60**	**0.93**	**-253**	**0.03**	**0.63**	**-2179**	**0.75*****	**0.40**	**0.94**	**-3403**	**0.03**

Note: Frugivore richness was log transformed and proportion of frugivores was arcsine square root transformed. GLM = non–spatial generalized linear model, SLM = spatial linear model (calculated as spatial autoregressive error model), Moran = Moran's *I* values. A ^{2} symbol indicates that both the linear and quadratic terms were included. The direction of effect of single predictor variables is indicated with + or -. R²–values of SLM indicate the non–spatial smooth (R^2_{trend}) and the total fit (R^2_{fit}: composed of non–spatial and spatial smooth). All values are mean values which were obtained from bootstrapping the whole dataset (*n* = 8,563 equal area grid cells) 100 times with a 10% random subsample (*n* = 856). Standard errors (not shown) of all mean values were generally much smaller than 10% of the mean values.

Mnemonics of variables: PET = potential evapotranspiration; TEMP = mean annual temperature; FROST = number of frost days; PREC = annual precipitation; WET = number of wet days; AET = actual evapotranspiration; NPPann = total annual above ground productivity; NPPmin = total productivity of the least productive three months; NPPmax = total productivity of the most productive three months; NPPratio = ratio of total productivity of the least productive three months and total productivity of the most productive three months; NPPpulse = seasonal pulse of production in relation to productivity of the most productive three months; NPPcv = coefficient of variation of monthly NPP values; TOPO = difference between maximum and minimum elevation; HABDIV = number of vegetation classes according to the Olson global land cover classification; REALM = biogeographic realm membership.

No other single climatic predictor than AET was similarly strong although most other water–energy, productivity, or seasonality variables explained around 40–60% of variation in frugivore richness and proportion (Table 3.2 and Appendix 3). The best explaining environmental variable in each category (i.e., water–energy and productivity, seasonality, and habitat heterogeneity) were AET, the coefficient of variation of monthly NPP values (NPPcv), and the number of vegetation classes (HABDIV). Total productivity of the most productive three months (NPPmax) as well as variables related to habitat heterogeneity (TOPO, HABDIV) had little explanatory power (Table 3.2 and Appendix 3). Non–spatial single–predictor GLMs generally contained a high amount of spatial autocorrelation in model residuals as indicated by highly significant Moran's I values (Table 3.2 and Appendix 3). The fitted single–predictor SLMs successfully removed the spatial autocorrelation structure in model residuals but generally showed similar results to non–spatial analyses (Table 3.2 and Appendix 3).

When considering the potential influence of the biogeographic history on frugivore distribution I found that realm membership (REALM) as a single predictor variable explained 63–65% of spatial variation in frugivore richness and proportion (see Table 3.2 for 1° and Appendix 3 for 2° equivalent models). Results from SLMs also revealed this important role of biogeographic realm membership (Table 3.2 and Appendix 3). Further analyses revealed that frugivore richness and proportion of frugivores significantly differed between all major biogeographical regions except between the Palearctic and Nearctic (Figure 3.3A, B). The Neotropics had the highest species richness and proportion of frugivorous birds, followed by Indo–Malaya and the Afrotropics (Figure 3.3A, B). Australasia had the lowest species richness and proportion of frugivorous birds of all tropical tropical realms and the temperate realms (Palearctic, Nearctic) generally had low numbers and proportions of frugivorous species (Figure 3.3A, B).

Multiple predictor models that included AET and REALM were found to explain between 80–85% variation in frugivore richness and proportion (Table 3.2, Appendix 4). Once accounting for environment (i.e., AET) frugivore richness and proportion of frugivores, respectively, still showed significant differences between almost all biogeographic regions (Figure 3.3C, D). However, once AET had been accounted for, variation in frugivore richness between the Afrotropics and Indo–Malaya and the Neotropics, respectively, was no longer statistically distinguishable. Most notably, the temperate Nearctic and Palearctic regions had the lowest residual richness and proportion (Figure 3.3C, D).

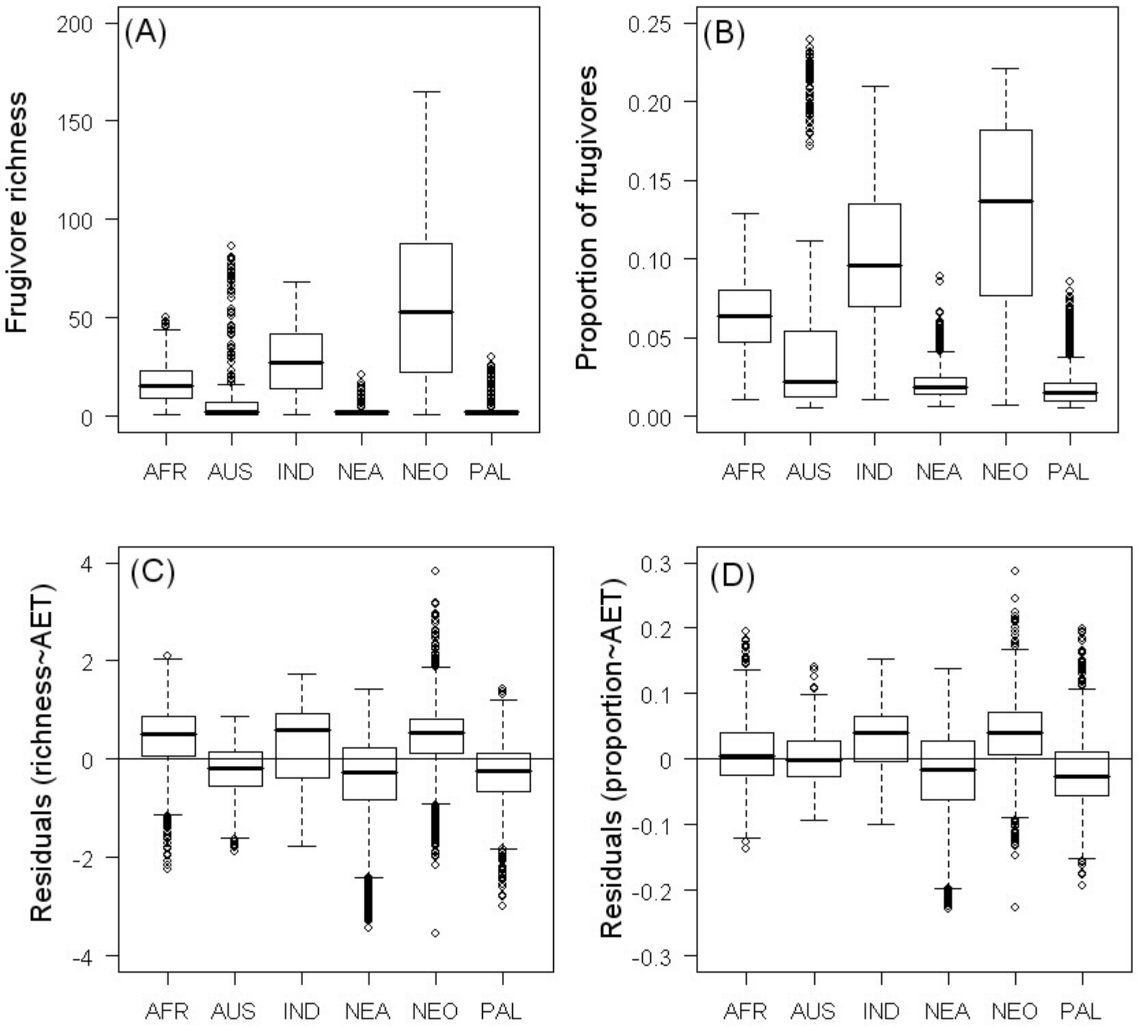


Figure 3.3: Biogeographic realm effects on avian frugivore diversity. (A) frugivore richness, (B) proportion of frugivores, (C) avian frugivore richness after controlling for actual evapotranspiration (AET), and (D) proportion of frugivores after controlling for AET. (C) and (D) illustrates residuals from a linear regression model with frugivore richness (log transformed) and proportion of frugivores (arcsine square root transformed), respectively, as response variables and AET as predictor variable. Biogeographic realms: AFR = Afrotropics, AUS = Australasia, IND = Indo–Malaya, NEA = Nearctic, NEO = Neotropics, PAL = Palearctic. In (A), (B) and (D), all group means were significantly different ($P < 0.05$) from each other except PAL and NEA (multiple pair wise comparisons with Tukey's HSD test). In (C), all group means were significantly different from each other except between AFR and IND, and between AFR and NEO.

The two–predictor models (including AET and REALM) were improved when including an interaction term between both variables, and these models explained between 88–89% variation in frugivore richness and proportion (Table 3.4 and Appendix 4). Examining the interaction between AET and REALM in more detail revealed that the proportion of frugivores increased linearly with AET in all tropical realms but that the slope of this relationship differed, decreasing from the Neotropics, Australasia, and Indo–Malaya to the

Afrotropics. In the Palearctic and the Nearctic there was no linear relationship between proportion of frugivores and AET (Figure 3.4).

Table 3.3: Results of multiple predictor models examined at resolution equivalent to 1° to explain global avian frugivore richness and the proportion of frugivores in avian assemblages. The multiple predictor model with the highest R²–value is highlighted in bold.

	GLM			SLM			
Variables	R^2	AIC	Moran	R^2_{trend}	R^2_{fit}	AIC	Moran
Frugivore richness							
AET + REALM	0.84	119	0.61***	0.83	0.94	-510	0.03
AET + REALM + AET:REALM	**0.88**	**-105**	**0.46*****	**0.85**	**0.94**	**-524**	**0.03**
AET + HABDIV	0.74	549	0.70***	0.69	0.94	-449	0.02
AET + NPPcv²	0.73	587	0.74***	0.71	0.94	-445	0.03
AET + NPPcv²+ HABDIV	0.74	549	0.70***	0.69	0.94	-461	0.02
AET + REALM + HABDIV	0.84	120	0.60***	0.82	0.94	-525	0.03
AET + REALM + NPPcv²	0.84	113	0.59***	0.82	0.94	-528	0.03
AET + REALM + HABDIV + NPPcv²	0.84	114	0.59***	0.81	0.94	-541	0.03
Proportion of frugivores							
AET + REALM	0.80	-2729	0.69***	0.75	0.95	-3616	0.02
AET + REALM + AET:REALM	**0.88**	**-3166**	**0.44*****	**0.80**	**0.95**	**-3657**	**0.01**
AET + HABDIV	0.76	-2548	0.67***	0.71	0.95	-3581	0.01
AET + NPPcv²	0.74	-2482	0.71***	0.70	0.95	-3596	0.01
AET + NPPcv²+ HABDIV	0.77	-2586	0.64***	0.70	0.95	-3596	0.02
AET + REALM + HABDIV	0.82	-2806	0.62***	0.75	0.95	-3615	0.02
AET + REALM + NPPcv²	0.83	-2848	0.58***	0.74	0.95	-3628	0.02
AET + REALM + HABDIV + NPPcv²	0.84	-2882	0.56***	0.74	0.95	-3628	0.02

Note: Frugivore richness was log transformed and proportion of frugivores was arcsine square root transformed. GLM = non–spatial generalized linear model, SLM = spatial linear model (calculated as spatial autoregressive error model), Moran = Moran's *I* values. A ^{2} symbol indicates that both the linear and quadratic terms were included. R²–values of SLM indicate the non–spatial smooth (R^2_{trend}) and the total fit (R^2_{fit}: composed of non–spatial and spatial smooth). All values are mean values which were obtained from bootstrapping the whole dataset (*n* = 8,563 equal area grid cells) 100 times with a 10% random subsample (*n* = 856). Standard errors of all mean values (not shown) were generally much smaller than 10% of the mean values.

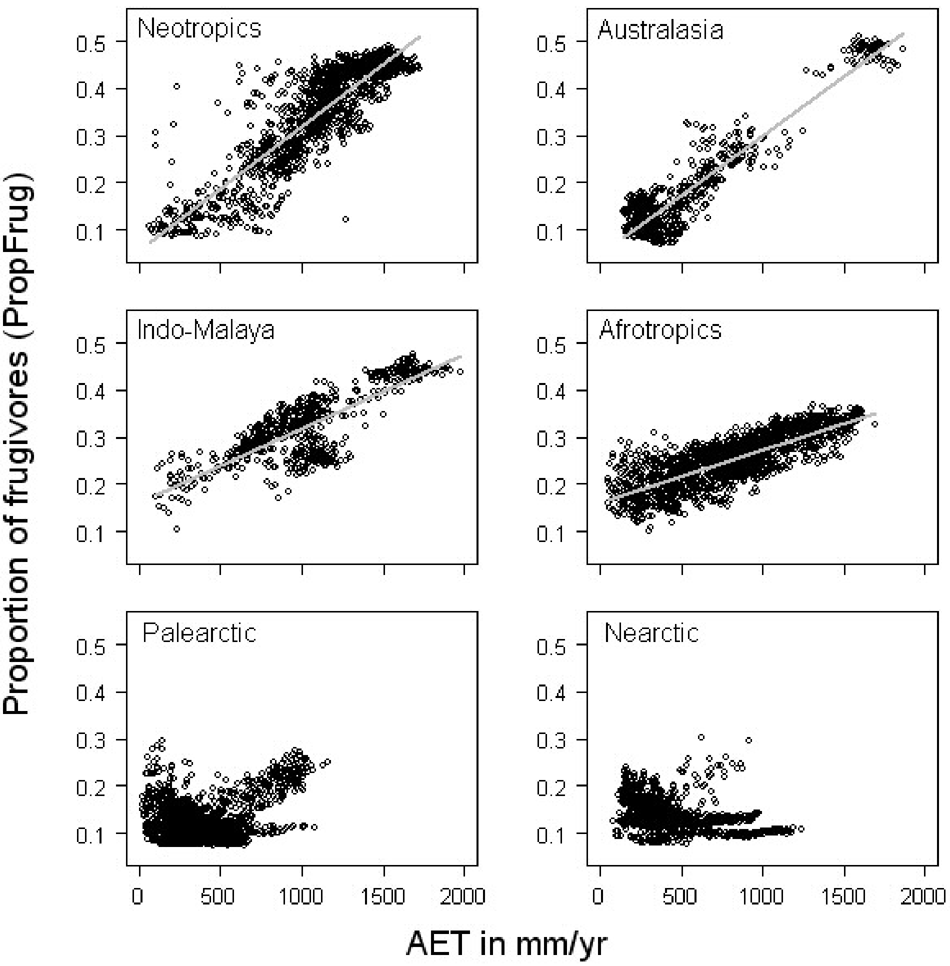


Figure 3.4: Relationships between proportion of frugivores (PropFrug) and actual evapotranspiration (AET) within six biogeographic realms. Analyses were done with arcsine square root transformed PropFrug across an equal area grid equivalent to 1° grid cell size (12,364 km² area). Note that PropFrug increases linearly with AET in all tropical realms but that the slope of this relationship decreases from the Neotropics to the Afrotropics. The relationship is not significant in the Palearctic and Nearctic. Neotropics: PropFrug = 0.06 + 2.63e-04 AET, $F_{[1,13]} = 45$, $P < 0.001$; Australasia: PropFrug = 0.05 + 2.51e-04 AET, $F_{[1,20]} = 170$, $P < 0.001$; Indo–Malay: PropFrug = 0.16 + 1.57e-04 AET, $F_{[1,8]} = 18$, $P < 0.01$; Afrotropics: PropFrug = 0.16 + 1.12e-04 AET, $F_{[1,13]} = 23$, $P < 0.001$; Palearctic: PropFrug = 0.11 + 0.50e-04 AET, $F_{[1,41]} = 3$, $P = 0.09$; Nearctic: PropFrug = 0.16 – 0.55e-04 AET, $F_{[1,14]} = 3$, $P = 0.12$. Significance levels and F–statistics were corrected for spatial autocorrelation using geographically effective degrees of freedom (Dutilleul 1993).

3.5 Discussion

Although continental–scale patterns and biogeographic comparisons of frugivore diversity have been elucidated before (Karr 1976b; Fleming et al. 1987; Fleming 2005; Primack and Corlett 2005; Kissling et al. 2007), my study constitutes the first comprehensive global–scale analysis on geographic and taxonomic patterns of avian frugivore diversity and their potential environmental and historical determinants. My analyses revealed that the global distribution of frugivorous birds is determined by contemporary climate (especially water–energy availability and region- and clade-specific patterns of diversification of frugivorous clades, as indicated by the strong statistical signal of biogeographic region. High species numbers and proportions of frugivores are found in all tropical realms (with exceptionally high species richness in the Neotropics) but temperate regions and the Australian continent are generally species–poor. Significant differences in frugivore richness and proportion exist between most biogeographic regions (Figure 3.3A, B) and remain even once environmental factors (i.e., AET) have been accounted for (Figure 3.3C, D). Together with realm–specific responses of frugivores to water–energy dynamics (Figure 3.4) and geographic patterns of diversification within major clades (Figure 3.2) my results suggest that historical influences on global patterns of avian frugivore diversity cannot be neglected.

My analyses with a wide range of environmental variables showed that the global diversity of frugivorous birds is best explained by actual evapotranspiration and other measures of productivity. This is in line with recent findings from global–scale analyses that variables related to water–energy dynamics are the core predictors of vascular plant (Kreft & Jetz 2007) and overall bird diversity (Hawkins et al. 2003b). Some evidence suggests that AET and other water–energy measures may act indirectly on bird species richness via effects on plants (Hawkins et al. 2005), but a rigorous broad-scale scrutiny of this putative pathway is still missing. The signal of such a connection should be particularly strong for frugivorous birds where water and energy act indirectly via effects on food plants (Kissling et al. 2007). These indirect climatic effects on frugivore richness via plants could be composed of climatic effects on fruit production (e.g., Karr 1976a; Levey 1988) and fruiting phenologies (van Schaik et al. 1993). However, there could also be "hidden" historical and evolutionary components in the statistical relationship between AET and frugivore richness if AET covaries with past climate history and/or with the evolutionary diversification of fleshy-fruited plants.

The extremely high Neotropical bird diversity has been attributed to a number of factors including the great extent of rainforests, a substantial faunal exchange when North and South America met (the "Great American Interchange"), a great complexity of geographic dispersal barriers (rivers, mountains) in interaction with past climate change, and the location and extent of past wet–forest refuge areas (Karr 1976b; Haffer 1969, 1997; Newton 2003). I find that the geographic pattern of avian frugivore richness in the Neotropics (Figure 3.1A) largely resembles that of overall bird species richness in this region (Newton 2003; Orme et al. 2005; Appendix 2). Many bird clades which have undergone extensive recent evolutionary radiations in the Neotropics (Ricklefs 2002; Ericson et al. 2003; Newton 2003) include orders and families with large numbers of frugivorous species (Table 3.1; Figure 3.2). The overall pattern of avian frugivore diversity is driven to a large extent by the Passeriformes (Figure 3.2A) and by a relatively high proportion of frugivorous species in the Psittaciformes, Piciformes, and Craciformes (Figure 3.2C-E, Table 3.1). For frugivores in particular, there is an exceptionally high diversity of fleshy–fruited plants in the Neotropics (Snow 1981; Gentry 1982) which is composed of two major radiations, an Amazonian centered radiation of canopy trees and an Andean–centered radiation of epiphytes and understorey shrubs (Gentry 1982). This high food plant diversity in both lowland as well as mountain regions in the Neotropics could explain the high species richness of frugivores in the Andes and the relatively similar proportion of frugivores in lowland and mountain habitats at equatorial latitudes in South America (Figure 3.1B). A recent cross–continental comparison of 27 field studies on plant–frugivore communities supports the idea that the relationship between food plant diversity and species richness of vertebrate frugivores is particularly strong in the Neotropics (Fleming 2005).

The hypothesis that the geographic distribution of fleshy–fruited plant taxa has profoundly influenced the diversification of frugivorous birds could explain the realm–specific richness–environment relationships (Figure 3.4) if AET co-varies with food plant diversity. In contrast to the Neotropics, hotspots of overall bird species richness in other tropical or subtropical mountain ranges (e.g., the East African mountains or the Himalayas, see Orme et al. 2005) are not reflected by frugivores. Instead, in these regions frugivorous birds are more common in the lowland tropical rainforests where the diversity of food plants is higher (Kissling et al. 2007). In Africa, the low number and proportion of frugivorous bird species (Figure 3.3A, B) parallels a very low species richness of fleshy–fruited plants (Snow 1981; Fleming 2005). Similarly, in Southeast Asia the lower species number and proportion of frugivores relative to the Neotropics (Figure 3.3A, B) could be explained by the dominance of non–fleshy fruited trees (Dipterocarpaceae) which could have limited the diversification of co–occurring fleshy fruited canopy and understorey plants (Fleming et al. 1987; Primack & Corlett 2005). There is, however, an exceptionally high diversity of fig trees (*Ficus* spp., a keystone resource for frugivores in the tropics; Shanahan et al. 2001; Harrison 2005) in the Indo–Pacific region, which could explain why Indo–Malaya and New Guinea harbor higher species numbers and proportion of frugivores than the Afrotropics (Figures 3.1 and 3.3).

Even after accounting for AET (and possibly for potential co-variation with food plant diversity), Australasia and the Northern temperate regions (Nearctic, Palearctic) show significantly lower species richness than the three other realms (Neotropics, Indo–Malaya, Afrotropics; Figure 3.3C). These differences might be explained by historical legacies related to climate change and niche conservatism (Hawkins et al. 2005, 2007; Wiens and Donogue 2004; Wiens and Graham 2005). During the Cretaceous and early Tertiary the Australian continent was warm and wet, but at the end of the Miocene it experienced increasing aridity and major decreases in precipitation. These long–term climatic shifts had a profound impact on speciation and extinction rates in Australia likely leaving an imprint on the contemporary bird richness pattern (Hawkins et al. 2005). Bird clades which initially evolved under wetter conditions may have failed to adapt to drier conditions or arid habitats suggesting that ancestral niches are conserved over evolutionary time (Hawkins et al. 2005; Wiens and Donogue 2004; Wiens and Graham 2005). We hypothesize that the extraordinary low frugivore richness and proportion in the Nearctic and Palearctic (Figure 3.1) might similarly reflect phylogenetic niche conservatism: frugivorous bird species or their food plants may have predominantly originated in tropical climates and harsh climates acted as barriers to the invasion of temperate zones by tropical clades (Prinzing et al. 2001; Wiens and Donogue 2004; Hawkins et al. 2007).

Additionally to availability of food plants, niche conservatism, and past climate change, some authors have suggested that the evolution or immigration of ecological competitors such as fruit–eating mammals might have influenced geographic patterns of avian frugivore distribution (Fleming et al. 1987; Primack & Corlett 2005). For instance, it has been hypothesized that the evolution of medium– to large–sized ground–living frugivorous birds like the Neotropical chachalacas, guans, and curassows (Cracidae, Figure 3.2E) could have been favored by the absence of terrestrial frugivorous mammals whereas the presence of terrestrial fruit-eating primates in the forests of Africa may have prevented the evolution of such ground-living frugivorous birds (Fleming et al. 1987; Primack & Corlett 2005). The Indomalayan region and Oceania have seen exceptional radiations of fruit-eating pigeons and doves (Columbiformes), perching birds (Passeriformes), and hornbills (Bucerotiformes) which could have been favored by the absence of competition for fruits with primates. Similarly, the high diversity of parrots (Psittaciformes) in the Neotropics (Figure 3.2c) might be partly a result of the low number of squirrel species with which parrot diets often overlap (Primack & Corlett 2005). I hypothesize that the lower proportion of avian frugivores in the Afrotropics compared to Indomalayan and Neotropical regions once AET had been accounted for (Figure 3.3D) and the lower slope in the relationship between AET and frugivore proportion (Figure 3.4) could be due to higher competition with mammals. Future studies should investigate the temporal and spatial co-occurrence of frugivorous bird and mammal species at biogeographic scales.

Although the global distribution of avian frugivore diversity is statistically best explained by water–energy dynamics, the variation in geographic patterns of frugivore richness across biogeographic realms cannot be understood without taking historical processes into account. My results suggest that major differences in avian frugivore diversity between biogeographic regions have likely been influenced by the diversification of food plants, niche conservatism, and past climate change. This supports the idea that the availability of food resources over geographic and evolutionary time scales ultimately determines geographic patterns of frugivore richness (Fleming et al. 1987; Fleming 2005). Future research will likely benefit from using phylogenetic reconstructions to examine the diversification of fleshy–fruited plants and frugivores in different biogeographic regions. Broad-scale distribution data for other frugivorous taxa (e.g., mammals) would allow assessing the potential effects of competitors on the diversification and distribution of frugivorous birds. Frugivores and their food plants promise to be a rewarding model system to better understand how biotic interactions and environmental constraints affect community assembly over macroevolutionary timescales and broad geographic scales.

4 FOOD PLANT DIVERSITY AS BROAD-SCALE DETERMINANT OF AVIAN FRUGIVORE RICHNESS

4.1 Abstract

The causes of variation in animal species richness at large spatial scales are intensively debated. Here I examine whether the diversity of food plants, contemporary climate and energy, or habitat heterogeneity determine species richness patterns of avian frugivores across sub-Saharan Africa. Path models indicate that species richness of *Ficus* (their fruits being one of the major food resources for frugivores in the tropics) has the strongest direct effect on richness of avian frugivores whereas the influences of variables related to water-energy and habitat heterogeneity are mainly indirect. The importance of *Ficus* richness for richness of avian frugivores diminishes with decreasing specialization of birds on fruit eating, but is retained when accounting for spatial autocorrelation. I suggest that a positive relationship between food plant and frugivore species richness could result from niche assembly mechanisms (e.g. coevolutionary adaptations to fruit size, fruit color, or vertical stratification of fruit presentation) or, alternatively, from stochastic speciation-extinction processes. In any case, the close relationship between species richness of *Ficus* and avian frugivores suggests that figs are keystone resources for animal consumers, even at continental scales.

Keywords: Africa, coevolution, community assembly, macroecology, plant-frugivore interactions, spatial autoregressive model.

4.2 Introduction

A large number of hypotheses have been proposed to explain patterns of species richness at broad spatial scales (Willig et al. 2003). Based on high correlations with species richness, contemporary climate and energy variables (e.g. precipitation, temperature and/or evapotranspiration) are often thought to explain spatial variation in species richness better than any other non-climatic variable (Wright 1983; Hawkins et al. 2003a; Currie et al. 2004). However, a number of other factors also determine broad-scale patterns of species richness, including topography, habitat diversity, or regional and evolutionary history (e.g. Rahbek & Graves 2001; Jetz & Rahbek 2002; Willig et al. 2003). Despite a century of debate about the primary determinants of species richness, the underlying causal mechanisms behind the patterns still remain vague (Willig et al. 2003; Currie et al. 2004; Rahbek et al. 2007).

For vascular plants it is widely argued that precipitation and ambient energy are the main drivers of species richness (Hawkins et al. 2003a; Field et al. 2005). Water availability, heat, and light directly influence plant growth and productivity and are essential to plant physiological processes (Waide et al. 1999; Field et al. 2005). Higher productivity might result in more species because physiological tolerances of individual species vary for different climatic conditions (the ‘physiological tolerance hypothesis’; Currie et al. 2004), or, alternatively, because more productive areas are warmer and evolutionary rates might be faster at higher ambient temperatures, e.g. due to shorter generation times, higher mutation rates, and/or faster physiological processes (‘speciation rate hypothesis’; Allen et al. 2006). For animals, especially for endotherms, the relationships between species richness and water, energy, and climate are less pronounced than for plants (Rahbek & Graves 2001; Jetz & Rahbek 2002; Hawkins et al. 2003a, b). One likely explanation is that energy might not directly influence animal species richness via its effect on animal’s physiological requirements or evolutionary rates but rather indirectly via trophic relationships (Wright 1983; Hawkins et al. 2003a, b; Currie et al. 2004). This hypothesis assumes that richness of animals is determined by the abundance, distribution, and diversity of food resources (e.g. plant biomass for herbivores, fruits for frugivores).

At small spatial scales, animal species richness can be associated with the abundance, diversity, or partitioning of food resources (e.g., Herrera 1985; Siemann et al. 1998; Novotny et al. 2006). This relationship is, however, difficult to test at large spatial extents because it is difficult to map food resources for animal groups at continental scales (e.g., insects for insectivorous birds). One possibility to test for a link between animal species richness and resources is to relate the species richness of animals to the species richness of their food items (e.g., food plants; Hawkins & Porter 2003; Márquez et al. 2004; Novotny et al. 2006). However, correlations between animal and plant species richness can also result from both groups responding similarly to the same environmental variables. After accounting for these environmental variables, a convincing dependency of animal on plant species richness has not been demonstrated so far at broad spatial scales (Hawkins & Porter 2003; Hawkins & Pausas 2004; Márquez et al. 2004).

Plant-frugivore interactions might be an ideal model system for continental analyses of animal and plant species richness. Most frugivorous animals heavily rely on fruits, particularly in the tropics (Fleming et al. 1987). In a number of fine-scale field studies it has been shown that the richness of frugivorous animals is largely dependent on fruit availability (e.g., Herrera 1985; Fleming et al. 1987; Bleher et al. 2003). Among fruiting plants, the fig genus (*Ficus*) has been considered to be a keystone plant resource for many frugivores because of large crop sizes and asynchronous fruiting patterns throughout the year (Terborgh 1986; Lambert & Marshall 1991; Shanahan et al. 2001a; Bleher et al. 2003; Harrison 2005; but see Gautier-Hion & Michaloud 1989). Thus, the diversity and abundance of figs might set the carrying capacity for frugivorous animals in the tropics. Correspondingly, Goodman & Ganzhorn (1997) proposed that avian frugivore richness might depend directly on species richness of *Ficus* trees. However, no rigorous test of this ‘fig-frugivore-richness hypothesis’ has been conducted at a large regional scale such as a continent.

In this study I examine whether the richness of *Ficus* species at a continental scale (i.e., sub-Saharan Africa) influences avian consumer richness by examining a comprehensive database with a resolution of 1° latitude and longitude, summarizing the distribution of all breeding birds (n = 1,771), all *Ficus* species (n = 86), and five climatic and environmental variables (precipitation, temperature, productivity, topography, and ecosystem diversity). I classify frugivorous birds into three classes (obligate, partial, and opportunistic fruit-eaters) and predict the association between frugivore and *Ficus* richness to be stronger for those frugivores that are more specialised on fruit eating. I apply path analysis to disentangle inter-correlations between variables and compare the results of this non-spatial method with results from spatial regression models that account for the spatial autocorrelation structure within the dataset.

4.3 Methods

4.3.1 Bird data

I used an updated version (September 29, 2005) of the comprehensive distribution database of African breeding birds compiled by the Zoological Museum, University of Copenhagen (see Burgess et al. 1998 and Brooks et al. 2001 for methodology, and Jetz & Rahbek 2002 for sources used for mapping). Maps for each species represent a conservative extent-of-occurrence extrapolation of the breeding range at a resolution of 1° x 1° cells (latitude-longitude). Data were compiled from standard reference works and dozens of other published references (including recent atlases and unpublished research) and, for difficult regions and taxa, experts' opinions were sought (the full list of sources is available at http://www.zmuc.dk/commonweb/research/biodata.htm). Most of the northern part of continental Africa, the Sahara, is marked by extreme species scarcity (Jetz & Rahbek 2002) and almost all species in it and North of it belong to the Eurasian biome. I thus focused my analyses on all 1,771 breeding bird species south of the Saharan desert ecoregion (Figure 1E) with ecoregion boundaries for the South Sahara as Northern boundary (Olson et al. 2001). The sub-Saharan database contains 434,789 records on 1,737 cells. The extent of the grid was chosen to be similar to the one used by Jetz & Rahbek (2002) to make results comparable. I therefore excluded cells containing less than 50% dry land. Cell size varies only slightly with latitude, ranging from 10,188 km^2 to 12,308 km^2. The WORLDMAP computer program, version 4.20.24 (1999, P. H. Williams, Natural History Museum, London) was used to overlay the distributional data.

4.3.2 Frugivore classification

The diets of all bird species in the sub-Saharan database were determined from a comprehensive literature survey (see Appendix 5 for references and classification procedure). I distinguished major and minor food items for each species from the literature by using keywords on food and feeding behavior (e.g. the terms "almost exclusively", "entirely", "almost entirely", "mainly", "prefers" were taken to define major food items, and "occasionally", "probably", "sometimes", "when available" etc. to define minor food items). I classified all species into three frugivore guilds depending on diet preference for fruits: (i) obligate frugivores (species that primarily feed on fruits, i.e. the only major food item are fruits), (ii) partial frugivores (species that have, beside fruits, other major food items, e.g., terrestrial invertebrates), and (iii) opportunistic fruit-eaters (species that only occasionally eat fruits as supplementary food). The three frugivore guilds were characterized by the degree of avian specialization on fruits, with obligate frugivores being most dependent and opportunistic fruit-eaters being least dependent on availability of fruits. This classification of frugivorous bird species integrates the best knowledge currently available on feeding behavior of African birds (Appendix 5). For the interested reader I also provide species lists of all African frugivores (Appendix 6).

4.3.3 *Ficus* data

Individual distribution maps for all *Ficus* species were provided by the Iziko Museums of Cape Town (2005, S. van Noort and J.-Y. Rasplus, available at http://www.figweb.org/Ficus/Species_index/afrotropical_species.htm). The maps are based on country records and the extent of species occurrence is approximated based on habitat affiliations of each species (S. van Noort, Iziko Museums of Cape Town, pers. comm.). To create a *Ficus* richness map for sub-Saharan Africa, I first georeferenced the maps of each species and digitized the geographic ranges. The ranges of all individual *Ficus* species were then overlaid on a 1° x 1° grid cell map. For each species I assigned the value 1 indicating species presence for each 1° grid cell when the cell contained more than 10% distribution cover. *Ficus* richness values were then calculated for each cell by adding all presence values. I tested the sensitivity of the 10% distribution cover threshold by calculating *Ficus* richness values from *Ficus* presence maps based on thresholds of 0, 5, 15, and 20% distribution cover. All of the resulting *Ficus* richness patterns were highly correlated with each other (Spearman rank correlations $r_s > 0.98$) indicating that the arbitrarily chosen threshold of 10% did not distort the overall *Ficus* richness pattern. Geoprocessing was done with the software ArcView 3.2 and ArcGIS 9. Taxonomy of *Ficus* follows Berg & Wiebes (1992) and Shanahan et al. (2001a: appendix 1). The geographic distributions of different subspecies were pooled as one species. *Ficus thonningii* was used as a synonym for *Ficus petersii* and *Ficus burkei*. A total of 86 *Ficus* species were thus finally distinguished in my study (Appendix 7).

4.3.4 Environmental variables

Besides species richness of *Ficus* I included five environmental variables as potential determinants of the richness pattern of avian frugivores. The environmental variables included two climatic variables related to water input (precipitation) and ambient energy (temperature), a measure of productivity, a measure of topographic heterogeneity, and habitat diversity (see Table 4.1 for details). These variables have previously been shown to be strongly correlated with species richness of birds and woody plants at continental scales (Waide et al. 1999;

Rahbek & Graves 2001; Jetz & Rahbek 2002; Hawkins et al. 2003a, b; Field et al. 2005). Data for precipitation and temperature were extracted from the mean monthly climatic database for the period 1961-1990 provided by the Intergovernmental Panel on Climate Change (IPCC), available online at http://ipcc-ddc.cru.uea.ac.uk/obs/get_30yr_means.html (see New et al. 1999 for methodology). I used mean annual precipitation (mm/yr) and mean daily maximum temperature (°C) (following Jetz & Rahbek 2002), degraded from 0.5° to 1° resolution. For productivity, I chose net primary productivity (NPP) predictions from the DOLY global model (Woodward et al. 1995). Topographic heterogeneity was quantified as altitudinal range (difference between maximum and minimum elevation) of the 1-minute digital elevation model presented by Hutchinson et al. (1996). Ecosystem diversity was estimated by counting the number of distinct ecosystems in each cell from a recently published map of global ecosystems (Olson 1994; available at http://edcsns17.cr.usgs.gov/glcc/). While both ecosystem diversity and topographic relief are potential important predictors in their own right (Rahbek & Graves 2001), they are also rough surrogate variables for habitat heterogeneity.

Table 4.1: Predictor variables used to explain spatial variation in richness of avian frugivore species across sub-Saharan Africa.

Mnemonic	Predictor variables (units)	Hypothesis (reference*)
FigRich	Number of *Ficus* species per 1° cell (count)	Food plant diversity (1, 2)
Prec	Mean annual precipitation (mm/yr)	Water availability (3, 4, 5, 6)
MaxTemp	Mean daily maximum temperature (C°)	Ambient energy (4, 5)
NPP	Net primary productivity (t C ha^{-1} yr^{-1})	Productivity (4, 5, 7)
AltRange	Topographic relief (altitudinal range in m)	Topographic heterogeneity (4, 6)
EcoDiv	Number of ecosystems in cell (count)	Ecosystem diversity (6)

* (1) Goodman & Ganzhorn (1997); (2) Bleher et al. (2003); (3) Field et al. (2005); (4) Jetz & Rahbek (2002); (5) Hawkins et al. (2003a); (6) Rahbek & Graves (2001); (7) Waide et al. (1999)

4.3.5 Statistical analysis

To disentangle the relative roles of predictor variables, many of which co-varied (Appendix 9), and to assess the potential influence of spatial autocorrelation on the robustness of my results, the analysis comprised a three-step process.

