Spatial and temporal patterns in bird communities along an elevational gradient in the tropical Andes

Dissertation

for attaining the PhD degree

submitted to the faculty of Biology

of the Johann Wolfgang Goethe University

in Frankfurt am Main

by

Vinicio Estuardo Santillán Rodríguez

from Riobamba, Ecuador

Frankfurt 2019

(D30)

Faculty of Biology of the

Johann Wolfgang Goethe University accepted as a dissertation.

Dean:	Prof. Dr. Sven Klimpel
First reviewer:	Prof. Dr. Katrin Böhning-Gaese
Second reviewer:	Prof. Dr. Roland Brandl

Date of disputation: ___________

TABLE OF CONTENS

1. Summary ... 1
2. Introduction ... 4
  2.1 Global biodiversity patterns ... 4
  2.2 Spatial variation in biodiversity ... 5
    2.2.1 Abiotic drivers of biodiversity ... 6
    2.2.2 Biotic drivers of biodiversity ... 6
    2.2.3 Local and regional biodiversity ... 7
  2.3 Temporal variation in biodiversity ... 8
    2.3.1 Historical factors influencing biodiversity ... 8
    2.3.2 Factors causing seasonal variation in biodiversity ... 9
  2.4 Biodiversity and environmental change ... 9
    2.4.1 Climate change ... 10
    2.4.2 Land-use change ... 10
  2.5 Different facets of biodiversity ... 11
    2.5.1 Taxonomic diversity ... 11
    2.5.2 Functional diversity ... 12
  2.6 Tropical biodiversity ... 14
    2.6.1 Biodiversity in tropical mountain forests ... 14
3. Thesis structure, conceptual framework and research questions ... 16
  3.1 How do direct and indirect effects of elevation structure spatial variation in bird communities? ... 19
  3.2 Which factors shape the temporal variation of bird communities across elevations? ... 19
  3.3 How are taxonomic and functional bird diversity affected by forest fragmentation? ... 20
4. Tropical system, study area and research design ... 21
  4.1 Ecosystem and patterns of biodiversity in southern Ecuador ... 21
  4.2 Study area ... 22
  4.3 Methods and research design ... 23
5. Main results and discussion ... 25
  5.1 Direct and indirect effects of elevation, climate and vegetation structure on bird communities ... 25
  5.2 Climate, but not resource availability drive temporal variation in bird communities ... 27

5.3 Functional indicators respond differently to forest fragmentation than taxonomic indicators of biodiversity 29
6. Synthesis and conclusions 31
7. Zusammenfassung 34
7.1 Einleitung 34
7.2 Studiengebiet und Studiensystem 35
7.3 Methoden und Studiendesign 35
7.4 Fragen und Hypothesen 36
7.5 Ergebnisse und Diskussion 37
7.6 Zusammenfassung und Synthese 39
8. Resumen 40
8.1 Introducción 40
8.2 Sistema y área de estudio 41
8.3 Métodos y diseño del estudio 41
8.4 Preguntas e hipótesis 42
8.5 Resultados y discusión 43
8.6 Síntesis y conclusiones 44
9. References 46
10. Acknowledgements 67
11. Appendices 69
Appendix 1. Direct and indirect effects of elevation, climate and vegetation structure on bird communities on a tropical mountain 70
Appendix 2. Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient ... 95
Appendix 3. Different responses of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient 136
Appendix 4. Curriculum vitae 180

To my parents for a lifetime of love and support...

1. Summary

Understanding global biodiversity patterns is one of the main objectives of ecology. Spatial variation in species richness can be explained by several environmental factors. The relationships between species richness and environmental factors have been associated with latitudinal, longitudinal and elevational gradients. The number of species is determined by birth, death and migration rates of species in a given area. These rates are affected by abiotic and biotic factors acting at local and regional scales. Climatic seasonal variation may also influence biodiversity, directly through physiological limitations and indirectly through biotic interactions, vegetation structure and food availability. Climate and land-use change are the main factors for landscape simplification and biotic homogenization. Thus, the study of community patterns across environmental gradients may help to predict the effect of projected environmental change.

I investigated how abiotic and biotic factors influence different facets of bird diversity across an elevational gradient. My study was conducted along an elevational gradient spanning 2000 m within and around Podocarpus National Park and San Francisco reserve on the southeastern slope of the Andes in Ecuador. The climate is humid tropical montane with a bimodal rain regime. The region is characterized by evergreen premontane forest at low elevations, evergreen lower montane forest at mid elevations and upper montane forest at high elevations. The elevational gradient has natural continuous forests within the protected reserves and fragmented forests surrounding the reserves in a matrix of cattle pastures. To monitor bird diversity, I placed nine 20-m radius point counts within 18 one-hectare plots, in continuous and fragmented forest at 1000, 2000 and 3000 m a.s.l. I recorded and identified all birds for 10 minutes within each point count. Bird communities were sampled eight times per plot, in the most humid season and in the least humid season of 2014 and 2015. To estimate flower and fruit availability, I recorded all plants with open flowers and ripe fruits within each point count. To obtain the relative invertebrate availability, I assessed understory invertebrate fresh biomass using a standardized sweep-netting design along 100-metre borders of each plot. Vertical vegetation heterogeneity was estimated at eight layers above the ground within each point count. Temperature for each plot was obtained using an air temperature regionalization tool and precipitation through remote sensing techniques and meteorological data.

In the first chapter of this thesis, I explored the effects of elevation, climate and vegetation structure on overall bird communities as well as on frugivorous and insectivorous birds. I found that elevation was mostly indirectly associated with bird diversity, jointly mediated via temperature, precipitation and vegetation structure. Additionally, elevation was directly and positively associated with both the overall bird community and with insectivores, but not with frugivores. My findings indicate a reduction of bird diversity due to climatic factors and vegetation structure with increasing elevation. However, the direct, positive effect of elevation suggests that bird diversity was higher than expected towards high elevations, probably due to spatial, biotic and evolutionary settings.

In the second chapter, I analysed the influence of climate and resource availability on temporal variation of bird communities. I found a higher bird diversity in the least humid season than in the most humid season. The seasonality of the bird communities was mainly driven by temperature and precipitation. While temperature had a significant positive effect at high elevations, precipitation had a significant negative effect at low elevations. Resource availability had no significant effect. My findings suggest that the temporal fluctuations in bird communities likely occur due to climate constraints rather than due to resource limitations.

In the third chapter, I studied the effect of forest fragmentation on taxonomic and functional bird diversity. I found that taxonomic diversity was higher in fragmented compared to continuous forests, while functional diversity was negatively affected by fragmentation, but only at low elevations. The increase of taxonomic diversity in disturbed habitats suggests an increase of habitat generalists, which may compensate the loss of forest specialists. My findings suggest that taxonomic diversity can be uncoupled from functional diversity in diverse communities at low elevations.

My results show the effects of environmental factors on the spatio-temporal patterns of bird communities and the potentially uncoupled responses of taxonomic and functional diversity to forest fragmentation. My findings highlight that bird communities respond differently to abiotic and biotic factors across elevational gradients. Overall, my study helps to better understand the mechanisms that drive species communities in response to complex environmental conditions, which could be an essential contribution for the conservation of bird communities in the tropical Andes.

2. Introduction

2.1 Global biodiversity patterns

Biological diversity is distributed heterogeneously across the different regions of the Earth (Gaston 2000), and changes in relation to the environmental factors of the respective region (Mori et al. 2013). The relationships between biodiversity and the environment are associated with spatial gradients, such as latitude, longitude and elevation (Brown and Lomolino 1998). No single environmental factor, but rather the combination of different abiotic and biotic factors shape the variation of biodiversity (Waide et al. 1999; Keith et al. 2012). These environmental factors may determine speciation, extinction and migration of species in ecological communities (Ricklefs 2008), and are acting at local and regional scales (Huston 1999). In addition, biodiversity is affected by temporal patterns at evolutionary and ecological times (Rosenzweig 1995), due to natural and anthropogenic causes (Dornelas et al. 2013). Seasonal variation of climate is another important factor for the evolution and distribution of organisms (Boyce 1979), affecting biodiversity directly through physiological limitations (Hawkins et al. 2003a) or indirectly through biotic interactions, vegetation structure and resources availability (O'Brien 1998). Climate, land-cover, evolutionary processes and biotic interactions have been proposed as the main drivers of biodiversity (Willig et al. 2003). However, other environmental factors such as habitat and environmental productivity can also drive biodiversity patterns (Rosenzweig 1995). Today, climate and land-use change are the main factors that affect biodiversity (Brown et al. 2004), producing landscape simplification and driving biotic homogenization (Gámez-Virués et al. 2015). In order to infer and forecast spatio-temporal patterns of biodiversity, the number of species observed in a given area and time has often been used (Brown et al. 2001; Orme et al. 2005). However, the relative species abundance (Hubbell 2001), and other diversity facets, such as functional diversity (Meynard et al. 2011) are also important dimensions of biodiversity. Studying the relationship of different facets of biodiversity have led to a significant improvement of our knowledge of the effects of environmental factors on species patterns and their functional relationships (Mori et al. 2013).

2.2 Spatial variation in biodiversity

Environmental factors are the main determinants of spatial variation of biodiversity (Cavender-Bares et al. 2016). Abiotic and biotic environmental factors are influenced by latitudinal, longitudinal and altitudinal or topographical gradients (O'Brien et al. 2000). For instance, species diversity increases from the poles towards the equator (Condamine et al. 2012) and depends on mechanisms such as speciation, extinction and dispersion that directly change biodiversity patterns between temperate and tropical regions (Willig et al. 2003; Mittelbach et al. 2007). The latitudinal gradient of biodiversity is mainly related to temperature effects. However, water availability also plays an important role in shaping biodiversity patterns (O'Brien 1998; Hawkins et al. 2003a). Water-energy dynamics affect the rates of ecological interactions and coevolution across latitudinal gradients (Rohde 1992; Brown 2014). Longitudinal gradients show regional differences in biodiversity structure, composition, and dynamics (Slik et al. 2018), and are a strong structural element in shaping species ranges and genetic diversity (Stewart et al. 2010; Conord et al. 2012). Latitudinal and longitudinal gradients work together to define the biodiversity in a given ecosystem (Stewart et al. 2010).

Mountains are hotspots of global biodiversity, endemism and threatened species (Orme et al. 2005; Quintero and Jetz 2018). Elevational gradients present different climatic, spatial, historical and biotic settings (Gaston 2000). Climatic drivers can be temperature, precipitation, humidity or cloud cover (McCain and Grytnes 2010). Spatial constraints include the species–area relationship and the mid-domain effect (Colwell et al. 2004). The species-area relationship predicts that low elevations with larger areas should harbour more species than smaller areas at higher elevations (Rahbek 1997). The mid-domain effect predicts that the species' spatial boundaries between low and high elevations result in higher biodiversity towards the centre of a given area (Colwell et al. 2004). Evolutionary history is linked to speciation rates, extinction rates, clade age and phylogenetic niche conservatism (Hawkins et al. 2012). Biotic conditions, such as vegetation structure, competition or mutualisms can also change along elevational gradients (Bascompte 2009; Quitián et al. 2017). Mountains are ideally suited to explore the natural patterns of communities and species distributions that could be applied to global scales (McCain and Grytnes 2010).

2.2.1 Abiotic drivers of biodiversity

Abiotic drivers include aspects of climate, physical environment and edaphic conditions (Soberón and Peterson 2005), and drive the distribution of biodiversity in their surroundings (Ricklefs and Miller 2000). Climate conditions are the main abiotic factors to shape patterns of biodiversity over all spatial scales (Hawkins et al. 2003a; Evans et al. 2005; Clarke and Gaston 2006), regulating environmental productivity, and driving evolutionary processes and biotic interactions (O'Brien 1998; Currie et al. 2004). Temperature is generally a strong biodiversity predictor in temperate latitudes and at high elevations (Hawkins et al. 2003a; McCain and Colwell 2011), while precipitation is often important in the tropics and subtropics (Hawkins et al. 2003a, b). Low or extremely high temperatures could affect the metabolic processes of plants and animals (Allen et al. 2002), and heavy precipitation or water limitation may restrict activity, mobility and interactions of animals (Boyle et al. 2010, 2011). For instance, the variation of biodiversity with elevation has mainly been associated with temperature decrease with increasing elevation, and the resulting reduction in environmental productivity (Rahbek 1995). The effect of precipitation on the biodiversity of montane ecosystems is more complex and difficult to evaluate, and has been associated with temperature variation (McCain and Colwell 2011). Water-energy dynamics affect global diversity patterns of plants and animals (O'Brien 1998), directly via physiological effects (Allen et al. 2006) and indirectly via biotic interactions (Wright 1983), which in turn drive growth and reproduction rates as well as population sizes (Evans et al. 2005). However, the effects of climate factors are often not comparable among different taxa (O'Brien 1998; Khaliq et al. 2017). In addition, water-energy dynamics may directly influence plant productivity (O'Brien 1998; Francis and Currie 2003), which, depending on the capacity of animals to obtain the available resources, can translate into species diversity of animals (Rosenzweig 1995).

2.2.2 Biotic drivers of biodiversity

Several biological processes have been proposed to explain biodiversity patterns. For instance, habitat structure may influence diversity and composition of animal communities (Tews et al. 2004). However, the effect of habitat structure on biodiversity is complex, may involve a number of independent connections, and may differ between taxa or even between functional groups (MacArthur and MacArthur 1961; Terborgh 1977). Ecotone effects refer to overlap areas between communities (Harris 1988), and are related to a high diversity of plants and animals (Terborgh 1985; Colwell et al. 2004). Ecotone effects have been considered to be more important for temperate species distributions, while biotic interactions appear to be the main factor for diverse tropical fauna (Terborgh 1985; Harris 1988).

Biotic interactions such as mutualism, facilitation, competition, predation and parasitism (Bascompte 2009) determine birth, death and short-distance migration of species at local scales (Ricklefs and Miller 2000; Begon et al. 2006), and speciation, extinctions and long-distance migrations at regional scales (Ricklefs 2008; Brooker et al. 2009). Biotic factors can affect the distribution of biodiversity both positively and negatively (Soberón and Peterson 2005) as well as at local and regional scales (Wiens 2011). Mutualism and competition are considered as the main biotic factors that drive biodiversity patterns (O'Brien 1998). For instance, mutualistic networks (e.g., pollination and seed dispersal networks) have been shown to minimize competition and increase biodiversity (Bastolla et al. 2009). At the same time, competition may regulate the coexistence of species that compete for a resource, affecting the structure and diversity of natural communities (Tilman 1994). Theoretical and empirical studies document that biotic interactions are not necessarily robust to environmental changes (Gilman et al. 2010). In fact, biotic interactions may be lost even before the species involved disappear (Jordano 2016).

2.2.3 Local and regional biodiversity

To understand global biodiversity patterns, it is necessary to observe the relationship between local and regional scales (Gaston 2000). Both local and regional communities are influenced by abiotic and biotic factors (Huston 1999). Although local processes are important, most evidence indicates that local species richness mainly derives from regional species richness (Cornell and Lawton 1992). However, biotic interactions such as competition can only be identified at local scales, because at regional scales it is often masked by abiotic factors (Huston 1999). Local biodiversity, independent of biotic interactions, may increase proportionally with regional biodiversity, whereas local diversity, limited by biotic interactions, becomes independent of regional biodiversity

(Cornell and Lawton 1992). Additionally, different regions differ in environmental conditions that affect local processes (Huston 1999).

2.3 Temporal variation in biodiversity

Temporal patterns of biodiversity can be measured on both evolutionary and ecological timescales (Rosenzweig 1995). Historical events and past environmental conditions influence evolutionary processes (Brown 2014). Current environmental changes, such as succession processes and seasonal variation, may influence the occupation and reoccupation of habitats by species (Rosenzweig 1995). Seasonality has strong effects on resource availability (Boyce 1979), and on community dynamics such as population growth, migration, colonisation and local extinctions (Shimadzu et al. 2015). Climatic seasonality influences biodiversity through physiological constraints or via environmental productivity (Evans et al. 2005). It may also influence biotic interactions, minimizing competition and finally stabilizing the number of individuals of each species in a community (Kot and Schaffer 1984; Shimadzu et al. 2013). The analysis of temporal cycles in biodiversity could help to predict the ecological impacts of future climate change (Grøtan et al. 2012).

2.3.1 Historical factors influencing biodiversity

To understand the timing and rate of diversification of contemporary organisms is a key scientific challenge (Rosenzweig 1995). Historical data can give valuable information about the biological processes that shaped current global biodiversity (Tingley and Beissinger 2009). Theoretical and empirical information suggest that historic temperature is the most important factor for diversification (McCain 2009a; Brown 2014). Generally, species diversity increases with increasing historic temperature along latitudinal and elevational gradients (Allen et al. 2002). Nevertheless, historical variation of precipitation could also lead to changes in biodiversity at different spatial scales (Adler and Levine 2007). Other historical environmental factors such as habitat variability due to water-energy dynamics can also affect diversification rates (Weir 2006; Hawkins et al. 2012). For instance, Weir (2006) found that lowland and highland bird communities in neotropical mountains have different timing and diversification rates due to different environmental factors in their history. Therefore, it is necessary to understand the link between historical environmental processes and the resulting contemporary diversity (Brown 2014).

2.3.2 Factors causing seasonal variation in biodiversity

Seasonal variation of species richness and abundance has been mainly associated with water-energy dynamics (O'Brien 1998). Seasonality of temperature and precipitation at high latitudes may cause dormancy and hibernation, and may regulate the timing of migration and breeding season of species (Grøtan et al. 2012). In contrast, in tropical biomes most species remain active all year and reproduce continuously. However, the seasonality of climatic factors can have different effects on the number of individuals rather than on species richness (Rosenzweig 1995; Magurran 2007). For instance, theoretical and empirical studies from tropical ecosystems suggest that seasonal environmental variability affects mainly species abundance, while species richness often remains constant (Greenberg 1981; Loiselle 1988; Williams and Middleton 2008; Grøtan et al. 2012). In addition, climatic variability could also indirectly influence biodiversity through seasonal changes in vegetation structure and resource availability (Loiselle and Blake 1991; Mulwa et al. 2013). Seasonal variability may affect patterns of biotic interactions by increasing or reducing the number of individuals, niche occupancy and resource availability (Boyce 1979; Wikelski et al. 2003; Adler and Levine 2007). Thus, seasonality may be an important factor for the geographic variation of organisms (Boyce 1979), driving temporal biodiversity patterns due to physiological responses of species, but also through biotic factors, such as ecological interactions (Brown et al. 2004).

2.4 Biodiversity and environmental change

Climate and land-use change are by far the main factors of environmental change (Frishkoff et al. 2016). The effects of warming climate are strongest at high latitudes and high elevations (Anderson et al. 2011), and their influence on the structure and function of terrestrial ecosystems is in general still little understood (Walker and Steffen 1999). Land-use change is considered the most important factor for biotic homogenization (Gámez-Virués et al. 2015), reducing critical ecosystem functions and services (Jarvis et al. 2010). However, climate change is often superimposed to human alterations of the landscape (Anderson et al. 2011). Disentangling the differential effects of environmental changes such as climate and land-use change on natural communities is still an unsolved issue (Cadotte and Tucker 2017). Thus, information about the relationship between environmental conditions and community structure can provide useful evidence on the potential effects of environmental change on biodiversity (Helmus et al. 2010).

2.4.1 Climate change

Ecological and physiological processes of biodiversity are sensitive to climate alterations especially of temperature and precipitation (Walther et al. 2002). The relationship between ambient climatic variability and water-energy tolerance of species varies across taxa (Khaliq et al. 2014), has strong effects on species abundance (Bowler et al. 2017), and alters species interactions (Gilman et al. 2010) in terrestrial communities. The greenhouse effect has been considered as the main factor of global temperature increase (Walker and Steffen 1999), resulting in severe range contractions and local extinctions of biodiversity (Parmesan 2006), especially in species with restricted ranges (e.g., tropical mountain species, see Brown 2014). For instance, warmer temperatures have caused tropical mountain bird species to migrate to higher elevations, which could lead to declining species abundances at lower elevations (Anderson et al. 2013; Blake and Loiselle 2015). Warmer temperatures might also be beneficial for highland species, but extreme climate events could negatively affect communities at high elevations (Boyle 2011). In addition, climate change could alter the amount of precipitation and its temporal variation, thus affecting the spatio-temporal movements of lowland bird assemblages (Larsen et al. 2011). So far, the effect of climate change on biodiversity is difficult to assess due to natural climatic variability, and the effect of local non-climatic environmental changes (Walker and Steffen 1999; Parmesan and Yohe 2003).

2.4.2 Land-use change

Land-use change and human disturbance are among the most important factors of global environmental change (Newbold et al. 2015). Land-use change may affect population dynamics, local adaptation, dispersion and speciation (Gámez-Virués et al. 2015; Cote et al. 2017; Legrand et al. 2017; Emer et al. 2018), leading to species homogenization and spatial cohesion of biodiversity (Opdam and Wascher 2004; Frishkoff et al. 2016). However, the effect of land-use change on biodiversity generally depends on habitat type (Nogués-Bravo et al. 2008), disturbance intensity (Flynn et al. 2009), taxonomic group (Lawton et al. 1998; Schulze et al. 2004), and functional groups within each taxon (Lehouck et al. 2009; Breitbach et al. 2012; Petit 2015). This has been shown across several taxa, such as plants (Pakeman 2014), bees (Forrest et al. 2015), hummingbirds (Tinoco et al. 2018), and bats (Cisneros et al. 2014). Nevertheless, the conversion of natural continuous forests into human-disturbed habitats may support a surprisingly high diversity, contributing to the overall biodiversity of each ecosystem (Mayfield et al. 2010; Mulwa et al. 2012). Therefore, the effect of human disturbance on ecosystems should be measured by different facets of diversity and functional groups (Corbelli et al. 2015; Bregman et al. 2016).

2.5 Different facets of biodiversity

Understanding the spatio-temporal variation of biodiversity across different environments is the core challenge of community ecology (Dornelas et al. 2013; Mori et al. 2013). In order to assess changes of biodiversity, ecologists have focused on taxonomic indicators such as species richness and abundance (Lawton et al. 1998; Laurance et al. 2011). However, changes in biodiversity can be extended to other diversity facets, such as functional diversity (Meynard et al. 2011), which is associated with ecosystem functions (Mason et al. 2005). The use of both taxonomic and functional diversity can improve predictions of responses of biodiversity and its associated ecosystem functions to environmental change (Mayfield et al. 2005). Both diversity facets are complementary, potentially responding differently to environmental change (Mayfield et al. 2010).

2.5.1 Taxonomic diversity

Magurran (2004) defines biodiversity as the variability among living organisms from all ecosystems in space and time. Biodiversity in the strict sense measures the number of species in a sample (Whittaker 1972). However, ecologists have long accepted biodiversity as synonymous to the number of species and species abundance (Hubbell 2001). The variation in species abundance has also motivated the use of species evenness as an additional dimension of taxonomic diversity (Hill 1973; Magurran

2004), which measures the importance of species in a community (Whittaker 1972). In addition, several taxonomic diversity indices have been developed to expresses the dominance and evenness of species in a sample (Whittaker 1972). However, while the real meaning, benefit and utility of taxonomic diversity indices are widely discussed (e.g., Hurlbert 1971; Feinsinger 2001), species richness, abundance and evenness remain the most accepted biodiversity metrics in community ecology (Noss 1990; Willig et al. 2003; Magurran 2004).

Species richness is the natural, simplest and most intuitive biological diversity measure (Magurran 2004), representing the number of species in a community of a given taxon (Whittaker 1972). Unfortunately, detecting all species in a community is a complex task due to communities inhabiting highly complex and heterogeneous environments (Grenyer et al. 2006; Jarzyna and Jetz 2016). In order to record biodiversity through species richness, population size variation should be taken into account (Gotelli and Colwell 2001; Guillera-Arroita 2017). Thus, the inclusion of the number of individuals helps to understand the differences of species in their abundance (Hubbell 2001). Estimating abundance is critical for quantifying population dynamics and the impact of environmental change (Dénes et al. 2015). Spatio-temporal variation of abundance reflects the relationship between species and environmental gradients (Brown et al. 1995; Mac Nally 2007), mainly through birth, death and migration rates (Begon et al. 2006). Investigating the number of individuals helps to determine variation in species richness (Currie et al. 2004), to recognize common and rare species, and to estimate population densities between ecosystems (Magurran 2004). Therefore, the relative abundance of species is an important attribute of ecological communities (Hubbell 2001). Evenness is an additional dimension of taxonomic diversity and analyses how individuals are distributed across species within a community (Hill 1973). Thus, evenness determines the community uniformity or the dominance of one or some species within the community (Whittaker 1972). As species richness and abundance are often correlated, evenness is considered as a valuable and independent biodiversity measure (Smith and Wilson 1996).

2.5.2 Functional diversity

Functional group richness and functional trait diversity are important components of biodiversity (Tilman 2001; Petchey and Gaston 2006), allowing the evaluation of factors that drive community structure and ecosystem functioning (Díaz et al. 2007). Functional groups according to taxonomic guild level, feeding guilds (Hawkins and MacMahon 1989; Simberloff and Dayan 1991), and species trait diversity (Mason et al. 2005) have provided a valid measure to evaluate the functional structure of communities (Cadotte et al. 2011) and their ecosystem functions across environmental gradients (Mayfield et al. 2010).

The higher taxon approach (taxonomic guilds) measures the hierarchical structure of included taxa (Cracraft 1981). This approach has been applied to a number of species within genera, families and orders (Gaston and Williams 1993; Balmford et al. 1996a; Larsen and Rahbek 2005). The taxonomic relationship is framed within a guild concept as a set of species with similar niche requirements (Hawkins and MacMahon 1989; Simberloff and Dayan 1991). Taxonomic guilds have been tested in several ecosystems and habitats, and at various scales for different taxa such as plants (Villaseñor et al. 2005), benthic communities (Greffard et al. 2011), terrestrial invertebrates (Williams and Gaston 1994), amphibians and reptiles (Pawar et al. 2007), birds (Balmford et al. 1996a, b) and mammals (Larsen and Rahbek 2005). Higher-taxon level studies have proved to be cost-effective for predicting biodiversity patterns (Kallimanis et al. 2012), and the loss of key functional groups (Simberloff and Dayan 1991). In contrast, Burns (1989) defined a feeding guild as an aggregation of species with similar trophic resources. Feeding guilds are related to food webs that shape communities and ecosystems basically through mutualism, competition and predation (Begon et al. 2006). However, MacNally (1983) proposed that feeding guild structure is mainly influenced by interspecific competition. Foraging behaviour is highly related to feeding guild structure (Simberloff and Dayan 1991). The feeding guild concept has been widely applied to several taxonomic groups (Adams 1985), but has in particular been studied in species-rich taxa such as birds (Verner 1984; Gray et al. 2007; Pigot et al. 2016).