In the first step, I calculated Spearman rank correlations (r_s) between all variables in the data set to examine the strength of the relationships between predictor variables, and between predictor and response variables. In the second step, I applied path analysis (Mitchell 1992; Quinn & Keough 2002), which allows considering hypothesized causal relationships in datasets with more than one dependent variable and effects of dependent variables on one another. Whereas path analysis cannot replace experimental manipulations for detecting causal links between variables it is one of the few methods to test ecological and evolutionary hypotheses at broad spatial scales (Hawkins & Porter 2003; Márquez et al. 2004). Path models are usually presented in path diagrams where hypothesized causal relationships between response and predictor variables are indicated by arrows, and the effect of one variable on another is measured by standardized partial regression coefficients from multiple regression models (Mitchell 1992; Quinn & Keough 2002). Path analysis further allows to partition correlation between predictor and response variables (so called “total effects”) into direct and indirect effects. Direct effects are measured by the standardized partial regression coefficients between a predictor variable and a response variable (i.e., the direct link) whereas indirect effects are calculated by adding the products of all standardized partial regression coefficients over all paths between a predictor and a response variable (i.e. including indirect links via other correlated predictor variables, see Mitchell 1992; Quinn & Keough 2002).

The path models were designed to represent hypotheses of how predictor variables might interact with each other to influence avian frugivore richness, and the links were thus based on a priori knowledge or logical relationships among the predictor variables (see references in Table 4.1). Because the main focus was on the potential influence of *Ficus* richness on frugivore richness, I first generated a path model that excluded *Ficus* richness followed by a model to which *Ficus* richness was added. Comparison of the first model with the second model allowed us to evaluate whether *Ficus* richness had a significant effect on frugivore richness itself, or whether it only acted upon frugivore richness through causal relationships with other environmental variables. I assessed the path models using Structural Equation Modeling (SEM), which is an extension of path analysis (see Mitchell 1992 for an introduction). Model evaluation was done by comparing the fitted path models to a baseline model where observed variables were assumed to be uncorrelated with each other (Arbuckle 2003: Appendix C). I used the normed fit index (NFI) as a fit measure (Bentler and Bonett 1980), which ranges between zero and one, with values close to one indicating a good fit (Arbuckle 2003). The χ^2 goodness of fit test (which is often used to assess the null hypothesis that a path model fits to the data) is invalid in this case because the large sample size (n = 1737) would have almost certainly resulted in significant departures from the null hypothesis (see Arbuckle 2003 and his Appendix C). I additionally tested whether multiple regression models with all explanatory variables (Table 4.1) explained frugivore species richness better than multiple regression models where *Ficus* richness was excluded as explanatory variable. These model comparisons were done with the Akaike Information Criterion (AIC), a model selection criterion which accounts for both model fit and model complexity (Burnham & Anderson 2002).

In my third analysis I tested for the presence of spatial autocorrelation because the data violate the assumption of independently distributed errors in regression models (Legendre & Legendre 1998), and, as a consequence, the effects of explanatory variables might thus be exaggerated (Lichstein et al. 2002). To quantify the pattern of autocorrelation in the data set, I calculated Moran's I values (i.e. a measure of autocorrelation) across twenty distance classes (one distance class corresponds to 112 km) and plotted them in so-called correlograms (Legendre & Legendre 1998). I first calculated Moran's I for all raw bird richness data (i.e. obligate frugivores, partial frugivores, opportunistic fruit-eaters, and all birds), and then fitted multiple regression models with all predictor variables (i.e. models which are equivalent to all direct effects on avian richness in the path models) and recalculated Moran's I on the residuals. Any reduction in spatial autocorrelation among residuals reflects the amount of spatial structure in the species richness data that can be explained by the spatial structure in predictor variables. Because fitting the multiple regression models with all predictor variables did not remove all of the spatial autocorrelation in the richness variables, I fitted spatial autoregressive models (Cliff & Ord 1981; Cressie 1993) which augment the multiple regression models with an additional term that accounts for patterns in the response variable that are not predicted by explanatory variables, but are instead related to values in neighboring locations. I then compared the standardized partial regression coefficients (Quinn & Keough 2002) from the spatial autoregressive models to those of the path models (i.e. direct effects on avian richness) to assess whether the relative importance of parameter estimates changes when the spatial autocorrelation structure in the response variables is removed.

All statistical analysis was done with the free software R (R Development Core Team 2005) except for the path models which were calculated with the AMOS software (Arbuckle 2003). The spatial models were calculated as "spatial simultaneous autoregressive error models" using the R library "spdep", version 0.3-25 (2006, R. Bivand, available at http://cran.r-project.org/src/contrib/Descriptions/spdep.html). These models are a special type of simultaneous autoregressive models and assume that the response at each location (i) is a function not only of the explanatory variable at i, but of the values of the response at neighboring locations (j) as well (Cliff & Ord 1981; Anselin 1988; Cressie 1993). I defined the spatial neighborhood with a distance of 112 km including the four neighboring cells that directly join each focal cell (the rook's case). The spatial weights matrix was calculated with a row standardized coding scheme that scales the co-variances based on the number of neighbors of each region (see R library "spdep" for details, reference above). Moran's I values and correlograms were calculated with the R library "ncf", version 1.0-9 (2006, O. N. Bjørnstad, available at http://asi23.ent.psu.edu/onb1/). To improve the normality of distributions I transformed all endogenous variables (i.e., those with incoming arrows in the path models) and used transformed values in all regression analyses. Precipitation, maximum temperature, and NPP+1 were log-transformed whereas all richness measures (i.e. species richness of *Ficus*, obligate frugivores, partial frugivores, opportunistic fruit-eaters, all birds, and ecosystem diversity) were square-root transformed. These transformations yielded the best approximations of normal distributions and were performed to meet the normality of errors assumption (Mitchell 1992; Quinn & Keough 2002). Analyses with untransformed values gave qualitatively similar results.

4.4 Results

4.4.1 Geographic patterns of species richness

Species richness of obligate avian frugivores (*n* = 92) across sub-Saharan Africa is highest in tropical rainforest regions at equatorial latitudes (Figure 4.1A), particularly in coastal areas of West Africa and in the Congo Basin, but also within the East African mountains. Hotspots of obligate frugivore richness are thus not congruent with hotspots of overall bird species richness, which are mainly found in the Eastern parts of sub-Saharan Africa (Figure 4.1E). Geographic patterns of species richness of partial frugivores (*n* = 200; Figure 4.1B) are more similar to obligate frugivore richness (Figure 4.1A) than to overall bird species richness (*n* = 1,771; Figure 4.1E) whereas opportunistic fruit-eaters (*n* = 290; Figure 4.1D) closely resemble overall bird species richness (Figure 4.1E) rather than obligate frugivore richness (Figure 4.1A). The species richness of *Ficus* trees (*n* = 86) is highest in the Congo Basin and relatively low in South Africa and along the Eastern parts of Africa (Figure 4.1C), and thus largely congruent with obligate frugivore richness patterns (Figure 4.1A).

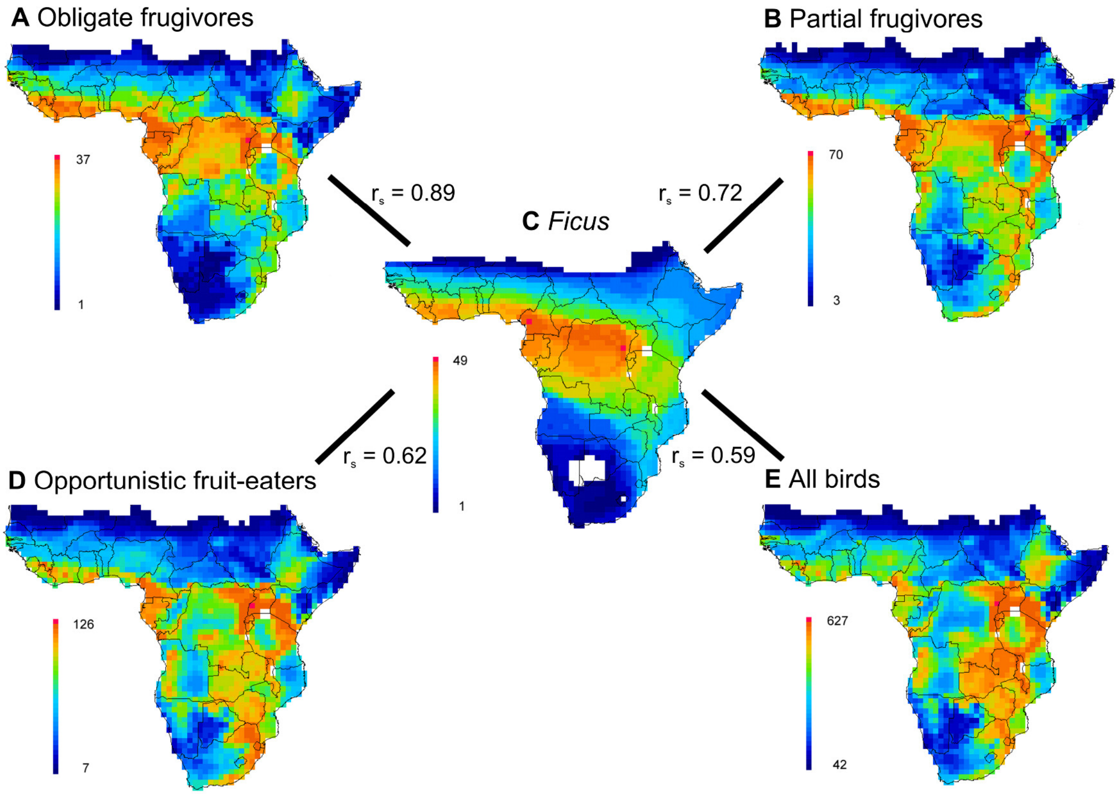


Figure 4.1: Geographic patterns of species richness in Sub-Saharan Africa. (A) obligate frugivores (92 species), (B) partial frugivores (200 species), (C) all *Ficus* trees (86 species), (D) opportunistic fruit-eaters (290 species), and (E) all breeding birds (1771 species). Equal-frequency classification is shown, with color ramps indicating minimum (dark blue, bottom of legend) and maximum (dark red, top of legend) species richness. Note that the scale of richness differs among figures.

4.4.2 Determinants of frugivore richness

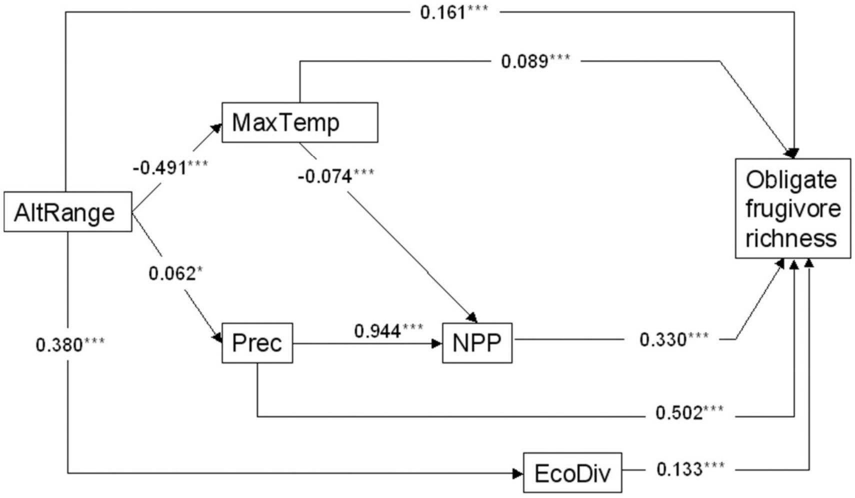
Simple correlations between *Ficus* and bird species richness indicated that they positively co-vary across sub-Saharan Africa (Figure 4.1 and Appendix 8). As expected, the relationship was strongest for obligate frugivores ($r_s = 0.89$), intermediate for partial frugivores ($r_s = 0.72$), and lowest for opportunistic fruit-eaters ($r_s = 0.62$) and overall bird species richness ($r_s = 0.59$). Precipitation, NPP, ecosystem diversity, and maximum temperature were also strongly correlated ($r_s > 0.60$) with avian species richness in almost all cases, and precipitation and NPP highly co-varied with each other and with species richness of *Ficus* trees ($r_s > 0.84$). Maximum temperature, altitudinal range, and ecosystem diversity generally showed weaker correlations ($r_s < 0.50$) with other predictor variables (Appendix 9).

The path model without *Ficus* richness (Figure 4.2A) explained 74.2% of the variance in richness of obligate frugivorous birds, and the measure of fit (NFI = 0.891) indicated that the model adequately described the data structure. Precipitation had the strongest direct effect on richness of obligate frugivorous birds followed by NPP, altitudinal range, ecosystem diversity, and maximum temperature (Figure 4.2A). Including richness of *Ficus* trees in the path model improved the explanatory power (81.7%) and the overall fit of the model (NFI = 0.920), and I thus consider this path model (Figure 4.2B) as a better description of obligate frugivore richness patterns. Model selection based on AIC values also indicated that a multiple regression model with *Ficus* species richness (AIC = 2245) supported the obligate frugivore richness data better (i.e. had a lower AIC value) than a multiple regression where *Ficus* richness had been excluded (AIC = 2838, ΔAIC = 593). In the path model with *Ficus* richness (Figure 4.2B), the direct effect of precipitation on richness of obligate frugivorous birds was very low (0.095) and richness of *Ficus* trees instead became the most important variable with the strongest direct effect (0.546) on richness of obligate frugivorous birds (Table 4.2; Figure 4.2B). When including indirect effects, the relative importance of precipitation increased (Table 4.2) because it was very strongly correlated with NPP and *Ficus* richness (Figure 4.2B). The total effects of other predictor variables were also higher than their direct effects (Table 4.2) indicating that they indirectly affected frugivore richness via other variables.

Table 4.2: Standardized direct and total effects of predictor variables on species richness of obligate frugivores (OBL), partial frugivores (PAR), opportunistic fruit-eaters (OPP), and all birds (ALL). Values are derived from path models (see Figure 4.2), which include species richness of *Ficus* trees as predictor variable. Indirect effects are total effects minus direct effects and equal zero if total effects and direct effects have the same values. Mnemonics of predictor variables are explained in Table 4.1.

Predictor	Direct effects				Total effects			
variable	OBL	PAR	OPP	ALL	OBL	PAR	OPP	ALL
FigRich	0.546	0.454	0.252	0.172	0.546	0.454	0.252	0.172
Prec	0.095	0.018	0.193	0.410	0.814	0.626	0.604	0.611
MaxTemp	0.003	-0.362	-0.421	-0.264	0.064	-0.311	-0.398	-0.243
NPP	0.271	0.236	0.209	0.058	0.330	0.285	0.236	0.077
AltRange	0.110	0.044	0.043	0.137	0.230	0.383	0.388	0.416
EcoDiv	0.099	0.250	0.220	0.267	0.133	0.278	0.235	0.278

A $r^2 = 0.742$, model fit: NFI = 0.891



B $r^2 = 0.817$, model fit: NFI = 0.920

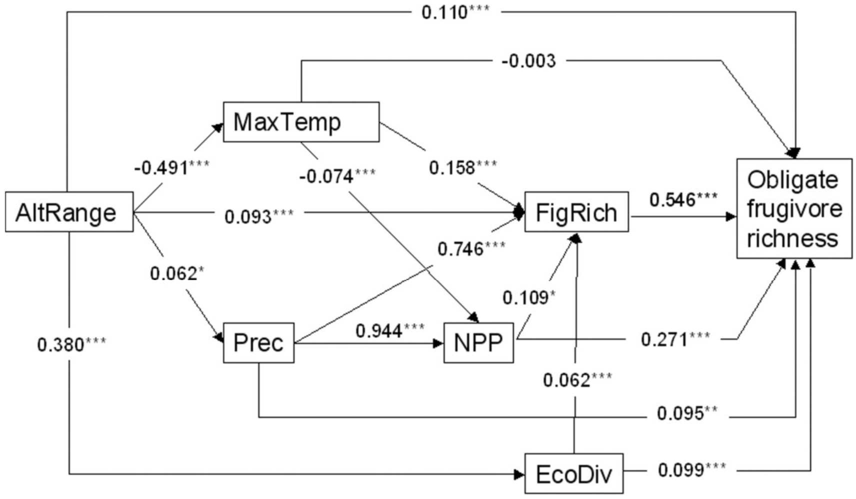


Figure 4.2: Path models for richness of obligate frugivorous bird species. (A) *Ficus* richness excluded; (B) *Ficus* richness included. Illustrated are direct effects (i.e., standardized partial regression coefficients) and their significance levels (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). R-square and NFI (normed fit index) are given for each model (see methods for details).

Replacing obligate frugivores in the path model (Figure 4.2B) with partial frugivores, opportunistic fruit-eaters, and all birds, resulted in less explained variance in avian species richness (partial frugivores: 73.7%; opportunistic fruit-eaters: 70.3%; all birds: 66.4%) than the original path model (obligate frugivore richness: 81.7%). This trend is consistent with the expectation that the hypothesized causal relationships in the path models should be stronger for birds that are more specialized on fruit-eating. Furthermore, these path models showed that direct effects of *Ficus* richness became weaker with decreasing specialization of birds on fruit-eating (Table 4.2) which also confirms the expectations. Correspondingly, the AIC values of multiple regression models with all explanatory variables increased with decreasing specialization on fruit eating ($AIC_{obligate\ frugivores} = 2{,}245$; $AIC_{partial\ frugivores} = 3{,}452$; $AIC_{opportunistic\ fruit\text{-}eaters} = 4{,}275$; $AIC_{all\ birds} = 7{,}214$).

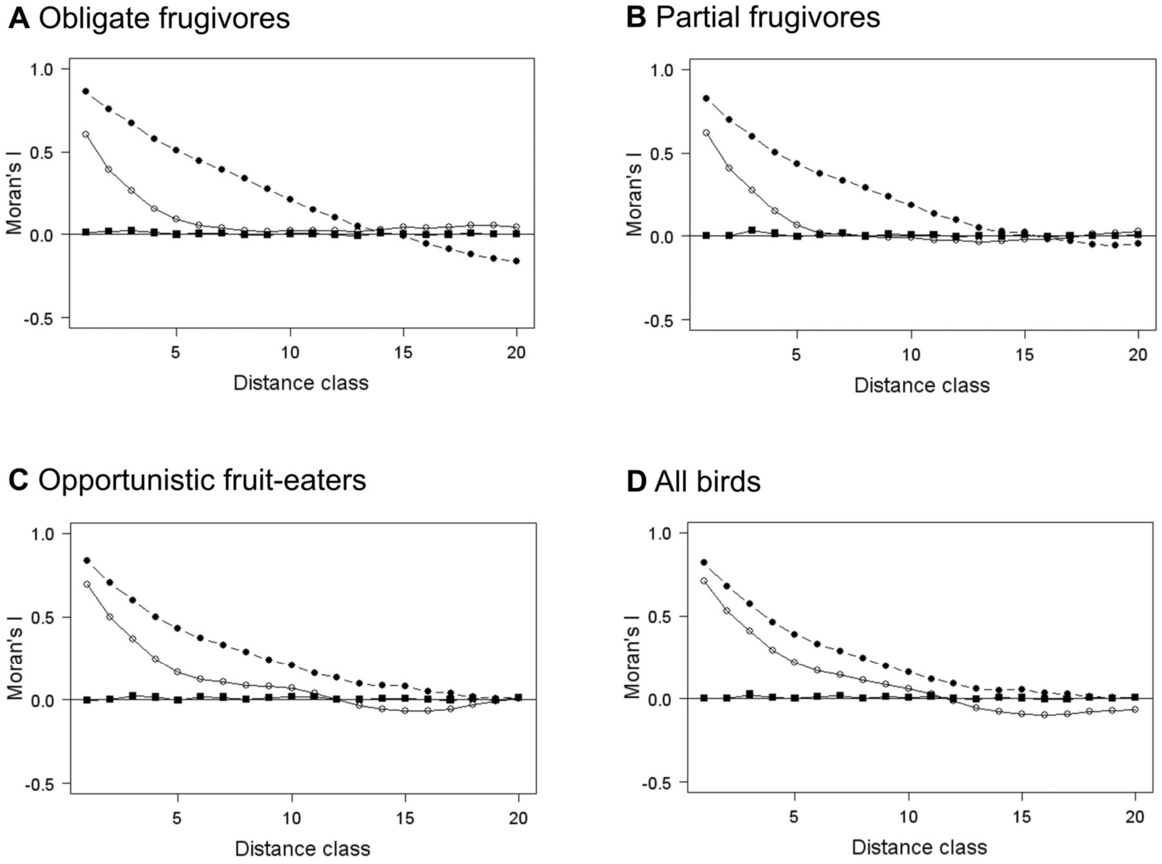


Figure 4.3: Correlograms for raw data on species richness (solid circles), residuals of multiple regression models (open circles), and residuals of spatial autoregressive error models (solid squares). Both models included all predictor variables (see Table 4.1) and species richness of obligate frugivores (A), partial frugivores (B), opportunistic fruit-eaters (C), and all birds (D), respectively, as response variables. Multiple regression models thus include all direct effects of predictor variables on avian species richness from the path models. One unit distance class corresponds to 112 km.

4.4.3 Effect of spatial autocorrelation

All avian species richness data were spatially autocorrelated over more than 1,000 km, although the extent (i.e. distance) differed slightly between frugivore guilds (Figure 4.3). Fitting multiple regression models with all predictor variables (i.e. models with those variables that show direct effects on avian species richness in the path models) reduced spatial autocorrelation in all richness data indicating that the spatial structure of explanatory variables accounted for some of the spatial autocorrelation structure in the avian richness data. However, the set of explanatory variables could not account for all of the observed spatial structure in the response variables (Figure 4.3). I therefore fitted spatial autoregressive models, which removed almost all of the spatial autocorrelation in richness data across all distance classes (Figure 4.3), indicating that the spatial structure can be explained by including information on the covariance structure from the four neighboring cells directly joining each focal cell.

Table 4.3: Standardized partial regression coefficients from spatial autoregressive error models (see methods for details). All models were calculated as multiple regression models with avian species richness (obligate frugivores OBL, partial frugivores PAR, opportunistic fruit-eaters OPP, and all birds ALL, respectively) as response variable and all other variables as predictor variables (see Table 4.1 for explanation of mnemonics).

Predictor variable	OBL	PAR	OPP	ALL
FigRich	0.382	0.266	0.222	0.231
Prec	0.259	0.253	0.322	0.248
MaxTemp	-0.023	-0.082	-0.032	-0.037
NPP	0.165	0.162	0.160	0.163
AltRange	0.086	0.097	0.070	0.065
EcoDiv	0.077	0.083	0.081	0.123

The standardized partial regression coefficients of the spatial autoregressive models (Table 4.3) differed from those of the path models (direct effects in Table 4.2) demonstrating that the effects of predictor variables might be exaggerated when using traditional multiple regression or path models. However, despite the changes in parameter estimates, richness of *Ficus* trees still remained the strongest predictor variable to explain the richness pattern of obligate and partial frugivorous birds, respectively. Moreover, its effect still decreased with decreasing specialization of birds on fruit-eating (Table 4.3). Besides, the relative importance of other predictor variables to explain obligate frugivore richness did not change when using spatial autoregressive models except precipitation, which became more important in spatial analyses (compare direct effects in Table 4.2 and Table 4.3).

4.5 Discussion

My analyses indicate that a positive relationship between species richness patterns of figs (*Ficus* spp.) and avian frugivores exists across sub-Saharan Africa, which suggests that both are linked via resource-consumer interactions rather than being caused by similar responses to environmental variables. I thus provide evidence that food plant diversity is an important determinant of avian frugivore richness in tropical regions, even after controlling for confounding environmental variables and spatial autocorrelation. The results also underline the potential role of *Ficus* as a keystone plant resource for avian frugivores in the tropics (Shanahan et al. 2001a; Bleher et al. 2003; Harrison 2005).

There are a number of mechanisms that could potentially explain a positive relationship between food plant and animal consumer species richness. Some can be based on deterministic processes and niche assembly theory (Graves & Rahbek 2005) whereas others are based on stochastic processes and ecological drift (i.e. neutral theory; Hubbell 2001; see also Colwell et al. 2004). One possible explanation for a positive relationship between food plant and frugivore species richness is that a greater number of plant species could potentially provide more niches for the coexistence of animal species (‘niche assembly hypothesis’) (Hutchinson 1959). This explanation assumes that animal species specialize on certain food plants or on specific types of resources provided by the plants (Price 2002). For instance, the latitudinal gradient in species richness of herbivorous insects from temperate to tropical regions has been suggested to be a direct function of an increase in plant species richness (Novotny et al. 2006). However, this ‘reciprocal specialization hypothesis’ is unlikely to be relevant for plant-frugivore interactions (Herrera 2002). Most fruit-eating bird species do not specialize on the fruits of a particular plant species. Instead, frugivorous bird species often treat fleshy-fruited plant species as interchangeable (Zamora 2000; Herrera 2002). For this study system I know of only one frugivorous bird species (Bruce’s Green-pigeon *Treron waalia*) that feeds particularly on one single fig species (*Ficus platyphylla*) with the ranges of the two species largely overlapping. Other examples might exist, but evidence for strong reciprocal specialization between frugivore species and fig or fleshy-fruited plant species is generally scarce (Herrera 2002).

Alternatively, a greater number of food plant species could potentially provide more niches for animal consumer species by providing a larger range of resources types. For instance, fruit size is an important attribute of fruits and varies greatly between species (e.g. fruit sizes of *Ficus* species range from 0.5 cm to 10 cm in diameter; Berges & Wiebes 1992). If frugivores show some specialization on differently sized fruits, then frugivore species richness is likely to increase with a greater range of fruit sizes. There is some evidence for this ‘size-related coupling hypothesis’ (Herrera 2002; Githiru et al. 2002; Lord 2004) because fruit size sets limits to fruit ingestion, at least to relatively small-sized birds that swallow whole fruits. It is thus likely that a greater number of *Ficus* species is accompanied with a larger diversity of fruit sizes (Berges & Wiebes 1992), which may attract a greater size range of fruit-eating birds increasing frugivore species richness (Shanahan et al. 2001a). If size-related coupling of fruits and frugivores is the underlying mechanism in this study system, then the correlations between fig and frugivore species richness could result as a bi-product of this relationship.

Similarly to fruit size, other fruit traits could potentially influence food choice and partitioning of the available fruit spectrum among consumer species (Gautier-Hion et al. 1985; Herrera 2002). For instance, frugivorous birds can discriminate among fruits on the basis of color and might exhibit distinct color preferences (Herrera 2002). A larger number of *Ficus* species is likely to increase the range of fruit colors (fig colors vary greatly from red, yellow, orange, green, brown to black fruits; Berges & Wiebes 1992), and this might attract a wider range of frugivorous species ('fruit color-richness hypothesis'). There is some evidence that differences in fruit color can explain differences in frugivore assemblage structure, at least when considering consumer species across taxa (e.g. when comparing primates and birds, Voigt et al. 2004). However, to my knowledge no study has shown convincingly that certain frugivorous bird species specialize on specific fruit colors. Other fruit traits such as fruit pulp quality (i.e. nutrient composition) could also be critical in food selection of frugivorous animals, but there is generally little evidence that they play an important role in shaping mutual adaptations between fleshy-fruited plants and frugivores (Herrera 2002).

Another potential mechanism underlying a positive relationship between fleshy-fruited plant and frugivore species richness is that a larger number of food plants is likely to increase the diversity of fruit presentation. For instance, depending on the *Ficus* species, figs are presented at different heights above ground level and at different locations (e.g., at groundlevel runners, on stems or trunks, or in leaf axis; Berges & Wiebes 1992). The architecture of fruit display is likely to determine fruit suitability for particular frugivores, especially if frugivores exhibit different feeding behaviours. The variability of fruit presentation within *Ficus* thus allows discrete guilds of *Ficus* species to attract different subsets of the total frugivore community (Shanahan & Compton 2001). This might result in a distinct vertical stratification of fig-frugivore communities (the 'vertical stratification hypothesis'; Shanahan & Compton 2001) and could, at least partly, explain the positive relationship between *Ficus* and frugivore species richness.

All mechanisms outlined so far explain the positive relationship between food plant and animal consumer species richness with an increased availability of niches provided by a larger number of plant species (niche assembly hypothesis). In contrast, the species richness of trophically similar species (e.g. frugivores) competing for similar resources (e.g. fruits) could also result from stochastic ecological and evolutionary processes (Hubbell 2001). For instance, areas with high species richness of fleshy-fruited plants could potentially produce more fruit biomass due to either more food plant individuals or higher total fruit production (e.g. Ortiz-Pulido & Rico-Gray 2000). If the total abundance of fruit resources increases with food plant species richness, than more individuals of frugivores could be sustained in areas with high food plant diversity. The high species richness of frugivorous birds could then be governed by neutral speciation and extinction processes where differences in traits of food plant and animal consumer species might be irrelevant for structuring plant-frugivore assemblages (Hubbell 2001; see also Burns 2006). In this case, *Ficus* species richness would then be positively associated with species richness of frugivorous birds because it also correlates with the overall abundance and availability of fruit resources (the 'resource-abundance hypothesis').

Finally, the spatial congruence in patterns of fig and frugivore richness could not only be driven by figs as resources for frugivores but also vice versa if frugivores constrain the spatial distribution and species richness of figs at continental scales. I tested this idea by interchanging *Ficus* richness and obligate frugivore richness in this path model (Figure 4.2B) and found an influence of similar magnitude between frugivores and figs (direct effect: 0.532). This pattern could result if the large-scale distribution of fig species and their colonization of new sites is constrained by seed dispersal of frugivorous birds (see e.g. Shanahan et al. 2001b for fig colonization of new volcanic islands). With a greater species richness of frugivorous dispersers the seeds are more likely to arrive in a greater variety of sites and at different distances, as different species of birds have different foraging behaviours, perching locations, and movement patterns. Furthermore, a higher species richness of frugivores might lead to better seed dispersal, more long-distance dispersal events, and the foundation of new *Ficus* populations, potentially resulting in higher speciation rates of *Ficus* species (see also Phillimore et al. 2006).

In contrast to my study, many thoroughly conducted studies on plant-frugivore interactions have failed to document strong adaptive relationships (e.g. through demographic sorting or coevolutionary processes) between fruits and frugivores (e.g. Herrera 1998) suggesting that non-adaptive processes such as climate, historical or phylogenetic effects constrain the development of mutual adaptations (Herrera 2002). For instance, similar to my study Márquez et al. (2004) analyzed plant-frugivore richness at the scale of major river basins across Europe and found that avian frugivore richness was more dependent on environmental factors than on fleshy fruited plant-species richness. Fleming (2005) examined the relationship between species richness of fruit-eating birds and their food plants in New and Old World communities and found hemispheric differences in plant-frugivore mutualisms. Recent plant-frugivore research suggests that these kind of differences are often generated by analyses at different spatio-temporal scales (Burns 2004; García & Ortiz-Pulido 2004).

To understand the causal mechanisms of animal species richness patterns at continental and global scales, predictions from competing mechanistic hypothesis should be tested (Willig et al. 2003; Currie et al. 2004; Rahbek et al. 2007), ideally across multiple spatial and temporal scales (Böhning-Gaese 1997; Burns 2004; Rahbek 2005). The results demonstrate a close relationship between the species richness of *Ficus* and avian frugivores in sub-Saharan Africa suggesting that figs are keystone resources for animal consumers at continental scales. This relationship might be driven by niche assembly mechanisms, e.g. coevolutionary adaptations to fruit size, fruit color, or vertical stratification of fruit presentation, or, alternatively, by a neutral speciation-extinction process. In both cases, however, the present study suggests that climatic variables influence frugivore species richness only indirectly via food webs rather than having a direct effect on the physiological tolerances of the organisms.

5 SPATIAL PATTERNS OF WOODY PLANT AND BIRD DIVERSITY: FUNCTIONAL RELATIONSHIPS OR ENVIRONMENTAL EFFECTS?

5.1 Abstract

The aim of this study was to test the relative roles of functional relationships between birds and woody plants and direct and indirect environmental effects on broad-scale species richness of both groups. Based on comprehensive range maps of all birds and woody plants (native species > 2.5 m in height) in Kenya, I mapped species richness of both groups. I distinguished species richness of four different avian frugivore guilds (obligate, partial, opportunistic and non-frugivores) and fleshy-fruited and non-fleshy-fruited woody plants and used structural equation modeling and spatial regressions to test for effects of functional relationships (resource-consumer interactions, vegetation structural complexity) and environment (climate, habitat heterogeneity) on the richness patterns. Path analyses suggested that bird and woody plant species richness are linked via functional relationships, probably driven by vegetation structural complexity rather than trophic interactions. Bird species richness was determined in my models by both environmental variables and the functional relationships with woody plants. Direct environmental effects on woody plant richness differed from those on bird richness, and different avian consumer guilds showed distinct responses to climatic factors when woody plant species richness was included in path models. The results imply that bird and woody plant diversity are linked at this scale via vegetation structural complexity, and that environmental factors differ in their direct effects on plants and avian trophic guilds. I conclude that climatic factors influence broad-scale tropical bird species richness in large part indirectly, via effects on plants, rather than only directly as often assumed. This could have important implications for future predictions of animal species richness in response to climate change.

Keywords: autoregressive model, biodiversity, community assembly, cross-taxon congruence, indirect effects, frugivory, Kenya, plant-animal interactions, species-energy theory, trophic guild.

5.2 Introduction

Geographic patterns of species richness are central to ecology and have gained much attention in recent years (e.g. Jetz & Rahbek 2002; Hawkins et al. 2003a; Currie et al. 2004; Field et al. 2005). Although the precise mechanisms for the creation and maintenance of geographic gradients in species diversity are still hotly debated (e.g. Rahbek & Graves 2001; Currie et al. 2004; Hawkins et al. 2007a), there seems to be consensus that variables related to climate and habitat heterogeneity play a prominent role at broad spatial scales (Rahbek & Graves 2001; Jetz & Rahbek 2002; Hawkins et al. 2003a). Likely mechanisms include potential effects on the physiological tolerances of individual species (Currie et al. 2004), on diversification rates (Jetz et al. 2004; Allen et al. 2006), or on energy flow through food webs (Wright 1983; Kissling et al. 2007). If different groups of organisms show similar direct or indirect responses to environmental factors, I might expect that species richness patterns of different taxa are spatially congruent. Such patterns could have profound implications for biodiversity conservation, e.g. for global conservation planning (Lamoreux et al. 2005), the selection of nature reserves (Howard et al. 1998), and for assessing effects of habitat modification across taxa (Schulze et al. 2004). However, the results from studies on species richness congruence have been mixed and often poor relationships between taxa have been reported (Wolters et al. 2006). A better understanding of the functional relationships and mechanisms underlying richness correlations and the potential direct and indirect effects of climate and habitat heterogeneity variables is therefore urgently needed (Menéndez et al. 2007).

One possibility to test for functional relationships in cross-taxon congruence patterns is to relate the species richness of animals to the species richness of plants (e.g. Currie 1991; Hawkins & Porter 2003; Lee & Rotenberry 2005; Kissling et al. 2007). Plants are at the base of terrestrial food webs and provide a great variety of food resources relevant for animal consumers (e.g. Hutchinson 1959; Herrera 1985; Shanahan et al. 2001a; Kissling et al. 2007). A positive relationship between animal and plant species richness might therefore result from trophic relationships, with consumer diversity reflecting the diversity of the food plants (hypothesis 1, the “food plant diversity hypothesis”; Kissling et al. 2007). Plants are also key structural elements of terrestrial ecosystems and thus determine habitat configuration for many animal species, including birds (MacArthur & MacArthur 1961). An increase in animal species richness with plant species richness might therefore result from an increase in the diversity and complexity of vegetation structure, providing more niches for animal species to coexist (hypothesis 2, the “vegetation structure hypothesis”; MacArthur & MacArthur 1961;

Tews et al. 2004; Lee & Rotenberry 2005). This relationship has been convincingly demonstrated at local scales (MacArthur & MacArthur 1961; Pearson 1975; Cody 1985) but has not yet been found at broad spatial scales, and a similar local relationship was found not to hold at the macro scale for butterflies (Hawkins & Porter 2003). Finally, a positive correlation between animal and plant species richness could also result from both groups responding similarly to the same environmental variables. In this case, interactions between the two taxonomic groups would not be expected to affect the species richness of birds (hypothesis 3, which I call the “similar environmental effects hypothesis”; Hawkins & Porter 2003).