Morphological, physiological and behavioural traits of species can influence biodiversity and ecosystem functioning (Tilman 2001), and are reliable indicators of an organism's function in an evolutionary and environmental context (Wainwright 1994). Functional trait diversity measures the range and relative abundance of functional traits present in a community (Díaz et al. 2007). Several indices have been developed to measure functional diversity (Petchey and Gaston 2006). However, Villéger et al.

(2008) and Laliberté and Legendre (2010) implemented a general framework for applying functional indices (e.g. functional richness, functional dispersion and functional evenness) using a principal coordinate analyses (PCoA) that projects Euclidian distances among species into a multidimensional trait space. Functional richness estimates the volume of multidimensional trait space occupied by an entire community (Villéger et al. 2008). Functional dispersion quantifies the distance of species to the community centroid in a multidimensional trait space, while considering the relative abundance of each species (Laliberté and Legendre 2010). Finally, functional evenness shows the distribution of abundance in the functional trait space (Mason et al. 2005). Thus, complementary functional diversity indices provide a tool to evaluate niche complementarity in different ecological contexts (Mason et al. 2013).

2.6 Tropical biodiversity

Tropical forests are vast and complex systems (Carson and Schnitzer 2008). The tropics have the most diverse genomes and clades of species of higher taxa (Willig et al. 2003). The high diversity of tropical forests is probably due to their complex water-energy dynamics, forest structure and biotic interactions (Leigh 2008). Theoretical and empirical studies suggest that the relatively high temperature at low latitudes is the most important factor that shapes the high tropical biodiversity (Brown 2014). Additionally, the effects of precipitation (Hawkins et al. 2003b), habitat diversity (Newbold et al. 2015), evolutionary and ecological patterns have been associated with the high diversity in the tropics (Orme et al. 2005). Overall high environmental productivity in tropical rainforests could support more individuals per species and more species per area than in temperate systems (Currie et al. 2004; Brown 2014).

2.6.1 Biodiversity in tropical mountain forests

Tropical mountains are among the top-five biodiversity hotspots, housing 20% of all plant and 16% of all vertebrate species (Myers et al. 2000). Tropical elevational gradients have a wide range of temperatures, warmer at the base and colder at the top, and show a variable pattern of precipitation and water availability across all elevations (McCain and Grytnes 2010). In addition, tropical mountains harbour different forest types, such as lowland tropical rainforest, premontane rainforest, montane rainforest, cloud forest, elfin forest and paramo (McCain and Grytnes 2010). Daniel Janzen (1967) proposed that “mountain passes are higher in the tropics”. With this statement he pointed out that organisms have more physiological constraints in tropical mountains than in temperate mountains, because tropical organisms do not experience the strong seasonal climatic fluctuations that temperate organisms are exposed to. The limited seasonal climatic variation could cause the narrow thermal niches and restricted distributions of tropical organisms (McCain 2009a), which would explain the high speciation rates and species diversity on tropical mountains (Brown 2014).

3. Thesis structure, conceptual framework and research questions

My PhD research assesses the spatio-temporal patterns of bird diversity, and the environmental factors that shape bird communities along an elevational gradient in the Ecuadorian Andes. First, I identified the main drivers of bird diversity across a 2000 m elevational gradient (Figure 1, Q1). Then, I linked the temporal variation of bird communities with the abiotic and biotic factors of each elevation (Figure 1, Q2). Finally, I evaluated the different responses of taxonomic and functional bird diversity to forest fragmentation (Figure 1, Q3). My work contributes to the understanding of the effects of abiotic and biotic factors on tropical bird communities across disturbance and elevational gradients. Birds are one of the most sensitive and cost-efficient taxonomic groups for biodiversity monitoring (McCain 2009b). They play a key role for ecosystem functioning, occupying a wide range of trophic niches (Sekercioglu 2006; Kissling et al. 2012). Thus, understanding the drivers of bird diversity is important for predicting how ecosystems might change under projected future environmental change (McCain and Grytnes 2010).

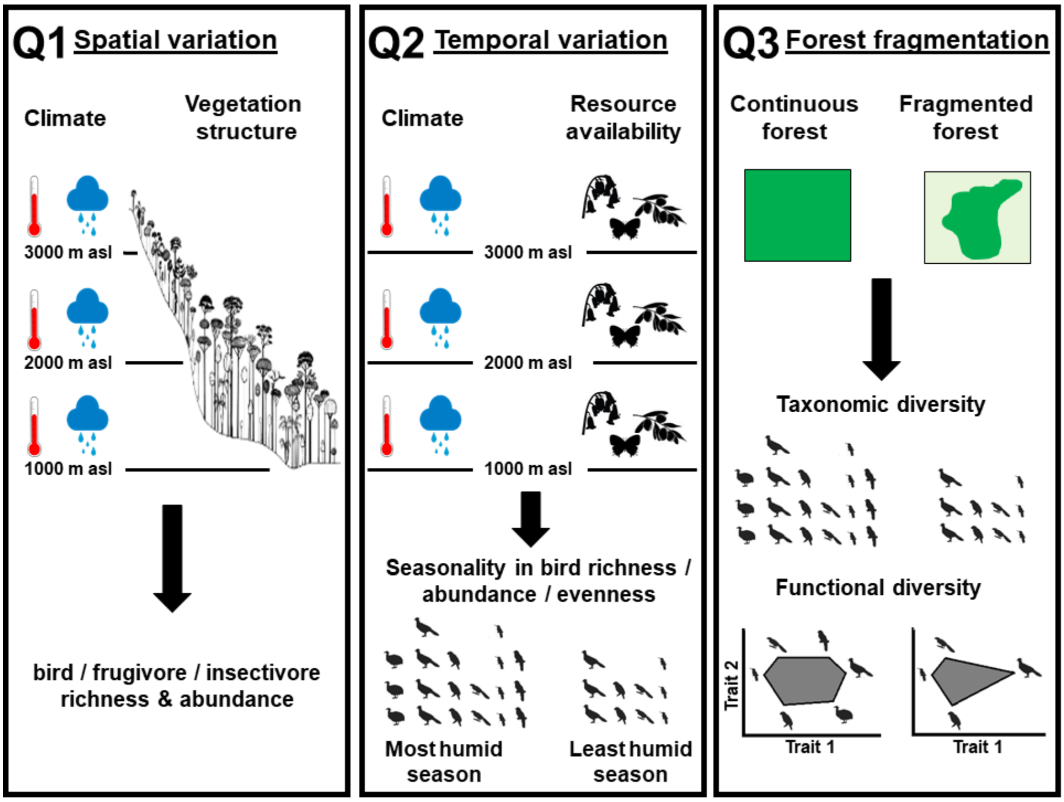
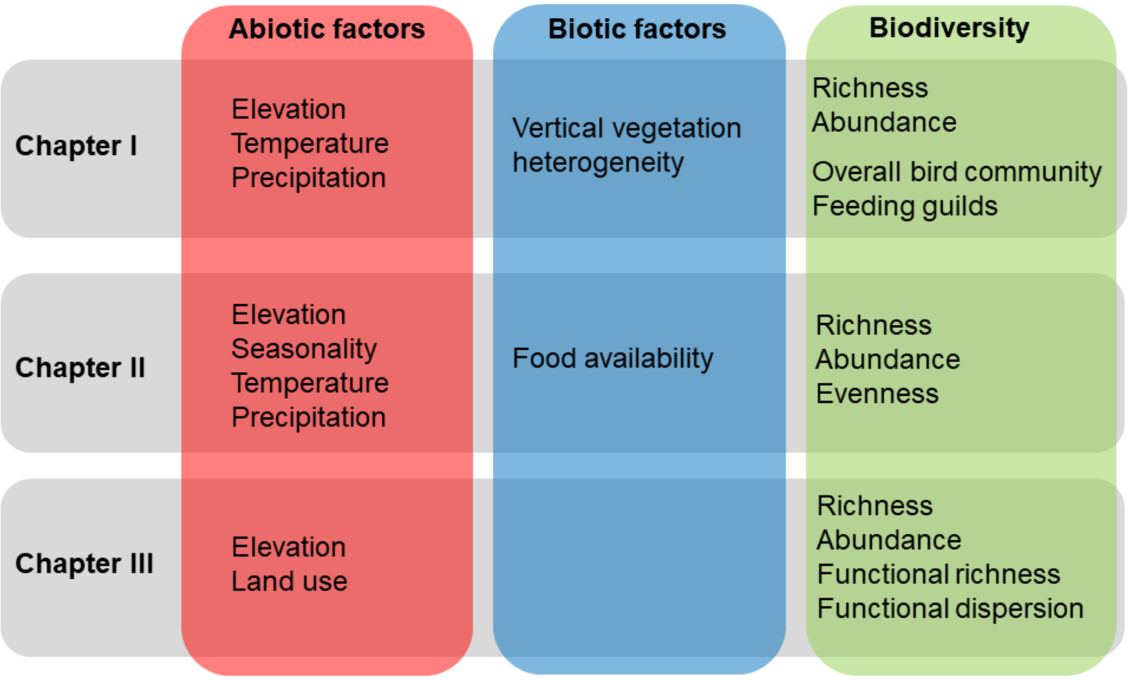


Figure 1. The conceptual framework shows the study design and the abiotic and biotic factors that drive biodiversity, i.e. elevation, climate, vegetation structure, resource availability and land-use change. The aim of my thesis was to gain a deeper understanding of the drivers that shape bird community patterns across an elevational gradient in the tropical Andes. In the first chapter, I investigated the direct effects of elevation, and indirect effects of elevation mediated via climate and vegetation structure on bird communities (Q1). In the second chapter, I investigated the temporal variation of bird communities, and which abiotic and biotic factors drive bird diversity patterns between the most humid and the least humid season (Q2). Finally, in my last chapter, I aimed at investigating the taxonomic and functional response of bird communities to forest fragmentation (Q3).

I structured my PhD thesis in three chapters, which analyse the abiotic and biotic factors that shape different facets of bird diversity across the elevational gradient (Figure 2). In the first chapter, I tested how abiotic and biotic factors directly and indirectly affect bird communities and frugivorous and insectivorous birds in particular (Figure 2). In the second chapter, I examined which abiotic and biotic factors explain temporal fluctuations in bird communities (Figure 2). In the third chapter, I evaluated taxonomic and functional bird diversity in both continuous and fragmented forest (Figure 2).



	Abiotic factors	**Biotic factors**	**Biodiversity**
Chapter I	Elevation Temperature Precipitation	Vertical vegetation heterogeneity	Richness Abundance Overall bird community Feeding guilds
Chapter II	Elevation Seasonality Temperature Precipitation	Food availability	Richness Abundance Evenness
Chapter III	Elevation Land use		Richness Abundance Functional richness Functional dispersion

Figure 2. Thesis structure highlighting the abiotic and biotic factors that I used in my study to test the effect of environmental conditions on different facets of biodiversity. Each chapter is elaborated as a single scientific research paper, which I submitted to and published in international peer-reviewed journals.

Each chapter of my thesis is presented as a scientific research paper that can be found in the appendix of this dissertation. I am the lead author on all these papers that have been submitted to or have been published in international and peer-reviewed scientific journals. The first chapter has been submitted to Acta Oecologica (Appendix A1), the second chapter has been published in PloS ONE (Santillán et al. 2018, Appendix A2), and the third chapter has been published in Oecologia (Santillán et al. 2019, Appendix A3). Each scientific paper contains the complete research question and the detailed methodologies used in the specific study.

3.1 How do direct and indirect effects of elevation structure spatial variation in bird communities?

In the first chapter (Appendix A1), I explored the effects of abiotic and biotic drivers on bird communities across an elevational gradient (Santillán et al. submitted). I used structural equation models (SEMs) to disentangle the direct and indirect effects of elevation, temperature, precipitation, and vegetation structure on species richness and abundance of the overall bird communities, as well as on frugivorous and insectivorous birds, respectively. I expected that direct effects of elevation should be more important for overall bird diversity, while indirect effects of elevation jointly mediated via temperature, precipitation and vegetation structure should be more important for the specific feeding guilds (Ferger et al. 2014). I also expected different responses of frugivores and insectivores to abiotic and biotic factors; for instance, vegetation structure should have a stronger effect on insectivorous than on frugivorous birds (Tscharntke et al. 2008; Jankowski et al. 2013; Bregman et al. 2014).

3.2 Which factors shape the temporal variation of bird communities across elevations?

In the second chapter (Appendix A2), I examined the spatio-temporal dynamics of bird assemblages along an elevational gradient (Santillán et al. 2018). I tested the effects of seasonality (most humid and least humid season) on bird richness, abundance, and evenness. I also examined whether temperature, precipitation and/or resource availability explain the temporal fluctuations in bird diversity. I expected that temperature and precipitation should limit bird richness, abundance and evenness mostly at high elevations, due to physiological constraints (Hawkins et al. 2003a; McCain 2009b). In contrast, I expected resource availability to affect bird richness, abundance and evenness in particular at low elevations, due to higher competition for resources (Brown et al. 1996a).