From these hypotheses, testable predictions can be derived. First, if functional (i.e. trophic or structural complexity) relationships between animals and plants shape broad-scale patterns of species richness (hypotheses 1 and 2), then a positive correlation between species richness of both taxa should persist when environmental variables have been accounted for (see Hawkins & Porter 2003; Kissling et al. 2007). Second, according to hypothesis 1 (food plant diversity hypothesis), the plant–animal correlation should be stronger for those subgroups of animals and plants that are more specialised on each other than for subgroups with weaker trophic interactions (Kissling et al. 2007). Third, hypothesis 2 (vegetation structure hypothesis) predicts a relatively strong positive plant–animal correlation regardless of whether plants are food resources for animals or not (e.g. Lee & Rotenberry 2005). Finally, hypothesis 3 (similar environmental effects hypothesis) predicts relatively strong environment–species richness correlations that are similar for plant and animal taxa. These predictions are not mutually exclusive and may be additive. To date, however, there have been few attempts to test these predictions, or to distinguish between the three hypotheses. In particular, there have been few attempts to disentangle the relative roles of trophic relationships and vegetation structural complexity in shaping geographic patterns of animal species richness at broad spatial scales (Hawkins & Porter 2003; Márquez et al. 2004; Kissling et al. 2007; Menéndez et al. 2007).

Plant–frugivore interactions represent a good study system for such broad-scale analyses of animal and plant species richness. Most frugivorous animals rely heavily on fruits, particularly in the tropics (Herrera 1985; Fleming et al. 1987; Shanahan et al. 2001a; Kissling et al. 2007). Accordingly, the food plant diversity hypothesis predicts relatively strong positive relationships between food plant and frugivore species richness (Kissling et al. 2007), e.g. due to evolutionary or ecological responses of frugivores to fruit size, fruit color, fruit biomass or vertical stratification of fruit presentation (Herrera 2002; Kissling et al. 2007).

Fruit-eating vertebrate species can be classified into frugivore guilds (e.g. obligate, partial, and opportunistic frugivores), and plant species into those with fleshy fruits and those without. This allows examination of trends in the strength of the relationship between different frugivore guilds and food plant species richness. Finally, habitat selection of frugivores and other birds is not only influenced by food availability but also by vegetation structure and complexity and other factors. Species richness of different feeding guilds might therefore respond differently to changes in vegetation structure and complexity across tropical ecosystems (Waltert et al. 2005).

In this study, I investigate the three hypotheses using a comprehensive geographic database at a spatial resolution of ~55 km (0.5° grid cells) that includes 1,005 bird species, 1,417 woody plant species and six environmental variables related to climate (precipitation, temperature, potential evapotranspiration, seasonality) and habitat heterogeneity (topographic relief, land cover diversity). I classify bird species into four frugivore groups (obligate frugivores, partial frugivores, opportunistic fruit-eaters, non-fruit-eaters), and woody plant species into two resource groups (fleshy-fruited plants, non-fleshy-fruited plants). I particularly aimed to test the following five predictions. The first I call 'prediction 0' because it concerns functional relationships and therefore applies to both hypotheses 1 and 2: a significant positive correlation between bird and woody plant species richness when environmental effects have been accounted for. Secondly, hypothesis 1 (trophic relationships) predicts a stronger plant richness–animal richness correlation between fleshy-fruited plants and frugivores than between non-fleshy-fruited plants and frugivores (prediction 1a). Hypothesis 1 also predicts that the plant–animal correlation should be successively weaker between fleshy-fruited plants and obligate frugivores, partial frugivores, opportunistic fruit-eaters and non-fruit-eaters (prediction 1b). Hypothesis 2 (vegetation structure) predicts relatively strong correlations between trophically independent groups, i.e. between frugivores and non-fleshy-fruited plants and between non-frugivores and fleshy-fruited plants (prediction 2). Finally, hypothesis 3 (similar environmental effects) predicts both very similar total effects of environmental variables on the richness variables and relatively strong direct effects of environmental variables on the richness variables, which should be similar for woody plant and bird species richness (prediction 3).

5.3 Methods

5.3.1 Bird species richness

The Bird Atlas of Kenya (Lewis & Pomeroy 1989) provides the most comprehensive information available on the distribution of birds in East Africa, with presence/absence data of species (mainly collected for the period 1970-1984) at a spatial resolution of 0.5° x 0.5° cells, so-called quarter square degrees (QSDs). This spatial resolution corresponds to ~55.5 km and QSD cell area is effectively constant (~3,080 km^2). In total, 1,065 bird species are listed in the atlas, of which 871 species are presented with distribution maps; for the remaining 194 species QSD records are only listed in the text. For this analysis, I used all available distribution information (i.e. maps and listed records, including pre-1970 records) but excluded vagrant species and those species represented only by anecdotal records (1,005 bird species were thus analyzed). Using the software ArcView 3.2, I transferred all presence data (i.e. maps and information on listed species records) of all included species into a digital QSD grid system (described below for the plant data).

I classified all the bird species (n = 1,005) into four frugivore guilds, depending on diet preference for fruits (see Kissling et al. 2007 for details on this classification procedure): (i) obligate frugivores (species that primarily feed on fruits, i.e. the only major food items are fruits, n = 43), (ii) partial frugivores (species that eat fruits and other major food items such as terrestrial invertebrates, n = 98), (iii) opportunistic fruit-eaters (species only occasionally eating fruits as supplementary food, n = 145), and (iv) non-fruit-eaters (not eating any fruits, n = 719). These four frugivore guilds are characterized by declining degree of specialization on fruits. I calculated species richness values for all four guilds for each QSD grid cell.

5.3.2 Plant species richness

I estimated the species richness of woody plants for each QSD cell from a comprehensive set of distribution maps and site location data for trees and shrubs in Kenya (Beentje, 1994). I followed the same criteria as in Field et al. (2005) to determine which species to include, and thus retained 1,417 out of 1,862 species. Those eliminated were non-native species, plants ≤ 2.5 m in height, and plants that are not truly woody. Beentje's (1994) distribution maps use the same QSD grid system as the bird data, so I transferred the presence/absence information directly into the grid cells. Species whose distribution information is reported by Beentje in terms of collecting localities (see Field et al. 2005 for details) were included in these data. The initial grid system contained 228 QSD cells (including cells that cross the border of Kenya) from which I excluded cells that (1) lie partly outside the borders of Kenya (*n* = 52), (2) are known to be botanically undercollected (*n* = 9; Beentje, 1994), or (3) have more than 50% lake area (*n* = 7). These cells were excluded because they are known to underestimate plant and bird diversity. The final database contained 160 QSD cells and this was used for all the analyses.

I classified all woody plants (*n* = 1,417) into two resource groups: (i) fleshy-fruited plant species (*n* = 788), and (ii) non-fleshy-fruited plant species (*n* = 629). Fleshy-fruited plant species were identified according to the presence or absence of fleshy parts (information from Beentje 1994), including species with berries, drupes, and dehiscent fruits with fleshy arils. Where fruit types were unclear, expert opinions were obtained (see acknowledgements) and/or specimens examined.

5.3.3 Environmental variables

I included six environmental variables (Table 5.1) related to climate (precipitation, temperature, potential evapotranspiration [PET], seasonality) and habitat heterogeneity (topographic relief, land cover diversity). These variables have previously been shown to be important determinants of species richness of birds and plants at broad spatial scales (see references in Table 5.1).

Table 5.1: Environmental variables used to account for spatial variation in bird and woody plant species richness.

Abbreviation	Predictor variables (units)	Hypothesis (reference*)
Climate		
Prec	Mean annual precipitation (mm/yr)	Water availability (1, 2)
Temp	Mean monthly temperature (°C)	Temperature (2, 3)
PET	Mean annual potential evapotranspiration (mm/yr)	Energy (1, 2)
Seas	Seasonality, measured as coefficient of variation of monthly precipitation values (mm/month)	Seasonality (4)
Habitat heterogeneity		
Topo	Topographic relief (altitudinal range in m)	Topographic heterogeneity (5, 6)
LCov	Land cover diversity (Shannon–Wiener diversity)	Habitat diversity (5, 7)

* (1) Field et al. (2005); (2) Hawkins et al. (2003a); (3) Allen et al. (2006); (4) Hurlbert & Haskell (2003); (5) Rahbek & Graves (2001); (6) Jetz & Rahbek (2002); (7) Tews et al. (2004);

Climate variables

Data for precipitation and temperature were extracted from the WorldClim database (version 1.4; Hijmans et al. 2005), which yields interpolated mean monthly climatic data from the period 1950-2000 (available online at http://www.worldclim.org/). I used mean annual precipitation and mean monthly temperature, degraded from 1 km to ~55 km (i.e. QSD) resolution. PET data were obtained from the United Nations Environmental Program (UNEP), available at 0.5° (i.e. QSD) resolution (http://www.grid.unep.ch/, see also Ahn & Tateishi 1994. This PET dataset is widely used in studies of species richness (e.g. Francis & Currie 2003) and widely accepted. Note also that, in Kenya, Thornthwaite's PET is almost completely collinear with temperature, unlike the Ahn & Tateishi data. Seasonality was calculated as the coefficient of variation of the monthly precipitation values, to quantify seasonal changes in precipitation.

Habitat heterogeneity

I selected two potentially relevant measures of habitat heterogeneity for the study (Table 5.1): (i) topographic relief, and (ii) land cover diversity. Topographic relief was quantified for each QSD cell as altitudinal range (maximum minus minimum elevation). Elevation data were extracted from the 30 arc-second SRTM-GTOPO30 dataset provided by The Global Land Cover Facility (available at http://glcf.umiacs.umd.edu/data/srtm/). Land cover diversity was calculated from the Kenya Spatially Aggregated Multipurpose Landcover database provided by FAO-Africover (available at http://www.africover.org). For each QSD cell, I calculated the proportion of each of the 101 recognized land cover types in Kenya and then computed the Shannon-Wiener function (Krebs 1999) as an index of land cover diversity. This index varied between 0 and 4.63, with higher values indicating more (and more evenly sized) land cover types and, therefore, greater habitat diversity within a cell.

5.3.4 Statistical analysis

I used path analysis and structural equation models (SEMs) (Shipley 2000) to investigate the relative roles of environmental predictor variables and to test the five predictions. In contrast to traditional multiple regression models (which can only deal with one response variable) SEMs allow the consideration of hypothesized causal relationships in datasets with more than one dependent variable and effects of dependent variables on one another. As a consequence, SEMs allow the partitioning of correlations between predictor and response variables (so called "total effects") into direct and indirect effects. Direct effects are measured by standardized partial regression coefficients between a predictor variable and a response variable (i.e. the direct link), whereas indirect effects can be calculated by adding the products of all standardized partial regression coefficients over all paths between a predictor and a response variable (i.e. including indirect links via other correlated predictor variables; see Shipley 2000). Although SEMs cannot replace experimental manipulations they are one of the few methods to test ecological hypotheses at broad spatial scales (e.g. Hawkins & Porter 2003; Hawkins et al. 2005, 2007b; Menéndez et al. 2007).

Based on logical and established relationships among the predictor variables (see references in Table 5.1) I first constructed an a priori theoretical SEM with bird species richness, plant species richness, and all environmental variables (see Figure 5.2A). This a priori model included all the hypothesized potential links between variables. I then constructed 15 nested SEMs, representing each plant–bird richness combination in turn: one measure of plant richness (all woody plants, fleshy-fruited plants, non-fleshy-fruited plants) and one measure of bird species richness (all birds, obligate frugivores, partial frugivores, opportunistic fruit-eaters, non-fruit-eaters). Figure 5.2B is an example, showing the model for all woody plants and all birds. These nested SEMs shared the same causal structure as the a priori theoretical SEM but some of the paths were eliminated. Elimination of paths was guided by calculating, for each richness response variable, traditional multiple ordinary least squares (OLS) regression models with all predictor variables (including plants for birds) and then selecting the minimal adequate OLS model for each richness variable based on the Akaike Information Criterion (AIC) (Burnham & Anderson 2002). This information theoretic approach evaluates the relative support in the observed data for a given candidate set of models and selects the most parsimonious model based on model fit and model complexity (Burnham & Anderson 2002). Using these minimal adequate models for each richness variable I then constructed nested SEMs within the a priori theoretical model by removing those paths from the a priori model that were redundant for the most parsimonious explanation of the response variables. All nested SEMs showed high goodness of fit as indicated by a number of fit measures including high goodness-of fit indices (all between 0.75-0.82) and Bentler-Bonett normed fit indices (NFI) of 0.77-0.84 (values close to 1 indicate a good fit). As alternatives, I also tested SEMs using the full a priori model structure, and these models yielded similar results to those presented here.

The following SEMs were used to test the five predictions. A SEM with overall bird and woody species richness (Figure 5.2B) was used to test prediction 0 (the presence of any functional relationship; see also Hawkins & Porter 2003). To test prediction 1a (a stronger correlation between food plants and frugivores than between non-food plants and frugivores) I examined SEMs with the two plant resource groups in turn (fleshy-fruited plant species and non-fleshy-fruited plant species), and the species richness of avian frugivores (obligate and partial frugivores, respectively). Similarly, to test prediction 1b (decreasing trend in the relationship between food plants and specialization of birds on fruit eating) I used SEMs with fleshy-fruited plants and the species richness of the different avian guilds in turn (obligate frugivores, partial frugivores, opportunistic fruit-eaters and non-fruit-eaters). To test prediction 2 (vegetation structural complexity) I assessed the direct paths between plants and bird of SEMs with trophically independent groups (i.e. between frugivores and non-fleshy-fruited plants and between non-fruit-eating birds and fleshy-fruited plants). Finally, to test prediction 3 (similar environmental effects) I examined the direct environmental effects on species richness in all SEMs, i.e. the paths between climate and habitat heterogeneity variables and plant and bird species richness, respectively. I also compared the total effects of the environmental variables on plant and bird species richness.

The presence of spatial autocorrelation violates the assumption of independently distributed errors in regression models, and, as a consequence, Type I errors of traditional tests might be inflated (Legendre 1993). Moreover, spatial autocorrelation can affect inference from statistical models and the ability to evaluate the importance of explanatory variables (Diniz-Filho et al. 2003; Dormann et al. 2007). To explore the influence of spatial autocorrelation on inference from the path models, I therefore tested for the presence of spatial autocorrelation by calculating Moran’s I values (i.e. a measure of spatial autocorrelation; Legendre 1993) on the residuals of the minimal adequate (OLS) regression models. Since most of these OLS models contained significant spatial autocorrelation in their residuals, I fitted spatial linear models (SLMs; here “spatial simultaneous autoregressive error models”; see Kissling & Carl 2008) which can include the spatial autocorrelation structure of a given dataset. Final model assessment was based on the reduction of spatial autocorrelation in model residuals (evaluated with Moran’s I values), the increase in r^2-values (for the spatial models, pseudo-r^2-values were calculated as the squared Pearson correlation between predicted and observed values), and the minimization of the AIC value (see Kissling & Carl 2008). To compare the relative importance of predictor variables from SLMs and OLS regressions, I calculated standardized partial regression coefficients from both model types. For the non-spatial (OLS) models, these standardized partial regression coefficients are equivalent to the direct effects on species richness in my SEMs.

All statistical analyses were done with the free software R (available at http://www.R-project.org). SEMs were calculated with the R library “sem”, v. 0.9-6, and Moran’s I values and SLMs were calculated using the R library “spdep”, v. 0.3-32 (both packages are available at http://cran.r-project.org/src/contrib/PACKAGES.html). The spatial neighborhood of the SLMs was defined with a distance of 57 km including the four neighboring cells that directly join each focal cell (the rook’s case). The spatial weights matrix was calculated with a row standardized coding style that scales the covariances based on the number of neighbors of each region (for details see Kissling & Carl 2008). To improve normality and linearity in the response of richness variables to environmental predictor variables I square-root transformed all richness variables and log(x+1) transformed mean annual precipitation and altitudinal range.

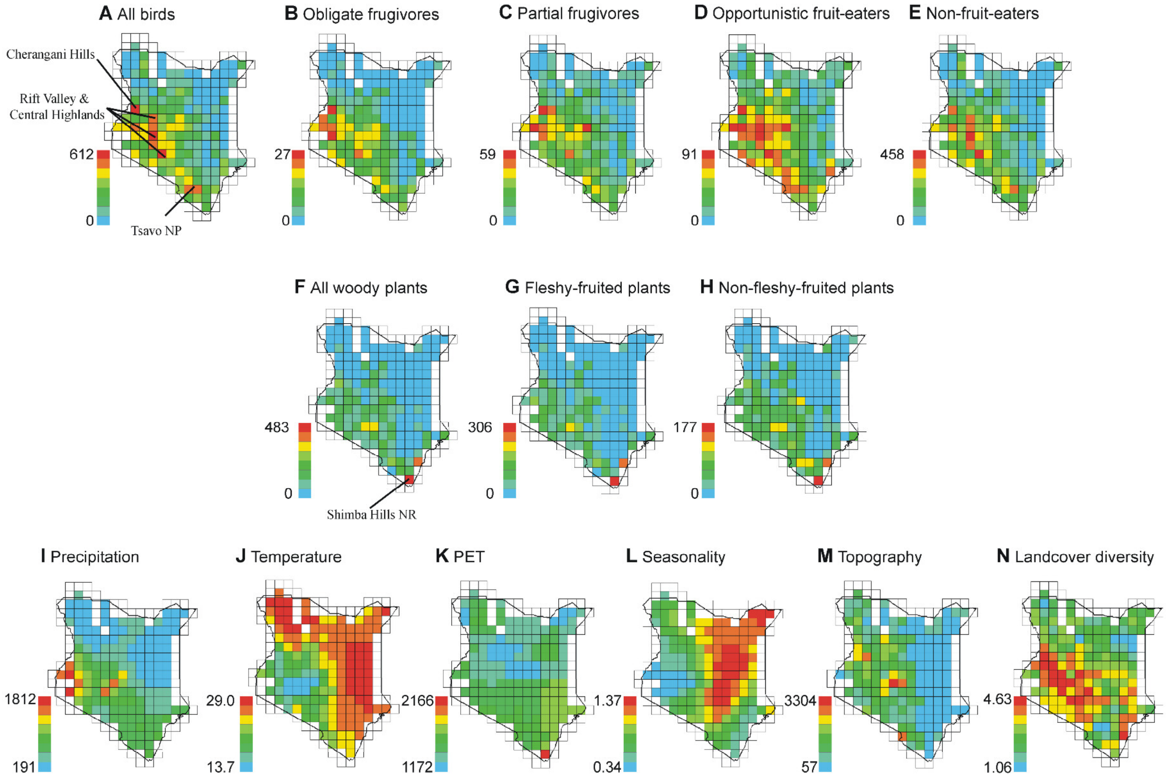


Figure 5.1: Spatial patterns of species richness and environmental variables across Kenya. (A–E) Species richness of all birds and avian frugivore guilds. (F–H) Species richness of woody plants, fleshy-fruited plants, and non-fleshy-fruited plants. (I–N) Environmental variables (see Table 5.1). Equal frequency classification is shown, with color ramps indicating minimum (blue, bottom of legend) and maximum (red, top of legend) values.

5.4 Results

5.4.1 Geographic patterns of species richness and environment

Overall bird species richness across Kenya was highest in the south-western parts of the country, with hotspots in the Cherangani Hills, the Rift Valley, the Central Highlands, and the

Tsavo National Park (Figure 5.1A). In contrast, the arid bushlands and deserts of northern Kenya and the coastal plains in the East were characterized by relatively low bird diversity. The spatial patterns of species richness change somewhat when considering different avian frugivore guilds (Figure 5.1B-E). Species richness of obligate and partial frugivores was highest in the West close to the border of Uganda whereas opportunistic fruit eaters were also very common much further southeast. Woody plant species richness, in contrast to bird species richness, peaked in the southernmost part of the country which included the Shimba Hills National Reserve (Figure 5.1F). Fleshy-fruited and non-fleshy-fruited plants (Figure 5.1G & H) showed similar patterns to all woody plants but medium to high species richness values of non-fleshy-fruited plants appeared to be spatially spread out more than those of fleshy-fruited plants. Geographic patterns of the environmental variables revealed strong and markedly different broad-scale spatial gradients across Kenya (Figure 5.1I-N).

5.4.2 Functional relationships

Bivariate Pearson correlation coefficients between all variables are given in Appendix 10. The simple correlation between woody plant species richness and overall bird species richness indicated that they positively covary across Kenya ($r = 0.81$). A strong correlation between the two variables remained when accounting for environmental effects with a SEM (Figure 5.2B, bold coefficient), supporting prediction 0. This suggests an important role for functional relationships, either via resource–consumer interactions or vegetation structural complexity, though other explanations are possible. Dissecting the overall species richness patterns into avian guilds and plant resource groups revealed that all bird groups showed high spatial congruence ($r \geq 0.76$) with the plant groups (Appendix 10). SEMs with species richness of the four avian guilds and the two plant resource groups supported this general trend (all standardized partial regression coefficients ≥ 0.44; see Figure 5.3). In contradiction to prediction 1a, both species richness of fleshy-fruited plants and non-fleshy-fruited plants had similarly strong direct effects on obligate and partial avian frugivores (compare white with gray bars for OBL and PAR in Figure 5.3). Moreover, the effect of fleshy-fruited plant species richness on species richness of avian guilds in my SEMs did not decrease from obligate frugivores, partial frugivores, opportunistic fruit-eaters to non-fruit-eaters (compare the white bars in Figure 5.3), in contradiction to prediction 1b. Thus I found little support for hypothesis 1 (food plant diversity hypothesis). Consistent with prediction 2, the direct relationships between trophically independent groups of species were often strong, which can be interpreted as supporting hypothesis 2 (vegetation structural hypothesis).

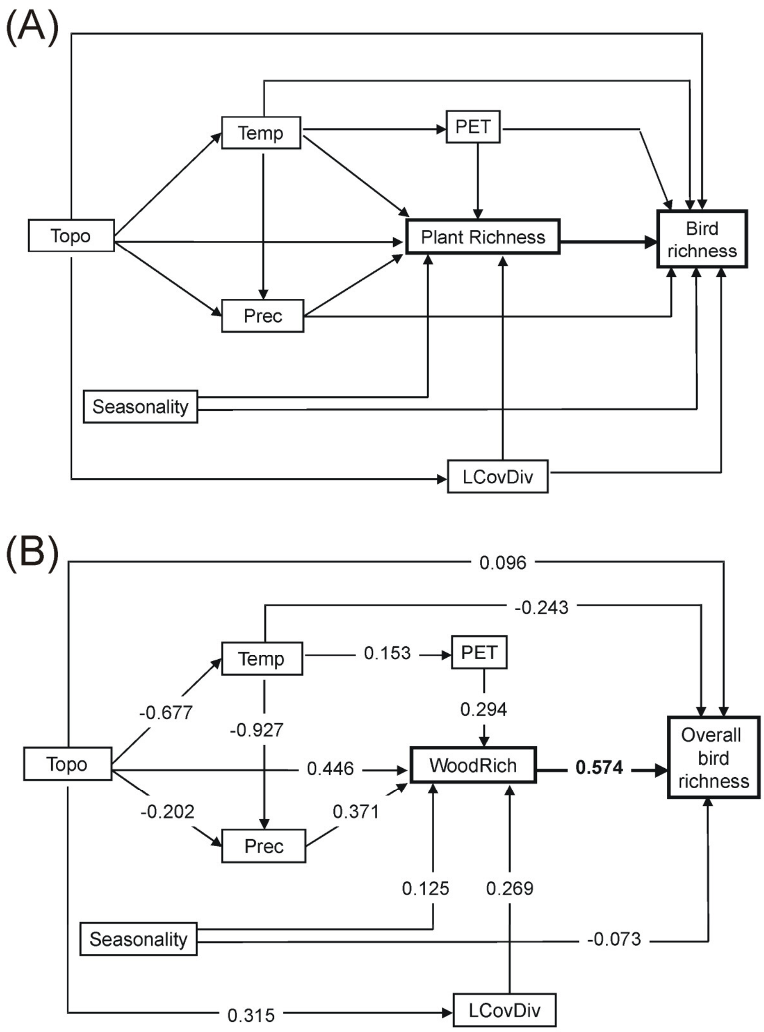


Figure 5.2: Structural equation model (SEM) of the influence of plant species richness and environmental variables on bird species richness. (A) A priori theoretical SEM including all variables and the potential relationships among them. (B) Nested SEM testing the effect of woody plant species richness (WoodRich) on overall bird species richness (goodness-of-fit index = 0.75; Bentler–Bonnett NFI = 0.78). Due to the presence of spatial autocorrelation (see Tables 5.2 and 5.3) significance levels for standardized partial regression coefficients are not given. See Table 5.1 for abbreviations of environmental variables.

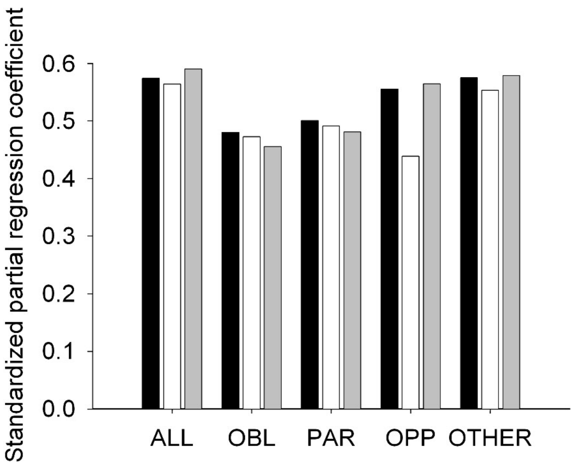


Figure 5.3: Direct effects of plant species richness (black: all woody plants; white: fleshy-fruited plants; gray: non-fleshy-fruited plants) on species richness of birds (ALL: all birds; OBL: obligate frugivores; PAR: partial frugivores; OPP: opportunistic fruit-eaters; OTHER: non-fruit-eating birds). Direct effects are standardized partial regression coefficients from structural equation models similar to Figure 5.2A where bird richness has been replaced by ALL, OBL, PAR, OPP and OTHER, and plant richness by richness of woody plants, fleshy-fruited plants and non-fleshy-fruited plants, respectively. See text for details on model selection.

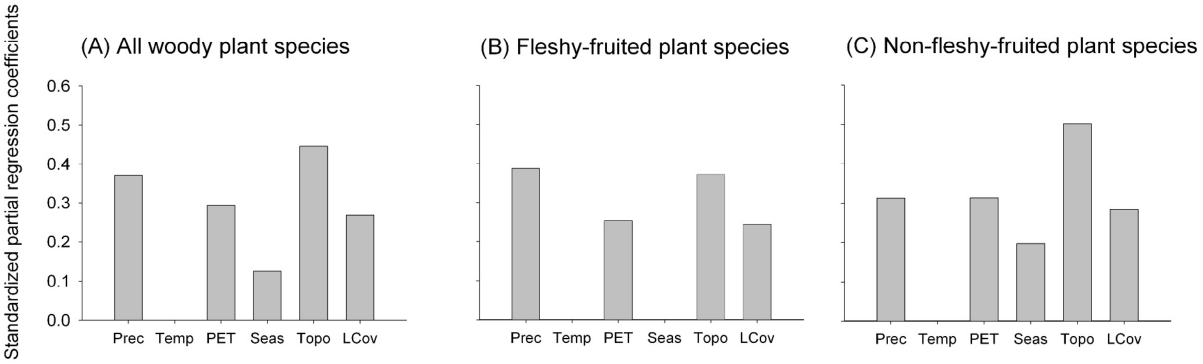


Figure 5.4: Absolute direct effects of environmental predictor variables on species richness of plants (A: all woody plants; B: fleshy-fruited plants; C: non-fleshy-fruited plants). Values are derived from structural equation models similar to Figure 5.2A, where plant richness has been replaced by species richness of woody plants, fleshy-fruited or non-fleshy-fruited plants. See text for details on model selection. Zero values indicate that the variable was not selected in the minimal adequate model.

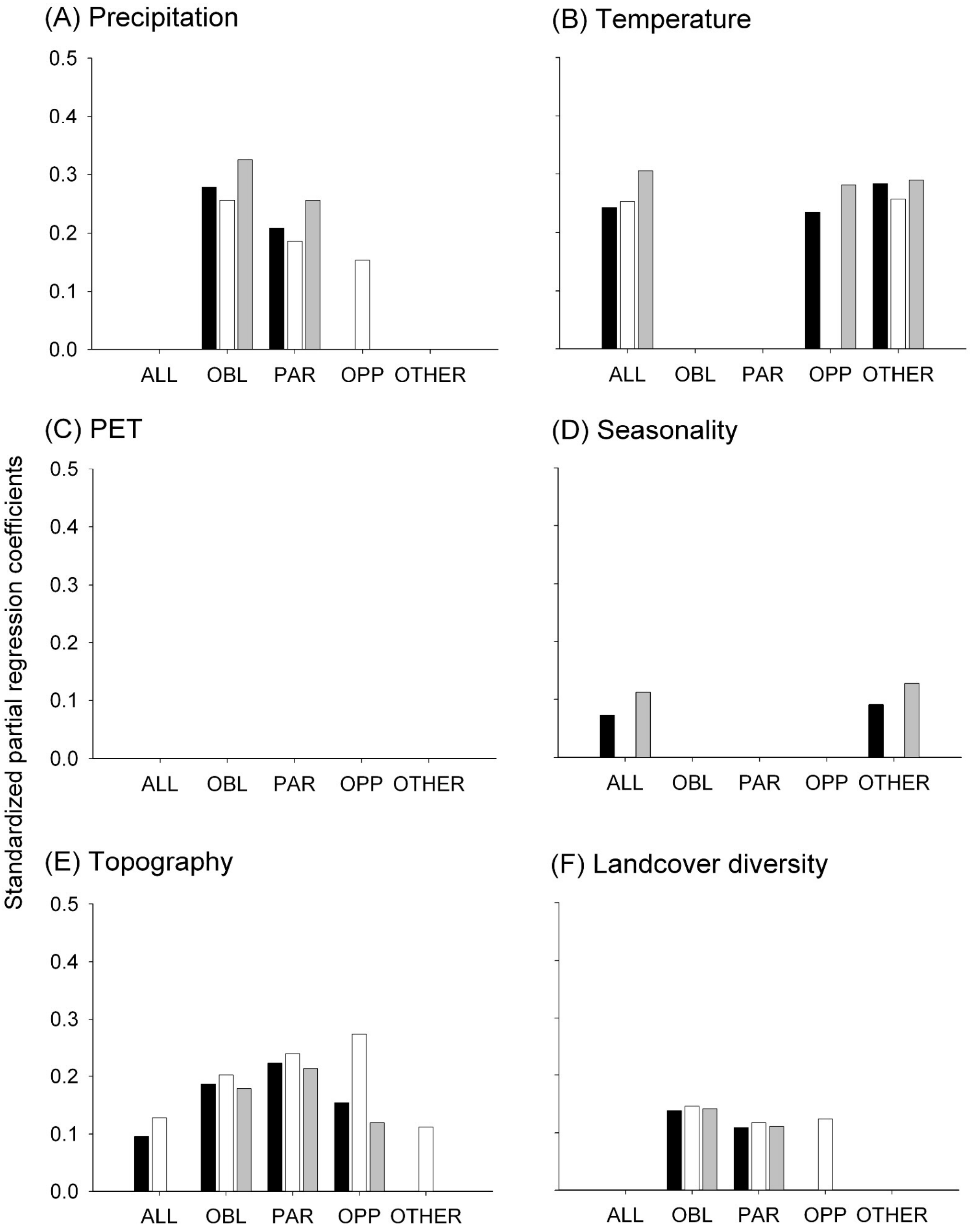


Figure 5.5: Absolute direct effects of environmental predictor variables on species richness of birds (ALL: all birds; OBL: obligate frugivores; PAR: partial frugivores; OPP: opportunistic fruit-eaters; OTHER: non-fruit-eating birds). Values are derived from structural equation models similar to Figure 5.2A, where plant richness was replaced by species richness of woody plants (black columns), fleshy-fruited plants (white) or non-fleshy-fruited plants (gray), and bird richness by ALL, OBL, PAR, OPP and OTHER. See text for details on model selection. Zero values indicate that the variable was not selected in the minimal adequate model.

5.4.3 Environmental effects

Direct effects of environmental variables on the species richness of both woody plants (Figure 5.4) and birds (Figure 5.5) were often strong in my SEMs. The strongest direct effects of environmental variables on species richness of woody plants came from topographic relief, precipitation, and PET, though their relative importance differed between the two plant resource groups (Figure 5.4). Avian guilds differed in terms of direct effects of environmental variables on their species richness when woody plant species richness was included in SEMs (Figure 5.5). For instance, precipitation showed strong direct effects on species richness of frugivores (OBL and PAR; Figure 5.5A) whereas direct effects of temperature were strong for birds that are not specialized on fruit-eating (OPP and OTHER, Figure 5.5B). These direct environmental effects on both bird and woody plant diversity differed from the total (i.e. direct + indirect) effects of environmental variables in the path models (see Appendix 11 and 12). Total effects of some environmental variables differed a little between the plant groups (e.g. precipitation and seasonality, Appendix 11) while others were very consistent. The total effects were also relatively similar across bird groups (Appendix 12), with precipitation being the main exception as it was stronger for frugivores than non-frugivores. Strong direct and indirect environmental effects on species richness in the SEMs are consistent with prediction 3, as are broadly similar total effects of environmental variables on bird and plant species richness. However, the differences that do exist (e.g. PET and precipitation – compare Appendix 11 and 12) are not consistent with hypothesis 3 (similar environmental effects hypothesis) as the sole cause of bird species richness. Nor is the important role of woody plant species richness in all the models. The contrasting nature of the direct effects of environment on richness (compare Figures 5.4 and 5.5) can be interpreted as being inconsistent with hypothesis 3.

5.4.4 Effects of spatial autocorrelation

In most cases, the residuals from the minimal adequate OLS models which included avian species richness as response variable showed a spatial autocorrelation structure pattern, as indicated by significant Moran’s I values (Table 5.2). Only OLS regressions with obligate frugivore richness as response variable showed no spatial autocorrelation structure in model residuals (Table 5.2). When fitting SLMs with the same variables, the spatial autocorrelation structure in OLS model residuals disappeared (i.e. non-significant Moran’s I values around 0; see Table 5.2) indicating that the non-independence assumption was no longer violated.

Table 5.2: Standardized partial regression coefficients of traditional ordinary least squares (OLS) regressions and spatial linear models (SLM) with bird species richness (ALL: all bird species; OBL: obligate frugivores; PAR: partial frugivores; OPP: opportunistic fruit-eaters; OTHER: non-fruit-eating birds) as response variable, and plant species richness (woody plants, fleshy-fruited plants and non-fleshy-fruited plants, respectively) and six environmental variables (see Table 5.1 for abbreviations) as potential predictor variables. Minimal adequate OLS models were chosen from the full set of explanatory variables based on the Akaike Information Criterion (AIC) (see text for details). The high spatial autocorrelation of errors in most OLS analyses (all Moran's I, $P < 0.05$) confirms the expected violation of the non-independence assumption. Coefficients from OLS analyses are identical to direct effects in structural equation models.

	Bird species richness									
	ALL		OBL		PAR		OPP		OTHER	
Variables	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM	OLS	SLM
Models with all woody plants (WoodRich)										
WoodRich	0.574	0.533	0.480	0.477	0.500	0.489	0.555	0.504	0.575	0.545
Prec	-	-	0.278	0.273	0.208	0.164	-	-	-	-
Temp	-0.243	-0.163	-	-	-	-	-0.234	-0.212	-0.283	-0.197
PET	-	-	-	-	-	-	-	-	-	-
Seas	-0.073	-0.126	-	-	-	-	-	-	-0.091	-0.153
Topo	0.096	0.123	0.187	0.187	0.224	0.222	0.155	0.189	-	-
LCovDiv	-	-	0.139	0.142	0.109	0.144	-	-	-	-
Model r^2	0.73	0.76	0.82	0.82	0.76	0.79	0.69	0.71	0.70	0.74
Model *AIC*	835	823	294	296	432	421	554	548	804	791
Moran's *I*	0.21***	0.01	0.05	0.00	0.22***	0.02	0.17**	0.00	0.23***	0.01
Models with fleshy-fruited plants (FleshRich)										
FleshRich	0.564	0.511	0.472	0.467	0.491	0.472	0.439	0.387	0.553	0.501
Prec	-	-	0.256	0.250	0.186	0.139	0.153	0.122	-	-
Temp	-0.253	-0.204	-	-	-	-	-	-	-0.257	-0.201
PET	-	-	-	-	-	-	-	-	-	-
Seas	-	-	-	-	-	-	-	-	-	-
Topo	0.128	0.161	0.202	0.204	0.240	0.243	0.274	0.292	0.112	0.138
LCovDiv	-	-	0.147	0.151	0.117	0.154	0.124	0.144	-	-
Model r^2	0.70	0.74	0.81	0.81	0.75	0.78	0.67	0.71	0.67	0.71
Model *AIC*	847	836	304	305	440	428	565	555	817	804
Moran's *I*	0.21***	0.00	0.06	0.00	0.22***	0.01	0.21***	0.01	0.22***	0.00
Models with non-fleshy-fruited plants (NonFlesh)										
NonFlesh	0.590	0.569	0.456	0.455	0.481	0.480	0.565	0.524	0.579	0.561
Prec	-	-	0.326	0.321	0.256	0.214	-	-	-	-
Temp	-0.305	-0.241	-	-	-	-	-0.281	-0.258	-0.289	-0.204
PET	-	-	-	-	-	-	-	-	-	-
Seas	-0.112	-0.160	-	-	-	-	-	-	-0.128	-0.186
Topo	-	-	0.179	0.179	0.214	0.207	0.119	0.151	-	-
LCovDiv	-	-	0.143	0.145	0.111	0.144	-	-	-	-
Model r^2	0.75	0.78	0.83	0.83	0.77	0.80	0.71	0.73	0.72	0.76
Model *AIC*	821	809	290	292	427	415	543	538	790	776
Moran's *I*	0.21***	0.01	0.05	0.00	0.22***	0.02	0.17**	0.00	0.23***	0.01

Table 5.3: Standardized partial regression coefficients from traditional ordinary least squares (OLS) regressions and spatial linear models (SLM) with plant species richness (all woody plants, fleshy-fruited plants and non-fleshy-fruited plants, respectively) as response variable, and six environmental variables (see Table 5.1 for abbreviations) as potential predictor variables. Minimal adequate OLS models were chosen from the full set of explanatory variables based on the Akaike Information Criterion (AIC) (see text for details). The high spatial autocorrelation of errors in OLS analysis (all Moran's I, $P < 0.05$) confirms the expected violation of the non-independence assumption. Coefficients from OLS analyses are identical to direct effects in structural equation models.

	Plant species richness					
	All woody		Fleshy		Non-fleshy	
Variables	OLS	SLM	OLS	SLM	OLS	SLM
Prec	0.371	0.364	0.388	0.377	0.313	0.295
Temp	-	-	-	-	-	-
PET	0.294	0.306	0.254	0.267	0.314	0.315
Seas	0.125	0.150	-	-	0.197	0.217
Topo	0.446	0.472	0.372	0.390	0.502	0.524
LCovDiv	0.269	0.279	0.244	0.250	0.284	0.294
Model r^2	0.64	0.66	0.66	0.68	0.59	0.62
Model *AIC*	788	783	706	704	663	656
Moran's *I*	0.16**	-0.01	0.12*	-0.01	0.18**	-0.01

Comparison of parameter estimates (i.e. standardized partial regression coefficients) from SLM and non-spatial OLS models suggests that their strengths are generally very similar (Table 5.2). Moreover, in almost all cases the relative importance of predictor variables to explain avian species richness did not change (Table 5.2). OLS models with woody, fleshy-fruited, or non-fleshy-fruited plant species richness as response variables and all environmental variables as predictor variables similarly indicated that differences in parameter estimates between SLM and non-spatial OLS models were unimportant (Table 5.3). Overall, these results suggest that inference from SLM and OLS models is very similar for the dataset.

5.5 Discussion

My analyses suggest that geographic patterns of tropical bird and woody plant diversity across Kenya are linked via functional relationships and that environmental factors differ in their direct effects on both groups. These functional relationships may be largely driven by vegetation structural effects (hypothesis 2); this is consistent with the strong correlations that I found between the species richness of trophically independent bird and plant taxa. There was no evidence for an important role of resource–consumer interactions (hypothesis 1) since the direct effects of woody species richness on bird species richness in the SEMs were not consistent with the predictions based on trophic relationships. The results were robust to the presence of spatial autocorrelation in the dataset since both spatial and non-spatial analyses yielded very similar results (Tables 5.2 and 5.3).

It is often speculated that resource–consumer interactions play an important role in shaping geographic patterns of animal species richness (e.g. Wright 1983; Hawkins et al. 2003a). However few studies have addressed this issue explicitly, and the results are contrasting. In a seminal paper, Hawkins & Porter (2003) analyzed species richness of butterflies across California and found no relationship between butterfly and food plant diversity once environmental variables had been accounted for, despite strong specificity of butterflies to host plants. Across Britain, however, Menéndez et al. (2007) demonstrated that host-plant richness is an important determinant of butterfly diversity, even when accounting for environmental correlations. For avian consumers, Márquez et al. (2004) showed that the species richness of wintering birds in Europe is more dependent on environmental factors than on food plant diversity whereas Kissling et al. (2007) demonstrated the opposite for avian frugivores in sub-Saharan Africa. Recently published studies indicate that generalizations about resource–consumer diversity at broad spatial scales are difficult to make, probably because the relationship between food plant diversity and animal consumers varies with geographic location (Hawkins & Porter 2003; Márquez et al. 2004; Kissling et al. 2007; Menéndez et al. 2007), evolutionary history (Fleming et al. 1987), spatial and temporal scales of analysis (Burns 2004), and the metabolic ecology of animal consumers (ecto- vs. endotherms; Currie et al. 2004).

For tropical frugivorous bird species it has been shown that their species richness patterns at the continental scale of sub-Saharan Africa are very strongly linked to the species richness of fig trees (*Ficus* spp.; Kissling et al. 2007) – a major fruit resource for frugivores in the tropics (Shanahan et al. 2001a). Such positive relationships between species richness of animal consumers and their food plants can potentially be explained by niche assembly mechanisms, e.g. evolutionary or ecological responses to fruit size, fruit color or vertical stratification of fruit presentation (Herrera 2002; Kissling et al. 2007). I tested the 'fig–frugivore richness hypothesis' (Kissling et al. 2007) with the Kenyan dataset by extracting all *Ficus* species ($n = 32$) from the fleshy-fruited plants, and re-calculated all path models by interchanging woody plant species richness with *Ficus* richness (compare Figure 5.2). The direct effects of *Ficus* diversity on species richness of avian guilds in the path models, however, were similar to (but weaker than) those of all fleshy-fruited plants (Appendix 6) providing only weak evidence for a keystone resource effect of *Ficus* richness on avian frugivore diversity at the spatial scale of Kenya. The differences at the Kenyan and African scale in the importance of *Ficus* for frugivorous birds might be explained by a lack of lowland tropical rain forest in Kenya, which is the habitat type that harbors the highest diversity of *Ficus* and frugivorous birds at the continental scale of sub-Saharan Africa (Kissling et al. 2007).

A higher species richness of woody plants may also be associated with more architectural complexity (hypothesis 2) and thus more structural niches to be occupied by animal species (MacArthur & MacArthur 1961; Cody 1985; Tews et al. 2004). Although a number of studies have demonstrated that the species richness of birds is associated with woody plant diversity at a number of spatial scales and across many habitats (e.g. MacArthur & MacArthur 1961; Lee & Rotenberry 2005; Rompré et al. 2007), very few studies have attempted to separate the effects of resource–consumer interactions and vegetation structural complexity on bird diversity at scales comparable to my study, and none that I am aware of in the tropics. For North America, Rotenberry (1985) and Lee & Rotenberry (2005) analyzed bird diversity in relation to vegetation structure and plant species composition and concluded that plant–bird species associations are not only mediated by vegetation structural complexity but also by food resources. In contrast, my analyses suggest that functional relationships between bird and woody plant diversity across Kenya may be more associated with vegetation structural complexity than resource–consumer interactions. Vegetation structural complexity thus may be more important in shaping geographic gradients of tropical bird diversity than has previously been thought (e.g. Oindo et al. 2001; Jetz & Rahbek 2002; Hawkins et al. 2003a; Kissling et al. 2007; but see Hawkins et al. 2005, 2007b). This requires further investigation.

Although recent research has shown that diversity hotspots of a wide variety of organisms are correlated with environmental variables (see references in Table 5.1), few studies have tried to disentangle the relative direct and indirect effects of environmental predictor variables on plant–animal diversity (Hawkins & Porter 2003; Kissling et al. 2007; Menéndez et al. 2007). My results for woody plants are consistent with recent evidence showing that contemporary water and energy availability play a dominant role in shaping geographic patterns of plant diversity (Field et al. 2005; Kreft & Jetz 2007). However, the path models suggest that climate as well as habitat heterogeneity act in large part indirectly on bird species richness via effects on plants rather than having strong direct effects on bird species distributions (Figure 5.2B). Strong direct effects of climatic factors on animal species richness are more likely for butterflies (Hawkins & Porter 2003; Menéndez et al. 2007), or other solar ectotherms such as reptiles (Hawkins et al. 2003a), which appear to be limited by direct effects of temperature on their physiological tolerances (“physiological tolerance hypothesis”; Currie et al. 2004). For endotherms such as birds, however, it is more likely that contemporary species diversity gradients are predominantly determined by indirect effects of climate, either mediated through trophic relationships and the production of food items (Wright 1983; Kissling et al. 2007), or via habitat composition and vegetation structural complexity (MacArthur & MacArthur 1961; Tews et al. 2004; Rompré et al. 2007; this study). However, some climatic variables might be important in directly determining spatial richness patterns of certain avian trophic guilds (Figure 5.5 and Table 5.2). Further work would be interesting to examine why there is an apparent switch from direct effects of precipitation for frugivorous birds to temperature for non-frugivorous birds.

Recent models for predicting climate change impacts on animal species richness largely rely on statistical relationships between species richness and environmental factors (e.g. Lemoine et al. 2007). It is, however, unclear under which circumstances these assumptions are valid for accurately predicting future species distributions (Araújo & Rahbek 2006). Concerns have arisen because such models assume that species interactions are of minor importance at broad geographic scales and that species assemblages are in a steady-state relationship with contemporary climate (Araújo & Rahbek 2006). However, there is now increasing evidence that species interactions can indeed strongly influence responses to changing climates (e.g. Suttle et al. 2007) and that predictions of ecological responses to climate change cannot simply be based on direct environmental effects on species (e.g. Menéndez et al. 2006, 2007). The results support this view by implying that bird species richness, at least in the tropics, is likely to respond indirectly to changing climates via direct climatic effects on plants. The SEMs further suggest that direct environmental effects on birds and plants differ once functional relationships between birds and woody plants have been accounted for (Figures 5.4 & 5.5). This suggests that climate change could alter the spatial synchrony and reshuffle plant–animal richness, species composition and community organization in tropical ecosystems (Parmesan 2006).

If we are to use indicator taxa for spatially explicit forecasting of changes in biodiversity we need to know much more about what underlies richness correlations, including species interactions and direct and indirect environmental effects on species richness (Wolters et al. 2006). Forecasts of changes in species richness are more likely to fail if climate is not the only factor limiting the distribution of bird species and assemblages, e.g. if functional relationships (resource–consumer interactions, vegetation structural complexity), interspecific interactions (predation, competition, mutualism) or dispersal limitation play a prominent role (Parmesan 2006). Changes in woody plant species richness could lag behind those expected on the basis of climate-change scenarios because of dispersal limitation and longevity of the species. This in turn could affect the future distribution of bird species richness via effects on species' food and especially habitat resources. Recent research from Britain has demonstrated 'colonization lags', at least for butterflies (Menéndez et al. 2006), and Svenning & Skov (2007) suggest that changes in plant species distributions may lag behind climate change by centuries. I thus conclude that direct climatic effects on plants and animals are likely to differ and that future predictions of animal species richness in response to climate change therefore need to include indirect climatic effects, e.g. via plants.

6 GENERAL CONCLUSIONS

6.1 What have we learned?

This thesis provides a first comprehensive assessment of geographic patterns of avian frugivore richness and their environmental and historical determinants at broad spatial scales. In doing so it takes advantage of recent developments in data availability, geoinformatics, and statistical modeling and applies path analyses and structural equation models, spatial and nonspatial regressions, and bootstrapping techniques to disentangle the relative roles of predictor variables. At least three major findings have to be highlighted from the results of the three preceding chapters. First, analyses at continental and global scales indicate that geographic patterns of frugivore richness differ significantly from those of all birds, at least in the Afrotropics and in Southeast Asia. These differences are likely related to the spatial distribution of food resources which appear to be fundamental in determining species distributions. Second, analyses at continental and regional scales imply that most climatic variables largely act indirectly on frugivore richness, via effects on plants, rather than only directly as often assumed. Direct effects of plants on frugivore richness include trophic interactions with major food plants (e.g. *Ficus*) or functional relationships driven by vegetation structural complexity. Finally, the global scale analysis revealed that historical influences on regional patterns of avian frugivore diversity cannot be neglected. These are likely related to the evolutionary history of fleshy–fruited plant taxa, niche conservatism, and past climate change. Overall the results of this thesis imply an important role of plant-animal interactions and contemporary and historical environmental constraints on community assembly over macroecological and macroevolutionary scales.

6.2 Prospects for future research

6.2.1 Macroecology of plant-frugivore interactions

Macroecological research on frugivores is in its infancy and we still know little about how patterns and processes at smaller spatial and temporal scales relate to those at broader scales (Burns 2004). Due to the vast knowledge on plant-frugivore interactions at small spatial and temporal scales this field offers great potential to link patterns and processes across scales (Böhning-Gaese 1997; Burns 2004; Rahbek 2005). Moreover, frugivorous species and their food plants appear to be an interesting model system to better understand how environmental, historical and evolutionary constraints affect community assembly at local and regional scales (Ricklefs 1987). For instance, comparisons of plant-frugivore systems between regions with different biogeographic history could shed light on ecological and evolutionary processes and species interactions (Voigt et al. 2004; Böhning-Gaese 2007). In particularly, there is little knowledge about the biogeography and phylogeography of frugivorous species and how frugivores have co–diversified with fleshy–fruited plants in different biogeographic regions (Fleming et al. 1987; Fleming 2005; Primack and Corlett 2005). Moreover, the geographic co-occurrence of other frugivorous taxa (e.g., mammals) has not been examined in detail at broader spatial scales and might be an interesting avenue for future research. One of the challenges will be to compile high-quality distribution data across several taxa and to combine them with phylogenetic information (see below).

6.2.2 Biotic interactions and climate change projections

Accelerated climate change and habitat destruction through direct human activities are two of the greatest threats to terrestrial biodiversity (Sala et al. 2000; Jetz et al. 2007). Climate change in particular has tremendous effects on the phenology and distribution of species (Parmesan 2006), and by the end of the 21st century, large portions of the Earth's surface may experience climates not found at present (Williams et al. 2007). With the releases of the Intergovernmental Panel on Climate Change (IPCC) reports this year it has become even clearer that global warming's impacts will only worsen (Kerr 2007). Although recent changes in climate have already resulted in observable changes in the phenology, reproductive success, abundance, and geographical ranges of plant and animal species (e.g., Thomas & Lennon 1999; Root et al. 2003; Crick 2004; Parmesan 2006; Lemoine et al. 2007), it is far from clear how climate-change impacts on biodiversity can be forecasted (Araújo & Rahbek 2006; Dormann 2007). The macroecological approach has much to offer to global change solutions (Kerr et al. 2007).

Recent models for predicting climate change impacts on animal species richness largely rely on statistical relationships between species richness and environmental factors (e.g. Lemoine et al. 2007). It is, however, unclear under which circumstances these assumptions are valid for accurately predicting future species distributions (Araújo & Rahbek 2006). Concerns have arisen because such models assume that species interactions are of minor importance at broad geographic scales and that species assemblages are in a steady-state relationship with contemporary climate (Araújo & Rahbek 2006). However, the results of this thesis show that biotic interactions (here plant-frugivore interactions) need to be understood if we are to predict how species and communities will respond to climate. Moreover, these results as well as increasing evidence from other studies imply that species interactions can indeed strongly influence responses to changing climates (e.g. Suttle et al. 2007) and that predictions of ecological responses to climate change cannot simply be based on direct environmental effects on species (e.g. Menéndez et al. 2006, 2007). The consideration of biotic interactions when modeling species distributions under climate change has widely been neglected but will be a major challenge for future research (Araújo & Luoto 2007; Heikkinen et al. 2007).

6.2.3 Macroevolution and the integration of phylogenies

Results from this thesis have shown that historical processes need to be taken into account to fully understand geographic patterns of species richness. Representing history as biogeographic realm membership is certainly a very crude approximation for the evolutionary and biogeographic processes that have shaped geographic patterns of species richness and communities. A better and potentially more rewarding approach is to use phylogenetic analyses to assess the influence of historical and evolutionary processes on the structure of contemporary ecological systems (Webb et al. 2002; Wiens & Donoghue 2004; Ricklefs 2007). The integration of evolutionary and ecological approaches at broad spatial scales is still in its infancy but has great potential for a better understanding of geographic gradients in species richness (Wiens & Donoghue 2004; Wiens & Graham 2005; Harrison & Cornell 2007; Johnson & Stinchcombe 2007). Linking broad-scale distribution databases with phylogenetic information could, for instance, help to better understand centers of diversification (Fjeldså & Rahbek 2006; Hawkins et al. 2007b), speciation mechanisms (Raikow & Bledsoe 2000; Graham et al. 2004; Mittelbach et al. 2007), and spatial variation in diversification rates (Ricklefs 2006b; Diniz-Filho et al. 2007).

6.3 Concluding remarks

Understanding geographic patterns of biological diversity and their underlying processes has ever fascinated ecologists and evolutionary biologists (Darwin 1859; Wallace 1878; MacArthur 1972; Brown 1995) and will continue to be one of the big challenges of science in the next few decades (Pennisi 2005). To answer the question "what determines species diversity” will require a major interdisciplinary effort, including knowledge and people from disciplines such as ecology, biogeography, palaeontology, systematics, evolutionary biology, and the earth sciences. Recent developments in ecological theory, data availability, DNA technology and bio- and geoinformatics provide ample opportunities to advance this field. Progress in understanding the distribution of life on earth will likely benefit from merging evolutionary and ecological approaches at broad spatial scales.

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Appendix 1: References for classification and global species list

The following references were used to extract food information:

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Table A1: List of frugivorous species (n = 1,230) with references used to extract food information.

No	Order	Family	Species	Source of food information
1	Struthioniformes	Casuariidae	*Casuarius casuarius*	Hoyo et al. (1992)
2	Struthioniformes	Casuariidae	*Casuarius bennetti*	Hoyo et al. (1992)
3	Struthioniformes	Casuariidae	*Casuarius unappendiculatus*	Hoyo et al. (1992)
4	Tinamiformes	Tinamidae	*Tinamus tao*	Hoyo et al. (1992)
5	Tinamiformes	Tinamidae	*Tinamus major*	Hoyo et al. (1992)
6	Tinamiformes	Tinamidae	*Tinamus guttatus*	Hoyo et al. (1992)
7	Tinamiformes	Tinamidae	*Nothocercus bonapartei*	Hoyo et al. (1992)
8	Tinamiformes	Tinamidae	*Nothocercus julius*	Hoyo et al. (1992)
9	Tinamiformes	Tinamidae	*Crypturellus berlepschi*	Hoyo et al. (1992)
10	Tinamiformes	Tinamidae	*Crypturellus cinereus*	Hoyo et al. (1992)
11	Tinamiformes	Tinamidae	*Crypturellus soui*	Hoyo et al. (1992)
12	Tinamiformes	Tinamidae	*Crypturellus ptaritepui*	Hoyo et al. (1992)
13	Tinamiformes	Tinamidae	*Crypturellus cinnamomeus*	Hoyo et al. (1992)
14	Tinamiformes	Tinamidae	*Crypturellus undulatus*	Hoyo et al. (1992)
15	Tinamiformes	Tinamidae	*Crypturellus transfasciatus*	Hoyo et al. (1992)
16	Tinamiformes	Tinamidae	*Crypturellus strigulosus*	Hoyo et al. (1992)

17	Tinamiformes	Tinamidae	*Crypturellus boucardi*	Hoyo et al. (1992)
18	Tinamiformes	Tinamidae	*Crypturellus kerriae*	Hoyo et al. (1992)
19	Tinamiformes	Tinamidae	*Crypturellus erythropus*	Hoyo et al. (1992)
20	Tinamiformes	Tinamidae	*Crypturellus duidae*	Hoyo et al. (1992)
21	Tinamiformes	Tinamidae	*Crypturellus atrocapillus*	Hoyo et al. (1992)
22	Tinamiformes	Tinamidae	*Crypturellus variegatus*	Hoyo et al. (1992)
23	Tinamiformes	Tinamidae	*Crypturellus brevirostris*	Hoyo et al. (1992)
24	Tinamiformes	Tinamidae	*Crypturellus bartletti*	Hoyo et al. (1992)
25	Tinamiformes	Tinamidae	*Crypturellus casiquiare*	Hoyo et al. (1992)
26	Craciformes	Cracidae	*Ortalis vetula*	Elliott et al. (1994)
27	Craciformes	Cracidae	*Ortalis cinereiceps*	Elliott et al. (1994)
28	Craciformes	Cracidae	*Ortalis garrula*	Elliott et al. (1994)
29	Craciformes	Cracidae	*Ortalis ruficauda*	Elliott et al. (1994)
30	Craciformes	Cracidae	*Ortalis erythroptera*	Elliott et al. (1994)
31	Craciformes	Cracidae	*Ortalis wagleri*	Elliott et al. (1994)
32	Craciformes	Cracidae	*Ortalis poliocephala*	Elliott et al. (1994)
33	Craciformes	Cracidae	*Ortalis leucogastra*	Elliott et al. (1994)
34	Craciformes	Cracidae	*Ortalis guttata*	Elliott et al. (1994)
35	Craciformes	Cracidae	*Ortalis motmot*	Elliott et al. (1994)
36	Craciformes	Cracidae	*Ortalis superciliaris*	Elliott et al. (1994)
37	Craciformes	Cracidae	*Penelope argyrotis*	Elliott et al. (1994)
38	Craciformes	Cracidae	*Penelope barbata*	Elliott et al. (1994)
39	Craciformes	Cracidae	*Penelope ortoni*	Elliott et al. (1994)
40	Craciformes	Cracidae	*Penelope montagnii*	Elliott et al. (1994)
41	Craciformes	Cracidae	*Penelope marail*	Elliott et al. (1994)
42	Craciformes	Cracidae	*Penelope superciliaris*	Elliott et al. (1994)
43	Craciformes	Cracidae	*Penelope dabbenei*	Elliott et al. (1994)
44	Craciformes	Cracidae	*Penelope purpurascens*	Elliott et al. (1994)
45	Craciformes	Cracidae	*Penelope perspicax*	Elliott et al. (1994)
46	Craciformes	Cracidae	*Penelope albipennis*	Elliott et al. (1994)
47	Craciformes	Cracidae	*Penelope jacquacu*	Elliott et al. (1994)
48	Craciformes	Cracidae	*Penelope obscura*	Elliott et al. (1994)
49	Craciformes	Cracidae	*Penelope pileata*	Elliott et al. (1994)
50	Craciformes	Cracidae	*Penelope ochrogaster*	Elliott et al. (1994)
51	Craciformes	Cracidae	*Penelope jacucaca*	Elliott et al. (1994)
52	Craciformes	Cracidae	*Pipile pipile*	Elliott et al. (1994)
53	Craciformes	Cracidae	*Pipile cumanensis*	Elliott et al. (1994)
54	Craciformes	Cracidae	*Pipile cujubi*	Elliott et al. (1994)
55	Craciformes	Cracidae	*Pipile jacutinga*	Elliott et al. (1994)

56	Craciformes	Cracidae	*Aburria aburri*	Elliott et al. (1994)
57	Craciformes	Cracidae	*Chamaepetes unicolor*	Elliott et al. (1994)
58	Craciformes	Cracidae	*Chamaepetes goudotii*	Elliott et al. (1994)
59	Craciformes	Cracidae	*Penelopina nigra*	Elliott et al. (1994)
60	Craciformes	Cracidae	*Oreophasis derbianus*	Elliott et al. (1994)
61	Craciformes	Cracidae	*Nothocrax urumutum*	Elliott et al. (1994)
62	Craciformes	Cracidae	*Mitu tomentosa*	Elliott et al. (1994)
63	Craciformes	Cracidae	*Mitu salvini*	Elliott et al. (1994)
64	Craciformes	Cracidae	*Mitu tuberosa*	Elliott et al. (1994)
65	Craciformes	Cracidae	*Mitu mitu*	Elliott et al. (1994)
66	Craciformes	Cracidae	*Pauxi pauxi*	Elliott et al. (1994)
67	Craciformes	Cracidae	*Pauxi unicornis*	Elliott et al. (1994)
68	Craciformes	Cracidae	*Crax rubra*	Elliott et al. (1994)
69	Craciformes	Cracidae	*Crax alberti*	Elliott et al. (1994)
70	Craciformes	Cracidae	*Crax daubentoni*	Elliott et al. (1994)
71	Craciformes	Cracidae	*Crax alector*	Elliott et al. (1994)
72	Craciformes	Cracidae	*Crax fasciolata*	Elliott et al. (1994)
73	Craciformes	Cracidae	*Crax blumenbachii*	Elliott et al. (1994)
74	Craciformes	Megapodiidae	*Aepypodius arfakianus*	Elliott et al. (1994)
75	Craciformes	Megapodiidae	*Macrocephalon maleo*	Elliott et al. (1994)
76	Galliformes	Phasianidae	*Pternistis camerunensis*	Elliott et al. (1994)
77	Galliformes	Phasianidae	*Rhizothera longirostris*	Elliott et al. (1994)
78	Galliformes	Phasianidae	*Arborophila orientalis*	Elliott et al. (1994)
79	Galliformes	Phasianidae	*Haematortyx sanguiniceps*	Elliott et al. (1994)
80	Galliformes	Phasianidae	*Lophura inornata*	Elliott et al. (1994)
81	Galliformes	Phasianidae	*Lophura diardi*	Elliott et al. (1994)
82	Galliformes	Phasianidae	*Lophura bulweri*	Elliott et al. (1994)
83	Galliformes	Phasianidae	*Syrmaticus humiae*	Elliott et al. (1994)
84	Galliformes	Phasianidae	*Polyplectron inopinatum*	Elliott et al. (1994)
85	Galliformes	Phasianidae	*Polyplectron schleiermacheri*	Elliott et al. (1994)
86	Galliformes	Phasianidae	*Afropavo congensis*	Elliott et al. (1994)
87	Galliformes	Odontophoridae	*Dendrortyx barbatus*	Elliott et al. (1994)
88	Galliformes	Odontophoridae	*Odontophorus capueira*	Elliott et al. (1994)
89	Piciformes	Picidae	*Melanerpes candidus*	Hoyo et al. (2002)
90	Piciformes	Picidae	*Melanerpes flavifrons*	Hoyo et al. (2002)
91	Piciformes	Picidae	*Melanerpes hypopolius*	Hoyo et al. (2002)
92	Piciformes	Megalaimidae	*Psilopogon pyrolophus*	Hoyo et al. (2002)
93	Piciformes	Megalaimidae	*Megalaima virens*	Hoyo et al. (2002)
94	Piciformes	Megalaimidae	*Megalaima lagrandieri*	Hoyo et al. (2002)

95	Piciformes	Megalaimidae	*Megalaima zeylanica*	Hoyo et al. (2002)
96	Piciformes	Megalaimidae	*Megalaima lineata*	Hoyo et al. (2002)
97	Piciformes	Megalaimidae	*Megalaima viridis*	Hoyo et al. (2002)
98	Piciformes	Megalaimidae	*Megalaima faiostricta*	Hoyo et al. (2002)
99	Piciformes	Megalaimidae	*Megalaima corvina*	Hoyo et al. (2002)
100	Piciformes	Megalaimidae	*Megalaima chrysopogon*	Hoyo et al. (2002)
101	Piciformes	Megalaimidae	*Megalaima rafflesii*	Hoyo et al. (2002)
102	Piciformes	Megalaimidae	*Megalaima mystacophanos*	Hoyo et al. (2002)
103	Piciformes	Megalaimidae	*Megalaima javensis*	Hoyo et al. (2002)
104	Piciformes	Megalaimidae	*Megalaima flavifrons*	Hoyo et al. (2002)
105	Piciformes	Megalaimidae	*Megalaima franklinii*	Hoyo et al. (2002)
106	Piciformes	Megalaimidae	*Megalaima oorti*	Hoyo et al. (2002)
107	Piciformes	Megalaimidae	*Megalaima asiatica*	Hoyo et al. (2002)
108	Piciformes	Megalaimidae	*Megalaima monticola*	Hoyo et al. (2002)
109	Piciformes	Megalaimidae	*Megalaima incognita*	Hoyo et al. (2002)
110	Piciformes	Megalaimidae	*Megalaima henricii*	Hoyo et al. (2002)
111	Piciformes	Megalaimidae	*Megalaima armillaris*	Hoyo et al. (2002)
112	Piciformes	Megalaimidae	*Megalaima pulcherrima*	Hoyo et al. (2002)
113	Piciformes	Megalaimidae	*Megalaima australis*	Hoyo et al. (2002)
114	Piciformes	Megalaimidae	*Megalaima eximia*	Hoyo et al. (2002)
115	Piciformes	Megalaimidae	*Megalaima rubricapilla*	Hoyo et al. (2002)
116	Piciformes	Megalaimidae	*Megalaima haemacephala*	Hoyo et al. (2002)
117	Piciformes	Megalaimidae	*Calorhamphus fuliginosus*	Hoyo et al. (2002)
118	Piciformes	Lybiidae	*Gymnobucco calvus*	Hoyo et al. (2002)
119	Piciformes	Lybiidae	*Gymnobucco peli*	Hoyo et al. (2002)
120	Piciformes	Lybiidae	*Gymnobucco sladeni*	Hoyo et al. (2002)
121	Piciformes	Lybiidae	*Gymnobucco bonapartei*	Hoyo et al. (2002)
122	Piciformes	Lybiidae	*Stactolaema leucotis*	Hoyo et al. (2002)
123	Piciformes	Lybiidae	*Stactolaema anchietae*	Hoyo et al. (2002)
124	Piciformes	Lybiidae	*Stactolaema whytii*	Hoyo et al. (2002)
125	Piciformes	Lybiidae	*Stactolaema olivacea*	Hoyo et al. (2002)
126	Piciformes	Lybiidae	*Pogoniulus scolopaceus*	Hoyo et al. (2002)
127	Piciformes	Lybiidae	*Pogoniulus coryphaeus*	Hoyo et al. (2002)
128	Piciformes	Lybiidae	*Pogoniulus leucomystax*	Hoyo et al. (2002)
129	Piciformes	Lybiidae	*Pogoniulus simplex*	Hoyo et al. (2002)
130	Piciformes	Lybiidae	*Pogoniulus atroflavus*	Hoyo et al. (2002)
131	Piciformes	Lybiidae	*Pogoniulus subsulphureus*	Hoyo et al. (2002)
132	Piciformes	Lybiidae	*Pogoniulus bilineatus*	Hoyo et al. (2002)
133	Piciformes	Lybiidae	*Pogoniulus chrysoconus*	Hoyo et al. (2002)

134	Piciformes	Lybiidae	*Pogoniulus pusillus*	Hoyo et al. (2002)
135	Piciformes	Lybiidae	*Buccanodon duchaillui*	Hoyo et al. (2002)
136	Piciformes	Lybiidae	*Tricholaema hirsuta*	Hoyo et al. (2002)
137	Piciformes	Lybiidae	*Tricholaema diademata*	Hoyo et al. (2002)
138	Piciformes	Lybiidae	*Tricholaema frontata*	Hoyo et al. (2002)
139	Piciformes	Lybiidae	*Tricholaema lacrymosa*	Hoyo et al. (2002)
140	Piciformes	Lybiidae	*Lybius undatus*	Hoyo et al. (2002)
141	Piciformes	Lybiidae	*Lybius vieilloti*	Hoyo et al. (2002)
142	Piciformes	Lybiidae	*Lybius leucocephalus*	Hoyo et al. (2002)
143	Piciformes	Lybiidae	*Lybius chaplini*	Hoyo et al. (2002)
144	Piciformes	Lybiidae	*Lybius rubrifacies*	Hoyo et al. (2002)
145	Piciformes	Lybiidae	*Lybius guifsobalito*	Hoyo et al. (2002)
146	Piciformes	Lybiidae	*Lybius torquatus*	Hoyo et al. (2002)
147	Piciformes	Lybiidae	*Lybius minor*	Hoyo et al. (2002)
148	Piciformes	Lybiidae	*Lybius bidentatus*	Hoyo et al. (2002)
149	Piciformes	Lybiidae	*Lybius dubius*	Hoyo et al. (2002)
150	Piciformes	Lybiidae	*Lybius rolleti*	Hoyo et al. (2002)
151	Piciformes	Lybiidae	*Trachyphonus margaritatus*	Hoyo et al. (2002)
152	Piciformes	Lybiidae	*Trachyphonus erythrocephalus*	Hoyo et al. (2002)
153	Piciformes	Ramphastidae	*Capito aurovirens*	Hoyo et al. (2002)
154	Piciformes	Ramphastidae	*Capito wallacei*	Hoyo et al. (2002)
155	Piciformes	Ramphastidae	*Capito maculicoronatus*	Hoyo et al. (2002)
156	Piciformes	Ramphastidae	*Capito squamatus*	Hoyo et al. (2002)
157	Piciformes	Ramphastidae	*Capito hypoleucus*	Hoyo et al. (2002)
158	Piciformes	Ramphastidae	*Capito dayi*	Hoyo et al. (2002)
159	Piciformes	Ramphastidae	*Capito quinticolor*	Hoyo et al. (2002)
160	Piciformes	Ramphastidae	*Capito niger*	Hoyo et al. (2002)
161	Piciformes	Ramphastidae	*Eubucco richardsoni*	Hoyo et al. (2002)
162	Piciformes	Ramphastidae	*Eubucco bourcierii*	Hoyo et al. (2002)
163	Piciformes	Ramphastidae	*Eubucco tucinkae*	Hoyo et al. (2002)
164	Piciformes	Ramphastidae	*Eubucco versicolor*	Hoyo et al. (2002)
165	Piciformes	Ramphastidae	*Semnornis frantzii*	Hoyo et al. (2002)
166	Piciformes	Ramphastidae	*Semnornis ramphastinus*	Hoyo et al. (2002)
167	Piciformes	Ramphastidae	*Aulacorhynchus prasinus*	Hoyo et al. (2002)
168	Piciformes	Ramphastidae	*Aulacorhynchus sulcatus*	Hoyo et al. (2002)
169	Piciformes	Ramphastidae	*Aulacorhynchus derbianus*	Hoyo et al. (2002)
170	Piciformes	Ramphastidae	*Aulacorhynchus haematopygus*	Hoyo et al. (2002)
171	Piciformes	Ramphastidae	*Aulacorhynchus huallagae*	Hoyo et al. (2002)
172	Piciformes	Ramphastidae	*Aulacorhynchus coeruleicinctis*	Hoyo et al. (2002)

173	Piciformes	Ramphastidae	*Pteroglossus inscriptus*	Hoyo et al. (2002)
174	Piciformes	Ramphastidae	*Pteroglossus viridis*	Hoyo et al. (2002)
175	Piciformes	Ramphastidae	*Pteroglossus bitorquatus*	Hoyo et al. (2002)
176	Piciformes	Ramphastidae	*Pteroglossus azara*	Hoyo et al. (2002)
177	Piciformes	Ramphastidae	*Pteroglossus castanotis*	Hoyo et al. (2002)
178	Piciformes	Ramphastidae	*Pteroglossus aracari*	Hoyo et al. (2002)
179	Piciformes	Ramphastidae	*Pteroglossus torquatus*	Hoyo et al. (2002)
180	Piciformes	Ramphastidae	*Pteroglossus frantzii*	Hoyo et al. (2002)
181	Piciformes	Ramphastidae	*Pteroglossus pluricinctus*	Hoyo et al. (2002)
182	Piciformes	Ramphastidae	*Pteroglossus beauharnaesii*	Hoyo et al. (2002)
183	Piciformes	Ramphastidae	*Baillonius bailloni*	Hoyo et al. (2002)
184	Piciformes	Ramphastidae	*Andigena laminirostris*	Hoyo et al. (2002)
185	Piciformes	Ramphastidae	*Andigena hypoglauca*	Hoyo et al. (2002)
186	Piciformes	Ramphastidae	*Andigena cucullata*	Hoyo et al. (2002)
187	Piciformes	Ramphastidae	*Andigena nigrirostris*	Hoyo et al. (2002)
188	Piciformes	Ramphastidae	*Selenidera spectabilis*	Hoyo et al. (2002)
189	Piciformes	Ramphastidae	*Selenidera reinwardtii*	Hoyo et al. (2002)
190	Piciformes	Ramphastidae	*Selenidera nattereri*	Hoyo et al. (2002)
191	Piciformes	Ramphastidae	*Selenidera culik*	Hoyo et al. (2002)
192	Piciformes	Ramphastidae	*Selenidera maculirostris*	Hoyo et al. (2002)
193	Piciformes	Ramphastidae	*Selenidera gouldii*	Hoyo et al. (2002)
194	Piciformes	Ramphastidae	*Ramphastos sulfuratus*	Hoyo et al. (2002)
195	Piciformes	Ramphastidae	*Ramphastos brevis*	Hoyo et al. (2002)
196	Piciformes	Ramphastidae	*Ramphastos vitellinus*	Hoyo et al. (2002)
197	Piciformes	Ramphastidae	*Ramphastos dicolorus*	Hoyo et al. (2002)
198	Piciformes	Ramphastidae	*Ramphastos ambiguus*	Hoyo et al. (2002)
199	Piciformes	Ramphastidae	*Ramphastos tucanus*	Hoyo et al. (2002)
200	Piciformes	Ramphastidae	*Ramphastos toco*	Hoyo et al. (2002)
201	Bucerotiformes	Bucerotidae	*Ocyceros griseus*	Hoyo et al. (2001)
202	Bucerotiformes	Bucerotidae	*Ocyceros gingalensis*	Hoyo et al. (2001)
203	Bucerotiformes	Bucerotidae	*Ocyceros birostris*	Hoyo et al. (2001)
204	Bucerotiformes	Bucerotidae	*Anthracoceros coronatus*	Hoyo et al. (2001)
205	Bucerotiformes	Bucerotidae	*Anthracoceros albirostris*	Hoyo et al. (2001)
206	Bucerotiformes	Bucerotidae	*Anthracoceros malayanus*	Hoyo et al. (2001)
207	Bucerotiformes	Bucerotidae	*Anthracoceros marchei*	Hoyo et al. (2001)
208	Bucerotiformes	Bucerotidae	*Anthracoceros montani*	Hoyo et al. (2001)
209	Bucerotiformes	Bucerotidae	*Buceros rhinoceros*	Hoyo et al. (2001)
210	Bucerotiformes	Bucerotidae	*Buceros bicornis*	Hoyo et al. (2001)
211	Bucerotiformes	Bucerotidae	*Buceros hydrocorax*	Hoyo et al. (2001)