3.3 How are taxonomic and functional bird diversity affected by forest fragmentation?

In the third chapter (Appendix A3), I compared taxonomic and functional indicators of bird diversity in response to human-induced forest fragmentation (Santillán et al. 2019). First, I expected a decrease of bird species richness in fragmented forests compared to continuous forests (Nogués-Bravo et al. 2008; Montaño-Centellas and Garitano-Zavala 2015). Second, I expected a decrease of functional diversity in fragmented forests (Tscharntke et al. 2008; Sitters et al. 2016) in association with a decrease in taxonomic diversity (Flynn et al. 2009). Finally, I hypothesised a stronger effect of forest fragmentation on the functional diversity of species-rich lowland communities (because these are often functionally over-dispersed and prone to the loss of functionally extreme species) than on functional diversity of species-poor highland communities (because these are functionally clustered and thus, more robust due to functional redundancies) (Dehling et al. 2014).

4. Tropical system, study area and research design

4.1 Ecosystem and patterns of biodiversity in southern Ecuador

The research area is located in the Andes of southeast Ecuador. The area is a low transition zone (Huancabamba depression) between the northern and southern central tropical Andes. The area is located on the eastern slope of the Cordillera Real with a complex topography presenting a great habitat variety, which produces and maintains high biodiversity and endemism (Richter et al. 2013). The area is characterized by humid tropical montane climate (Kottek et al. 2006), with a strong climatic variation across the elevational gradient. While temperature decreases with increasing elevation (0.37K per 100m), precipitation has a unimodal distribution and shows most humid and least humid periods during the year across the elevational gradient (Emck 2007).

The research area is influenced by the dry Catamayo-Alamor and the moist Paramo-South eastern cordillera biogeographic regions (Ministerio de Ambiente del Ecuador 2012). The area is considered a hotspot of biodiversity, reporting a high diversity of vascular plants (1206), lichens (323), ferns (257), mosses (515), butterflies (2739), bats (24), and birds (379, Brehm et al. 2008). At the landscape level, the vegetation structure can be classified in four forest types: primary forest of the ridge of Cajanuma (3000 m a.s.l.) with a high percentage of *Weinmannia* species and vascular epiphytes and a high coverage of epiphytic mosses; primary ravine forest of higher altitudes (above 2000 m a.s.l.) with some vascular epiphytes and conspicuous climber plants; primary ravine forest of lower altitudes (below 2000 m a.s.l.) with tall and thick trees and a high percentage of emergent trees; and low ridge forest (1000 m a.s.l.) with dense canopy, high number of trees, climbers and lianas, and the highest canopy stratum compared to all other forest types (Paulsch et al. 2008).

The research area is located within and around *Podocarpus* National Park (PNP) and the Biological Reserve San Francisco (BRSF). PNP belongs to the national system of protected areas since December 15, 1982. The national park has an area of 1468.8 km^2, which includes several ecosystems, i.e. lower mountain rainforest, upper mountain rainforest, subpáramo and páramo. The BRSF is located in the valley of the San

Francisco river between the provincial capitals of Loja and Zamora, and has an area of 11.2 km^2 with an elevational range from 1800 to 3160 m a.s.l. (Beck et al. 2008). The region has a heterogenic ethnic, socio-cultural and socioeconomic structure (Pohle 2008). Land use outside the protected areas depends on the decisions of individual farming households, which has led to three main habitat types: forest, scrub and pasture (Pohle 2008; Pohle et al. 2013). The main reason of deforestation is pasture expansion for livestock (Pohle et al. 2013).

4.2 Study area

I carried out this study within and around *Podocarpus* National Park and San Francisco reserve on the south-eastern slope of the Andes in Ecuador (Figure 3). The study was conducted at three elevations (1000 m a.s.l., 4° 6′ S, 78° 58′ W; 2000 m a.s.l., 3° 58′ S, 79° 4′ W; 3000 m a.s.l., 4° 6′ S, 79° 10′ W), in natural continuous forests within the protected reserves that are mostly undisturbed by humans (Homeier et al. 2008) and in fragmented forests surrounding the reserves that are embedded in a matrix of cattle pastures (Tapia-Armijos et al. 2015). The study area is characterized by humid tropical montane climate (Kottek et al. 2006) with a bimodal rain regime across the elevational gradient (most humid season: May to June; least humid season: October to November; Emck 2007). At low elevations mean annual temperature is 20 °C and mean annual precipitation is 2432 mm. At mid elevations mean annual temperature is 15.5 °C and mean annual precipitation 2079 mm. At high elevations mean annual temperature is 10 °C and mean annual precipitation is 4522 mm (Emck 2007).

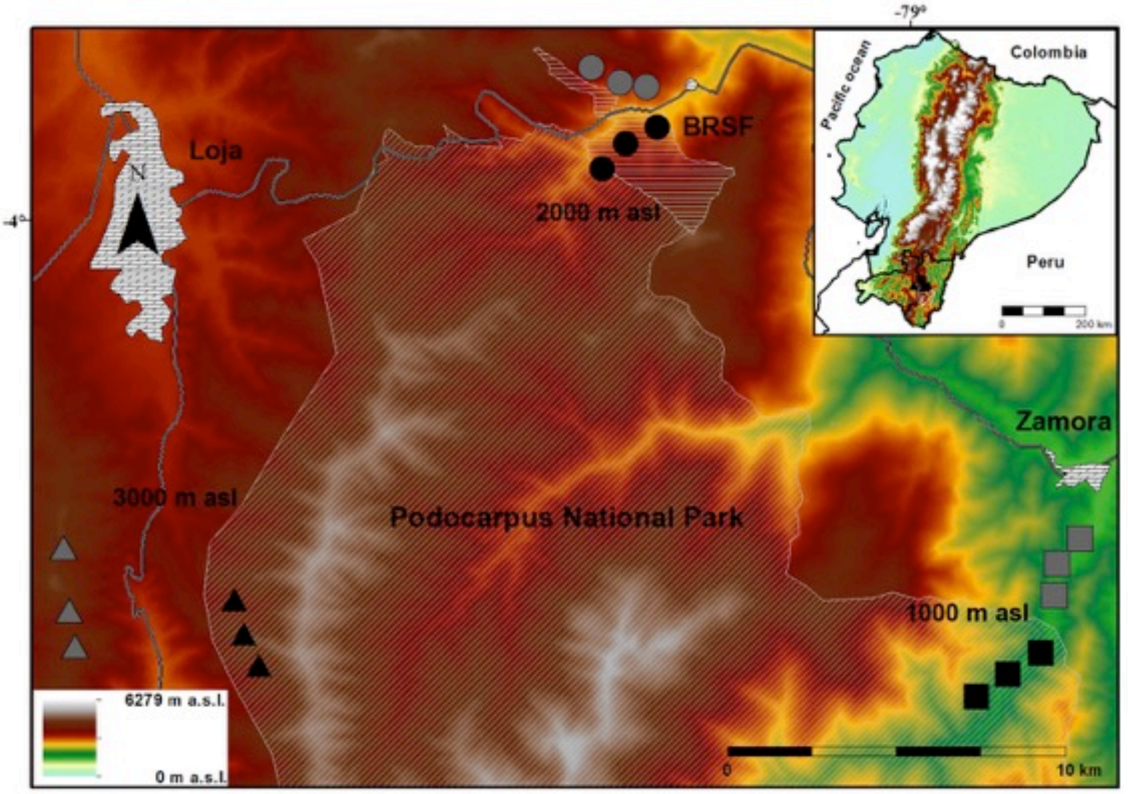


Figure 3. Map of the study area showing the sampling plots with the elevational range, the main cities and roads, the area of the *Podocarpus* National Park and the Biological Reserve San Francisco. The squares represent the sampling plots at low elevations, the circles those at medium elevations and the triangles those at high elevations. The plots in black are located in natural continuous forest and the plots in grey are located in fragmented forest.

4.3 Methods and research design

I conducted the study on a total of 18 1-ha plots covering three continuous and three fragmented forest patches at each elevation (Figure 3, Figure 4). On each 1-ha plot I placed nine point counts, eight at the borders and one in the centre (total sampling area per plot ~ 1.1 ha). I sampled bird communities twice per most humid season (May-July) and twice per least humid season (September-November) in 2014 and 2015, resulting in eight temporal replicates per plot, and a total of 144 replicates across all 18 plots. I recorded and identified all birds to species level within a 20-metre radius around the centre of each point count for 10 minutes. Finally, I quantified bird species richness and bird abundance by pooling the records of all point counts per plot and temporal replicates (216 hours in total). I used published data (Wilman et al. 2014) for the classification of feeding guilds (i.e., nectarivores, frugivores, insectivores and omnivores). To quantify the functional richness (FRic) and functional dispersion (FDis), I used six ecomorphological trait indices measuring flight performance, food intake and bipedal locomotion (Dawideit et al. 2009; Pigot et al. 2016), as well as body mass. Bird traits were measured on four specimens, two female and two male individuals, of each species in museum collections (Natural History Museum, Berlin, Germany; Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; Zoological Research Museum Alexander Koenig, Bonn, Germany; Zoological Museum of the University of Copenhagen, Denmark). To estimate flower and fruit availability, I summed the number of open flowers and ripe fruits within each of the nine point counts to obtain the overall abundance per plot (Mulwa et al. 2013). I assessed understory invertebrate biomass by using a standardized sweep-netting design to obtain the cumulative invertebrate fresh biomass across all plots (Mulwa et al. 2013). I estimated vegetation structure by calculating vertical vegetation heterogeneity. For this, I used the Shannon–Wiener diversity index across different layers of vegetation cover at 0, 1, 2, 4, 8, 16 and 32 m above ground (Bibby et al. 2000). The average monthly within-forest temperatures for each plot were obtained through an air temperature regionalization tool developed for the study region (Fries et al. 2012). Monthly mean precipitation was obtained through remote sensing techniques and meteorological data (Rollenbeck and Bendix 2011).

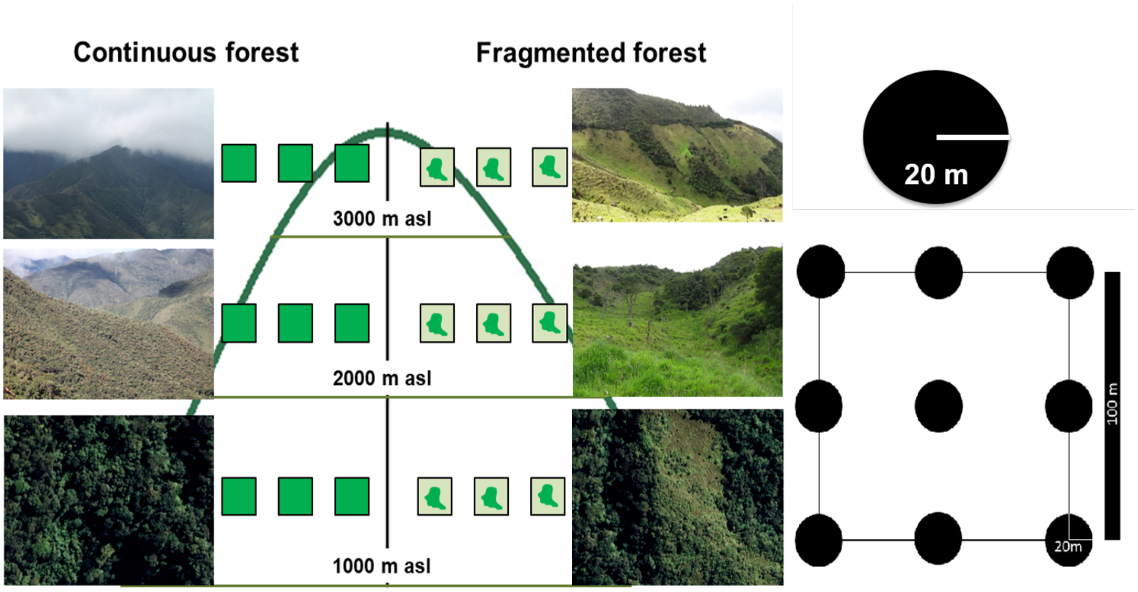


Figure 4. Sampling design: squares represent 18 1-ha plots placed at three elevations in continuous and fragmented forests. On each 1-ha plot a total of nine bird point counts are placed, eight at the borders and one in the centre.

5. Main results and discussion

5.1 Direct and indirect effects of elevation, climate and vegetation structure on bird communities

In the first chapter of my dissertation, I used structural equation models (SEM) to examine the direct and indirect effects of elevation, climate and vegetation structure on bird communities along a tropical mountain slope. Elevation was mostly indirectly associated with bird diversity, jointly mediated via temperature, precipitation and vegetation structure. Elevation also had a direct effect on overall bird diversity and on insectivores, whereas frugivorous birds were not directly affected by elevation. In turn, temperature had a positive effect and precipitation had a negative effect on bird diversity in all SEMs. The effect of vegetation structure was twice as large for insectivorous than for frugivorous birds.

These findings indicate a reduction of bird diversity due to climatic factors and vegetation structure with increasing elevation. However, the positive direct effect of elevation on bird diversity also suggest that, while accounting for the negative indirect effects of elevation, bird diversity was higher than expected at high elevations. This pattern might result from other factors related to elevation, such as spatial factors, biotic factors and evolutionary history (McCain and Grytnes 2010). a) Spatial factors, such as the species-area relationship and the mid-domain effect, predict that different habitat sizes and ecotone effects shape bird communities across elevational gradients (Rahbek 1997; Colwell et al. 2004). b) Biotic factors, such as resource availability and competition for food could also explain the positive effect of elevation on patterns of bird diversity (Dehling et al. 2014; Ferger et al. 2014). c) Evolutionary history can explain the diversification of contemporary fauna (Hawkins et al. 2006, 2012), such as divergent timing and diversification processes in lowland and highland Neotropical birds (Weir 2006; Hawkins et al. 2007).

The positive effect of temperature on bird community patterns has been previously demonstrated across elevational and latitudinal gradients (Hawkins et al. 2003a; Evans et al. 2005; Ruggiero and Hawkins 2008; McCain 2009b), related to a higher productivity under high temperatures (Allen et al. 2002). However, temperature is not the only climatic factor explaining patterns of bird diversity (McCain 2009b; McCain and Grytnes 2010). Precipitation is considered to be among the most important climate factors shaping biodiversity in tropical ecosystems (Hawkins et al. 2003a). A negative effect of precipitation has previously been recorded for some flying taxa (Grindal et al. 1992; Aizen 2003; Santillán et al. 2018). For instance, heavy rain can limit flight performance (Ortega-Jimenez and Dudley 2012) and restrict foraging time (Boyle et al. 2010) of birds.

Vegetation structure has previously been shown to be highly correlated with mountain bird diversity (Terborgh 1977; Jankowski et al. 2013), as it provides refuge, as well as nesting and foraging habitats for birds (MacArthur and MacArthur 1961; Tews et al. 2004; Mulwa et al. 2012). In my study I found a stronger effect of vegetation structure on insectivore richness than on frugivore richness, which is in concordance with several previous studies (Waltert et al. 2005; Jankowski et al. 2013; Ferger et al. 2014). Insectivorous birds have specialized foraging techniques in specific microhabitats within complex vegetation structure (Willson 1974; Naoki 2007; Pigot et al. 2016). In contrast, frugivorous birds are usually independent of vegetation structure (Kissling et al. 2007, 2008), as they are more associated to plant diversity and fruit abundance (Loiselle and Blake 1991; Kissling et al. 2007).

I found both a direct and indirect effect of elevation on patterns of bird diversity along a tropical mountain slope. Additionally, temperature, precipitation and vegetation structure were jointly shaping patterns of biodiversity along the elevational gradient. However, spatial, biological and evolutionary settings associated with mountains may play an important role for bird communities, which may be more important for insectivorous birds than for frugivorous birds. My study highlights the mechanisms shaping patterns of bird diversity, and reveals the interaction of several drivers across tropical mountain slopes. Understanding the effects of environmental factors across elevational gradients could help to better predict bird community patterns in response to global environmental change.

5.2 Climate, but not resource availability drive temporal variation in bird communities

In the second chapter, I investigated the effect of seasonality (most humid season and least humid season) on bird richness, abundance and evenness across an elevational gradient. I tested whether temperature, precipitation and/or food resource availability explained temporal fluctuations in bird richness, abundance and evenness over eight temporal replicates. Additionally, I tested whether temporal fluctuations of nectarivores, frugivores, insectivores, and omnivores differ in relation to climate and their respective resource type. I found that bird species richness decreased significantly at high elevations, and bird richness, abundance and species evenness varied significantly between the most humid season and least humid season across all elevations. The temporal fluctuations in bird diversity were explained by temperature and precipitation, but not by resource availability. Temperature had a significant, positive effect on bird abundance at mid and high elevations, while precipitation had a significant, negative effect at mid and low elevations. These results suggest that in my study area temporal fluctuations of bird communities occur mainly in response to climatic constraints rather than are limited by food availability.

The decline of bird species richness at the highest elevation is in line with previous studies, showing a decline of species richness along elevational gradients (McCain 2009b). In contrast, the non-significant changes in bird abundance across the elevational gradient indicate that in relatively species-poor communities at high elevations the abundance of species is often higher compared to species-rich lowland assemblages (Willig and Presley 2015).

I found changes in species richness between seasons across all three elevations, but these changes were largely driven by changes in abundance. The increase in abundance in the least humid season corresponded to a consistent decline of bird evenness, indicating an increase in abundance of the dominant species in the respective communities. These results suggest medium- to long-distance seasonal movements of birds (Terborgh 1985) rather than short-distance elevational migrations (Boyle et al. 2011). This pattern is in concordance with the narrow thermal tolerance of tropical species (Brown 2014), that may force birds to leave their habitat in unsuitable climatic conditions (Hau 2001).

The contrasting effects of temperature and precipitation on bird abundance along the elevational gradient support the argument that lowland and highland bird communities may be affected by different climatic factors (Ruggiero and Hawkins 2008; McCain 2009b). In my study area temperature decreases with increasing elevation, and precipitation has a U-shaped distribution across the elevational gradient (Emck 2007; Rollenbeck and Bendix 2011). In fact, forests at high elevations are characterized by persistent cloud cover and fog throughout the year (Bendix et al. 2006; Emck 2007). This pattern indicates that highland bird communities are limited by temperature but are adapted to high water availability. In contrast, lowland bird communities are limited by heavy rainfall but are not limited by temperature. Previous studies have identified precipitation as a main constraint of tropical bird communities, as severe rain events may cause physiological constraints and result in migrations of birds (Williams and Middleton 2008; Boyle et al. 2010; Tingley et al. 2012). My results highlight that temporal bird community patterns are shaped by specific climate conditions at each elevation.

Resource availability did not explain temporal fluctuations in bird communities in contrast to several previous studies (Loiselle and Blake 1991; Poulin et al. 1992; Borghesio and Laiolo 2004; Mulwa et al. 2013). However, most of these studies have focused on particular species or feeding guilds rather than on the overall bird community. In my study, temporal variation of bird feeding guilds was not explained by temporal variation of their respective food resource. A valid explanation for this pattern could be the high plant productivity of the studied ecosystems (Fiedler et al. 2008; Homeier et al. 2008) which may provide a surplus of resources for birds, which might lead to a decoupling of resource availability and consumer diversity (Feinsinger 1976).

I found a significant decline of bird species richness towards high elevations and a strong seasonal variation of bird diversity in relation to changing climatic factors. The climate effect was different across the elevational gradient. Low temperature and high precipitation affected mainly bird abundance. In contrast, food resource availability had no significant effect on bird communities across the elevational gradient. My results thus emphasize the importance of temporal dynamics of temperature and precipitation for the community structure of birds, highlighting the potential sensitivity of bird communities to projected climate change (Blake and Loiselle 2015).

5.3 Functional indicators respond differently to forest fragmentation than taxonomic indicators of biodiversity

In the third chapter, I compared the effects of forest fragmentation on species richness, abundance and evenness, as well as on functional richness (FRic), dispersion (FDis) and evenness (FEve), across the elevational gradient. I found a decline of bird taxonomic diversity towards high elevations, but a more complex relationship of functional diversity across the elevational gradient. Species richness and abundance were higher in fragmented compared to continuous forests. Fragmentation had stronger effects on bird species abundance than on species richness across the elevational gradient. Bird functional richness and dispersion showed different responses to forest fragmentation at low compared to mid and high elevations. In fact, both functional indices declined in fragmented forest only at low elevations. I did not find significant differences of species evenness between continuous and fragmented forests and among elevations. Functional evenness had a significant interaction between fragmented forests and elevation at mid elevations. These results indicate that forest fragmentation has different effects on bird taxonomic diversity than on bird functional diversity, particularly in diverse lowland communities.

The decline of bird diversity with increasing elevation (Nogués-Bravo et al. 2008; McCain 2009b), and in response to human disturbance (Lehouck et al. 2009; Mulwa et al. 2013; Montaño-Centellas and Garitano-Zavala 2015) is widely reported in previous studies. However, the increase of bird taxonomic diversity in disturbed habitats that I found in my study has also been recorded by other previous studies (Loiselle and Blake 1991; Mulwa et al. 2012). Such particular increases of diversity could be the result of an increase of generalist species in the community, which may compensate the loss of specialists (Neuschulz et al. 2011). Additionally, in my study area continuous and fragmented forests have similar vegetation structure and the distance of forest fragments to the border of the nearest natural continuous forest is relatively small (Quitián et al. 2017).

The strong effect of fragmentation on bird abundance could be explained by the fact that environmental changes typically affect species abundance first, before species richness is affected (Currie et al. 2004; Dulle et al. 2016). Thus, species abundance may be an important measure to detect subtle changes in bird communities along land-use and elevational gradients (Brown et al. 1995; Mac Nally 2007).

The decline of FRic and FDis in fragmented forests only at low elevations was probably due to the loss of functionally distinct species with extreme morphological traits on these sites (Flynn et al. 2009; Bregman et al. 2016). The weak effects of fragmentation on FRic and FDis at mid elevations suggest a simultaneous loss or gain of functionally distinct species in both forest types. The increase of FRic in fragmented compared to continuous forests at high elevations indicates a gain of habitat generalists with distinct morphologies (Stotz et al. 1996; Bregman et al. 2014), resulting in changes in the functional composition of these communities. Previous studies have reported that highland bird communities are more sensitive to forest fragmentation than lowland bird communities (Soh et al. 2006; Harris et al. 2014). However, most of these studies have focused on taxonomic diversity, endemic or threatened species, but not on the functional diversity of bird communities. In fact, highland communities often show a higher adaptability to environmental change than lowland communities (Loiselle and Blake 1991), probably because they host a functionally diverse set of generalist species that can better cope with harsh environmental conditions (Louthan et al. 2015) and forest fragmentation (Soh et al. 2006; Montaño-Centellas and Garitano-Zavala 2015).

My results suggest a decoupled response of taxonomic and functional diversity in diverse and functionally over-dispersed lowland communities compared to functionally clustered highland communities (Petchey and Gaston 2006; Flynn et al. 2009; Mayfield et al. 2010). In fact, some recent studies have highlighted contrasting responses of species and functional trait diversity for different taxa (Niu et al. 2014; Forrest et al. 2015; Seymour et al. 2015; Bässler et al. 2016). For instance, Seymour et al. (2015) showed opposite patterns of bird species richness and functional diversity along a gradient of vegetation structure in an arid landscape. My study thus stands in line with previous findings and demonstrates that including different facets of diversity can improve our understanding of the effects of human disturbance on biodiversity (Petchey and Gaston 2006; Mayfield et al. 2010).

6. Synthesis and conclusions

In my PhD thesis, I studied how abiotic and biotic factors affect different facets of bird diversity. I used an elevational gradient on the eastern slopes of the tropical Andes of Ecuador to test for direct and indirect effects of elevation, climate and vegetation structure on bird communities; the effects of abiotic and biotic factors on temporal variation of bird diversity; and the effects of forest fragmentation on taxonomic and functional diversity. The study area is a hotspot of biodiversity that covers both an elevational gradient from lower mountain rainforest to upper mountain rainforest, as well as a gradient of land use from continuous to fragmented forest. The decrease of temperature with increasing elevation, seasonal precipitation pattern, and different vegetation structures across the elevational gradient constitute a powerful natural experiment to study potential drivers of biodiversity patterns.

My results highlight the importance of current climate conditions and vegetation structure on bird community patterns across an elevational gradient. The direct, positive effect of elevation on bird communities suggests the importance of other elevation-related factors such as spatial conditions, biotic interactions and evolutionary history (Gaston 2000). Area effects, such as species-area relationships and mid-domain effects (Rahbek 1997; Colwell et al. 2004), resource availability and competition (Dehling et al. 2014; Ferger et al. 2014), and divergent evolutionary history between lowland and highland bird communities (Weir 2006; Hawkins et al. 2007) could be important determinants of bird diversity. These elevation-related factors might explain the different structure of bird communities across elevational gradients (Patterson et al. 1998; Herzog et al. 2005; Graham et al. 2009; Dehling et al. 2014), and therefore potentially different responses to current environmental conditions (Herzog et al. 2005; Jankowski et al. 2013). My study also shows the importance of environmental factors (i.e. temperature, precipitation and vegetation structure) to understand community patterns across elevational gradients. The positive effect of temperature (Ruggiero and Hawkins 2008; McCain 2009b) and the negative effect of precipitation (Boyle et al. 2010; Santillán et al. 2018) on bird communities has been previously reported across elevational gradients. Climate has been shown to be an important predictor of bird species richness (Hawkins et al. 2003a; Evans et al. 2005). Positive effects of vegetation structure on bird diversity have previously been reported in tropical mountain systems

(Jankowski et al. 2013) and on a global scale (Kissling et al. 2012). The stronger effect of vegetation structure on insectivores than on frugivores that I find in my study is probably due to the use of specific microhabitats and specialized foraging techniques of insectivorous birds (Naoki 2007; Jankowski et al. 2013; Pigot et al. 2016). In contrast, frugivorous birds are usually independent from overall vegetation structure (Kissling et al. 2007, 2008). Overall, my results emphasize the importance of understanding the mechanisms that shape biodiversity patterns due to joint effects of several drivers in complex tropical mountain systems.