212	Bucerotiformes	Bucerotidae	*Buceros vigil*	Hoyo et al. (2001)
213	Bucerotiformes	Bucerotidae	*Anorrhinus tickelli*	Hoyo et al. (2001)
214	Bucerotiformes	Bucerotidae	*Anorrhinus austeni*	Hoyo et al. (2001)
215	Bucerotiformes	Bucerotidae	*Anorrhinus galeritus*	Hoyo et al. (2001)
216	Bucerotiformes	Bucerotidae	*Penelopides affinis*	Hoyo et al. (2001)
217	Bucerotiformes	Bucerotidae	*Penelopides manillae*	Hoyo et al. (2001)
218	Bucerotiformes	Bucerotidae	*Penelopides mindorensis*	Hoyo et al. (2001)
219	Bucerotiformes	Bucerotidae	*Penelopides panini*	Hoyo et al. (2001)
220	Bucerotiformes	Bucerotidae	*Penelopides exarhatus*	Hoyo et al. (2001)
221	Bucerotiformes	Bucerotidae	*Aceros comatus*	Hoyo et al. (2001)
222	Bucerotiformes	Bucerotidae	*Aceros nipalensis*	Hoyo et al. (2001)
223	Bucerotiformes	Bucerotidae	*Aceros corrugatus*	Hoyo et al. (2001)
224	Bucerotiformes	Bucerotidae	*Aceros waldeni*	Hoyo et al. (2001)
225	Bucerotiformes	Bucerotidae	*Aceros leucocephalus*	Hoyo et al. (2001)
226	Bucerotiformes	Bucerotidae	*Aceros cassidix*	Hoyo et al. (2001)
227	Bucerotiformes	Bucerotidae	*Aceros undulatus*	Hoyo et al. (2001)
228	Bucerotiformes	Bucerotidae	*Aceros narcondami*	Hoyo et al. (2001)
229	Bucerotiformes	Bucerotidae	*Aceros everetti*	Hoyo et al. (2001)
230	Bucerotiformes	Bucerotidae	*Aceros subruficollis*	Hoyo et al. (2001)
231	Bucerotiformes	Bucerotidae	*Aceros plicatus*	Hoyo et al. (2001)
232	Bucerotiformes	Bucerotidae	*Ceratogymna bucinator*	Hoyo et al. (2001)
233	Bucerotiformes	Bucerotidae	*Ceratogymna fistulator*	Hoyo et al. (2001)
234	Bucerotiformes	Bucerotidae	*Ceratogymna brevis*	Hoyo et al. (2001)
235	Bucerotiformes	Bucerotidae	*Ceratogymna subcylindricus*	Hoyo et al. (2001)
236	Bucerotiformes	Bucerotidae	*Ceratogymna cylindricus*	Hoyo et al. (2001)
237	Bucerotiformes	Bucerotidae	*Ceratogymna atrata*	Hoyo et al. (2001)
238	Bucerotiformes	Bucerotidae	*Ceratogymna elata*	Hoyo et al. (2001)
239	Trogoniformes	Trogonidae	*Pharomachrus mocinno*	Hoyo et al. (2001)
240	Trogoniformes	Trogonidae	*Pharomachrus antisianus*	Hoyo et al. (2001)
241	Trogoniformes	Trogonidae	*Pharomachrus fulgidus*	Hoyo et al. (2001)
242	Trogoniformes	Trogonidae	*Pharomachrus auriceps*	Hoyo et al. (2001)
243	Trogoniformes	Trogonidae	*Pharomachrus pavoninus*	Hoyo et al. (2001)
244	Trogoniformes	Trogonidae	*Priotelus temnurus*	Hoyo et al. (2001)
245	Trogoniformes	Trogonidae	*Trogon melanurus*	Hoyo et al. (2001)
246	Trogoniformes	Trogonidae	*Trogon clathratus*	Hoyo et al. (2001)
247	Trogoniformes	Trogonidae	*Trogon comptus*	Hoyo et al. (2001)
248	Trogoniformes	Trogonidae	*Trogon bairdii*	Hoyo et al. (2001)
249	Trogoniformes	Trogonidae	*Trogon viridis*	Hoyo et al. (2001)
250	Trogoniformes	Trogonidae	*Trogon citreolus*	Hoyo et al. (2001)

251	Trogoniformes	Trogonidae	*Trogon elegans*	Hoyo et al. (2001)
252	Trogoniformes	Trogonidae	*Trogon personatus*	Hoyo et al. (2001)
253	Trogoniformes	Trogonidae	*Trogon violaceus*	Hoyo et al. (2001)
254	Coliiformes	Coliidae	*Colius striatus*	Hoyo et al. (2001)
255	Coliiformes	Coliidae	*Colius leucocephalus*	Hoyo et al. (2001)
256	Coliiformes	Coliidae	*Colius castanotus*	Hoyo et al. (2001)
257	Coliiformes	Coliidae	*Colius colius*	Hoyo et al. (2001)
258	Coliiformes	Coliidae	*Urocolius macrourus*	Hoyo et al. (2001)
259	Coliiformes	Coliidae	*Urocolius indicus*	Hoyo et al. (2001)
260	Cuculiformes	Cuculidae	*Microdynamis parva*	Hoyo et al. (1997)
261	Cuculiformes	Cuculidae	*Eudynamys scolopacea*	Hoyo et al. (1997)
262	Cuculiformes	Cuculidae	*Scythrops novaehollandiae*	Hoyo et al. (1997)
263	Cuculiformes	Cuculidae	*Phaenicophaeus pyrrhocephalus*	Hoyo et al. (1997)
264	Cuculiformes	Cuculidae	*Coua serriana*	Hoyo et al. (1997)
265	Psittaciformes	Cacatuidae	*Cacatua ophthalmica*	Hoyo et al. (1997)
266	Psittaciformes	Cacatuidae	*Cacatua ducorpsii*	Hoyo et al. (1997)
267	Psittaciformes	Psittacidae	*Eos histrio*	Hoyo et al. (1997)
268	Psittaciformes	Psittacidae	*Nestor notabilis*	Hoyo et al. (1997)
269	Psittaciformes	Psittacidae	*Nestor meridionalis*	Hoyo et al. (1997)
270	Psittaciformes	Psittacidae	*Psittaculirostris edwardsii*	Hoyo et al. (1997)
271	Psittaciformes	Psittacidae	*Bolbopsittacus lunulatus*	Hoyo et al. (1997)
272	Psittaciformes	Psittacidae	*Psittinus cyanurus*	Hoyo et al. (1997)
273	Psittaciformes	Psittacidae	*Psittacella modesta*	Hoyo et al. (1997)
274	Psittaciformes	Psittacidae	*Psittacella madaraszi*	Hoyo et al. (1997)
275	Psittaciformes	Psittacidae	*Geoffroyus heteroclitus*	Hoyo et al. (1997)
276	Psittaciformes	Psittacidae	*Prioniturus montanus*	Hoyo et al. (1997)
277	Psittaciformes	Psittacidae	*Prioniturus waterstradti*	Hoyo et al. (1997)
278	Psittaciformes	Psittacidae	*Prioniturus platenae*	Hoyo et al. (1997)
279	Psittaciformes	Psittacidae	*Prioniturus luconensis*	Hoyo et al. (1997)
280	Psittaciformes	Psittacidae	*Prioniturus discurus*	Hoyo et al. (1997)
281	Psittaciformes	Psittacidae	*Prioniturus verticalis*	Hoyo et al. (1997)
282	Psittaciformes	Psittacidae	*Prioniturus flavicans*	Hoyo et al. (1997)
283	Psittaciformes	Psittacidae	*Prioniturus platurus*	Hoyo et al. (1997)
284	Psittaciformes	Psittacidae	*Prioniturus mada*	Hoyo et al. (1997)
285	Psittaciformes	Psittacidae	*Tanygnathus megalorynchos*	Hoyo et al. (1997)
286	Psittaciformes	Psittacidae	*Tanygnathus lucionensis*	Hoyo et al. (1997)
287	Psittaciformes	Psittacidae	*Tanygnathus sumatranus*	Hoyo et al. (1997)
288	Psittaciformes	Psittacidae	*Tanygnathus gramineus*	Hoyo et al. (1997)
289	Psittaciformes	Psittacidae	*Eclectus roratus*	Hoyo et al. (1997)

290	Psittaciformes	Psittacidae	*Psittrichas fulgidus*	Hoyo et al. (1997)
291	Psittaciformes	Psittacidae	*Prosopeia splendens*	Hoyo et al. (1997)
292	Psittaciformes	Psittacidae	*Prosopeia tabuensis*	Hoyo et al. (1997)
293	Psittaciformes	Psittacidae	*Alisterus chloropterus*	Hoyo et al. (1997)
294	Psittaciformes	Psittacidae	*Aprosmictus jonquillaceus*	Hoyo et al. (1997)
295	Psittaciformes	Psittacidae	*Barnardius zonarius*	Hoyo et al. (1997)
296	Psittaciformes	Psittacidae	*Coracopsis vasa*	Hoyo et al. (1997)
297	Psittaciformes	Psittacidae	*Coracopsis nigra*	Hoyo et al. (1997)
298	Psittaciformes	Psittacidae	*Psittacus erithacus*	Hoyo et al. (1997)
299	Psittaciformes	Psittacidae	*Poicephalus senegalus*	Hoyo et al. (1997)
300	Psittaciformes	Psittacidae	*Poicephalus meyeri*	Hoyo et al. (1997)
301	Psittaciformes	Psittacidae	*Poicephalus flavifrons*	Hoyo et al. (1997)
302	Psittaciformes	Psittacidae	*Poicephalus rufiventris*	Hoyo et al. (1997)
303	Psittaciformes	Psittacidae	*Loriculus vernalis*	Hoyo et al. (1997)
304	Psittaciformes	Psittacidae	*Loriculus galgulus*	Hoyo et al. (1997)
305	Psittaciformes	Psittacidae	*Loriculus amabilis*	Hoyo et al. (1997)
306	Psittaciformes	Psittacidae	*Loriculus pusillus*	Hoyo et al. (1997)
307	Psittaciformes	Psittacidae	*Loriculus flosculus*	Hoyo et al. (1997)
308	Psittaciformes	Psittacidae	*Psittacula eupatria*	Hoyo et al. (1997)
309	Psittaciformes	Psittacidae	*Psittacula krameri*	Hoyo et al. (1997)
310	Psittaciformes	Psittacidae	*Psittacula cyanocephala*	Hoyo et al. (1997)
311	Psittaciformes	Psittacidae	*Psittacula calthropae*	Hoyo et al. (1997)
312	Psittaciformes	Psittacidae	*Psittacula alexandri*	Hoyo et al. (1997)
313	Psittaciformes	Psittacidae	*Psittacula caniceps*	Hoyo et al. (1997)
314	Psittaciformes	Psittacidae	*Psittacula longicauda*	Hoyo et al. (1997)
315	Psittaciformes	Psittacidae	*Anodorhynchus hyacinthinus*	Hoyo et al. (1997)
316	Psittaciformes	Psittacidae	*Ara glaucogularis*	Hoyo et al. (1997)
317	Psittaciformes	Psittacidae	*Ara militaris*	Hoyo et al. (1997)
318	Psittaciformes	Psittacidae	*Ara manilata*	Hoyo et al. (1997)
319	Psittaciformes	Psittacidae	*Ara auricollis*	Hoyo et al. (1997)
320	Psittaciformes	Psittacidae	*Aratinga acuticaudata*	Hoyo et al. (1997)
321	Psittaciformes	Psittacidae	*Aratinga guarouba*	Hoyo et al. (1997)
322	Psittaciformes	Psittacidae	*Aratinga rubritorques*	Hoyo et al. (1997)
323	Psittaciformes	Psittacidae	*Aratinga mitrata*	Hoyo et al. (1997)
324	Psittaciformes	Psittacidae	*Aratinga erythrogenys*	Hoyo et al. (1997)
325	Psittaciformes	Psittacidae	*Aratinga finschi*	Hoyo et al. (1997)
326	Psittaciformes	Psittacidae	*Aratinga leucophthalmus*	Hoyo et al. (1997)
327	Psittaciformes	Psittacidae	*Aratinga euops*	Hoyo et al. (1997)
328	Psittaciformes	Psittacidae	*Aratinga chloroptera*	Hoyo et al. (1997)

329	Psittaciformes	Psittacidae	*Aratinga solstitialis*	Hoyo et al. (1997)
330	Psittaciformes	Psittacidae	*Aratinga jandaya*	Hoyo et al. (1997)
331	Psittaciformes	Psittacidae	*Aratinga auricapilla*	Hoyo et al. (1997)
332	Psittaciformes	Psittacidae	*Aratinga weddellii*	Hoyo et al. (1997)
333	Psittaciformes	Psittacidae	*Aratinga nana*	Hoyo et al. (1997)
334	Psittaciformes	Psittacidae	*Aratinga canicularis*	Hoyo et al. (1997)
335	Psittaciformes	Psittacidae	*Pyrrhura devillei*	Hoyo et al. (1997)
336	Psittaciformes	Psittacidae	*Pyrrhura lepida*	Hoyo et al. (1997)
337	Psittaciformes	Psittacidae	*Pyrrhura perlata*	Hoyo et al. (1997)
338	Psittaciformes	Psittacidae	*Pyrrhura molinae*	Hoyo et al. (1997)
339	Psittaciformes	Psittacidae	*Pyrrhura picta*	Hoyo et al. (1997)
340	Psittaciformes	Psittacidae	*Pyrrhura viridicata*	Hoyo et al. (1997)
341	Psittaciformes	Psittacidae	*Pyrrhura egregia*	Hoyo et al. (1997)
342	Psittaciformes	Psittacidae	*Pyrrhura melanura*	Hoyo et al. (1997)
343	Psittaciformes	Psittacidae	*Pyrrhura orcesi*	Hoyo et al. (1997)
344	Psittaciformes	Psittacidae	*Pyrrhura rupicola*	Hoyo et al. (1997)
345	Psittaciformes	Psittacidae	*Pyrrhura albipectus*	Hoyo et al. (1997)
346	Psittaciformes	Psittacidae	*Pyrrhura calliptera*	Hoyo et al. (1997)
347	Psittaciformes	Psittacidae	*Pyrrhura rhodocephala*	Hoyo et al. (1997)
348	Psittaciformes	Psittacidae	*Enicognathus leptorhynchus*	Hoyo et al. (1997)
349	Psittaciformes	Psittacidae	*Forpus cyanopygius*	Hoyo et al. (1997)
350	Psittaciformes	Psittacidae	*Forpus xanthopterygius*	Hoyo et al. (1997)
351	Psittaciformes	Psittacidae	*Forpus coelestis*	Hoyo et al. (1997)
352	Psittaciformes	Psittacidae	*Brotogeris tirica*	Hoyo et al. (1997)
353	Psittaciformes	Psittacidae	*Brotogeris chiriri*	Hoyo et al. (1997)
354	Psittaciformes	Psittacidae	*Brotogeris pyrrhopterus*	Hoyo et al. (1997)
355	Psittaciformes	Psittacidae	*Brotogeris jugularis*	Hoyo et al. (1997)
356	Psittaciformes	Psittacidae	*Brotogeris cyanoptera*	Hoyo et al. (1997)
357	Psittaciformes	Psittacidae	*Brotogeris chrysopterus*	Hoyo et al. (1997)
358	Psittaciformes	Psittacidae	*Brotogeris sanctithomae*	Hoyo et al. (1997)
359	Psittaciformes	Psittacidae	*Nannopsittaca panychlora*	Hoyo et al. (1997)
360	Psittaciformes	Psittacidae	*Touit huetii*	Hoyo et al. (1997)
361	Psittaciformes	Psittacidae	*Touit costaricensis*	Hoyo et al. (1997)
362	Psittaciformes	Psittacidae	*Touit dilectissima*	Hoyo et al. (1997)
363	Psittaciformes	Psittacidae	*Touit purpurata*	Hoyo et al. (1997)
364	Psittaciformes	Psittacidae	*Touit melanonotus*	Hoyo et al. (1997)
365	Psittaciformes	Psittacidae	*Touit surda*	Hoyo et al. (1997)
366	Psittaciformes	Psittacidae	*Touit stictoptera*	Hoyo et al. (1997)
367	Psittaciformes	Psittacidae	*Pionites leucogaster*	Hoyo et al. (1997)

368	Psittaciformes	Psittacidae	*Pionopsitta pileata*	Hoyo et al. (1997)
369	Psittaciformes	Psittacidae	*Pionopsitta haematotis*	Hoyo et al. (1997)
370	Psittaciformes	Psittacidae	*Pionopsitta pulchra*	Hoyo et al. (1997)
371	Psittaciformes	Psittacidae	*Pionopsitta pyrilia*	Hoyo et al. (1997)
372	Psittaciformes	Psittacidae	*Gypopsitta vulturina*	Hoyo et al. (1997)
373	Psittaciformes	Psittacidae	*Hapalopsittaca melanotis*	Hoyo et al. (1997)
374	Psittaciformes	Psittacidae	*Hapalopsittaca fuertesi*	Hoyo et al. (1997)
375	Psittaciformes	Psittacidae	*Hapalopsittaca pyrrhops*	Hoyo et al. (1997)
376	Psittaciformes	Psittacidae	*Graydidascalus brachyurus*	Hoyo et al. (1997)
377	Psittaciformes	Psittacidae	*Pionus sordidus*	Hoyo et al. (1997)
378	Psittaciformes	Psittacidae	*Pionus tumultuosus*	Hoyo et al. (1997)
379	Psittaciformes	Psittacidae	*Pionus senilis*	Hoyo et al. (1997)
380	Psittaciformes	Psittacidae	*Pionus chalcopterus*	Hoyo et al. (1997)
381	Psittaciformes	Psittacidae	*Pionus fuscus*	Hoyo et al. (1997)
382	Psittaciformes	Psittacidae	*Amazona leucocephala*	Hoyo et al. (1997)
383	Psittaciformes	Psittacidae	*Amazona collaria*	Hoyo et al. (1997)
384	Psittaciformes	Psittacidae	*Amazona ventralis*	Hoyo et al. (1997)
385	Psittaciformes	Psittacidae	*Amazona xantholora*	Hoyo et al. (1997)
386	Psittaciformes	Psittacidae	*Amazona agilis*	Hoyo et al. (1997)
387	Psittaciformes	Psittacidae	*Amazona vittata*	Hoyo et al. (1997)
388	Psittaciformes	Psittacidae	*Amazona pretrei*	Hoyo et al. (1997)
389	Psittaciformes	Psittacidae	*Amazona autumnalis*	Hoyo et al. (1997)
390	Psittaciformes	Psittacidae	*Amazona rhodocorytha*	Hoyo et al. (1997)
391	Psittaciformes	Psittacidae	*Amazona brasiliensis*	Hoyo et al. (1997)
392	Psittaciformes	Psittacidae	*Amazona festiva*	Hoyo et al. (1997)
393	Psittaciformes	Psittacidae	*Amazona xanthops*	Hoyo et al. (1997)
394	Psittaciformes	Psittacidae	*Amazona barbadensis*	Hoyo et al. (1997)
395	Psittaciformes	Psittacidae	*Amazona aestiva*	Hoyo et al. (1997)
396	Psittaciformes	Psittacidae	*Amazona ochrocephala*	Hoyo et al. (1997)
397	Psittaciformes	Psittacidae	*Amazona amazonica*	Hoyo et al. (1997)
398	Psittaciformes	Psittacidae	*Amazona mercenaria*	Hoyo et al. (1997)
399	Psittaciformes	Psittacidae	*Amazona farinosa*	Hoyo et al. (1997)
400	Psittaciformes	Psittacidae	*Amazona kawalli*	Hoyo et al. (1997)
401	Psittaciformes	Psittacidae	*Amazona versicolor*	Hoyo et al. (1997)
402	Psittaciformes	Psittacidae	*Amazona arausiaca*	Hoyo et al. (1997)
403	Psittaciformes	Psittacidae	*Amazona guildingii*	Hoyo et al. (1997)
404	Psittaciformes	Psittacidae	*Amazona imperialis*	Hoyo et al. (1997)
405	Psittaciformes	Psittacidae	*Deroptyus accipitrinus*	Hoyo et al. (1997)
406	Musophagiformes	Musophagidae	*Tauraco persa*	Hoyo et al. (1997)

407	Musophagiformes	Musophagidae	*Tauraco schuettii*	Hoyo et al. (1997)
408	Musophagiformes	Musophagidae	*Tauraco schalowi*	Hoyo et al. (1997)
409	Musophagiformes	Musophagidae	*Tauraco fischeri*	Hoyo et al. (1997)
410	Musophagiformes	Musophagidae	*Tauraco livingstonii*	Hoyo et al. (1997)
411	Musophagiformes	Musophagidae	*Tauraco corythaix*	Hoyo et al. (1997)
412	Musophagiformes	Musophagidae	*Tauraco bannermani*	Hoyo et al. (1997)
413	Musophagiformes	Musophagidae	*Tauraco erythrolophus*	Hoyo et al. (1997)
414	Musophagiformes	Musophagidae	*Tauraco macrorhynchus*	Hoyo et al. (1997)
415	Musophagiformes	Musophagidae	*Tauraco leucotis*	Hoyo et al. (1997)
416	Musophagiformes	Musophagidae	*Tauraco ruspolii*	Hoyo et al. (1997)
417	Musophagiformes	Musophagidae	*Tauraco hartlaubi*	Hoyo et al. (1997)
418	Musophagiformes	Musophagidae	*Tauraco leucolophus*	Hoyo et al. (1997)
419	Musophagiformes	Musophagidae	*Musophaga johnstoni*	Hoyo et al. (1997)
420	Musophagiformes	Musophagidae	*Musophaga porphyreolopha*	Hoyo et al. (1997)
421	Musophagiformes	Musophagidae	*Musophaga violacea*	Hoyo et al. (1997)
422	Musophagiformes	Musophagidae	*Musophaga rossae*	Hoyo et al. (1997)
423	Musophagiformes	Musophagidae	*Corythaixoides concolor*	Hoyo et al. (1997)
424	Musophagiformes	Musophagidae	*Corythaixoides personatus*	Hoyo et al. (1997)
425	Musophagiformes	Musophagidae	*Corythaixoides leucogaster*	Hoyo et al. (1997)
426	Musophagiformes	Musophagidae	*Crinifer piscator*	Hoyo et al. (1997)
427	Musophagiformes	Musophagidae	*Crinifer zonurus*	Hoyo et al. (1997)
428	Musophagiformes	Musophagidae	*Corythaeola cristata*	Hoyo et al. (1997)
429	Strigiformes	Steatornithidae	*Steatornis caripensis*	Hoyo et al. (1999)
430	Columbiformes	Columbidae	*Columba trocaz*	Hoyo et al. (1997)
431	Columbiformes	Columbidae	*Columba bollii*	Hoyo et al. (1997)
432	Columbiformes	Columbidae	*Columba junoniae*	Hoyo et al. (1997)
433	Columbiformes	Columbidae	*Columba unicincta*	Hoyo et al. (1997)
434	Columbiformes	Columbidae	*Columba sjostedti*	Hoyo et al. (1997)
435	Columbiformes	Columbidae	*Columba thomensis*	Hoyo et al. (1997)
436	Columbiformes	Columbidae	*Columba arquatrix*	Hoyo et al. (1997)
437	Columbiformes	Columbidae	*Columba pollenii*	Hoyo et al. (1997)
438	Columbiformes	Columbidae	*Columba hodgsonii*	Hoyo et al. (1997)
439	Columbiformes	Columbidae	*Columba albinucha*	Hoyo et al. (1997)
440	Columbiformes	Columbidae	*Columba pulchricollis*	Hoyo et al. (1997)
441	Columbiformes	Columbidae	*Columba elphinstonii*	Hoyo et al. (1997)
442	Columbiformes	Columbidae	*Columba torringtoni*	Hoyo et al. (1997)
443	Columbiformes	Columbidae	*Columba punicea*	Hoyo et al. (1997)
444	Columbiformes	Columbidae	*Columba argentina*	Hoyo et al. (1997)
445	Columbiformes	Columbidae	*Columba palumboides*	Hoyo et al. (1997)

446	Columbiformes	Columbidae	*Columba vitiensis*	Hoyo et al. (1997)
447	Columbiformes	Columbidae	*Columba leucomela*	Hoyo et al. (1997)
448	Columbiformes	Columbidae	*Columba pallidiceps*	Hoyo et al. (1997)
449	Columbiformes	Columbidae	*Columba leucocephala*	Hoyo et al. (1997)
450	Columbiformes	Columbidae	*Columba speciosa*	Hoyo et al. (1997)
451	Columbiformes	Columbidae	*Columba squamosa*	Hoyo et al. (1997)
452	Columbiformes	Columbidae	*Columba araucana*	Hoyo et al. (1997)
453	Columbiformes	Columbidae	*Columba caribaea*	Hoyo et al. (1997)
454	Columbiformes	Columbidae	*Columba cayennensis*	Hoyo et al. (1997)
455	Columbiformes	Columbidae	*Columba flavirostris*	Hoyo et al. (1997)
456	Columbiformes	Columbidae	*Columba inornata*	Hoyo et al. (1997)
457	Columbiformes	Columbidae	*Columba plumbea*	Hoyo et al. (1997)
458	Columbiformes	Columbidae	*Columba subvinacea*	Hoyo et al. (1997)
459	Columbiformes	Columbidae	*Columba nigrirostris*	Hoyo et al. (1997)
460	Columbiformes	Columbidae	*Columba goodsoni*	Hoyo et al. (1997)
461	Columbiformes	Columbidae	*Columba iriditorques*	Hoyo et al. (1997)
462	Columbiformes	Columbidae	*Columba malherbii*	Hoyo et al. (1997)
463	Columbiformes	Columbidae	*Columba delegorguei*	Hoyo et al. (1997)
464	Columbiformes	Columbidae	*Aplopelia larvata*	Hoyo et al. (1997)
465	Columbiformes	Columbidae	*Columba simplex*	Hoyo et al. (1997)
466	Columbiformes	Columbidae	*Streptopelia reichenowi*	Hoyo et al. (1997)
467	Columbiformes	Columbidae	*Macropygia rufipennis*	Hoyo et al. (1997)
468	Columbiformes	Columbidae	*Macropygia tenuirostris*	Hoyo et al. (1997)
469	Columbiformes	Columbidae	*Macropygia emiliana*	Hoyo et al. (1997)
470	Columbiformes	Columbidae	*Macropygia amboinensis*	Hoyo et al. (1997)
471	Columbiformes	Columbidae	*Macropygia magna*	Hoyo et al. (1997)
472	Columbiformes	Columbidae	*Macropygia phasianella*	Hoyo et al. (1997)
473	Columbiformes	Columbidae	*Macropygia ruficeps*	Hoyo et al. (1997)
474	Columbiformes	Columbidae	*Macropygia nigrirostris*	Hoyo et al. (1997)
475	Columbiformes	Columbidae	*Reinwardtoena browni*	Hoyo et al. (1997)
476	Columbiformes	Columbidae	*Reinwardtoena crassirostris*	Hoyo et al. (1997)
477	Columbiformes	Columbidae	*Turacoena manadensis*	Hoyo et al. (1997)
478	Columbiformes	Columbidae	*Turacoena modesta*	Hoyo et al. (1997)
479	Columbiformes	Columbidae	*Henicophaps albifrons*	Hoyo et al. (1997)
480	Columbiformes	Columbidae	*Henicophaps foersteri*	Hoyo et al. (1997)
481	Columbiformes	Columbidae	*Leucosarcia melanoleuca*	Hoyo et al. (1997)
482	Columbiformes	Columbidae	*Zenaida graysoni*	Hoyo et al. (1997)
483	Columbiformes	Columbidae	*Zenaida aurita*	Hoyo et al. (1997)
484	Columbiformes	Columbidae	*Caloenas nicobarica*	Hoyo et al. (1997)

485	Columbiformes	Columbidae	*Gallicolumba xanthonura*	Hoyo et al. (1997)
486	Columbiformes	Columbidae	*Phapitreron leucotis*	Hoyo et al. (1997)
487	Columbiformes	Columbidae	*Phapitreron amethystina*	Hoyo et al. (1997)
488	Columbiformes	Columbidae	*Phapitreron cinereiceps*	Hoyo et al. (1997)
489	Columbiformes	Columbidae	*Treron fulvicollis*	Hoyo et al. (1997)
490	Columbiformes	Columbidae	*Treron olax*	Hoyo et al. (1997)
491	Columbiformes	Columbidae	*Treron vernans*	Hoyo et al. (1997)
492	Columbiformes	Columbidae	*Treron bicincta*	Hoyo et al. (1997)
493	Columbiformes	Columbidae	*Treron pompadora*	Hoyo et al. (1997)
494	Columbiformes	Columbidae	*Treron curvirostra*	Hoyo et al. (1997)
495	Columbiformes	Columbidae	*Treron griseicauda*	Hoyo et al. (1997)
496	Columbiformes	Columbidae	*Treron floris*	Hoyo et al. (1997)
497	Columbiformes	Columbidae	*Treron teysmannii*	Hoyo et al. (1997)
498	Columbiformes	Columbidae	*Treron psittacea*	Hoyo et al. (1997)
499	Columbiformes	Columbidae	*Treron capellei*	Hoyo et al. (1997)
500	Columbiformes	Columbidae	*Treron phoenicoptera*	Hoyo et al. (1997)
501	Columbiformes	Columbidae	*Treron waalia*	Hoyo et al. (1997)
502	Columbiformes	Columbidae	*Treron calva*	Hoyo et al. (1997)
503	Columbiformes	Columbidae	*Treron sanctithomae*	Hoyo et al. (1997)
504	Columbiformes	Columbidae	*Treron pembaensis*	Hoyo et al. (1997)
505	Columbiformes	Columbidae	*Treron australis*	Hoyo et al. (1997)
506	Columbiformes	Columbidae	*Treron apicauda*	Hoyo et al. (1997)
507	Columbiformes	Columbidae	*Treron oxyura*	Hoyo et al. (1997)
508	Columbiformes	Columbidae	*Treron seimundi*	Hoyo et al. (1997)
509	Columbiformes	Columbidae	*Treron sphenura*	Hoyo et al. (1997)
510	Columbiformes	Columbidae	*Treron sieboldii*	Hoyo et al. (1997)
511	Columbiformes	Columbidae	*Treron formosae*	Hoyo et al. (1997)
512	Columbiformes	Columbidae	*Ptilinopus porphyreus*	Hoyo et al. (1997)
513	Columbiformes	Columbidae	*Ptilinopus cinctus*	Hoyo et al. (1997)
514	Columbiformes	Columbidae	*Ptilinopus dohertyi*	Hoyo et al. (1997)
515	Columbiformes	Columbidae	*Ptilinopus alligator*	Hoyo et al. (1997)
516	Columbiformes	Columbidae	*Ptilinopus marchei*	Hoyo et al. (1997)
517	Columbiformes	Columbidae	*Ptilinopus merrilli*	Hoyo et al. (1997)
518	Columbiformes	Columbidae	*Ptilinopus occipitalis*	Hoyo et al. (1997)
519	Columbiformes	Columbidae	*Ptilinopus fischeri*	Hoyo et al. (1997)
520	Columbiformes	Columbidae	*Ptilinopus jambu*	Hoyo et al. (1997)
521	Columbiformes	Columbidae	*Ptilinopus leclancheri*	Hoyo et al. (1997)
522	Columbiformes	Columbidae	*Ptilinopus subgularis*	Hoyo et al. (1997)
523	Columbiformes	Columbidae	*Ptilinopus bernsteinii*	Hoyo et al. (1997)

524	Columbiformes	Columbidae	*Ptilinopus magnificus*	Hoyo et al. (1997)
525	Columbiformes	Columbidae	*Ptilinopus perlatus*	Hoyo et al. (1997)
526	Columbiformes	Columbidae	*Ptilinopus ornatus*	Hoyo et al. (1997)
527	Columbiformes	Columbidae	*Ptilinopus tannensis*	Hoyo et al. (1997)
528	Columbiformes	Columbidae	*Ptilinopus aurantiifrons*	Hoyo et al. (1997)
529	Columbiformes	Columbidae	*Ptilinopus wallacii*	Hoyo et al. (1997)
530	Columbiformes	Columbidae	*Ptilinopus superbus*	Hoyo et al. (1997)
531	Columbiformes	Columbidae	*Ptilinopus perousii*	Hoyo et al. (1997)
532	Columbiformes	Columbidae	*Ptilinopus monacha*	Hoyo et al. (1997)
533	Columbiformes	Columbidae	*Ptilinopus coronulatus*	Hoyo et al. (1997)
534	Columbiformes	Columbidae	*Ptilinopus pulchellus*	Hoyo et al. (1997)
535	Columbiformes	Columbidae	*Ptilinopus regina*	Hoyo et al. (1997)
536	Columbiformes	Columbidae	*Ptilinopus roseicapilla*	Hoyo et al. (1997)
537	Columbiformes	Columbidae	*Ptilinopus greyii*	Hoyo et al. (1997)
538	Columbiformes	Columbidae	*Ptilinopus richardsii*	Hoyo et al. (1997)
539	Columbiformes	Columbidae	*Ptilinopus porphyraceus*	Hoyo et al. (1997)
540	Columbiformes	Columbidae	*Ptilinopus pelewensis*	Hoyo et al. (1997)
541	Columbiformes	Columbidae	*Ptilinopus rarotongensis*	Hoyo et al. (1997)
542	Columbiformes	Columbidae	*Ptilinopus huttoni*	Hoyo et al. (1997)
543	Columbiformes	Columbidae	*Ptilinopus purpuratus*	Hoyo et al. (1997)
544	Columbiformes	Columbidae	*Ptilinopus chalcurus*	Hoyo et al. (1997)
545	Columbiformes	Columbidae	*Ptilinopus insularis*	Hoyo et al. (1997)
546	Columbiformes	Columbidae	*Ptilinopus mercierii*	Hoyo et al. (1997)
547	Columbiformes	Columbidae	*Ptilinopus dupetithouarsii*	Hoyo et al. (1997)
548	Columbiformes	Columbidae	*Ptilinopus rivoli*	Hoyo et al. (1997)
549	Columbiformes	Columbidae	*Ptilinopus solomonensis*	Hoyo et al. (1997)
550	Columbiformes	Columbidae	*Ptilinopus viridis*	Hoyo et al. (1997)
551	Columbiformes	Columbidae	*Ptilinopus eugeniae*	Hoyo et al. (1997)
552	Columbiformes	Columbidae	*Ptilinopus hyogastra*	Hoyo et al. (1997)
553	Columbiformes	Columbidae	*Ptilinopus granulifrons*	Hoyo et al. (1997)
554	Columbiformes	Columbidae	*Ptilinopus iozonus*	Hoyo et al. (1997)
555	Columbiformes	Columbidae	*Ptilinopus insolitus*	Hoyo et al. (1997)
556	Columbiformes	Columbidae	*Ptilinopus naina*	Hoyo et al. (1997)
557	Columbiformes	Columbidae	*Ptilinopus melanospila*	Hoyo et al. (1997)
558	Columbiformes	Columbidae	*Ptilinopus arcanus*	Hoyo et al. (1997)
559	Columbiformes	Columbidae	*Ptilinopus victor*	Hoyo et al. (1997)
560	Columbiformes	Columbidae	*Ptilinopus luteovirens*	Hoyo et al. (1997)
561	Columbiformes	Columbidae	*Ptilinopus layardi*	Hoyo et al. (1997)
562	Columbiformes	Columbidae	*Drepanoptila holosericea*	Hoyo et al. (1997)

563	Columbiformes	Columbidae	*Alectroenas madagascariensis*	Hoyo et al. (1997)
564	Columbiformes	Columbidae	*Alectroenas sganzini*	Hoyo et al. (1997)
565	Columbiformes	Columbidae	*Alectroenas pulcherrima*	Hoyo et al. (1997)
566	Columbiformes	Columbidae	*Ducula poliocephala*	Hoyo et al. (1997)
567	Columbiformes	Columbidae	*Ducula forsteni*	Hoyo et al. (1997)
568	Columbiformes	Columbidae	*Ducula mindorensis*	Hoyo et al. (1997)
569	Columbiformes	Columbidae	*Ducula radiata*	Hoyo et al. (1997)
570	Columbiformes	Columbidae	*Ducula carola*	Hoyo et al. (1997)
571	Columbiformes	Columbidae	*Ducula aenea*	Hoyo et al. (1997)
572	Columbiformes	Columbidae	*Ducula perspicillata*	Hoyo et al. (1997)
573	Columbiformes	Columbidae	*Ducula concinna*	Hoyo et al. (1997)
574	Columbiformes	Columbidae	*Ducula pacifica*	Hoyo et al. (1997)
575	Columbiformes	Columbidae	*Ducula oceanica*	Hoyo et al. (1997)
576	Columbiformes	Columbidae	*Ducula aurorae*	Hoyo et al. (1997)
577	Columbiformes	Columbidae	*Ducula galeata*	Hoyo et al. (1997)
578	Columbiformes	Columbidae	*Ducula rubricera*	Hoyo et al. (1997)
579	Columbiformes	Columbidae	*Ducula myristicivora*	Hoyo et al. (1997)
580	Columbiformes	Columbidae	*Ducula pistrinaria*	Hoyo et al. (1997)
581	Columbiformes	Columbidae	*Ducula whartoni*	Hoyo et al. (1997)
582	Columbiformes	Columbidae	*Ducula rosacea*	Hoyo et al. (1997)
583	Columbiformes	Columbidae	*Ducula pickeringii*	Hoyo et al. (1997)
584	Columbiformes	Columbidae	*Ducula basilica*	Hoyo et al. (1997)
585	Columbiformes	Columbidae	*Ducula rufigaster*	Hoyo et al. (1997)
586	Columbiformes	Columbidae	*Ducula finschii*	Hoyo et al. (1997)
587	Columbiformes	Columbidae	*Ducula chalconota*	Hoyo et al. (1997)
588	Columbiformes	Columbidae	*Ducula latrans*	Hoyo et al. (1997)
589	Columbiformes	Columbidae	*Ducula brenchleyi*	Hoyo et al. (1997)
590	Columbiformes	Columbidae	*Ducula bakeri*	Hoyo et al. (1997)
591	Columbiformes	Columbidae	*Ducula goliath*	Hoyo et al. (1997)
592	Columbiformes	Columbidae	*Ducula pinon*	Hoyo et al. (1997)
593	Columbiformes	Columbidae	*Ducula melanochroa*	Hoyo et al. (1997)
594	Columbiformes	Columbidae	*Ducula mullerii*	Hoyo et al. (1997)
595	Columbiformes	Columbidae	*Ducula zoeae*	Hoyo et al. (1997)
596	Columbiformes	Columbidae	*Ducula badia*	Hoyo et al. (1997)
597	Columbiformes	Columbidae	*Ducula lacernulata*	Hoyo et al. (1997)
598	Columbiformes	Columbidae	*Ducula cineracea*	Hoyo et al. (1997)
599	Columbiformes	Columbidae	*Ducula bicolor*	Hoyo et al. (1997)
600	Columbiformes	Columbidae	*Ducula luctuosa*	Hoyo et al. (1997)
601	Columbiformes	Columbidae	*Ducula spilorrhoa*	Hoyo et al. (1997)

602	Columbiformes	Columbidae	*Lopholaimus antarcticus*	Hoyo et al. (1997)
603	Columbiformes	Columbidae	*Hemiphaga novaeseelandiae*	Hoyo et al. (1997)
604	Columbiformes	Columbidae	*Cryptophaps poecilorrhoa*	Hoyo et al. (1997)
605	Columbiformes	Columbidae	*Gymnophaps albertisii*	Hoyo et al. (1997)
606	Columbiformes	Columbidae	*Gymnophaps mada*	Hoyo et al. (1997)
607	Columbiformes	Columbidae	*Gymnophaps solomonensis*	Hoyo et al. (1997)
608	Columbiformes	Columbidae	*Goura victoria*	Hoyo et al. (1997)
609	Gruiformes	Psophiidae	*Psophia crepitans*	Hoyo et al. (1996)
610	Gruiformes	Psophiidae	*Psophia leucoptera*	Hoyo et al. (1996)
611	Gruiformes	Psophiidae	*Psophia viridis*	Hoyo et al. (1996)
612	Gruiformes	Rallidae	*Gallirallus australis*	Hoyo et al. (1996)
613	Passeriformes	Eurylaimidae	*Pseudocalyptomena graueri*	Hoyo et al. (2003)
614	Passeriformes	Eurylaimidae	*Calyptomena viridis*	Hoyo et al. (2003)
615	Passeriformes	Eurylaimidae	*Calyptomena hosii*	Hoyo et al. (2003)
616	Passeriformes	Eurylaimidae	*Calyptomena whiteheadi*	Hoyo et al. (2003)
617	Passeriformes	Tyrannidae	*Mionectes striaticollis*	Ridgely & Tudor (1994)
618	Passeriformes	Tyrannidae	*Mionectes olivaceus*	Ridgely & Tudor (1994)
619	Passeriformes	Tyrannidae	*Mionectes oleagineus*	Ridgely & Tudor (1994)
620	Passeriformes	Tyrannidae	*Mionectes macconnelli*	Ridgely & Tudor (1994)
621	Passeriformes	Tyrannidae	*Mionectes rufiventris*	Ridgely & Tudor (1994)
622	Passeriformes	Tyrannidae	*Zimmerius vilissimus*	Ridgely & Tudor (1994)
623	Passeriformes	Tyrannidae	*Zimmerius improbus*	Ridgely & Tudor (1994)
624	Passeriformes	Tyrannidae	*Zimmerius bolivianus*	Ridgely & Tudor (1994)
625	Passeriformes	Tyrannidae	*Zimmerius cinereicapillus*	Ridgely & Tudor (1994)
626	Passeriformes	Tyrannidae	*Zimmerius gracilipes*	Ridgely & Tudor (1994)
627	Passeriformes	Tyrannidae	*Zimmerius viridiflavus*	Ridgely & Tudor (1994)
628	Passeriformes	Tyrannidae	*Zimmerius chrysops*	Ridgely & Tudor (1994)
629	Passeriformes	Tyrannidae	*Tyrannulus elatus*	Ridgely & Tudor (1994)
630	Passeriformes	Tyrannidae	*Laniocera rufescens*	Ridgely & Tudor (1994)
631	Passeriformes	Tyrannidae	*Myiodynastes luteiventris*	Ridgely & Tudor (1994)
632	Passeriformes	Tyrannidae	*Legatus leucophaius*	Ridgely & Tudor (1994)
633	Passeriformes	Tyrannidae	*Phoenicircus nigricollis*	Ridgely & Tudor (1994)
634	Passeriformes	Tyrannidae	*Phoenicircus carnifex*	Ridgely & Tudor (1994)
635	Passeriformes	Tyrannidae	*Laniisoma buckleyi*	Ridgely & Tudor (1994)
636	Passeriformes	Tyrannidae	*Phibalura flavirostris*	Ridgely & Tudor (1994)
637	Passeriformes	Tyrannidae	*Tijuca atra*	Ridgely & Tudor (1994)
638	Passeriformes	Tyrannidae	*Tijuca condita*	Ridgely & Tudor (1994)
639	Passeriformes	Tyrannidae	*Carpornis cucullatus*	Ridgely & Tudor (1994)
640	Passeriformes	Tyrannidae	*Carpornis melanocephalus*	Ridgely & Tudor (1994)

641	Passeriformes	Tyrannidae	*Doliornis sclateri*	Ridgely & Tudor (1994)
642	Passeriformes	Tyrannidae	*Doliornis remseni*	Ridgely & Tudor (1994)
643	Passeriformes	Tyrannidae	*Ampelion rubrocristatus*	Ridgely & Tudor (1994)
644	Passeriformes	Tyrannidae	*Ampelion rufaxilla*	Ridgely & Tudor (1994)
645	Passeriformes	Tyrannidae	*Zaratornis stresemanni*	Ridgely & Tudor (1994)
646	Passeriformes	Tyrannidae	*Pipreola riefferii*	Ridgely & Tudor (1994)
647	Passeriformes	Tyrannidae	*Pipreola intermedia*	Ridgely & Tudor (1994)
648	Passeriformes	Tyrannidae	*Pipreola arcuata*	Ridgely & Tudor (1994)
649	Passeriformes	Tyrannidae	*Pipreola aureopectus*	Ridgely & Tudor (1994)
650	Passeriformes	Tyrannidae	*Pipreola jucunda*	Ridgely & Tudor (1994)
651	Passeriformes	Tyrannidae	*Pipreola lubomirskii*	Ridgely & Tudor (1994)
652	Passeriformes	Tyrannidae	*Pipreola pulchra*	Ridgely & Tudor (1994)
653	Passeriformes	Tyrannidae	*Pipreola chlorolepidota*	Ridgely & Tudor (1994)
654	Passeriformes	Tyrannidae	*Pipreola frontalis*	Ridgely & Tudor (1994)
655	Passeriformes	Tyrannidae	*Pipreola formosa*	Ridgely & Tudor (1994)
656	Passeriformes	Tyrannidae	*Pipreola whitelyi*	Ridgely & Tudor (1994)
657	Passeriformes	Tyrannidae	*Ampelioides tschudii*	Ridgely & Tudor (1994)
658	Passeriformes	Tyrannidae	*Iodopleura pipra*	Ridgely & Tudor (1994)
659	Passeriformes	Tyrannidae	*Iodopleura isabellae*	Ridgely & Tudor (1994)
660	Passeriformes	Tyrannidae	*Iodopleura fusca*	Ridgely & Tudor (1994)
661	Passeriformes	Tyrannidae	*Calyptura cristata*	Ridgely & Tudor (1994)
662	Passeriformes	Tyrannidae	*Lipaugus subalaris*	Ridgely & Tudor (1994)
663	Passeriformes	Tyrannidae	*Lipaugus cryptolophus*	Ridgely & Tudor (1994)
664	Passeriformes	Tyrannidae	*Lipaugus fuscocinereus*	Ridgely & Tudor (1994)
665	Passeriformes	Tyrannidae	*Lipaugus uropygialis*	Ridgely & Tudor (1994)
666	Passeriformes	Tyrannidae	*Lipaugus vociferans*	Ridgely & Tudor (1994)
667	Passeriformes	Tyrannidae	*Lipaugus unirufus*	Ridgely & Tudor (1994)
668	Passeriformes	Tyrannidae	*Lipaugus lanioides*	Ridgely & Tudor (1994)
669	Passeriformes	Tyrannidae	*Lipaugus streptophorus*	Ridgely & Tudor (1994)
670	Passeriformes	Tyrannidae	*Porphyrolaema porphyrolaema*	Ridgely & Tudor (1994)
671	Passeriformes	Tyrannidae	*Cotinga amabilis*	Ridgely & Tudor (1994)
672	Passeriformes	Tyrannidae	*Cotinga ridgwayi*	Ridgely & Tudor (1994)
673	Passeriformes	Tyrannidae	*Cotinga nattererii*	Ridgely & Tudor (1994)
674	Passeriformes	Tyrannidae	*Cotinga maynana*	Ridgely & Tudor (1994)
675	Passeriformes	Tyrannidae	*Cotinga cotinga*	Ridgely & Tudor (1994)
676	Passeriformes	Tyrannidae	*Cotinga maculata*	Ridgely & Tudor (1994)
677	Passeriformes	Tyrannidae	*Cotinga cayana*	Ridgely & Tudor (1994)
678	Passeriformes	Tyrannidae	*Xipholena punicea*	Ridgely & Tudor (1994)
679	Passeriformes	Tyrannidae	*Xipholena lamellipennis*	Ridgely & Tudor (1994)

680	Passeriformes	Tyrannidae	*Xipholena atropurpurea*	Ridgely & Tudor (1994)
681	Passeriformes	Tyrannidae	*Carpodectes nitidus*	Ridgely & Tudor (1994)
682	Passeriformes	Tyrannidae	*Carpodectes antoniae*	Ridgely & Tudor (1994)
683	Passeriformes	Tyrannidae	*Carpodectes hopkei*	Ridgely & Tudor (1994)
684	Passeriformes	Tyrannidae	*Conioptilon mcilhennyi*	Ridgely & Tudor (1994)
685	Passeriformes	Tyrannidae	*Gymnoderus foetidus*	Ridgely & Tudor (1994)
686	Passeriformes	Tyrannidae	*Haematoderus militaris*	Ridgely & Tudor (1994)
687	Passeriformes	Tyrannidae	*Querula purpurata*	Ridgely & Tudor (1994)
688	Passeriformes	Tyrannidae	*Pyroderus scutatus*	Ridgely & Tudor (1994)
689	Passeriformes	Tyrannidae	*Cephalopterus glabricollis*	Ridgely & Tudor (1994)
690	Passeriformes	Tyrannidae	*Cephalopterus penduliger*	Ridgely & Tudor (1994)
691	Passeriformes	Tyrannidae	*Cephalopterus ornatus*	Ridgely & Tudor (1994)
692	Passeriformes	Tyrannidae	*Perissocephalus tricolor*	Ridgely & Tudor (1994)
693	Passeriformes	Tyrannidae	*Procnias tricarunculata*	Ridgely & Tudor (1994)
694	Passeriformes	Tyrannidae	*Procnias alba*	Ridgely & Tudor (1994)
695	Passeriformes	Tyrannidae	*Procnias averano*	Ridgely & Tudor (1994)
696	Passeriformes	Tyrannidae	*Procnias nudicollis*	Ridgely & Tudor (1994)
697	Passeriformes	Tyrannidae	*Rupicola rupicola*	Ridgely & Tudor (1994)
698	Passeriformes	Tyrannidae	*Rupicola peruviana*	Ridgely & Tudor (1994)
699	Passeriformes	Tyrannidae	*Pipra aureola*	Ridgely & Tudor (1994)
700	Passeriformes	Tyrannidae	*Pipra fasciicauda*	Ridgely & Tudor (1994)
701	Passeriformes	Tyrannidae	*Pipra filicauda*	Ridgely & Tudor (1994)
702	Passeriformes	Tyrannidae	*Pipra mentalis*	Ridgely & Tudor (1994)
703	Passeriformes	Tyrannidae	*Pipra erythrocephala*	Ridgely & Tudor (1994)
704	Passeriformes	Tyrannidae	*Pipra rubrocapilla*	Ridgely & Tudor (1994)
705	Passeriformes	Tyrannidae	*Pipra chloromeros*	Ridgely & Tudor (1994)
706	Passeriformes	Tyrannidae	*Pipra cornuta*	Ridgely & Tudor (1994)
707	Passeriformes	Tyrannidae	*Pipra pipra*	Ridgely & Tudor (1994)
708	Passeriformes	Tyrannidae	*Lepidothrix coronata*	Ridgely & Tudor (1994)
709	Passeriformes	Tyrannidae	*Lepidothrix serena*	Ridgely & Tudor (1994)
710	Passeriformes	Tyrannidae	*Lepidothrix suavissima*	Ridgely & Tudor (1994)
711	Passeriformes	Tyrannidae	*Lepidothrix iris*	Ridgely & Tudor (1994)
712	Passeriformes	Tyrannidae	*Lepidothrix vilasboasi*	Ridgely & Tudor (1994)
713	Passeriformes	Tyrannidae	*Lepidothrix nattereri*	Ridgely & Tudor (1994)
714	Passeriformes	Tyrannidae	*Lepidothrix isidorei*	Ridgely & Tudor (1994)
715	Passeriformes	Tyrannidae	*Lepidothrix coeruleocapilla*	Ridgely & Tudor (1994)
716	Passeriformes	Tyrannidae	*Antilophia galeata*	Ridgely & Tudor (1994)
717	Passeriformes	Tyrannidae	*Chiroxiphia linearis*	Ridgely & Tudor (1994)
718	Passeriformes	Tyrannidae	*Chiroxiphia lanceolata*	Ridgely & Tudor (1994)

719	Passeriformes	Tyrannidae	*Chiroxiphia pareola*	Ridgely & Tudor (1994)
720	Passeriformes	Tyrannidae	*Chiroxiphia boliviana*	Ridgely & Tudor (1994)
721	Passeriformes	Tyrannidae	*Chiroxiphia caudata*	Ridgely & Tudor (1994)
722	Passeriformes	Tyrannidae	*Masius chrysopterus*	Ridgely & Tudor (1994)
723	Passeriformes	Tyrannidae	*Ilicura militaris*	Ridgely & Tudor (1994)
724	Passeriformes	Tyrannidae	*Corapipo gutturalis*	Ridgely & Tudor (1994)
725	Passeriformes	Tyrannidae	*Corapipo leucorrhoa*	Ridgely & Tudor (1994)
726	Passeriformes	Tyrannidae	*Manacus candei*	Ridgely & Tudor (1994)
727	Passeriformes	Tyrannidae	*Manacus aurantiacus*	Ridgely & Tudor (1994)
728	Passeriformes	Tyrannidae	*Manacus vitellinus*	Ridgely & Tudor (1994)
729	Passeriformes	Tyrannidae	*Manacus manacus*	Ridgely & Tudor (1994)
730	Passeriformes	Tyrannidae	*Machaeropterus pyrocephalus*	Ridgely & Tudor (1994)
731	Passeriformes	Tyrannidae	*Machaeropterus regulus*	Ridgely & Tudor (1994)
732	Passeriformes	Tyrannidae	*Machaeropterus deliciosus*	Ridgely & Tudor (1994)
733	Passeriformes	Tyrannidae	*Xenopipo atronitens*	Ridgely & Tudor (1994)
734	Passeriformes	Tyrannidae	*Chloropipo unicolor*	Ridgely & Tudor (1994)
735	Passeriformes	Tyrannidae	*Chloropipo uniformis*	Ridgely & Tudor (1994)
736	Passeriformes	Tyrannidae	*Chloropipo holochlora*	Ridgely & Tudor (1994)
737	Passeriformes	Tyrannidae	*Chloropipo flavicapilla*	Ridgely & Tudor (1994)
738	Passeriformes	Tyrannidae	*Heterocercus flavivertex*	Ridgely & Tudor (1994)
739	Passeriformes	Tyrannidae	*Heterocercus aurantiivertex*	Ridgely & Tudor (1994)
740	Passeriformes	Tyrannidae	*Heterocercus linteatus*	Ridgely & Tudor (1994)
741	Passeriformes	Ptilonorhynchidae	*Ailuroedus buccoides*	Coates (1990)
742	Passeriformes	Ptilonorhynchidae	*Ailuroedus melanotis*	Coates (1990)
743	Passeriformes	Ptilonorhynchidae	*Ailuroedus crassirostris*	Schodde et al. (1986)
744	Passeriformes	Ptilonorhynchidae	*Scenopooetes dentirostris*	Schodde et al. (1986)
745	Passeriformes	Ptilonorhynchidae	*Archboldia papuensis*	Coates (1990)
746	Passeriformes	Ptilonorhynchidae	*Archboldia sanfordi*	Coates (1990)
747	Passeriformes	Ptilonorhynchidae	*Amblyornis inornatus*	Coates (1990)
748	Passeriformes	Ptilonorhynchidae	*Amblyornis macgregoriae*	Coates (1990)
749	Passeriformes	Ptilonorhynchidae	*Amblyornis subalaris*	Coates (1990)
750	Passeriformes	Ptilonorhynchidae	*Amblyornis flavifrons*	Coates (1990)
751	Passeriformes	Ptilonorhynchidae	*Prionodura newtoniana*	Schodde et al. (1986)
752	Passeriformes	Ptilonorhynchidae	*Sericulus aureus*	Coates (1990)
753	Passeriformes	Ptilonorhynchidae	*Sericulus bakeri*	Coates (1990)
754	Passeriformes	Ptilonorhynchidae	*Sericulus chrysocephalus*	Schodde et al. (1986)
755	Passeriformes	Ptilonorhynchidae	*Ptilonorhynchus violaceus*	Schodde et al. (1986)
756	Passeriformes	Ptilonorhynchidae	*Chlamydera guttata*	Schodde et al. (1986)
757	Passeriformes	Ptilonorhynchidae	*Chlamydera maculata*	Schodde et al. (1986)

758	Passeriformes	Ptilonorhynchidae	*Chlamydera nuchalis*	Schodde et al. (1986)
759	Passeriformes	Ptilonorhynchidae	*Chlamydera lauterbachi*	Coates (1990)
760	Passeriformes	Ptilonorhynchidae	*Chlamydera cerviniventris*	Coates (1990)
761	Passeriformes	Meliphagidae	*Meliphaga montana*	Coates (1990)
762	Passeriformes	Meliphagidae	*Lichenostomus flavescens*	Marchant et al. (1990)
763	Passeriformes	Meliphagidae	*Oreornis chrysogenys*	Coates (1990)
764	Passeriformes	Meliphagidae	*Melipotes gymnops*	Coates (1990)
765	Passeriformes	Meliphagidae	*Melipotes fumigatus*	Coates (1990)
766	Passeriformes	Meliphagidae	*Melipotes ater*	Coates (1990)
767	Passeriformes	Meliphagidae	*Apalopteron familiare*	BirdLife International (2000)
768	Passeriformes	Irenidae	*Chloropsis aurifrons*	Hoyo et al. (2005)
769	Passeriformes	Corvidae	*Rhagologus leucostigma*	Coates (1990)
770	Passeriformes	Corvidae	*Pitohui dichrous*	Coates (1990)
771	Passeriformes	Corvidae	*Platysmurus leucopterus*	Madge & Burn (1994)
772	Passeriformes	Corvidae	*Cyanocorax caeruleus*	Madge & Burn (1994)
773	Passeriformes	Corvidae	*Cyanocorax affinis*	Madge & Burn (1994)
774	Passeriformes	Corvidae	*Urocissa caerulea*	Madge & Burn (1994)
775	Passeriformes	Corvidae	*Corvus typicus*	Madge & Burn (1994)
776	Passeriformes	Corvidae	*Corvus unicolor*	Madge & Burn (1994)
777	Passeriformes	Corvidae	*Corvus florensis*	Madge & Burn (1994)
778	Passeriformes	Corvidae	*Corvus validus*	Madge & Burn (1994)
779	Passeriformes	Corvidae	*Corvus meeki*	Madge & Burn (1994)
780	Passeriformes	Corvidae	*Corvus fuscicapillus*	Madge & Burn (1994)
781	Passeriformes	Corvidae	*Corvus tristis*	Madge & Burn (1994)
782	Passeriformes	Corvidae	*Corvus jamaicensis*	Madge & Burn (1994)
783	Passeriformes	Corvidae	*Corvus hawaiiensis*	Madge & Burn (1994)
784	Passeriformes	Corvidae	*Loboparadisea sericea*	Frith et al. (1998)
785	Passeriformes	Corvidae	*Cnemophilus macgregorii*	Frith et al. (1998)
786	Passeriformes	Corvidae	*Cnemophilus loriae*	Frith et al. (1998)
787	Passeriformes	Corvidae	*Macgregoria pulchra*	Frith et al. (1998)
788	Passeriformes	Corvidae	*Lycocorax pyrrhopterus*	Frith et al. (1998)
789	Passeriformes	Corvidae	*Manucodia atra*	Frith et al. (1998)
790	Passeriformes	Corvidae	*Manucodia chalybata*	Frith et al. (1998)
791	Passeriformes	Corvidae	*Manucodia comrii*	Frith et al. (1998)
792	Passeriformes	Corvidae	*Manucodia jobiensis*	Frith et al. (1998)
793	Passeriformes	Corvidae	*Manucodia keraudrenii*	Frith et al. (1998)
794	Passeriformes	Corvidae	*Semioptera wallacii*	Frith et al. (1998)
795	Passeriformes	Corvidae	*Paradigalla carunculata*	Frith et al. (1998)
796	Passeriformes	Corvidae	*Paradigalla brevicauda*	Frith et al. (1998)

797	Passeriformes	Corvidae	*Epimachus fastuosus*	Frith et al. (1998)
798	Passeriformes	Corvidae	*Epimachus bruijnii*	Frith et al. (1998)
799	Passeriformes	Corvidae	*Parotia sefilata*	Frith et al. (1998)
800	Passeriformes	Corvidae	*Parotia carolae*	Frith et al. (1998)
801	Passeriformes	Corvidae	*Parotia lawesii*	Frith et al. (1998)
802	Passeriformes	Corvidae	*Parotia helenae*	Frith et al. (1998)
803	Passeriformes	Corvidae	*Parotia wahnesi*	Frith et al. (1998)
804	Passeriformes	Corvidae	*Ptiloris magnificus*	Frith et al. (1998)
805	Passeriformes	Corvidae	*Ptiloris intercedens*	Frith et al. (1998)
806	Passeriformes	Corvidae	*Cicinnurus magnificus*	Frith et al. (1998)
807	Passeriformes	Corvidae	*Cicinnurus respublica*	Frith et al. (1998)
808	Passeriformes	Corvidae	*Cicinnurus regius*	Frith et al. (1998)
809	Passeriformes	Corvidae	*Astrapia nigra*	Frith et al. (1998)
810	Passeriformes	Corvidae	*Astrapia splendidissima*	Frith et al. (1998)
811	Passeriformes	Corvidae	*Astrapia mayeri*	Frith et al. (1998)
812	Passeriformes	Corvidae	*Astrapia stephaniae*	Frith et al. (1998)
813	Passeriformes	Corvidae	*Astrapia rothschildi*	Frith et al. (1998)
814	Passeriformes	Corvidae	*Pteridophora alberti*	Frith et al. (1998)
815	Passeriformes	Corvidae	*Seleucidis melanoleuca*	Frith et al. (1998)
816	Passeriformes	Corvidae	*Paradisaea rubra*	Frith et al. (1998)
817	Passeriformes	Corvidae	*Paradisaea minor*	Frith et al. (1998)
818	Passeriformes	Corvidae	*Paradisaea apoda*	Frith et al. (1998)
819	Passeriformes	Corvidae	*Paradisaea raggiana*	Frith et al. (1998)
820	Passeriformes	Corvidae	*Paradisaea decora*	Frith et al. (1998)
821	Passeriformes	Corvidae	*Paradisaea guilielmi*	Frith et al. (1998)
822	Passeriformes	Corvidae	*Paradisaea rudolphi*	Frith et al. (1998)
823	Passeriformes	Corvidae	*Oriolus melanotis*	Coates et al. (1997)
824	Passeriformes	Corvidae	*Oriolus bouroensis*	Coates et al. (1997)
825	Passeriformes	Corvidae	*Oriolus forsteni*	Coates et al. (1997)
826	Passeriformes	Corvidae	*Oriolus phaeochromus*	Coates et al. (1997)
827	Passeriformes	Corvidae	*Oriolus szalayi*	Coates (1990)
828	Passeriformes	Corvidae	*Oriolus sagittatus*	Schodde et al. (1986)
829	Passeriformes	Corvidae	*Oriolus flavocinctus*	Schodde et al. (1986)
830	Passeriformes	Corvidae	*Oriolus xanthonotus*	Robson (2000)
831	Passeriformes	Corvidae	*Oriolus steerii*	Kennedy (2000)
832	Passeriformes	Corvidae	*Oriolus albiloris*	Kennedy (2000)
833	Passeriformes	Corvidae	*Oriolus isabellae*	Kennedy (2000)
834	Passeriformes	Corvidae	*Oriolus oriolus*	Fry et al. (2000)
835	Passeriformes	Corvidae	*Oriolus auratus*	Fry et al. (2000)

836	Passeriformes	Corvidae	*Oriolus chinensis*	Robson (2000)
837	Passeriformes	Corvidae	*Oriolus chlorocephalus*	Fry et al. (2000)
838	Passeriformes	Corvidae	*Oriolus crassirostris*	BirdLife International (2000)
839	Passeriformes	Corvidae	*Oriolus monacha*	Fry et al. (2000)
840	Passeriformes	Corvidae	*Oriolus percivali*	Fry et al. (2000)
841	Passeriformes	Corvidae	*Oriolus hosii*	MacKinnon & Phillipps (1993)
842	Passeriformes	Corvidae	*Oriolus cruentus*	Robson (2000)
843	Passeriformes	Corvidae	*Sphecotheres hypoleucus*	Coates et al. (1997)
844	Passeriformes	Corvidae	*Sphecotheres viridis*	Schodde et al. (1986)
845	Passeriformes	Corvidae	*Sphecotheres vieilloti*	Simpson & Day (2004)
846	Passeriformes	Corvidae	*Coracina larvata*	MacKinnon & Phillipps (1993)
847	Passeriformes	Corvidae	*Coracina lineata*	Schodde et al. (1986)
848	Passeriformes	Corvidae	*Coracina schisticeps*	Coates (1990)
849	Passeriformes	Corvidae	*Coracina montana*	Coates (1990)
850	Passeriformes	Corvidae	*Lalage moesta*	Coates et al. (1997)
851	Passeriformes	Bombycillidae	*Dulus dominicus*	Raffaele (1998)
852	Passeriformes	Bombycillidae	*Ptilogonys cinereus*	Howell & Webb (1995)
853	Passeriformes	Bombycillidae	*Ptilogonys caudatus*	Stiles & Skutch (1989)
854	Passeriformes	Bombycillidae	*Phainopepla nitens*	Howell & Webb (1995)
855	Passeriformes	Bombycillidae	*Phainoptila melanoxantha*	Stiles & Skutch (1989)
856	Passeriformes	Bombycillidae	*Bombycilla garrulus*	Keith et al. (1992)
857	Passeriformes	Bombycillidae	*Bombycilla japonica*	Hoyo et al. (2005)
858	Passeriformes	Bombycillidae	*Bombycilla cedrorum*	De Schauensee & Phelps (1977)
859	Passeriformes	Muscicapidae	*Myophonus blighi*	Hoyo et al. (2005)
860	Passeriformes	Muscicapidae	*Myophonus melanurus*	Hoyo et al. (2005)
861	Passeriformes	Muscicapidae	*Zoothera peronii*	Hoyo et al. (2005)
862	Passeriformes	Muscicapidae	*Cataponera turdoides*	Hoyo et al. (2005)
863	Passeriformes	Muscicapidae	*Myadestes myadestinus*	Hoyo et al. (2005)
864	Passeriformes	Muscicapidae	*Myadestes lanaiensis*	Hoyo et al. (2005)
865	Passeriformes	Muscicapidae	*Myadestes obscurus*	Hoyo et al. (2005)
866	Passeriformes	Muscicapidae	*Myadestes palmeri*	Hoyo et al. (2005)
867	Passeriformes	Muscicapidae	*Myadestes genibarbis*	Hoyo et al. (2005)
868	Passeriformes	Muscicapidae	*Myadestes melanops*	Hoyo et al. (2005)
869	Passeriformes	Muscicapidae	*Myadestes coloratus*	Hoyo et al. (2005)
870	Passeriformes	Muscicapidae	*Myadestes unicolor*	Hoyo et al. (2005)
871	Passeriformes	Muscicapidae	*Platycichla flavipes*	Hoyo et al. (2005)
872	Passeriformes	Muscicapidae	*Platycichla leucops*	Hoyo et al. (2005)
873	Passeriformes	Muscicapidae	*Turdus pelios*	Hoyo et al. (2005)
874	Passeriformes	Muscicapidae	*Turdus ludoviciae*	Hoyo et al. (2005)

875	Passeriformes	Muscicapidae	*Turdus unicolor*	Hoyo et al. (2005)
876	Passeriformes	Muscicapidae	*Turdus albocinctus*	Hoyo et al. (2005)
877	Passeriformes	Muscicapidae	*Turdus pallidus*	Hoyo et al. (2005)
878	Passeriformes	Muscicapidae	*Turdus pilaris*	Hoyo et al. (2005)
879	Passeriformes	Muscicapidae	*Turdus fuscater*	Hoyo et al. (2005)
880	Passeriformes	Muscicapidae	*Turdus serranus*	Hoyo et al. (2005)
881	Passeriformes	Muscicapidae	*Turdus nigriceps*	Hoyo et al. (2005)
882	Passeriformes	Muscicapidae	*Turdus fulviventris*	Hoyo et al. (2005)
883	Passeriformes	Muscicapidae	*Turdus amaurochalinus*	Hoyo et al. (2005)
884	Passeriformes	Muscicapidae	*Turdus plebejus*	Hoyo et al. (2005)
885	Passeriformes	Muscicapidae	*Turdus obsoletus*	Hoyo et al. (2005)
886	Passeriformes	Muscicapidae	*Turdus nudigenis*	Hoyo et al. (2005)
887	Passeriformes	Muscicapidae	*Turdus maculirostris*	Hoyo et al. (2005)
888	Passeriformes	Muscicapidae	*Turdus jamaicensis*	Hoyo et al. (2005)
889	Passeriformes	Muscicapidae	*Turdus assimilis*	Hoyo et al. (2005)
890	Passeriformes	Muscicapidae	*Turdus migratorius*	Hoyo et al. (2005)
891	Passeriformes	Muscicapidae	*Chlamydochaera jefferyi*	MacKinnon & Phillipps (1993)
892	Passeriformes	Muscicapidae	*Cochoa purpurea*	Robson (2000)
893	Passeriformes	Muscicapidae	*Cochoa viridis*	Robson (2000)
894	Passeriformes	Muscicapidae	*Cochoa beccarii*	Hoyo et al. (2005)
895	Passeriformes	Muscicapidae	*Cochoa azurea*	Hoyo et al. (2005)
896	Passeriformes	Sturnidae	*Aplonis zelandica*	Feare & Craig (1999)
897	Passeriformes	Sturnidae	*Aplonis santovestris*	Feare & Craig (1999)
898	Passeriformes	Sturnidae	*Aplonis pelzelni*	Feare & Craig (1999)
899	Passeriformes	Sturnidae	*Aplonis atrifusca*	Feare & Craig (1999)
900	Passeriformes	Sturnidae	*Aplonis mavornata*	Feare & Craig (1999)
901	Passeriformes	Sturnidae	*Aplonis tabuensis*	Feare & Craig (1999)
902	Passeriformes	Sturnidae	*Aplonis striata*	Feare & Craig (1999)
903	Passeriformes	Sturnidae	*Aplonis opaca*	Feare & Craig (1999)
904	Passeriformes	Sturnidae	*Aplonis crassa*	Feare & Craig (1999)
905	Passeriformes	Sturnidae	*Aplonis cantoroides*	Feare & Craig (1999)
906	Passeriformes	Sturnidae	*Aplonis feadensis*	Feare & Craig (1999)
907	Passeriformes	Sturnidae	*Aplonis insularis*	Feare & Craig (1999)
908	Passeriformes	Sturnidae	*Aplonis grandis*	Feare & Craig (1999)
909	Passeriformes	Sturnidae	*Aplonis dichroa*	Feare & Craig (1999)
910	Passeriformes	Sturnidae	*Aplonis mysolensis*	Feare & Craig (1999)
911	Passeriformes	Sturnidae	*Aplonis minor*	Feare & Craig (1999)
912	Passeriformes	Sturnidae	*Aplonis panayensis*	Feare & Craig (1999)
913	Passeriformes	Sturnidae	*Aplonis magna*	Feare & Craig (1999)

914	Passeriformes	Sturnidae	*Aplonis mystacea*	Feare & Craig (1999)
915	Passeriformes	Sturnidae	*Aplonis brunneicapilla*	Feare & Craig (1999)
916	Passeriformes	Sturnidae	*Poeoptera stuhlmanni*	Feare & Craig (1999)
917	Passeriformes	Sturnidae	*Poeoptera kenricki*	Feare & Craig (1999)
918	Passeriformes	Sturnidae	*Poeoptera lugubris*	Feare & Craig (1999)
919	Passeriformes	Sturnidae	*Onychognathus neumanni*	Feare & Craig (1999)
920	Passeriformes	Sturnidae	*Grafisia torquata*	Feare & Craig (1999)
921	Passeriformes	Sturnidae	*Onychognathus walleri*	Feare & Craig (1999)
922	Passeriformes	Sturnidae	*Onychognathus nabouroup*	Feare & Craig (1999)
923	Passeriformes	Sturnidae	*Onychognathus tristramii*	Feare & Craig (1999)
924	Passeriformes	Sturnidae	*Onychognathus blythii*	Feare & Craig (1999)
925	Passeriformes	Sturnidae	*Onychognathus frater*	Feare & Craig (1999)
926	Passeriformes	Sturnidae	*Onychognathus tenuirostris*	Feare & Craig (1999)
927	Passeriformes	Sturnidae	*Onychognathus albirostris*	Feare & Craig (1999)
928	Passeriformes	Sturnidae	*Onychognathus salvadorii*	Feare & Craig (1999)
929	Passeriformes	Sturnidae	*Coccycolius iris*	Feare & Craig (1999)
930	Passeriformes	Sturnidae	*Lamprotornis cupreocauda*	Feare & Craig (1999)
931	Passeriformes	Sturnidae	*Lamprotornis purpureiceps*	Feare & Craig (1999)
932	Passeriformes	Sturnidae	*Lamprotornis purpureus*	Feare & Craig (1999)
933	Passeriformes	Sturnidae	*Lamprotornis nitens*	Feare & Craig (1999)
934	Passeriformes	Sturnidae	*Lamprotornis chloropterus*	Feare & Craig (1999)
935	Passeriformes	Sturnidae	*Lamprotornis acuticaudus*	Feare & Craig (1999)
936	Passeriformes	Sturnidae	*Lamprotornis splendidus*	Feare & Craig (1999)
937	Passeriformes	Sturnidae	*Lamprotornis ornatus*	Feare & Craig (1999)
938	Passeriformes	Sturnidae	*Lamprotornis caudatus*	Feare & Craig (1999)
939	Passeriformes	Sturnidae	*Cinnyricinclus sharpii*	Feare & Craig (1999)
940	Passeriformes	Sturnidae	*Cinnyricinclus femoralis*	Feare & Craig (1999)
941	Passeriformes	Sturnidae	*Cinnyricinclus leucogaster*	Feare & Craig (1999)
942	Passeriformes	Sturnidae	*Speculipastor bicolor*	Feare & Craig (1999)
943	Passeriformes	Sturnidae	*Saroglossa aurata*	Feare & Craig (1999)
944	Passeriformes	Sturnidae	*Sturnus senex*	Feare & Craig (1999)
945	Passeriformes	Sturnidae	*Sturnus erythropygius*	Feare & Craig (1999)
946	Passeriformes	Sturnidae	*Sturnus pagodarum*	Feare & Craig (1999)
947	Passeriformes	Sturnidae	*Sturnus burmannicus*	Feare & Craig (1999)
948	Passeriformes	Sturnidae	*Sturnus melanopterus*	Feare & Craig (1999)
949	Passeriformes	Sturnidae	*Leucopsar rothschildi*	Feare & Craig (1999)
950	Passeriformes	Sturnidae	*Ampeliceps coronatus*	Feare & Craig (1999)
951	Passeriformes	Sturnidae	*Mino anais*	Feare & Craig (1999)
952	Passeriformes	Sturnidae	*Mino dumontii*	Feare & Craig (1999)