Additionally, my study emphasizes the temporal variation of bird diversity, showing an increase of species richness and abundance in the least humid season compared to the most humid season, and a respective decrease of species evenness in this season. This effect was strongest in species abundance and was related to temporal variation of climatic factors rather than food resource availability. My results indicate that temperature had a strong effect on highland bird communities and precipitation on lowland bird communities. At mid elevations both climatic factors shaped bird diversity. Water-energy dynamics could explain the spatio-temporal variation of biodiversity across elevational gradients (McCain and Colwell 2011). However, how water-energy relationships affect montane bird diversity is still widely discussed (McCain 2009b). In fact, in my study system temperature had an opposite effect than precipitation on bird communities across the elevational gradient. My findings highlight the sensitivity of tropical birds to temporal variation of local climate. The spatio-temporal patterns of bird communities in response to water-energy dynamics should be accounted for, when projecting potential responses of birds to future climatic changes. Therefore, temperature and precipitation mainly drive temporal patterns of bird diversity on the eastern slopes of the tropical Andes of Ecuador.

Finally, I tested the effects of forest fragmentation on taxonomic and functional bird diversity. An increase of bird diversity in fragmented forests has been reported previously (Loiselle and Blake 1991; Mulwa et al. 2012). The strong effect of fragmentation on bird abundance suggests that disturbance might become best detectable in species abundance (Brown et al. 1995; Dulle et al. 2016). The decrease of functional richness and dispersion at low elevation, and increase of functional richness at high elevations, suggest a loss of functionally unique species in lowland communities, and an addition of species with extreme functional traits in highland communities

(Petchey and Gaston 2006; Mayfield et al. 2010). This result is supported by previous studies showing that species richness and abundance can be uncoupled from functional diversity (Petchey and Gaston 2006; Flynn et al. 2009; Mayfield et al. 2010). I conclude that the use of different measures of diversity can improve the detectability of human disturbance effects on bird communities. Species abundance is crucial to assess the effect of forest fragmentation on bird communities (Winfree et al. 2015), becoming an adequate measure to investigate the consequences of environmental changes (McCain and Grytnes 2010; Bowler et al. 2017). The functional diversity decline in fragmented forests only at low elevations was probably due to the loss of species with extreme morphological traits (Flynn et al. 2009; Bregman et al. 2016). In contrast, the increase of functional diversity in fragmented forests at high elevations indicates a gain of habitat generalists with distinct morphologies (Stotz et al. 1996; Bregman et al. 2014). Functional diversity was crucial to assess the effects of forest fragmentation at different elevations, helping to understand the mechanisms behind biodiversity and ecosystem function relationships (Tilman 2001; Mason et al. 2005). My results show that responses of taxonomic indicators can be uncoupled from functional indicators in diverse tropical ecosystem. These findings reveal that functional homogenization in ecological communities can be concealed by apparent increases in taxonomic diversity.

The global distribution of biodiversity, its role in shaping ecosystems processes and the likely effects of global environmental change on the maintenance of biodiversity have been a main challenge in ecology (Gaston 2000; Orme et al. 2005; Grenyer et al. 2006). Tropical mountains have an immense potential to understand the spatio-temporal patterns in species communities as a result of environmental changes across elevational gradients (McCain and Grytnes 2010; Quintero and Jetz 2018). Elevational gradients allow the testing of the effects of diverse environmental factors on biodiversity and its ecosystem functions across relatively short spatio-temporal gradients (Rahbek 1995), and assess the potential implications of environmental change (Blake and Loiselle 2015). My PhD thesis provides an overview of how bird communities respond to different environmental factors across an elevational gradient. My findings contribute to understanding the mechanisms that shape current bird communities in response to complex environmental conditions in the tropical Andes. My approach presents an effective tool for future community monitoring and conservation to assess the effects of potential environmental change.

7. Zusammenfassung

7.1 Einleitung

Die globalen Biodiversitätsmuster werden durch Umweltfaktoren bestimmt, die mit Längen-, Breiten- und Höhengradienten in Verbindung stehen (Gaston 2000). Diese abiotischen und biotischen Faktoren beeinflussen die raum-zeitlichen Muster ökologischer Gemeinschaften und bestimmen die Diversität und Verbreitung von Arten (Wiens 2011; Louthan et al. 2015). Zu den abiotischen Faktoren zählen physische Umwelt- und Klimaaspekte, welche die Produktivität der Umwelt regulieren. Ebenfalls spielen evolutionäre Prozesse sowie biotische Interaktionen eine wichtige Rolle für das Vorkommen von Arten. (Soberón and Peterson 2005). Temperatur und Niederschlag regulieren Wachstums- und Fortpflanzungsraten von ökologischen Gemeinschaften – entweder direkt durch physiologische Effekte (Allen et al. 2006) oder indirekt über biotische Interaktionen (Wright 1983) und die Produktivität der Umwelt (O'Brien 1998). Allerdings sind die Effekte solcher Wasser-Energie-Dynamiken nicht für alle Taxa und/oder funktionellen Teilgruppen innerhalb der Taxa gleich (O'Brien 1998). Biotische Faktoren beinhalten Habitatstruktur-, Habitatrand- und Ökotoneffekte, sowie biotische Wechselbeziehungen, wie Mutualismus oder Konkurrenz. Diese biotischen Faktoren bestimmen Geburten- und Sterblichkeitsraten, Artentstehungs- und Aussterbeereignisse, aber auch die Wanderung von Arten auf der lokalen und regionalen Ebene (Wisz et al. 2013). Mutualismen und Konkurrenz zwischen Arten werden als die wichtigsten biotischen Faktoren angesehen (Bascompte 2009). Mutualistische Interaktionsnetzwerke tragen zu einem Anstieg der Biodiversität bei und minimieren den Wettbewerb zwischen Arten (Bastolla et al. 2009). Im Gegensatz dazu reguliert Konkurrenz die Interaktionen zwischen Arten, was wiederum die Struktur ökologischer Gemeinschaften beeinflusst (Freeman 2015). Klimawandel und Landnutzung reduzieren und homogenisieren Biodiversität und beeinflussen ökologische Funktionen sowie biotische Interaktionen noch bevor die beteiligten Arten verschwinden (Opdam und Wascher 2004; Suárez et al. 2011). Die räumlichen und zeitlichen Veränderungen ökologischer Gemeinschaften entlang von Umweltgradienten zu verstehen, ist eine der größten Herausforderungen der Ökologie.

7.2 Studiengebiet und Studiensystem

Tropische Wälder sind weitläufige und komplexe Systeme mit einer hohen Diversität höherer Taxa (Carson und Schnitzer 2008). Insbesondere tropische Berge gehören zu den Ökosystemen mit der höchsten Diversität von Pflanzen und Wirbeltieren (Willig et al. 2003), die durch eine große Bandbreite an Temperaturen, sowie durch eine großen Niederschlagsvariabilität entlang ihrer Höhengradienten charakterisiert sind (Barry 2008). Die südöstlichen Hänge der Anden Ecuadors beherbergen auf Grund der komplexen Topografie und Habitatvielfalt, eine sehr hohe Biodiversität mit einem hohen Anteil endemischer Arten (Brehm et al. 2008). Das tropisch-humide Gebirge mit hoher Klimavariabilität wir maßgeblich durch zwei biogeografische Regionen beeinflusst: das aride Catamayo-Alamor und das humide Südost-Páramo (Umweltministerium von Ecudador 2012).

Die Studie wurde in und um den Podocarpus Nationalpark, sowie das Reservat San Francisco auf 1000, 2000 und 3000 m. ü. M. durchgeführt. Innerhalb der geschützten Flächen wurde in zusammenhängenden Waldflächen gearbeitet. Außerhalb der Schutzgebiete wurde in fragmentierten Waldstücken gearbeitet, welche in eine Matrix aus Weideflächen eingebettet sind. Das Studiengebiet weist ein tropisch-montanes Klima auf (Kottek et al. 2006) und der Niederaschlag ist bimodal über den Höhengradienten verteilt (sehr humide Jahreszeit und weniger humide Jahreszeit, Emck 2007). In den niederen Höhen liegt die mittlere Jahrestemperatur bei 20 °C und der mittlere Jahresniederschlag bei 2432 mm. In mittleren Höhen liegt die mittlere Jahrestemperatur bei 15.5 °C und der mittlere Jahresniederschlag bei 2079 mm. In den hohen Höhen liegt die mittlere Jahrestemperatur bei 10 °C und der mittlere Jahresniederschlag bei 4522 mm (Emck 2007).

7.3 Methoden und Studiendesign

Die Studie wurde auf 18, jeweils 1 Ha großen Flächen durchgeführt, von denen jeweils drei in den zusammenhängenden, sowie drei in den fragmentierten Waldstücken auf jeder Höhenstufe platziert wurden. Auf jeder dieser Flächen wurden neun Beobachtungspunkte eingerichtet und auf jedem dieser Punkte wurden für jeweils 10 Minuten alle Vogelarten innerhalb eines 20 Meter Radius registriert. Vogelgemeinschaften wurden zwischen 2014 und 2015 zweimal in der sehr humiden

Jahreszeit (Mai bis Juli) und zweimal in der weniger humiden Jahreszeit (September bis November) aufgenommen. Artenreichtum und -abundanz wurden berechnet, indem alle Aufnahmen pro Fläche und Zeitreplikat addiert wurden. Um Vögel in Nektarivore, Frugivore, Insektivore und Omnivore zu klassifizieren wurde die Einteilung durch Wilman et al. (2014) genutzt. Ökomorphologische, funktionelle Merkmale wurden an Museumsexemplaren gemessen. Funktioneller Reichtum (FRic) und funktionelle Dispersion (FDis) wurden mit sechs Merkmalsindizes sowie mit dem Körpergewicht quantifiziert. Die Ressourcenverfügbarkeit (Blüten, Früchte, Frischmasse von Invertebraten aus dem Unterholz), sowie die vertikale Vegetationsheterogenität wurden mit standardisierten Methoden erfasst (Bibby et al. 2000). Die monatlichen mittleren Temperatur- und Niederschlagswerte für jede Fläche wurden durch Fernerkundungstechnik auf der Basis von meteorologischen Daten ermittelt (Rollenbeck and Bendix 2011; Fries et al. 2012).

7.4 Fragen und Hypothesen

Im ersten Kapitel meiner Dissertation untersuchte ich, wie direkte und indirekte Effekte von Höhe die räumlichen Muster von Vogelgemeinschaften beeinflussen (Santillán et al. eingereicht). Ich erwartete, dass direkte Effekte wegen unterschiedlicher evolutionärer Geschichten von Tiefland- und Hochland-Gemeinschaften, wichtig für Artenreichtum und -abundanz der allgemeinen Vogelgemeinschaften entlang des Höhengradienten sind (Weir 2006). Ich erwartete auch, dass indirekte –über Klima und Vegetationsstruktur vermittelte – Höheneffekte, für spezifische Nahrungsgilden besonders wichtig sind (Ferger et al. 2014). Zusätzlich erwartete ich, dass Vegetationsstruktur wichtiger für Insektivore als für Frugivore Vögel ist (Jankowski et al. 2013; Ferger et al. 2014).

Im zweiten Kapitel untersuchte ich die Faktoren, welche die zeitlichen Veränderungen von Vogelgemeinschaften entlang von Höhengradienten bestimmen (Santillán et al. 2018). Ich erwartete eine Abnahme der Biodiversität mit zunehmender Höhe (McCain 2009). Zusätzlich erwartete ich zeitliche Veränderungen von Gemeinschaften auf Grund von saisonalen Effekten des Klimas, sowie der Nahrungsressourcen (Loiselle and Blake 1991). Speziell erwartete ich wegen physiologischen Limitierungen einen stärkeren Effekt von Temperatur auf Vogelabundanz, -äquität und -reichtum in den Hochlagen (Hawkins et al. 2003), während sich die Verfügbarkeit von Ressourcen wegen des stärkeren Wettbewerbs in den artenreicheren Gemeinschaften, besonders in den Tieflagen auf Vogelabundanz, -äquität und -reichtum auswirken sollte (Brown et al. 1996).

Im dritten Kapitel analysierte ich, wie sich Waldfragmentierung auf taxonomische und funktionelle Vogeldiversität auswirkt (Santillán et al. 2019). Ich erwartete, dass taxonomische und funktionelle Diversität in Waldfragmenten im Vergleich zu zusammenhängenden Waldflächen entlang des Höhengradienten jeweils niedriger ist (Nogués-Bravo et al. 2008; Flynn et al. 2009, Sitters et al. 2016). Ich erwartete auch, dass Fragmentierungseffekte bei funktionell überstreuten, artenreichen Tiefland-Gemeinschaften stärker zu Tage treten als in funktionell gruppierten, artenarmen Hochland-Gemeinschaften (Dehling et al. 2014).