953	Passeriformes	Sturnidae	*Basilornis celebensis*	Feare & Craig (1999)
954	Passeriformes	Sturnidae	*Basilornis galeatus*	Feare & Craig (1999)
955	Passeriformes	Sturnidae	*Basilornis corythaix*	Feare & Craig (1999)
956	Passeriformes	Sturnidae	*Basilornis miranda*	Feare & Craig (1999)
957	Passeriformes	Sturnidae	*Streptocitta albicollis*	Feare & Craig (1999)
958	Passeriformes	Sturnidae	*Streptocitta albertinae*	Feare & Craig (1999)
959	Passeriformes	Sturnidae	*Sarcops calvus*	Feare & Craig (1999)
960	Passeriformes	Sturnidae	*Gracula ptilogenys*	Feare & Craig (1999)
961	Passeriformes	Sturnidae	*Enodes erythrophris*	Feare & Craig (1999)
962	Passeriformes	Sturnidae	*Scissirostrum dubium*	Feare & Craig (1999)
963	Passeriformes	Sturnidae	*Margarops fuscus*	Feare & Craig (1999)
964	Passeriformes	Pycnonotidae	*Spizixos semitorques*	Hoyo et al. (2005)
965	Passeriformes	Pycnonotidae	*Pycnonotus striatus*	Hoyo et al. (2005)
966	Passeriformes	Pycnonotidae	*Pycnonotus leucogrammicus*	Hoyo et al. (2005)
967	Passeriformes	Pycnonotidae	*Pycnonotus tympanistrigus*	Hoyo et al. (2005)
968	Passeriformes	Pycnonotidae	*Pycnonotus melanoleucos*	Hoyo et al. (2005)
969	Passeriformes	Pycnonotidae	*Pycnonotus priocephalus*	Hoyo et al. (2005)
970	Passeriformes	Pycnonotidae	*Pycnonotus atriceps*	Hoyo et al. (2005)
971	Passeriformes	Pycnonotidae	*Pycnonotus melanicterus*	Hoyo et al. (2005)
972	Passeriformes	Pycnonotidae	*Pycnonotus squamatus*	Hoyo et al. (2005)
973	Passeriformes	Pycnonotidae	*Pycnonotus cyaniventris*	Hoyo et al. (2005)
974	Passeriformes	Pycnonotidae	*Pycnonotus xanthorrhous*	Hoyo et al. (2005)
975	Passeriformes	Pycnonotidae	*Pycnonotus sinensis*	Hoyo et al. (2005)
976	Passeriformes	Pycnonotidae	*Pycnonotus taivanus*	Hoyo et al. (2005)
977	Passeriformes	Pycnonotidae	*Pycnonotus aurigaster*	Hoyo et al. (2005)
978	Passeriformes	Pycnonotidae	*Pycnonotus eutilotus*	Hoyo et al. (2005)
979	Passeriformes	Pycnonotidae	*Pycnonotus nieuwenhuisii*	Hoyo et al. (2005)
980	Passeriformes	Pycnonotidae	*Pycnonotus urostictus*	Hoyo et al. (2005)
981	Passeriformes	Pycnonotidae	*Pycnonotus bimaculatus*	Hoyo et al. (2005)
982	Passeriformes	Pycnonotidae	*Pycnonotus finlaysoni*	Hoyo et al. (2005)
983	Passeriformes	Pycnonotidae	*Pycnonotus xantholaemus*	Hoyo et al. (2005)
984	Passeriformes	Pycnonotidae	*Pycnonotus penicillatus*	Hoyo et al. (2005)
985	Passeriformes	Pycnonotidae	*Pycnonotus flavescens*	Hoyo et al. (2005)
986	Passeriformes	Pycnonotidae	*Pycnonotus goiavier*	Hoyo et al. (2005)
987	Passeriformes	Pycnonotidae	*Pycnonotus plumosus*	Hoyo et al. (2005)
988	Passeriformes	Pycnonotidae	*Pycnonotus blanfordi*	Hoyo et al. (2005)
989	Passeriformes	Pycnonotidae	*Pycnonotus simplex*	Hoyo et al. (2005)
990	Passeriformes	Pycnonotidae	*Pycnonotus brunneus*	Hoyo et al. (2005)
991	Passeriformes	Pycnonotidae	*Pycnonotus erythropthalmos*	Hoyo et al. (2005)

992	Passeriformes	Pycnonotidae	*Calyptocichla serina*	Hoyo et al. (2005)
993	Passeriformes	Pycnonotidae	*Baeopogon indicator*	Hoyo et al. (2005)
994	Passeriformes	Pycnonotidae	*Baeopogon clamans*	Hoyo et al. (2005)
995	Passeriformes	Pycnonotidae	*Ixonotus guttatus*	Hoyo et al. (2005)
996	Passeriformes	Pycnonotidae	*Chlorocichla simplex*	Hoyo et al. (2005)
997	Passeriformes	Pycnonotidae	*Chlorocichla flavicollis*	Hoyo et al. (2005)
998	Passeriformes	Pycnonotidae	*Chlorocichla laetissima*	Hoyo et al. (2005)
999	Passeriformes	Pycnonotidae	*Chlorocichla prigoginei*	Hoyo et al. (2005)
1000	Passeriformes	Pycnonotidae	*Phyllastrephus strepitans*	Hoyo et al. (2005)
1001	Passeriformes	Pycnonotidae	*Alophoixus flaveolus*	Hoyo et al. (2005)
1002	Passeriformes	Pycnonotidae	*Tricholestes criniger*	Hoyo et al. (2005)
1003	Passeriformes	Pycnonotidae	*Iole virescens*	Hoyo et al. (2005)
1004	Passeriformes	Pycnonotidae	*Iole propinqua*	Hoyo et al. (2005)
1005	Passeriformes	Pycnonotidae	*Iole olivacea*	Hoyo et al. (2005)
1006	Passeriformes	Pycnonotidae	*Ixos palawanensis*	Hoyo et al. (2005)
1007	Passeriformes	Pycnonotidae	*Ixos philippinus*	Hoyo et al. (2005)
1008	Passeriformes	Pycnonotidae	*Ixos rufigularis*	Hoyo et al. (2005)
1009	Passeriformes	Pycnonotidae	*Ixos siquijorensis*	Hoyo et al. (2005)
1010	Passeriformes	Pycnonotidae	*Ixos everetti*	Hoyo et al. (2005)
1011	Passeriformes	Pycnonotidae	*Ixos malaccensis*	Hoyo et al. (2005)
1012	Passeriformes	Pycnonotidae	*Hemixos castanonotus*	Hoyo et al. (2005)
1013	Passeriformes	Pycnonotidae	*Hypsipetes mcclellandii*	Hoyo et al. (2005)
1014	Passeriformes	Pycnonotidae	*Hypsipetes virescens*	Hoyo et al. (2005)
1015	Passeriformes	Pycnonotidae	*Hypsipetes madagascariensis*	Hoyo et al. (2005)
1016	Passeriformes	Pycnonotidae	*Hypsipetes parvirostris*	Hoyo et al. (2005)
1017	Passeriformes	Pycnonotidae	*Hypsipetes borbonicus*	Hoyo et al. (2005)
1018	Passeriformes	Pycnonotidae	*Hypsipetes olivaceus*	Hoyo et al. (2005)
1019	Passeriformes	Pycnonotidae	*Hypsipetes leucocephalus*	Hoyo et al. (2005)
1020	Passeriformes	Pycnonotidae	*Hypsipetes nicobariensis*	Hoyo et al. (2005)
1021	Passeriformes	Pycnonotidae	*Hypsipetes thompsoni*	Hoyo et al. (2005)
1022	Passeriformes	Hypocoliidae	*Hypocolius ampelinus*	Fry et al. (2000)
1023	Passeriformes	Zosteropidae	*Apalopteron familiare*	BirdLife International (2000)
1024	Passeriformes	Sylviidae	*Garrulax bieti*	Hoyo et al. (2007)
1025	Passeriformes	Sylviidae	*Garrulax caerulatus*	Ali & Ripley (1996)
1026	Passeriformes	Sylviidae	*Garrulax sannio*	Ali & Ripley (1996)
1027	Passeriformes	Sylviidae	*Garrulax jerdoni*	Ali & Ripley (1996)
1028	Passeriformes	Sylviidae	*Garrulax henrici*	Ali & Ripley (1996)
1029	Passeriformes	Sylviidae	*Garrulax affinis*	Ali & Ripley (1996)
1030	Passeriformes	Sylviidae	*Garrulax morrisonianus*	Hoyo et al. (2007)

1031	Passeriformes	Sylviidae	*Liocichla phoenicea*	Robson (2000)
1032	Passeriformes	Sylviidae	*Liocichla omeiensis*	Hoyo et al. (2007)
1033	Passeriformes	Sylviidae	*Liocichla steerii*	Hoyo et al. (2007)
1034	Passeriformes	Sylviidae	*Lioptilus nigricapillus*	Fry et al. (2000)
1035	Passeriformes	Sylviidae	*Parophasma galinieri*	Fry et al. (2000)
1036	Passeriformes	Nectariniidae	*Dicaeum agile*	Cheke et al. (2001)
1037	Passeriformes	Nectariniidae	*Dicaeum aeruginosum*	Cheke et al. (2001)
1038	Passeriformes	Nectariniidae	*Dicaeum aureolimbatum*	Cheke et al. (2001)
1039	Passeriformes	Nectariniidae	*Dicaeum haematostictum*	Cheke et al. (2001)
1040	Passeriformes	Nectariniidae	*Dicaeum nitidum*	Cheke et al. (2001)
1041	Passeriformes	Nectariniidae	*Dicaeum monticolum*	Cheke et al. (2001)
1042	Passeriformes	Melanocharitidae	*Melanocharis arfakiana*	Coates (1990)
1043	Passeriformes	Melanocharitidae	*Melanocharis nigra*	Coates (1990)
1044	Passeriformes	Melanocharitidae	*Melanocharis longicauda*	Coates (1990)
1045	Passeriformes	Melanocharitidae	*Melanocharis versteri*	Coates (1990)
1046	Passeriformes	Melanocharitidae	*Melanocharis striativentris*	Coates (1990)
1047	Passeriformes	Melanocharitidae	*Melanocharis crassirostris*	Coates (1990)
1048	Passeriformes	Paramythiidae	*Oreocharis arfaki*	Coates (1990)
1049	Passeriformes	Paramythiidae	*Paramythia montium*	Coates (1990)
1050	Passeriformes	Passeridae	*Erythrura papuana*	Coates (1990)
1051	Passeriformes	Fringillidae	*Psittirostra psittacea*	BirdLife International (2000)
1052	Passeriformes	Fringillidae	*Conirostrum leucogenys*	De Schauensee & Phelps (1977)
1053	Passeriformes	Fringillidae	*Schistochlamys ruficapillus*	Isler & Isler (1999)
1054	Passeriformes	Fringillidae	*Schistochlamys melanopis*	Isler & Isler (1999)
1055	Passeriformes	Fringillidae	*Lamprospiza melanoleuca*	Isler & Isler (1999)
1056	Passeriformes	Fringillidae	*Cissopis leveriana*	Isler & Isler (1999)
1057	Passeriformes	Fringillidae	*Chlorornis riefferii*	Isler & Isler (1999)
1058	Passeriformes	Fringillidae	*Sericossypha albocristata*	Isler & Isler (1999)
1059	Passeriformes	Fringillidae	*Chlorospingus semifuscus*	Isler & Isler (1999)
1060	Passeriformes	Fringillidae	*Chlorospingus flavovirens*	Isler & Isler (1999)
1061	Passeriformes	Fringillidae	*Chrysothlypis chrysomelas*	Isler & Isler (1999)
1062	Passeriformes	Fringillidae	*Chrysothlypis salmoni*	Isler & Isler (1999)
1063	Passeriformes	Fringillidae	*Mitrospingus cassinii*	Isler & Isler (1999)
1064	Passeriformes	Fringillidae	*Mitrospingus oleagineus*	Isler & Isler (1999)
1065	Passeriformes	Fringillidae	*Chlorothraupis stolzmanni*	Isler & Isler (1999)
1066	Passeriformes	Fringillidae	*Heterospingus rubrifrons*	Isler & Isler (1999)
1067	Passeriformes	Fringillidae	*Heterospingus xanthopygius*	Isler & Isler (1999)
1068	Passeriformes	Fringillidae	*Piranga bidentata*	Isler & Isler (1999)
1069	Passeriformes	Fringillidae	*Calochaetes coccineus*	Isler & Isler (1999)

1070	Passeriformes	Fringillidae	*Phlogothraupis sanguinolenta*	Isler & Isler (1999)
1071	Passeriformes	Fringillidae	*Ramphocelus nigrogularis*	Isler & Isler (1999)
1072	Passeriformes	Fringillidae	*Ramphocelus dimidiatus*	Isler & Isler (1999)
1073	Passeriformes	Fringillidae	*Ramphocelus melanogaster*	Isler & Isler (1999)
1074	Passeriformes	Fringillidae	*Ramphocelus carbo*	Isler & Isler (1999)
1075	Passeriformes	Fringillidae	*Ramphocelus bresilius*	Isler & Isler (1999)
1076	Passeriformes	Fringillidae	*Ramphocelus passerinii*	Isler & Isler (1999)
1077	Passeriformes	Fringillidae	*Ramphocelus costaricensis*	Isler & Isler (1999)
1078	Passeriformes	Fringillidae	*Ramphocelus flammigerus*	Isler & Isler (1999)
1079	Passeriformes	Fringillidae	*Ramphocelus icteronotus*	Isler & Isler (1999)
1080	Passeriformes	Fringillidae	*Spindalis zena*	Isler & Isler (1999)
1081	Passeriformes	Fringillidae	*Spindalis dominicensis*	Isler & Isler (1999)
1082	Passeriformes	Fringillidae	*Spindalis nigricephala*	Isler & Isler (1999)
1083	Passeriformes	Fringillidae	*Spindalis portoricensis*	Isler & Isler (1999)
1084	Passeriformes	Fringillidae	*Thraupis episcopus*	Isler & Isler (1999)
1085	Passeriformes	Fringillidae	*Thraupis glaucocolpa*	Isler & Isler (1999)
1086	Passeriformes	Fringillidae	*Thraupis sayaca*	Isler & Isler (1999)
1087	Passeriformes	Fringillidae	*Thraupis cyanoptera*	Isler & Isler (1999)
1088	Passeriformes	Fringillidae	*Thraupis ornata*	Isler & Isler (1999)
1089	Passeriformes	Fringillidae	*Thraupis abbas*	Isler & Isler (1999)
1090	Passeriformes	Fringillidae	*Thraupis palmarum*	Isler & Isler (1999)
1091	Passeriformes	Fringillidae	*Thraupis cyanocephala*	Isler & Isler (1999)
1092	Passeriformes	Fringillidae	*Thraupis bonariensis*	Isler & Isler (1999)
1093	Passeriformes	Fringillidae	*Bangsia arcaei*	Isler & Isler (1999)
1094	Passeriformes	Fringillidae	*Bangsia melanochlamys*	Isler & Isler (1999)
1095	Passeriformes	Fringillidae	*Bangsia rothschildi*	Isler & Isler (1999)
1096	Passeriformes	Fringillidae	*Bangsia edwardsi*	Isler & Isler (1999)
1097	Passeriformes	Fringillidae	*Bangsia aureocincta*	Isler & Isler (1999)
1098	Passeriformes	Fringillidae	*Buthraupis montana*	Isler & Isler (1999)
1099	Passeriformes	Fringillidae	*Buthraupis eximia*	Isler & Isler (1999)
1100	Passeriformes	Fringillidae	*Buthraupis aureodorsalis*	Isler & Isler (1999)
1101	Passeriformes	Fringillidae	*Buthraupis wetmorei*	Isler & Isler (1999)
1102	Passeriformes	Fringillidae	*Wetmorethraupis sterrhopteron*	Isler & Isler (1999)
1103	Passeriformes	Fringillidae	*Anisognathus melanogenys*	Isler & Isler (1999)
1104	Passeriformes	Fringillidae	*Anisognathus lacrymosus*	Isler & Isler (1999)
1105	Passeriformes	Fringillidae	*Anisognathus igniventris*	Isler & Isler (1999)
1106	Passeriformes	Fringillidae	*Anisognathus somptuosus*	Isler & Isler (1999)
1107	Passeriformes	Fringillidae	*Anisognathus flavinuchus*	Isler & Isler (1999)
1108	Passeriformes	Fringillidae	*Anisognathus notabilis*	Isler & Isler (1999)

1109	Passeriformes	Fringillidae	*Stephanophorus diadematus*	Isler & Isler (1999)
1110	Passeriformes	Fringillidae	*Iridosornis porphyrocephala*	Isler & Isler (1999)
1111	Passeriformes	Fringillidae	*Iridosornis jelskii*	Isler & Isler (1999)
1112	Passeriformes	Fringillidae	*Iridosornis rufivertex*	Isler & Isler (1999)
1113	Passeriformes	Fringillidae	*Iridosornis reinhardti*	Isler & Isler (1999)
1114	Passeriformes	Fringillidae	*Dubusia taeniata*	Isler & Isler (1999)
1115	Passeriformes	Fringillidae	*Delothraupis castaneoventris*	Isler & Isler (1999)
1116	Passeriformes	Fringillidae	*Pipraeidea melanonota*	Isler & Isler (1999)
1117	Passeriformes	Fringillidae	*Euphonia jamaica*	Isler & Isler (1999)
1118	Passeriformes	Fringillidae	*Euphonia plumbea*	Isler & Isler (1999)
1119	Passeriformes	Fringillidae	*Euphonia affinis*	Isler & Isler (1999)
1120	Passeriformes	Fringillidae	*Euphonia luteicapilla*	Isler & Isler (1999)
1121	Passeriformes	Fringillidae	*Euphonia chlorotica*	Isler & Isler (1999)
1122	Passeriformes	Fringillidae	*Euphonia trinitatis*	Isler & Isler (1999)
1123	Passeriformes	Fringillidae	*Euphonia concinna*	Isler & Isler (1999)
1124	Passeriformes	Fringillidae	*Euphonia saturata*	Isler & Isler (1999)
1125	Passeriformes	Fringillidae	*Euphonia finschi*	Isler & Isler (1999)
1126	Passeriformes	Fringillidae	*Euphonia violacea*	Isler & Isler (1999)
1127	Passeriformes	Fringillidae	*Euphonia laniirostris*	Isler & Isler (1999)
1128	Passeriformes	Fringillidae	*Euphonia hirundinacea*	Isler & Isler (1999)
1129	Passeriformes	Fringillidae	*Euphonia chalybea*	Isler & Isler (1999)
1130	Passeriformes	Fringillidae	*Euphonia elegantissima*	Isler & Isler (1999)
1131	Passeriformes	Fringillidae	*Euphonia musica*	Isler & Isler (1999)
1132	Passeriformes	Fringillidae	*Euphonia cyanocephala*	Isler & Isler (1999)
1133	Passeriformes	Fringillidae	*Euphonia imitans*	Isler & Isler (1999)
1134	Passeriformes	Fringillidae	*Euphonia fulvicrissa*	Isler & Isler (1999)
1135	Passeriformes	Fringillidae	*Euphonia gouldi*	Isler & Isler (1999)
1136	Passeriformes	Fringillidae	*Euphonia chrysopasta*	Isler & Isler (1999)
1137	Passeriformes	Fringillidae	*Euphonia mesochrysa*	Isler & Isler (1999)
1138	Passeriformes	Fringillidae	*Euphonia minuta*	Isler & Isler (1999)
1139	Passeriformes	Fringillidae	*Euphonia anneae*	Isler & Isler (1999)
1140	Passeriformes	Fringillidae	*Euphonia xanthogaster*	Isler & Isler (1999)
1141	Passeriformes	Fringillidae	*Euphonia rufiventris*	Isler & Isler (1999)
1142	Passeriformes	Fringillidae	*Euphonia cayennensis*	Isler & Isler (1999)
1143	Passeriformes	Fringillidae	*Euphonia pectoralis*	Isler & Isler (1999)
1144	Passeriformes	Fringillidae	*Chlorophonia flavirostris*	Isler & Isler (1999)
1145	Passeriformes	Fringillidae	*Chlorophonia cyanea*	Isler & Isler (1999)
1146	Passeriformes	Fringillidae	*Chlorophonia pyrrhophrys*	Isler & Isler (1999)
1147	Passeriformes	Fringillidae	*Chlorophonia occipitalis*	Isler & Isler (1999)

1148	Passeriformes	Fringillidae	*Chlorophonia callophrys*	Isler & Isler (1999)
1149	Passeriformes	Fringillidae	*Chlorochrysa calliparaea*	Isler & Isler (1999)
1150	Passeriformes	Fringillidae	*Tangara inornata*	Isler & Isler (1999)
1151	Passeriformes	Fringillidae	*Tangara mexicana*	Isler & Isler (1999)
1152	Passeriformes	Fringillidae	*Tangara brasiliensis*	Isler & Isler (1999)
1153	Passeriformes	Fringillidae	*Tangara cabanisi*	Isler & Isler (1999)
1154	Passeriformes	Fringillidae	*Tangara palmeri*	Isler & Isler (1999)
1155	Passeriformes	Fringillidae	*Tangara chilensis*	Isler & Isler (1999)
1156	Passeriformes	Fringillidae	*Tangara fastuosa*	Isler & Isler (1999)
1157	Passeriformes	Fringillidae	*Tangara seledon*	Isler & Isler (1999)
1158	Passeriformes	Fringillidae	*Tangara cyanocephala*	Isler & Isler (1999)
1159	Passeriformes	Fringillidae	*Tangara desmaresti*	Isler & Isler (1999)
1160	Passeriformes	Fringillidae	*Tangara cyanoventris*	Isler & Isler (1999)
1161	Passeriformes	Fringillidae	*Tangara johannae*	Isler & Isler (1999)
1162	Passeriformes	Fringillidae	*Tangara schrankii*	Isler & Isler (1999)
1163	Passeriformes	Fringillidae	*Tangara florida*	Isler & Isler (1999)
1164	Passeriformes	Fringillidae	*Tangara arthus*	Isler & Isler (1999)
1165	Passeriformes	Fringillidae	*Tangara icterocephala*	Isler & Isler (1999)
1166	Passeriformes	Fringillidae	*Tangara xanthocephala*	Isler & Isler (1999)
1167	Passeriformes	Fringillidae	*Tangara chrysotis*	Isler & Isler (1999)
1168	Passeriformes	Fringillidae	*Tangara parzudakii*	Isler & Isler (1999)
1169	Passeriformes	Fringillidae	*Tangara xanthogastra*	Isler & Isler (1999)
1170	Passeriformes	Fringillidae	*Tangara punctata*	Isler & Isler (1999)
1171	Passeriformes	Fringillidae	*Tangara guttata*	Isler & Isler (1999)
1172	Passeriformes	Fringillidae	*Tangara varia*	Isler & Isler (1999)
1173	Passeriformes	Fringillidae	*Tangara rufigula*	Isler & Isler (1999)
1174	Passeriformes	Fringillidae	*Tangara gyrola*	Isler & Isler (1999)
1175	Passeriformes	Fringillidae	*Tangara lavinia*	Isler & Isler (1999)
1176	Passeriformes	Fringillidae	*Tangara cayana*	Isler & Isler (1999)
1177	Passeriformes	Fringillidae	*Tangara cucullata*	Isler & Isler (1999)
1178	Passeriformes	Fringillidae	*Tangara peruviana*	Isler & Isler (1999)
1179	Passeriformes	Fringillidae	*Tangara preciosa*	Isler & Isler (1999)
1180	Passeriformes	Fringillidae	*Tangara vitriolina*	Isler & Isler (1999)
1181	Passeriformes	Fringillidae	*Tangara meyerdeschauenseei*	Isler & Isler (1999)
1182	Passeriformes	Fringillidae	*Tangara rufigenis*	Isler & Isler (1999)
1183	Passeriformes	Fringillidae	*Tangara ruficervix*	Isler & Isler (1999)
1184	Passeriformes	Fringillidae	*Tangara cyanotis*	Isler & Isler (1999)
1185	Passeriformes	Fringillidae	*Tangara cyanicollis*	Isler & Isler (1999)
1186	Passeriformes	Fringillidae	*Tangara larvata*	Isler & Isler (1999)

1187	Passeriformes	Fringillidae	*Tangara nigrocincta*	Isler & Isler (1999)
1188	Passeriformes	Fringillidae	*Tangara dowii*	Isler & Isler (1999)
1189	Passeriformes	Fringillidae	*Tangara fucosa*	Isler & Isler (1999)
1190	Passeriformes	Fringillidae	*Tangara nigroviridis*	Isler & Isler (1999)
1191	Passeriformes	Fringillidae	*Tangara vassorii*	Isler & Isler (1999)
1192	Passeriformes	Fringillidae	*Tangara heinei*	Isler & Isler (1999)
1193	Passeriformes	Fringillidae	*Tangara phillipsi*	Isler & Isler (1999)
1194	Passeriformes	Fringillidae	*Tangara viridicollis*	Isler & Isler (1999)
1195	Passeriformes	Fringillidae	*Tangara argyrofenges*	Isler & Isler (1999)
1196	Passeriformes	Fringillidae	*Tangara cyanoptera*	Isler & Isler (1999)
1197	Passeriformes	Fringillidae	*Tangara velia*	Isler & Isler (1999)
1198	Passeriformes	Fringillidae	*Tangara callophrys*	Isler & Isler (1999)
1199	Passeriformes	Fringillidae	*Iridophanes pulcherrima*	Isler & Isler (1999)
1200	Passeriformes	Fringillidae	*Pseudodacnis hartlaubi*	Isler & Isler (1999)
1201	Passeriformes	Fringillidae	*Dacnis albiventris*	Isler & Isler (1999)
1202	Passeriformes	Fringillidae	*Dacnis lineata*	Isler & Isler (1999)
1203	Passeriformes	Fringillidae	*Dacnis flaviventer*	Isler & Isler (1999)
1204	Passeriformes	Fringillidae	*Dacnis nigripes*	Isler & Isler (1999)
1205	Passeriformes	Fringillidae	*Dacnis venusta*	Isler & Isler (1999)
1206	Passeriformes	Fringillidae	*Dacnis cayana*	Isler & Isler (1999)
1207	Passeriformes	Fringillidae	*Dacnis viguieri*	Isler & Isler (1999)
1208	Passeriformes	Fringillidae	*Dacnis berlepschi*	Isler & Isler (1999)
1209	Passeriformes	Fringillidae	*Chlorophanes spiza*	Isler & Isler (1999)
1210	Passeriformes	Fringillidae	*Tersina viridis*	Isler & Isler (1999)
1211	Passeriformes	Fringillidae	*Loxipasser anoxanthus*	Raffaele (1998)
1212	Passeriformes	Fringillidae	*Diglossopis indigotica*	Isler & Isler (1999)
1213	Passeriformes	Fringillidae	*Diglossopis glauca*	Isler & Isler (1999)
1214	Passeriformes	Fringillidae	*Caryothraustes canadensis*	Hilty & De Schauensee (2003)
1215	Passeriformes	Fringillidae	*Rhodothraupis celaeno*	Howell & Webb (1995)
1216	Passeriformes	Fringillidae	*Periporphyrus erythromelas*	Hilty & De Schauensee (2003)
1217	Passeriformes	Fringillidae	*Saltator orenocensis*	Hilty & De Schauensee (2003)
1218	Passeriformes	Fringillidae	*Psarocolius decumanus*	Jaramillo & Burke (1999)
1219	Passeriformes	Fringillidae	*Psarocolius viridis*	Jaramillo & Burke (1999)
1220	Passeriformes	Fringillidae	*Gymnostinops montezuma*	Jaramillo & Burke (1999)
1221	Passeriformes	Fringillidae	*Gymnostinops cassini*	Jaramillo & Burke (1999)
1222	Passeriformes	Fringillidae	*Gymnostinops bifasciatus*	Jaramillo & Burke (1999)
1223	Passeriformes	Fringillidae	*Psarocolius yuracares*	Jaramillo & Burke (1999)
1224	Passeriformes	Fringillidae	*Cacicus cela*	Jaramillo & Burke (1999)
1225	Passeriformes	Fringillidae	*Cacicus chrysopterus*	Jaramillo & Burke (1999)

1226	Passeriformes	Fringillidae	*Cacicus chrysonotus*	Jaramillo & Burke (1999)
1227	Passeriformes	Fringillidae	*Icterus laudabilis*	Jaramillo & Burke (1999)
1228	Passeriformes	Fringillidae	*Gymnomystax mexicanus*	Jaramillo & Burke (1999)
1229	Passeriformes	Fringillidae	*Hypopyrrhus pyrohypogaster*	Jaramillo & Burke (1999)
1230	Passeriformes	Fringillidae	*Curaeus forbesi*	Jaramillo & Burke (1999)

Appendix 2: Continental and island frugivores

Most frugivorous birds (*n* = 1,081, 88%) occurred on the continental parts of each realm whereas only 149 species (12%) occurred exclusively on islands (Table A1). Island frugivores were excluded in the statistical analyses – species which were mainly found within the orders of Passeriformes and Columbiformes (42% and 41% of all island frugivores, respectively).

Table A1: Numbers of breeding bird species in different biogeographical realms, with the numbers of frugivorous species ("FRUG") listed separately for the main continental part of each realm ("Continental"), islands associated with each realm ("Islands"), and the realm as a whole ("Total").

	FRUG species richness			Bird richness
Realm	Continental	Islands	Total	All
Neotropics	559(16)	18(+)	577(16)	3,553(100)
Australasia	182(12)	73(5)	255(17)	1,480(100)
Indo–Malaya	207(12)	23(1)	230(14)	1,679(100)
Afrotropics	139(8)	14(+)	153(8)	1,843(100)
Palaearctic	65(5)	3(+)	68(5)	1,393(100)
Nearctic	31(5)	0(0)	31(5)	664(100)
Oceania	0(0)	38(17)	38(17)	224(100)
All realms	1,081(12)	149(2)	1,230(14)	8,918(100)

Note: Frugivorous species that occur on both continent and islands of the same realm are listed under continental. The numbers of all terrestrial bird species ("Bird richness") are given for comparison. Figures in brackets are percentages of the total numbers of terrestrial bird species in a given realm. + = <1%. Note that numbers across realms (i.e., columns) do not add up to the overall number ("All realms") because some species occur in more than one realm.

Appendix 3: Results of single predictor models (2° resolution)

Table A2: Results of single predictor models examined at resolution equivalent to 2° to explain global avian frugivore richness and the proportion of frugivores in avian assemblages. Within each category the best single predictor variable is highlighted in bold.

		Frugivore richness							Proportion of frugivores						
		GLM			SLM				GLM			SLM			
Variables	+/-	R^2	AIC	Moran	R^2_{trend}	R^2_{fit}	AIC	Moran	R^2	AIC	Moran	R^2_{trend}	R^2_{fit}	AIC	Moran
NULL		–	1788	0.90***	–	0.94	-117	0.03	–	-1393	0.90***	–	0.96	-3496	0.00
Water–energy and productivity															
PET	+	0.53	1121	0.84***	0.53	0.94	-201	0.03	0.48	-1978	0.86***	0.48	0.96	-3551	0.01
PET^2		0.57	1040	0.80***	0.47	0.94	-209	0.03	0.59	-2176	0.80***	0.46	0.96	-3551	0.01
TEMP	+	0.43	1299	0.85***	0.43	0.94	-155	0.03	0.38	-1809	0.87***	0.38	0.96	-3554	0.00
TEMP^2		0.48	1216	0.82***	0.33	0.94	-161	0.03	0.49	-1994	0.84***	0.41	0.96	-3534	0.00
FROST	-	0.54	1105	0.80***	0.54	0.94	-136	0.03	0.52	-2035	0.82***	0.52	0.96	-3523	0.00
PREC	+	0.54	1091	0.76***	0.54	0.94	-183	0.02	0.62	-2243	0.74***	0.62	0.96	-3570	0.01
PREC^2		0.57	1039	0.77***	0.56	0.95	-241	0.01	–	–	–	–	–	–	–
WET	+	0.05	1748	0.91***	0.05	0.95	-207	0.02	0.05	-1440	0.91***	0.05	0.96	-3545	0.00
AET	**+**	**0.72**	**646**	**0.78*****	**0.72**	**0.95**	**-407**	**0.02**	**0.72**	**-2508**	**0.80*****	**0.72**	**0.96**	**-3716**	**0.01**
NPPann	+	0.50	1168	0.85***	0.50	0.95	-304	0.01	0.48	-1966	0.85***	0.48	0.96	-3633	0.01
NPPann^2		0.55	1070	0.80***	0.42	0.95	-324	0.00	0.59	-2180	0.77***	0.45	0.96	-3634	0.01
NPPmin	+	0.54	1108	0.79***	0.54	0.94	-169	0.03	0.62	-2246	0.77***	0.62	0.96	-3561	0.00
NPPmin^2		0.60	969	0.76***	0.60	0.94	-198	0.03	0.64	-2309	0.77***	0.64	0.96	-3581	0.00
NPPmax	+	0.04	1753	0.91***	0.04	0.95	-205	0.01	0.03	-1417	0.91***	0.03	0.96	-3541	0.00

Table A2 continued

NPPmax^2		0.20	1590	0.86***	0.12	0.95	-248	0.00	0.17	-1553	0.86***	0.08	0.96	-3556	0.00
Seasonality															
NPPratio	+	0.51	1150	0.79***	0.51	0.94	-160	0.03	0.59	-2187	0.78***	0.59	0.96	-3550	0.00
NPPratio^2		0.56	1064	0.78***	0.56	0.94	-177	0.03	0.61	-2217	0.77***	0.60	0.96	-3557	0.00
NPPpulse	+	0.52	1140	0.79***	0.52	0.94	-160	0.03	0.59	-2194	0.78***	0.59	0.96	-3551	0.00
NPPpulse^2		0.57	1051	0.78***	0.56	0.94	-178	0.03	0.61	-2224	0.77***	0.60	0.96	-3558	0.00
NPPcv	-	0.56	1067	0.82***	0.56	0.95	-227	0.03	0.51	-2020	0.85***	0.51	0.96	-3580	0.00
NPPcv^2		**0.60**	**983**	**0.80*** **	**0.58**	**0.95**	**-230**	**0.03**	**0.63**	**-2270**	**0.79*** **	**0.60**	**0.96**	**-3595**	**0.00**
Heterogeneity															
TOPO	-	0.00	1788	0.90***	0.00	0.95	-149	0.02	0.00	-1392	0.90***	0.00	0.96	-3497	0.00
HABDIV	**-**	**0.01**	**1783**	**0.89*** **	**0.01**	**0.95**	**-173**	**0.02**	**0.04**	**-1423**	**0.89*** **	**0.04**	**0.96**	**-3508**	**0.00**
History															
REALM		**0.70**	**722**	**0.72*** **	**0.61**	**0.94**	**-221**	**0.03**	**0.65**	**-2326**	**0.75*** **	**0.48**	**0.95**	**-3551**	**0.01**

Note: Frugivore richness was log transformed and proportion of frugivores was arcsine square root transformed. GLM = non–spatial generalized linear model, SLM = spatial linear model (calculated as spatial autoregressive error model), Moran = Moran's *I* values. A ^{2} symbol indicates that both the linear and quadratic terms were included. The direction of effect of single predictor variables is indicated with + or -. R^2–values of SLM indicate the non–spatial smooth (R^2_{trend}) and the total fit (R^2_{fit}: composed of non–spatial and spatial smooth). All values are mean values which were obtained from bootstrapping the whole dataset (n = 2,221 equal area grid cells) 100 times with a 40% random subsample (n = 888). Standard errors (not shown) of all mean values were generally much smaller than 10% of the mean values.

Mnemonics of variables: PET = potential evapotranspiration; TEMP = mean annual temperature; FROST = number of frost days; PREC = annual precipitation; WET = number of wet days; AET = actual evapotranspiration; NPPann = total annual above ground productivity; NPPmin = total productivity of the least productive three months; NPPmax = total productivity of the most productive three months; NPPratio = ratio of total productivity of the least productive three months and total productivity of the most productive three months; NPPpulse = seasonal pulse of production in relation to productivity of the most productive three months; NPPcv = coefficient of variation of monthly NPP values; TOPO = difference between maximum and minimum elevation; HABDIV = number of vegetation classes according to the Olson global land cover classification; REALM = biogeographic realm membership.

Appendix 4: Results of multiple predictor models (2° resolution)

Table A3: Results of multiple predictor models examined at resolution equivalent to 2° to explain global avian frugivore richness and the proportion of frugivores in avian assemblages. The multiple predictor model with the highest R²–value is highlighted in bold.

	GLM			SLM			
Variables	R^2	AIC	Moran	R^2_{trend}	R^2_{fit}	AIC	Moran
Frugivore richness							
AET + REALM	0.85	134	0.66***	0.83	0.95	-524	0.03
AET + REALM + AET:REALM	**0.88**	**-86**	**0.56*****	**0.86**	**0.95**	**-549**	**0.04**
AET + HABDIV	0.74	600	0.75***	0.70	0.95	-425	0.01
AET + NPPcv²	0.72	650	0.78***	0.71	0.95	-433	0.01
AET + NPPcv²+ HABDIV	0.74	596	0.75***	0.69	0.95	-440	0.01
AET + REALM + HABDIV	0.85	135	0.66***	0.83	0.95	-530	0.03
AET + REALM + NPPcv²	0.85	122	0.65***	0.82	0.95	-539	0.03
AET + REALM + HABDIV + NPPcv²	0.85	123	0.65***	0.82	0.95	-542	0.03
Proportion of frugivores							
AET + REALM	0.81	-2877	0.72***	0.79	0.96	-3756	0.00
AET + REALM + AET:REALM	**0.89**	**-3346**	**0.54*****	**0.85**	**0.96**	**-3797**	**0.01**
AET + HABDIV	0.77	-2681	0.74***	0.72	0.96	-3701	0.01
AET + NPPcv²	0.74	-2571	0.76***	0.71	0.96	-3704	0.01
AET + NPPcv²+ HABDIV	0.77	-2707	0.72***	0.71	0.96	-3704	0.01
AET + REALM + HABDIV	0.84	-3003	0.66***	0.80	0.96	-3757	0.00
AET + REALM + NPPcv²	0.84	-3018	0.63***	0.78	0.96	-3757	0.00
AET + REALM + HABDIV + NPPcv²	0.85	-3073	0.62***	0.79	0.96	-3758	0.01

Note: Frugivore richness was log transformed and proportion of frugivores was arcsine square root transformed. GLM = non–spatial generalized linear model, SLM = spatial linear model (calculated as spatial autoregressive error model), Moran = Moran's *I* values. A ^{2} symbol indicates that both the linear and quadratic terms were included. R²–values of SLM indicate the non–spatial smooth (R^2_{trend}) and the total fit (R^2_{fit}: composed of non–spatial and spatial smooth). All values are mean values which were obtained from bootstrapping the whole dataset (*n* = 2,221 equal area grid cells) 100 times with a 40% random subsample (*n* = 888). Standard errors of all mean values (not shown) were generally much smaller than 10% of the mean values.

Appendix 5: Classification of African frugivores

A5.1 African frugivore classification

I used all 1,771 sub-Saharan breeding bird species in the database to classify them into food guilds. The classification was based on food preference of each species as given in *The Birds of Africa* (Brown et al. 1982; Urban et al. 1986; Fry et al. 1988; Keith et al. 1992; Urban et al. 1997; Fry et al. 2000; Fry et al. 2004) and in the *Handbook of the Birds of the World* (del Hoyo et al. 1992, 1994, 1996, 1997, 1999, 2001, 2002, 2003, 2004, 2005). Diet categories were algae, amphibians and reptiles, aquatic invertebrates (aquatic insects and crustaceans), birds, carrion, fish, fruit, mammals (e.g. rodents, bats, squirrels, monkeys), nectar, seeds, omnivore, terrestrial plant parts (e.g. leaves, shoots, roots, flowers, bulbs), terrestrial invertebrates (incl. spiders, insects, and molluscs), and other food items (e.g. wax, human scraps, refuse). I distinguished major and minor food items by using keywords in the paragraphs on food and feeding behavior (e.g. "almost exclusively", "entirely", "almost entirely", "mainly", "prefers" taken to indicate major food items, and "occasionally", "probably", "sometimes", "when available" etc. identifying minor food items). I then classified three avian frugivore guilds depending on diet preference for fruits: (i) obligate frugivores (the only major food item are fruits), (ii) partial frugivores (other major food items besides fruits, e.g., terrestrial invertebrates), and (iii) opportunistic fruit-eaters (fruits only as minor food items). The full list of frugivorous bird species is given in Appendix 6.

A5.2 References for classification

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Appendix 6: African frugivores

A6.1 List of obligate frugivores

Andropadus chlorigula (inc. fusc.), Andropadus gracilirostris, Andropadus importunes, Andropadus montanus, Andropadus neumanni, Andropadus nigriceps, Andropadus tephrolaemus, Baeopogon clamans, Baeopogon indicator, Buccanodon duchaillui, Ceratogymna albotibialis, Ceratogymna atrata, Ceratogymna brevis, Ceratogymna bucinator, Ceratogymna cylindricus, Ceratogymna elata, Ceratogymna fistulator, Ceratogymna subcylindricus, Chlorocichla falkensteini, Chlorocichla flavicollis, Chlorocichla simplex, Cinnyricinclus femoralis, Cinnyricinclus leucogaster, Cinnyricinclus sharpii, Colius castanotus, Colius colius, Colius striatus, Columba delegorguei, Columba iriditorques, Corythaeola cristata, Corythaixoides concolor, Corythaixoides personatus, Crinifer piscator, Crinifer zonurus, Grafisia torquata, Gypohierax angolensis, Ixonotus guttatus, Lamprotornis acuticaudus, Lamprotornis purpureiceps, Lioptilus nigricapillus, Lybius chaplini, Lybius dubius, Lybius leucocephalus, Lybius rolleti, Lybius torquatus, Lybius vieilloti, Musophaga johnstoni, Musophaga porphyreolopha, Musophaga rossae, Musophaga violacea, Onychognathus albirostris, Onychognathus blythii, Onychognathus fulgidus, Onychognathus neumanni, Onychognathus tenuirostris, Parophasma galinieri, Petronia pyrgita, Ploceus weynsi, Poeoptera kenricki, Poeoptera stuhlmanni, Pogoniulus atroflavus, Pogoniulus bilineatus, Pogoniulus chrysoconus, Pogoniulus coryphaeus, Pogoniulus leucomystax, Pogoniulus pusillus, Pogoniulus simplex, Pogoniulus subsulphureus, Pycnonotus barbatus, Pycnonotus dodsoni, Pycnonotus somaliensis, Pycnonotus tricolor, Tauraco bannermani, Tauraco corythaix, Tauraco erythrolophus, Tauraco fischeri, Tauraco hartlaubi, Tauraco leucolophus, Tauraco leucotis, Tauraco livingstonii, Tauraco macrorhynchus, Tauraco persa, Tauraco ruspolii, Tauraco schalowi, Tauraco schuetti, Treron calva, Treron waalia, Tricholaema diademata, Tricholaema hirsuta, Tricholaema lacrymosa, Urocolius indicus, Urocolius macrourus

A6.2 List of partial frugivores

Acryllium vulturinum, Afropavo congensis, Agapornis pullarius, Agapornis swindernianus, Agapornis taranta, Amblyospiza albifrons, Anaplectes rubriceps, Andropadus ansorgei, Andropadus curvirostris, Andropadus gracilis, Andropadus kakamegae, Andropadus latirostris, Andropadus masukuensis, Andropadus milanjensis, Andropadus olivaceiceps, Andropadus virens, Anthoscopus flavifrons, Anthoscopus minutus, Anthreptes anchietae, Anthreptes aurantium, Anthreptes axillaris, Anthreptes collaris, Anthreptes fraseri, Anthreptes rectirostris, Bubalornis albirostris, Calyptocichla serina, Cercomela sinuata, Chlorocichla flaviventris, Chlorocichla laetissima, Chlorocichla prigoginei, Cichladusa ruficauda, Coccycolius iris, Colius leucocephalus, Columba albinucha, Columba arquatrix, Columba larvata, Columba sjostedti, Columba unicincta, Corythaixoides leucogaster, Cossypha caffra, Cossypha humeralis, Cossypha natalensis, Cossypha niveicapilla, Cossypha roberti, *Creatophora cinerea, Criniger barbatus, Dendrocygna bicolor, Estrilda astrild, Estrilda caerulescens, Francolinus adspersus, Francolinus afer, Francolinus ahantensis, Francolinus bicalcaratus, Francolinus camerunensis, Francolinus capensis, Francolinus clappertoni, Francolinus erckelii, Francolinus hartlaubi, Francolinus harwoodi, Francolinus icterorhynchus, Francolinus jacksoni, Francolinus leucoscepus, Francolinus levaillantoides, Francolinus natalensis, Francolinus ochropectus, Francolinus squamatus, Francolinus swainsonii, Guttera pucherani, Gymnobucco bonapartei, Gymnobucco calvus, Gymnobucco peli, Gymnobucco sladeni, Histurgops ruficauda, Lamprotornis caudatus, Lamprotornis chalcurus, Lamprotornis chalybaeus, Lamprotornis chloropterus, Lamprotornis corruscus, Lamprotornis cupreocauda, Lamprotornis elisabeth, Lamprotornis mevesii, Lamprotornis nitens, Lamprotornis pulcher, Lamprotornis purpureus, Lamprotornis purpuropterus, Lamprotornis shelleyi, Lamprotornis splendidus, Laniarius bicolour, Laniarius erythrogaster, Lybius bidentatus, Lybius guifsobalito, Lybius melanopterus, Lybius minor, Lybius rubrifacies, Lybius undatus, Malimbus ibadanensis, Melignomon eisentrauti, Monticola rupestris, Nectarinia johannae, Nectarinia olivacea, Nectarinia pembae, Nectarinia rubescens, Nectarinia violacea, Nigrita bicolor, Nigrita canicapilla, Nigrita fusconota, Nigrita luteifrons, Onychognathus morio, Onychognathus nabouroup, Onychognathus salvadorii, Onychognathus walleri, Oriolus auratus, Oriolus chlorocephalus, Oriolus larvatus, Oriolus nigripennis, Oriolus percivali, Phyllastrephus strepitans, Ploceus albinucha, Ploceus aurantius, Ploceus aureonucha, Ploceus bicolor, Ploceus cucullatus, Ploceus golandi, Ploceus insignis, Ploceus tricolor, Ploceus velatus, Ploceus xanthops, Poeoptera lugubris, Pogoniulus scolopaceus, Pogonocichla stellata, Poicephalus cryptoxanthus, Poicephalus flavifrons, Poicephalus gulielmi, Poicephalus meyeri, Poicephalus robustus, Poicephalus rueppellii, Poicephalus rufiventris, Poicephalus senegalus, Polyboroides typus, Pseudocalyptomena graueri, Psittacula krameri, Psittacus erithacus, Ptilopachus petrosus, Ptilostomus afer, Pycnonotus capensis, Pycnonotus nigricans, Rhynchostruthus socotranus, Serinus albogularis, Serinus burtoni, Serinus canicapillus, Serinus citrinelloides, Serinus gularis, Serinus leucopterus, Serinus mennelli, Serinus scotops, Serinus sulphuratus, Serinus whytii, Sheppardia gunningi, Speculipastor bicolour, Speirops melanocephalus, Spermophaga haematina, Spreo albicapillus, Stactolaema anchietae, Stactolaema leucotis, Stactolaema olivacea, Stactolaema whytii, Sylvia boehmi, Sylvia layardi, Sylvia leucomelaena, Sylvia subcaeruleum, Thamnolaea cinnamomeiventris, Thamnolaea coronata, Thescelocichla leucopleura, Tockus albotermінatus, Tockus fasciatus, Tockus flavirostris, Trachyphonus darnaudii, Trachyphonus erythrocephalus, Trachyphonus margaritatus, Trachyphonus purpuratus, Trachyphonus usambiro, Trachyphonus vaillantii, Tricholaema frontata, Tricholaema leucomelas, Tricholaema melanocephala, Turdoides fulvus, Turdus helleri, Turdus olivaceus, Turdus pelios, Turdus roehli, Turdus smithii, Turtur tympanistria, Zoothera gurneyi, Zoothera piaggiae, Zoothera tanganjicae, Zosterops kulalensis, Zosterops pallidus, Zosterops poliogaster, Zosterops silvanus, Zosterops winifredae*

A6.3 List of opportunistic fruit-eaters

Agapornis fischeri, Agapornis lilianae, Agelastes meleagrides, Agelastes niger, Alethe fuelleborni, Anas hottentota, Anthoscopus caroli, Anthoscopus sylviella, Anthreptes longuemarei, Anthreptes rubritorques, Apalis flavida, Apalis thoracica, Ardeotis arabs, Ardeotis kori, Bleda canicapillus, Bleda eximinius, Bleda notatus, Bleda syndactylus, Bradornis mariquensis, Bradornis pallidus, Bubalornis niger, Bubo leucostictus, Bubo poensis, Bubo vosseleri, Bubulcus ibis, Bucorvus abyssinicus, Bucorvus cafer, Camaroptera brachyura, Camaroptera brevicaudata, Camaroptera harterti, Campephaga flava, Cercomela familiaris, Cercomela melanura, Cercotrichas coryphaeus, Cercotrichas galactotes, Cercotrichas leucophrys, Cercotrichas paena, Cercotrichas signata, Certhilauda albescens, Certhilauda benguelensis, Certhilauda brevirostris, Certhilauda burra, Certhilauda curvirostris, Certhilauda semitorquata, Certhilauda subcoronata, Ceuthmochares aereus, Chrysococcyx cupreus, Chrysococcyx flavigularis, Chrysococcyx klaas, Cichladusa guttata, Columba guinea, Columba livia, Columba oliviae, Coracias cyanogaster, Coracina azurea, Coracina caesia, Corvinella melanoleuca, Corvus capensis, Corvus crassirostris, Corvus rhipidurus, Cosmopsarus regius, Cosmopsarus unicolor, Cossypha cyanocampter, Cossypha dichroa, Cossypha heuglini, Criniger calurus, Criniger chloronotus, Criniger ndussumensis, Criniger olivaceus, Cuculus solitarius, Dendrocygna viduata, Dendropicos fuscescens, Dendropicos obsoletus, Dicrurus adsimilis, Dinemellia dinemelli, Dioptrornis fischeri, Dryoscopus cubla, Eremomela badiceps, Eremomela pusilla, Eremopterix australis, Euplectes ardens, Euplectes hartlaubi, Eupodotis gindiana, Eupodotis melanogaster, Eupodotis ruficrista, Eupodotis savilei, Eupodotis senegalensis, Eupodotis vigorsii, Eurocephalus anguitimens, Eurocephalus rueppelli, Eurystomus gularis, Falco ardosiaceus, Francolinus africanus, Francolinus lathami, Francolinus sephaena, Fraseria cinerascens, Fraseria ocreata, Fulica cristata, Galerida magnirostris, Gallinula chloropus, Guttera plumifera, Halcyon malimbica, Hippolais pallida, Hirundo abyssinica, Hirundo cucullata, Hyliota violacea, Illadopsis pyrrhoptera, Indicator conirostris, Indicator exilis, Indicator indicator, Indicator maculates, Indicator meliphilus, Indicator variegates, Kupeornis rufocinctus, Lamprotornis australis, Lamprotornis hildebrandti, Lamprotornis superbus, Laniarius atrococcineus, Laniarius ferrugineus, Laniarius funebris, Laniarius mufumbiri, Lanius cabanisi, Lanius collaris, Larus leucophthalmus, Linurgus olivaceus, Lonchura bicolor, Lonchura nigriceps, Lophaetus occipitalis, Macrosphenus flavicans, Malcorus pectoralis, Malimbus cassini, Malimbus erythrogaster, Malimbus malimbicus, Malimbus nitens, Malimbus rubricollis, Mandingoa nitidula, Melaenornis pammelaina, Melichneutes robustus, Modulatrix stictigula, Monticola brevipes, Monticola explorator, Monticola pretoriae, Monticola rufocinereus, Muscicapa adusta, Muscicapa caerulescens, Muscicapa comitata, Muscicapa epulata, Muscicapa infuscata, Myioparus griseigularis, Myrmecocichla aethiops, Myrmecocichla formicivora, Myrmecocichla nigra, Namibornis herero, Nectarinia afra, Nectarinia batesi, Nectarinia chalybea, Nectarinia chloropygia, Nectarinia cyanolaema, Nectarinia hunteri, Nectarinia osea, Nectarinia seimundi, Nectarinia superba, Nectarinia ursulae, Neocossyphus fraseri, Neocossyphus poensis, *Neolestes torquatus, Neotis denhami, Neotis heuglinii, Neotis nuba, Nesocharis capistrata, Nesocharis shelleyi, Nicator chloris, Numida meleagris, Oenanthe leucopyga, Oenanthe monticola, Oriolus brachyrhynchus, Oriolus monacha, Oxylophus jacobinus, Oxylophus levaillantii, Pachyphantes superciliosus, Parmoptila woodhousei, Parus leucomelas, Parus niger, Passer diffusus, Passer griseus, Passer luteus, Passer melanurus, Philetairus socius, Phoeniculus bollei, Phoeniculus castaneiceps, Phoeniculus purpureus, Phragmacia substriata, Phyllanthus atripennis, Phyllastrephus albigularis, Phyllastrephus alfredi, Phyllastrephus baumanni, Phyllastrephus cabanisi, Phyllastrephus cerviniventris, Phyllastrephus flavostriatus, Phyllastrephus hypochloris, Phyllastrephus icterinus, Phyllastrephus placidus, Phyllastrephus poensis, Phyllastrephus scandens, Phyllastrephus terrestris, Phyllastrephus xavieri, Platysteira castanea, Platysteira concreta, Plectropterus gambensis, Ploceus alienus, Ploceus baglafecht, Ploceus capensis, Ploceus heuglini, Ploceus intermedius, Ploceus melanogaster, Ploceus nigerrimus, Ploceus nigricollis, Ploceus ocularis, Ploceus preussi, Porphyrio alleni, Porphyrio porphyrio, Prinia maculosa, Prionops caniceps, Prionops plumatus, Prionops rufiventris, Prionops scopifrons, Prodotiscus insignis, Prodotiscus regulus, Prodotiscus zambesiae, Pseudoalcippe abyssinica, Pseudoalcippe atriceps, Psophocichla litsipsirupa, Pyrenestes ostrinus, Pyrrhocorax pyrrhocorax, Rhinopomastus aterrimus, Rhinopomastus cyanomelas, Rhinopomastus minor, Rhodophoneus cruentus, Saxicola torquata, Serinus alario, Serinus ankoberensis, Serinus atrogularis, Serinus frontalis, Serinus leucolaema, Serinus mozambicus, Serinus striolatus, Sigelus silens, Sphenoaecus afer, Spreo bicolor, Spreo fischeri, Streptopelia capicola, Streptopelia decipiens, Streptopelia lugens, Streptopelia reichenowi, Streptopelia semitorquata, Streptopelia senegalensis, Streptopelia vinacea, Struthio camelus, Swynnertonia swynnertoni, Sylvia lugens, Sylvia rueppelli, Sylvietta virens, Tchagra senegala, Tchagra tchagra, Telophorus bocagei, Telophorus olivaceus, Telophorus zeylonus, Terpsiphone rufiventer, Terpsiphone viridis, Tockus albocristatus, Tockus bradfieldi, Tockus camurus, Tockus deckeni, Tockus erythrorhynchus, Tockus hartlaubi, Tockus hemprichii, Tockus jacksonii, Tockus leucomelas, Tockus monteiri, Tockus nasutus, Turdoides jardineii, Turdoides melanops, Turdoides reinwardtii, Turdoides sharpei, Turdoides tenebrosus, Turdus libonyanus, Turdus tephronotus, Uraeginthus granatina, Zoothera guttata, Zosterops senegalensis*

Appendix 7: *Ficus* species list

Ficus abscondita, Ficus abutilifolia, Ficus adolfi-friderici, Ficus amadiensis, Ficus ardisioides, Ficus artocarpoides, Ficus asperifolia, Ficus barteri, Ficus bizanae, Ficus bubu, Ficus burretiana, Ficus burtt-davyi, Ficus bussei, Ficus calyptrata, Ficus capreifolia, Ficus chirindensis, Ficus chlamydocarpa, Ficus conraui, Ficus cordata, Ficus crassicosta, Ficus craterostoma, Ficus cyathistipula, Ficus cyathistipuloides, Ficus densistipulata, Ficus dicranostyla, Ficus dryepondtiana, Ficus elasticoides, Ficus exasperata, Ficus faulkneriana, Ficus fischeri, Ficus glumosa, Ficus ilicina, Ficus ingens, Ficus jansii, Ficus kamerunensis, Ficus leonensis, Ficus lingua, Ficus louisii, Ficus lutea, Ficus lyrata, Ficus modesta, Ficus mucuso, Ficus muelleriana, Ficus natalensis, Ficus nigropunctata, Ficus oreodryadum, Ficus oresbia, Ficus ottoniifolia, Ficus ovata, Ficus pachyneura, Ficus palmata, Ficus persicifolia, Ficus platyphylla, Ficus polita, Ficus populifolia, Ficus preussii, Ficus pseudomangifera, Ficus psilopoga, Ficus pygmaea, Ficus recurvata, Ficus rokko, Ficus sagittifolia, Ficus salicifolia, Ficus sansibarica, Ficus saussureana, Ficus scassellatii, Ficus scott-elliotii, Ficus stuhlmannii, Ficus subcostata, Ficus subsagittifolia, Ficus sur, Ficus sycomorus, Ficus tesselata, Ficus tettensis, Ficus thonningii, Ficus tremula, Ficus trichopoda, Ficus umbellata, Ficus usambarensis, Ficus vallis-choudae, Ficus variifolia, Ficus vasta, Ficus verruculosa, Ficus vogeliana, Ficus wakefieldii, Ficus wildemaniana

Appendix 8: Fig-frugivore richness correlations

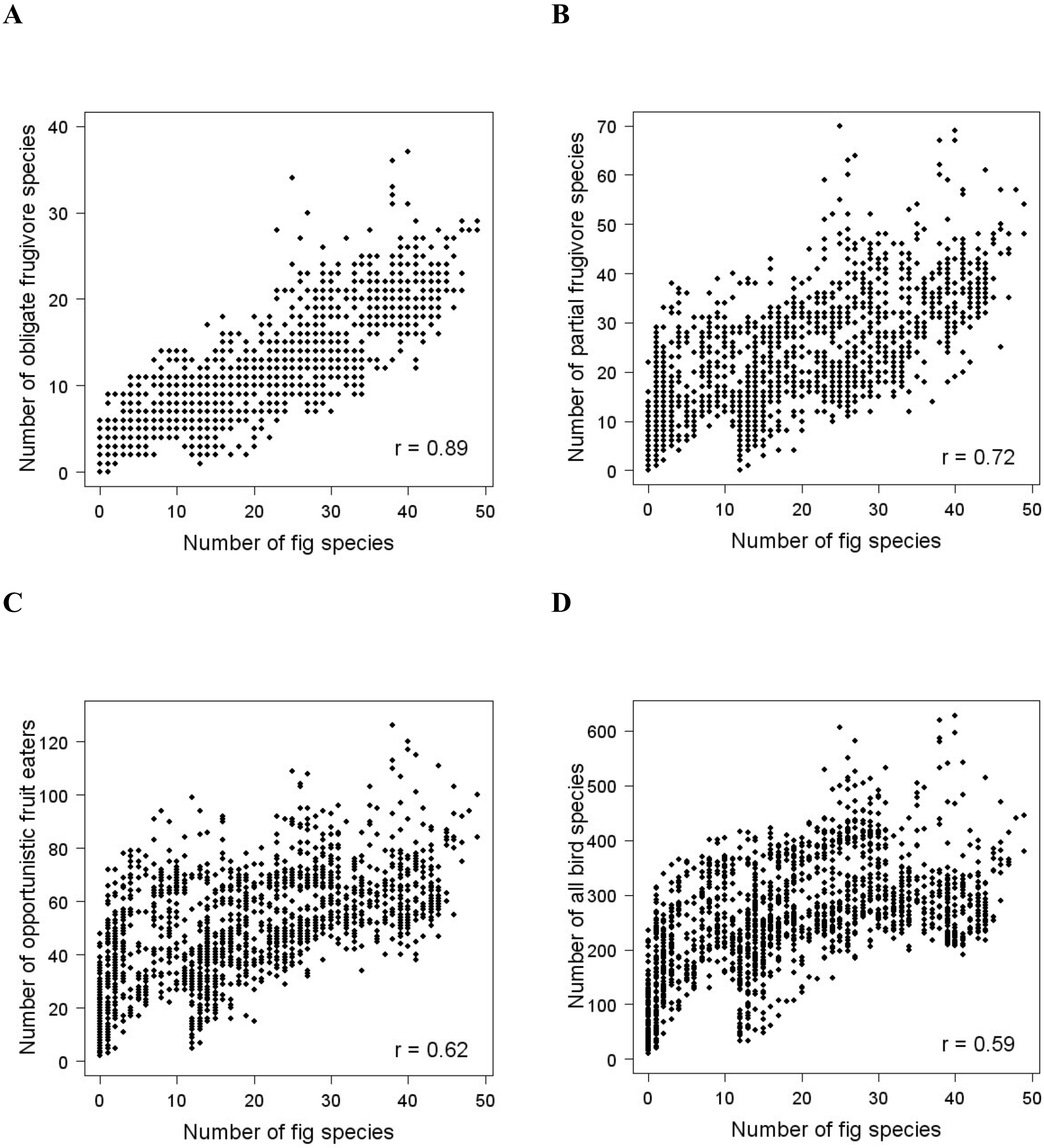

Figure A1: The relationship between fig (*Ficus* spp.) richness and species richness of obligate frugivores (A), partial frugivores (B), opportunistic fruit-eaters (C), and all breeding birds (D) in sub-Sahara Africa. Spearman rank correlations are given in the lower right corner of each graph.

Appendix 9: Correlation matrix

Table A4: Correlation matrix of untransformed predictor and response variables. OBL = obligate frugivores (*n* = 92); PAR = partial frugivores (*n* = 200); OPP = opportunistic frugivores (*n* = 290); ALL = all bird species (*n* = 1,772). Mnemonics of predictor variables are explained in Table 4.1.

	Spearman rank correlation (r_s)									
	Bird richness				Predictor variables					
Predictor variables	OBL	PAR	OPP	ALL	FigRich	Prec	MaxTemp	NPP	AltRange	EcoDiv
FigRich	0.89	0.72	0.62	0.59	1					
Prec	0.87	0.71	0.63	0.60	0.89	1				
MaxTemp	-0.33	-0.59	-0.65	-0.58	-0.20	-0.29	1			
NPP	0.85	0.75	0.68	0.63	0.85	0.93	-0.36	1		
AltRange	0.19	0.34	0.37	0.41	0.10	0.06	-0.52	0.06	1	
EcoDiv	0.57	0.68	0.66	0.67	0.46	0.48	0.45	0.51	0.34	1

Appendix 10: Pearson correlation matrix

Table A5: Pearson correlations of predictor and response variables. ALL: all birds; OBL = obligate frugivores; PAR = partial frugivores; OPP = opportunistic fruit-eaters; OTHER = non-fruit-eaters; Woody = all woody plants; Fleshy = fleshy-fruited plants; Non-fleshy = non-fleshy-fruited plants; *Ficus* = fig trees. Abbreviations of environmental predictor variables are explained in Table 5.1. Richness variables were square-root transformed and Prec and Topo were log(x+1) transformed. In the absence of correction for spatial autocorrelation or multiple tests, the threshold values for significance are 0.155 (alpha = 0.05) and 0.203 (alpha = 0.01).

	Bird richness					Plant richness				Environmental predictor variables					
Variables	ALL	OBL	PAR	OPP	OTHER	Woody	Fleshy	Non-fleshy	Ficus	Prec	Temp	PET	Seas	Topo	LCov
ALL	1	0.93	0.96	0.97	1	0.81	0.79	0.80	0.67	0.68	-0.70	0.04	-0.49	0.59	0.57
OBL	0.93	1	0.95	0.92	0.91	0.85	0.85	0.83	0.72	0.77	-0.74	0.08	-0.49	0.60	0.63
PAR	0.96	0.95	1	0.96	0.93	0.82	0.82	0.81	0.69	0.71	-0.71	0.02	-0.48	0.61	0.59
OPP	0.97	0.92	0.96	1	0.95	0.78	0.76	0.79	0.64	0.66	-0.68	0.00	-0.45	0.60	0.56
OTHER	1.00	0.91	0.93	0.95	1	0.79	0.78	0.79	0.66	0.66	-0.69	0.04	-0.50	0.57	0.56
Woody	0.81	0.85	0.82	0.78	0.79	1	0.99	0.98	0.82	0.69	-0.62	0.17	-0.43	0.52	0.59
Fleshy-fruited	0.79	0.85	0.82	0.76	0.78	0.99	1	0.95	0.82	0.73	-0.65	0.19	-0.48	0.51	0.59
Non-fleshy	0.80	0.83	0.81	0.79	0.79	0.98	0.95	1	0.79	0.63	-0.57	0.15	-0.36	0.52	0.56
Ficus	0.67	0.72	0.69	0.64	0.66	0.82	0.82	0.79	1	0.61	-0.56	0.13	-0.39	0.46	0.49
Prec	0.68	0.77	0.71	0.66	0.66	0.69	0.73	0.63	0.61	1	-0.79	0.18	-0.57	0.43	0.55
Temp	-0.70	-0.74	-0.71	-0.68	-0.69	-0.62	-0.65	-0.57	-0.56	-0.79	1	0.15	0.55	-0.68	-0.60
PET	0.04	0.08	0.02	0.00	0.04	0.17	0.19	0.15	0.13	0.18	0.15	1	-0.20	-0.41	0.07
Seas	-0.49	-0.49	-0.48	-0.45	-0.50	-0.43	-0.48	-0.36	-0.39	-0.57	0.55	-0.20	1	-0.40	-0.41
Topo	0.59	0.60	0.61	0.60	0.57	0.52	0.51	0.52	0.46	0.43	-0.68	-0.41	-0.40	1	0.32
Lcov	0.57	0.63	0.59	0.56	0.56	0.59	0.59	0.56	0.49	0.55	-0.60	0.07	-0.41	0.32	1

Appendix 11: Total effects on plant species richness

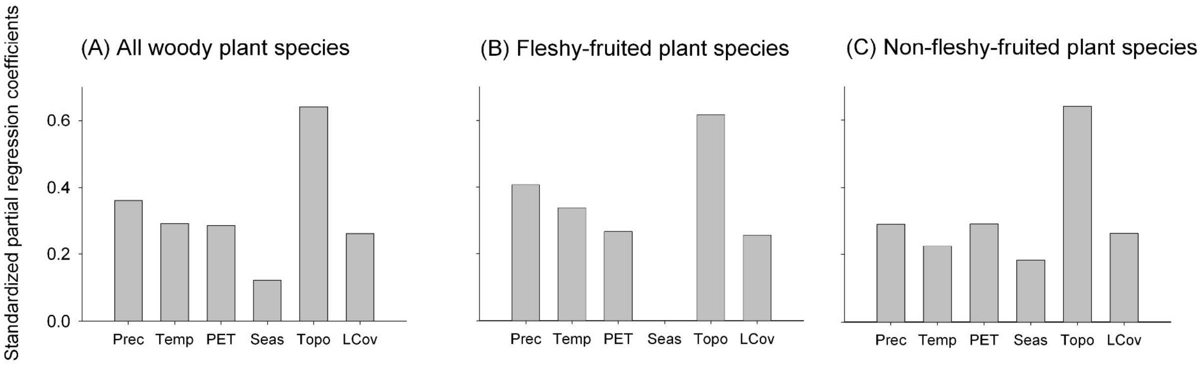

Figure A2: Absolute total effects (i.e. direct + indirect effects) of environmental predictor variables on species richness of plants (A: all woody plants; B: fleshy-fruited plants; C: non-fleshy-fruited plants). Values are derived from structural equation models similar to Figure 5.2A, where plant richness has been replaced by species richness of woody plants, fleshy-fruited or non-fleshy-fruited plants. See text for details on model selection. Zero values indicate that the variable was not selected in the minimal adequate model.

Appendix 12: Total effects on bird species richness

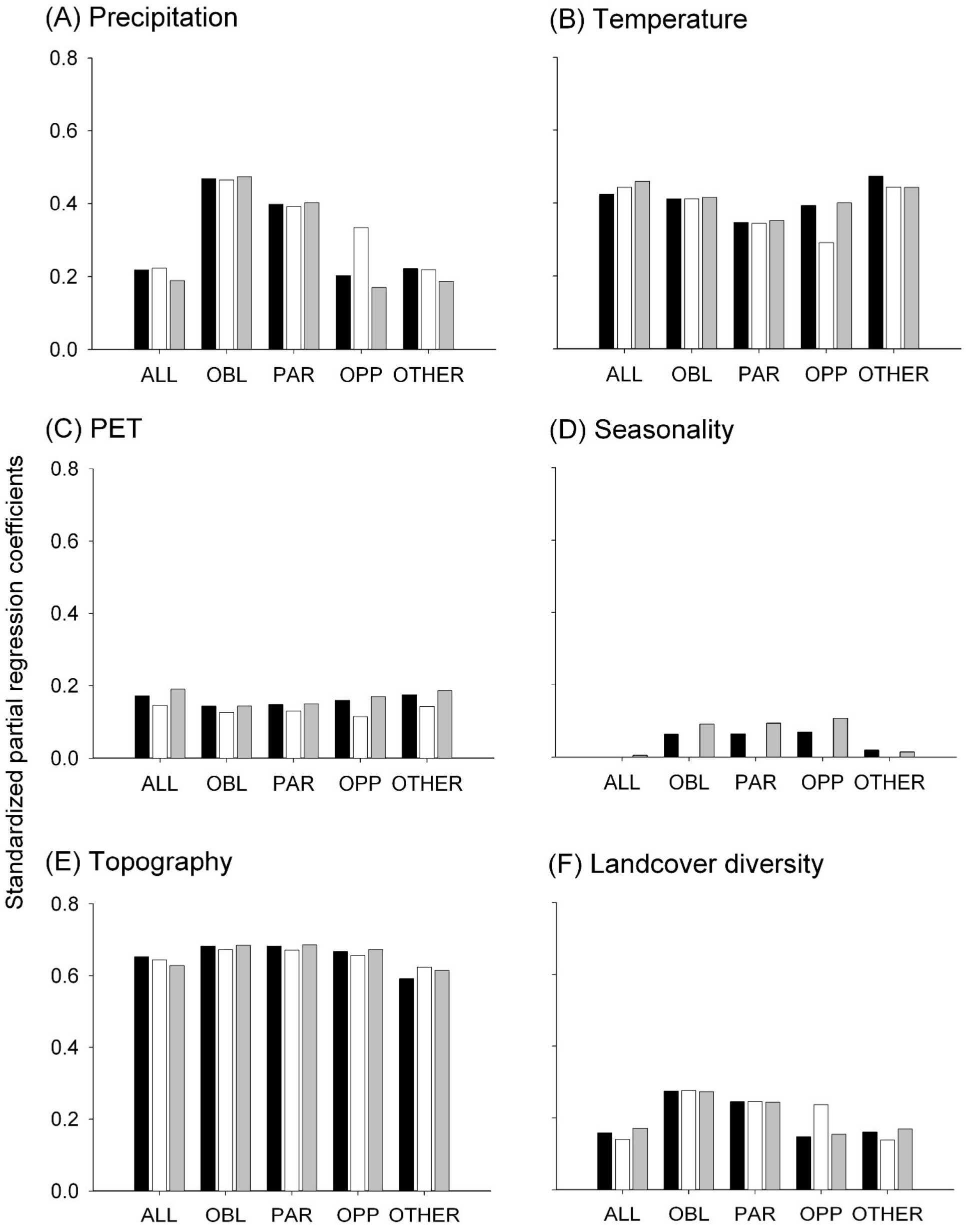

Figure A3: Absolute total effects (i.e. direct + indirect effects) of environmental predictor variables on species richness of birds (ALL: all birds; OBL: obligate frugivores; PAR: partial frugivores; OPP: opportunistic fruit-eaters; OTHER: non-fruit-eating birds). Values are derived from structural equation models similar to Figure 5.2A, where plant richness was replaced by species richness of woody plants (black columns), fleshy-fruited plants (white) or non-fleshy-fruited plants (gray), and bird richness by ALL, OBL, PAR, OPP and OTHER. See text for details on model selection. Zero values indicate that the variable was not selected in the minimal adequate model for both birds and plants.

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