7.5 Ergebnisse und Diskussion

Im ersten Kapitel konnte ich zeigen, dass sich Höhe vor allem indirekt auf Vogelgemeinschaften auswirkt, was über Temperatur, Niederschlag und Vegetationsstruktur vermittelt wird. Allerdings fand ich auch einen direkten Höheneffekt auf die allgemeine Vogelgemeinschaft, sowie auf insektivore, nicht aber auf frugivore Vögel (Santillán et al. eingereicht). Diese Ergebnisse legen nahe, dass Vogeldiversität in den Hochlagen höher ist als erwartet, was wahrscheinlich an anderen Faktoren liegt, die mit Höhe zusammenhängen, wie z.B. Art-Areal Effekte, biotische Interaktionen, oder der evolutionäre Kontext (McCain and Grytnes 2010). Der gegenläufige Effekt von Temperatur und Niederschlag auf Muster der ökologischen Gemeinschaften hängt mit physiologischen Limitierungen (Allen et al. 2002) und Beschränkungen in der Futtersuche zusammen (Boyle et al. 2010). Dass sich Vegetationsstruktur stärker auf Insektivore, als auf Frugivore auswirkt, liegt vermutlich an spezialisierten Futtersuche-Techniken der Insektivoren, welche eng an Vegetationsstruktur gebunden sind (Willson 1974; Pigot et al. 2016). Frugivore hingegen sind stärker von Pflanzendiversität und Fruchtabundanz abhängig (Loiselle and Blake 1991; Kissling et al. 2007). Meine Ergebnisse legen nahe, dass mehrere Umweltfaktoren in ihren Effekten auf Vogelgemeinschaften entlang tropischer Berghänge interagieren (McCain 2009), was wiederum die potenzielle Anfälligkeit von Biodiversität für den globalen Wandel unterstreicht.

Im zweiten Kapitel fand ich eine Abnahme der Vogeldiversität in den Hochlagen und saisonale Effekte in allen Höhenlagen (Santillán et al. 2018). Nicht-signifikante Abnahmen der Individuenzahlen entlang des Höhengradienten legen nahe, dass die Abundanz in relativ artenarmen Gemeinschaften in den Hochlagen im Vergleich zu artenreichen Gemeinschaften der Tieflagen höher ist (Willig and Presley 2015). Der positive Effekt von Temperatur auf Abundanz in mittleren und hohen Höhenlagen legt nahe, dass die Gemeinschaften durch Temperatur limitiert sind und an hohe Wasserverfügbarkeit angepasst sind. Im Gegensatz hierzu legt der negative Effekt von Niederschlag in mittleren und niedrigen Höhen nahe, dass die Gemeinschaften durch Wasserverfügbarkeit und nicht durch Temperatur limitiert sind. Die Tatsache, dass ich keinen Effekt von Nahrungsressourcen auf die zeitlichen Veränderungen der Vogelgemeinschaften finden konnte, könnte sich durch die in dem untersuchten Ökosystem sehr hohe Produktivität erklären (Brehm et al. 2008; Homeier et al. 2008), welche zu einer Entkopplung zwischen Ressourcenverfügbarkeit und Konsumentendiversität führen könnte (Feinsinger 1976). Diese Ergebnisse legen nahe, dass zeitliche Veränderungen in den Vogelgemeinschaften in meinem Untersuchungsgebiet hauptsächlich auf Grund von klimatischen Limitierungen erfolgen, was die potenzielle Empfindlichkeit von Vogelgemeinschaften gegenüber Klimawandel hervorhebt (Blake and Loiselle 2015).

Im dritten Kapitel konnte ich eine Abnahme der taxonomischen Vogeldiversität mit zunehmender Höhe zeigen, fand aber ein komplexeres Bild auf der Ebene der funktionellen Diversität (Santillán et al. 2019). Höherer Vogelreichtum und -abundanz in fragmentierten, verglichen mit zusammenhängenden Waldflächen, könnte das Ergebnis einer Zunahme von Habitatgeneralisten sein, welche den Verlust von Waldspezialisten in der Gemeinschaft kompensieren (Neuschulz et al. 2011). Dass sich Fragmentierung stärker auf die Anzahl der Individuen auswirkt, könnte daran liegen, dass sich Veränderungen in der Umwelt oftmals zuerst auf die Abundanz und dann erst auf den Artenreichtum auswirken (Currie et al. 2004). Die Abnahme von FRic und FDis in fragmentierten Waldflächen der Tieflagen, könnte am funktionellen Verlust verschiedener Arten mit extremen morphologischen Merkmalen liegen (Flynn et al. 2009; Bregman et al. 2016). Die Zunahme von FRic in fragmentierten Waldstücken der Hochlagen deutet auf eine Zunahme von generalisierten Arten mit unterschiedlichen Morphologieen hin (Stotz et al. 1996; Bregman et al. 2014), was die funktionelle

Zusammensetzung der Gemeinschaften verändert. Diese Ergebnisse legen nahe, dass sich taxonomische Diversität von funktioneller Diversität entkoppeln kann (Petchey and Gaston 2006), was besonders auf die hochdiversen Tiefland-Gemeinschaften zutrifft. Diese Ergebnisse unterstreichen auch, wie unser Verständnis der Effekte von menschlicher Störung auf Biodiversität davon profitieren kann, verschiedene Facetten der Diversität zu untersuchen (Mayfield et al. 2010).

7.6 Zusammenfassung und Synthese

Meine Ergebnisse legen nahe, dass raum-zeitliche Muster in Vogelgemeinschaften entlang von Höhengradienten von synergistischen Interaktionen zwischen Umweltfaktoren abhängen. Gegenläufige Effekte von Temperatur und Niederschlag, Vegetationsstruktur und Landnutzung, sowie anderer Faktoren, die mit der Höhe zusammenhängen, beeinflussen die raum-zeitlichen Muster von ökologischen Gemeinschaften und derer von funktionellen Gruppen. Dies hebt die Bedeutung der Interaktion von verschiedenen Umweltfaktoren für Biodiversität in komplexen, tropischen Bergsystemen hervor (McCain and Grytnes 2010).

Da die Struktur von ökologischen Gemeinschaften direkt und indirekt von den Effekten verschiedener abiotischer und biotischer Faktoren abhängig ist (Wiens 2011), sind Untersuchungen zu raum-zeitlichen Mustern von Biodiversität sehr komplex. Ein tieferes Verständnis von Umweltfaktoren ist jedoch wichtig, um die Effekte von Klima- und Landnutzungswandel auf Biodiversität besser zu verstehen. Zu erforschen, wie sich Biodiversität und die zugrundeliegenden ökologischen Funktionen in Zusammenhang mit klimatischen Bedingungen, Vegetationsstruktur und menschlicher Störung entlang von Höhengradienten verhält, ist somit unerlässlich, um den Verlust von Biodiversität und die funktionelle Homogenisierung von Artgemeinschaften vorherzusagen. Neben Untersuchungen zur Diversität ganzer Artgemeinschaften sind auch Studien zu spezifischen funktionellen Gruppen wichtig, um besser einschätzen zu können, wie Artengemeinschaften auf mögliche Änderungen des Ökosystems reagieren.

8. Resumen

8.1 Introducción

Los patrones globales de la biodiversidad están determinados por factores medio ambientales que están asociados a gradientes latitudinales, longitudinales y altitudinales (Gaston 2000). Estos factores abióticos y bióticos afectan espacial y temporalmente las comunidades, y determinan la diversidad y distribución de las especies (Wiens 2011; Louthan et al. 2015). Los factores abióticos incluyen aspectos del medio físico y clima, regulando la productividad ambiental y conduciendo los procesos evolutivos y las interacciones bióticas (Soberón and Peterson 2005). Las dinámicas de la temperatura y precipitación regulan las tasas de crecimiento y reproducción de las poblaciones naturales, directamente a través de efectos fisiológicos (Allen et al. 2006), e indirectamente a través de interacciones bióticas (Wright 1983) y productividad medio ambiental (O'Brien 1998). Sin embargo, los efectos de las dinámicas agua-energía no son iguales para todos los taxones y/o grupos funcionales dentro de estos taxones (O'Brien 1998). Los factores bióticos por su parte incluyen la estructura del hábitat, los efectos de borde y ecotono, y las interacciones bióticas. Estos factores bióticos determinan las tasas de natalidad y mortalidad, especiación y extinción, y migración de las especies a escalas locales y regionales (Wisz et al. 2013). Sin embargo, el mutualismo y la competencia son considerados los principales factores bióticos (Bascompte 2009). Las redes de interacción mutualistas aumentan la biodiversidad y minimizan la competición (Bastolla et al. 2009). Por su parte, la competencia regula la interacción entre las especies, afectando la estructura de las comunidades (Freeman 2015). El cambio climático y de uso del suelo simplifican y homogenizan de la biodiversidad, afectando las funciones ecológicas e interacciones bióticas de las especies, inclusive antes que las especies involucradas desaparezcan (Opdam and Wascher 2004; Suárez et al. 2011). Entender la variación espacial y temporal de las comunidades naturales a través de diferentes ecosistemas es uno de los principales desafíos de la ecología. Por lo tanto, es necesario analizar diferentes facetas de la diversidad, para mejorar las predicciones de las respuestas de la biodiversidad y sus funciones ecosistémicas a los cambios medio ambientales (Mayfield et al. 2010).

8.2 Sistema y área de estudio

Los bosques tropicales son vastos y complejos sistemas, con la mayor diversidad de taxones superiores (Carson and Schnitzer 2008). Las montañas tropicales son ecosistemas de alta diversidad de plantas y vertebrados (Willig et al. 2003), con un amplio rango de temperaturas de la base a la punta, y una gran disponibilidad y variabilidad de precipitación a través del gradiente de elevación (Barry 2008). La ladera sureste de los Andes ecuatorianos es conocida como una zona de gran diversidad y endemismo debido a su compleja topografía y gran hábitat variabilidad (Brehm et al. 2008). El área tiene un clima húmedo tropical de montaña con una gran variabilidad climática, influenciada por las regiones biogeográficas, seca Catamayo-Alamor y húmeda de páramo sudeste (Ministerio de Ambiente del Ecuador 2012).

El estudio fue conducido dentro y alrededor del Parque Nacional Podocarpus y la reserva San Francisco, a los 1000, 2000 y 3000 m s.n.m. En bosques continuos dentro de reservas protegidas y en bosques fragmentados que rodean las reservas, incrustados en una matriz de pastizales. El área de estudio se caracteriza por un clima montano tropical (Kottek et al. 2006) con un régimen de lluvia bimodal (temporada más húmeda, temporada menos húmeda, Emck 2007), en todo el gradiente de elevación. En elevaciones bajas, la temperatura media es 20 °C y la precipitación media es 2432 mm. En elevaciones medias, la temperatura media es 15,5 °C y la precipitación media es 2079 mm. En elevaciones altas, la temperatura media es 10 °C y la precipitación media es 4522 mm (Emck 2007).

8.3 Métodos y diseño del estudio

El estudio se realizó en 18 parcelas de 1 ha, instaladas en tres bosques continuos y tres fragmentados de cada elevación. En cada parcela se ubicó nueve puntos de conteo, donde se registró e identificó las especies dentro de un radio de 20 metros durante 10 minutos. Las comunidades de aves fueron monitoreadas dos veces en la temporada más húmeda (mayo-julio) y dos veces en la temporada menos húmeda (septiembre-noviembre), entre 2014 y 2015. La riqueza y abundancia de especies se obtuvo agrupando los registros por parcela y réplicas temporales. Se usó los datos de Wilman et al. (2014) para la clasificación de nectarívoros, frugívoros, insectívoros y omnívoros. Los rasgos funcionales ecomorfológicos se midieron en colecciones de museos. La riqueza funcional (FRic) y la dispersión funcional (FDis) fue cuantificada a través de seis índices de los rasgos funcionales y la masa corporal. La disponibilidad de flores y frutos, la biomasa fresca de invertebrados del sotobosque y la heterogeneidad de la vegetación vertical fue estimada mediante métodos estandarizados (Bibby et al. 2000). Los promedios mensuales de la temperatura y precipitación para cada parcela se obtuvieron a través de técnicas de detección remota y datos meteorológicos (Rollenbeck and Bendix 2011; Fries et al. 2012).

8.4 Preguntas e hipótesis

En el primer capítulo de esta tesis estudié cómo los efectos directos e indirectos de la elevación influyen la variación espacial de las comunidades de aves (Santillán et al. artículo enviado). Esperaba que los efectos de la elevación sean importantes para la diversidad en el gradiente altitudinal, debido a la diferente historia evolutiva de las comunidades de tierras bajas y altas (Weir 2006). También, esperaba que efectos indirectos de la elevación a través del clima y la estructura de la vegetación serían más importantes para las aves frugívoras e insectívoras (Ferger et al. 2014). Además, esperaba que la estructura de la vegetación esté más asociada con los insectívoros que con los frugívoros (Jankowski et al. 2013; Ferger et al. 2014).

En el segundo capítulo examiné los factores que determinan la variación temporal de las comunidades de aves a través del gradiente altitudinal (Santillán et al. 2018). Esperaba que la biodiversidad disminuya con el aumento de la elevación (McCain 2009b). Además, esperaba una variación temporal de las comunidades debido a la estacionalidad del clima y los recursos alimenticios (Loiselle and Blake 1991). En concreto, esperaba que la temperatura y la precipitación limiten la diversidad en elevadas altas, debido a limitaciones fisiológicas (Hawkins et al. 2003a); y la disponibilidad de recursos afecte la diversidad de aves a elevaciones bajas, debido a la competencia por los recursos (Brown et al. 1996b).

En el tercer capítulo analicé cómo la diversidad taxonómica y funcional de aves es afectada por la fragmentación de los bosques (Santillán et al. 2019). Esperaba de una disminución asociada de la diversidad taxonómica y funcional en bosques fragmentados en comparación con los bosques continuos en el gradiente de elevación (Nogués-Bravo et al. 2008; Flynn et al. 2009; Sitters et al. 2016). También, esperaba más fuertes efectos de la fragmentación en la diversidad funcional en comunidades diversas y funcionalmente dispersas de tierras bajas, que en las comunidades relativamente pobres y agrupadas funcionalmente de tierras altas (Dehling et al. 2014).

8.5 Resultados y discusión

En el primer capítulo, encontré que la elevación principalmente está indirectamente asociada con la comunidad de aves, a través de la combinación de la temperatura, precipitación y estructura de la vegetación. Sin embargo, el efecto directo en toda la comunidad e insectívoros, pero no en los frugívoros (Santillán et al. Artículo enviado), sugiere una diversidad mayor de la esperada en elevaciones altas, debido a otros factores relacionados con la elevación, como la configuración espacial, biótica y evolutiva (McCain and Grytnes 2010). El efecto opuesto de la temperatura y la precipitación en los patrones de la comunidad está relacionado con la productividad (Allen et al. 2002), y al tiempo efectivo de forrajeo de las aves (Boyle et al. 2010). El mayor efecto de la estructura de la vegetación en los insectívoros que en los frugívoros es probablemente debido a las técnicas de forrajeo especializadas de las aves insectívoras, fuertemente asociadas a la estructura de vegetación (Willson 1974; Pigot et al. 2016). En contraste, las aves frugívoras están más asociadas a la diversidad de platas y la abundancia de frutos (Loiselle and Blake 1991; Kissling et al. 2007). Mis resultados indican la interacción de varios factores medio ambientales en los patrones de las comunidades de aves a lo largo de las laderas de montañas tropicales (McCain 2009b). Por lo tanto, la potencial susceptibilidad de la biodiversidad al cambio medio ambiental global.

En el segundo capítulo, encontré la disminución de la diversidad de aves en elevaciones altas, y una estacionalidad de la abundancia, la uniformidad y la riqueza de aves en todas las elevaciones (Santillán et al. 2018). Los cambios no significativos en el número de individuos a lo largo del gradiente de elevación indican mayor abundancia en comunidades relativamente pobres en altas elevaciones, que en las ricas comunidades de elevaciones bajas (Willig and Presley 2015). El efecto positivo de la temperatura en la abundancia en elevaciones medias y altas, sugiere que estás comunidades están limitadas por la temperatura y adaptadas a la alta disponibilidad de agua. En contraste, el efecto negativo de la precipitación en elevaciones medias y bajas, sugiere que estás comunidades están limitadas por fuertes lluvias, pero no por la temperatura. El no efecto los recursos alimenticios en la variación temporal de la comunidad de aves podría ser debido la alta productividad de las plantas del ecosistema estudiado (Brehm et al. 2008; Homeier et al. 2008), lo que podría conducir a un desacoplamiento de la disponibilidad de recursos y el consumo (Feinsinger 1976). Estos resultados sugieren que en mi área de estudio las fluctuaciones temporales de las comunidades de aves ocurren principalmente debido a limitaciones climáticas, subrayando la potencial sensibilidad de las comunidades de aves al proyectado cambio climático (Blake and Loiselle 2015).

En el tercer capítulo, encontré una disminución de la diversidad taxonómica de las aves hacia elevaciones altas, pero un efecto más complejo de la diversidad funcional a través del gradiente de elevación (Santillán et al. 2019). La mayor riqueza y abundancia de especies en bosques fragmentados que en bosques continuos podría ser resultado del aumento de generalistas, compensando la pérdida de especialistas en la comunidad (Neuschulz et al. 2011). El mayor efecto de la fragmentación en el número de individuos podría deberse a que los cambios ambientales suelen afectar primero a la abundancia, y posteriormente a la riqueza de especies (Currie et al. 2004). La disminución de FRic y FDis en bosques fragmentados solo en elevaciones bajas, se debería a la pérdida de especies funcionalmente distintas con rasgos morfológicos extremos (Flynn et al. 2009; Bregman et al. 2016). El aumento de FRic en los bosques fragmentados en elevaciones altas, indica ganancia de generalistas con distintas morfologías (Stotz et al. 1996; Bregman et al. 2014), lo que resulta en cambios en la composición funcional de estas comunidades. Estos resultados indican que la diversidad taxonómica se puede desacoplar de la diversidad funcional en bosques fragmentados (Petchey and Gaston 2006), particularmente en diversas comunidades de tierras bajas. Destacando que incluir diferentes facetas de la diversidad puede mejorar la comprensión de la perturbación humana en la biodiversidad (Mayfield et al. 2010).

8.6 Síntesis y conclusiones

Mis resultados indican que los patrones espacio-temporales de la comunidad de aves dependen en gran medida de las interacciones sinérgicas entre los factores medio ambientales en el gradiente de elevación. El efecto opuesto de la temperatura y la precipitación, la estructura de la vegetación y uso del suelo, y otros factores relacionados con la elevación influenciaron los patrones espacio-temporales de la diversidad. Además, diferentes efectos de los factores medio ambientales en los grupos funcionales. Enfatizando la interacción de varios impulsores ambientales en los patrones de biodiversidad en los complejos sistemas de montañas tropicales (McCain and Grytnes 2010).

Dado que la estructura de las comunidades depende directamente e indirectamente del efecto conjunto de varios impulsores abióticos y bióticos (Wiens 2011), el estudio de los patrones espacio-temporales de la biodiversidad debería centrarse en las comunidades y sus diferentes grupos funcionales. Prediciendo las respuestas de la biodiversidad y sus funciones ecológicas a los efectos estructura de la vegetación y perturbación humana en el gradiente de elevación (Opdam and Wascher 2004). Para evaluar la variación de la biodiversidad y la homogeneización funcional de comunidades a través del estudio de la diversidad de toda la comunidad y de sus especialistas tróficos funcionalmente importantes.

Una mejor comprensión del efecto de los factores medio ambientales en las especies y sus roles funcionales es esencial para mantener la biodiversidad, garantizando la integridad de los ecosistemas (Cardinale et al. 2012). Los impulsores medio ambientales son fundamentales para predecir los impactos del cambio climático y del uso del suelo sobre la biodiversidad y sus roles en el ecosistema.

9. References

Publications marked with an asterisk (*) are included in the Appendices of this thesis.

Adams J. (1985) The definition and interpretation of guild structure in ecological communities. Journal of Animal Ecology 54:43–59

Adler PB, Levine JM (2007) Population variability of sparrows in space and time. Oikos 116:221–232

Aizen MA (2003) Down-facing flowers, hummingbirds and rain. Taxon 52:675–680

Allen AP, Brown JH, Gillooly JF (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Science 297:1545–1548

Allen AP, Gillooly JF, Savage VM, Brown JH (2006) Kinetic effects of temperature on rates of genetic divergence and speciation. Proceedings of the National Academy of Sciences 103:9130–9135

Anderson AS, Storlie CJ, Shoo LP, et al (2013) Current analogues of future climate indicate the likely response of a sensitive montane tropical avifauna to a warming world. PLoS ONE 8:e69393

Anderson P, Marengo J, Villalba R, et al (2011) Consequences of climate change for ecosystems and ecosystem services in the tropical Andes. In: Herzog S, Matínez R, Jørgensen P, Tiessen H (eds) Climate change and biodiversity in the tropical Andes. Inter-American Institute for Global Change Research, pp 1–18

Balmford A, Green MJB, Murray MG (1996a) Using higher-taxon richness as a surrogate for species richness: I. regional test. Proceedings of the Royal Society B: Biological Sciences 263:1267–1274

Balmford A, Jayasuriya AHM, Green MJB (1996b) Using higher-taxon richness as a surrogaye for species richness: II local applications. Proceedings of the Royal Society of London: Biological Sciences 263:1571–1575

Barry RG (2008) Mountain weather and climate, 3rd edn. Cambridge University Press, Cambridge, UK

Bascompte J (2009) Mutualistic networks. Frontiers in Ecology and the Environment 7:429–436

Bässler C, Cadotte MW, Beudert B, et al (2016) Contrasting patterns of lichen functional diversity and species richness across an elevation gradient. Ecography 39:689–698

Bastolla U, Fortuna MA, Pascual-García A, et al (2009) The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458:1018–1020

Beck E, Makeschin F, Haubrich F, et al (2008) The ecosystem (Reserva Biológica San Francisco). In: Beck E, Bendix J, Kottke I, et al. (eds) Gradients in a tropical mountain ecosystem of Ecuador. Ecological studies, vol 198. Springer-Verlag Berlin Heidelberg, Berlin, pp 1–13

Begon M, Townsend CR, Harper JL (2006) Ecology: from iondividuals to ecosystems, 4th edn. Blackwell Publishing Ltd., Oxford

Bendix J, Rollenbeck R, Göttlicher D, Cermak J (2006) Cloud occurrence and cloud properties in Ecuador. Climate Research 30:133–147

Bibby C, Burgess N, Hill D, Mustoe S (2000) Bird census techniques, 2nd edn. Academic Press, Cambridge, UK

Blake JG, Loiselle BA (2015) Enigmatic declines in bird numbers in lowland forest of eastern Ecuador may be a consequence of climate change. PeerJ 3:e1177

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

Bowler DE, Hof C, Haase P, et al (2017) Cross-realm assessment of climate change impacts on species' abundance trends. Nature Ecology and Evolution 1:1–7

Boyce MS (1979) Seasonality and patterns of natural selection for life histories. The American Naturalist 114:569–583

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

Boyle WA, Conway CJ, Bronstein JL (2011) Why do some, but not all, tropical birds migrate? A comparative study of diet breadth and fruit preference. Evolutionary Ecology 25:219–236

Boyle WA, Norris DR, Guglielmo CG (2010) Storms drive altitudinal migration in a tropical bird. Proceedings of the Royal Society B: Biological Sciences 277:2511–2519

Bregman TP, Lees AC, MacGregor HEA, et al (2016) Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. Proceedings of the Royal Society B: Biological Sciences 283:20161289

Bregman TP, Sekercioglu CH, Tobias JA (2014) Global patterns and predictors of bird species responses to forest fragmentation: implications for ecosystem function and conservation. Biological Conservation 169:372–383

Brehm G, Homeier J, Fiedler K, et al (2008) Mountain rain forests in southern Ecuador as a hotspot of biodiversity – limited knowledge and diverging patterns. In: Beck E, Bendix J, Kottke I, et al. (eds) Gradients in a Tropical Mountain Ecosystem of Ecuador. Springer-Verlag Berlin Heidelberg, Berlin, pp 15–23

Breitbach N, Tillmann S, Schleuning M, et al (2012) Influence of habitat complexity and landscape configuration on pollination and seed-dispersal interactions of wild cherry trees. Oecologia 168:425–437

Brooker RW, Callaway RM, Cavieres LA, et al (2009) Don’t Diss Integration: a Comment on Ricklefs’s Disintegrating Communities. The American Naturalist 174:919–927

Brown JH (2014) Why are there so many species in the tropics? Journal of Biogeography 41:8–22

Brown JH, Gillooly JF, Allen AP, et al (2004) Toward a metabolic theory of ecology. Ecology 85:1771–1789

Brown JH, Lomolino M V. (1998) Biogeography, 2nd edn. Sinauer Associates, Inc., Sunderland

Brown JH, Mehlman DW, Stevens GC (1995) Spatial variation in abundance. Ecology 76:2028–2043

Brown JH, Morgan Ernest SK, Parody JM, Haskell JP (2001) Regulation of diversity: maintenance of species richness in changing environments. Oecologia 126:321–332

Brown JH, Stevens GC, Kaufman DM (1996a) The geographic range: size, shape, boundaries, and internal structure. Annual Review of Ecology and Systematics 27:597–623

Brown JH, Stevens GC, Kaufman DM (1996b) The geographic range: size, shape, boundaries, and internal structure. Annual Review of Ecology and Systematics 27:597–623

Burns TP (1989) Lindeman's contradiction and the trophic structure of ecosystems. Ecology 70:1355–1362

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48:1079–1087

Cadotte MW, Tucker CM (2017) Should environmental filtering be abandoned? Trends in Ecology and Evolution 32:429–437

Cardinale BJ, Duffy JE, Gonzalez A, et al (2012) Biodiversity loss and its impacton humanity. Nature 486:59–67

Carson WP, Schnitzer SA (2008) Tropical forest community ecology, 1st edn. Blackwell Publishing Ltd, Oxford

Cavender-Bares J, Ackerly DD, Hobbie SE, Townsend PA (2016) Evolutionary legacy effects on ecosystems: biogeographic origins, plant traits, and implications for management in the era of global change. Annual Review of Ecology, Evolution, and Systematics 47:433–462

Cisneros LM, Fagan ME, Willig MR (2014) Effects of human-modified landscapes on taxonomic, functional and phylogenetic dimensions of bat biodiversity. Diversity and Distributions 21:1–11

Clarke A, Gaston KJ (2006) Climate, energy and diversity. Proceedings of the Royal Society B: Biological Sciences 273:2257–2266

Colwell RK, Rahbek C, Gotelli NJ (2004) The mid-domain effect and species richness patterns: what have we learned so far? The American Naturalist 163:1–23

Condamine FL, Sperling FAH, Wahlberg N, et al (2012) What causes latitudinal gradients in species diversity? Evolutionary processes and ecological constraints on swallowtail biodiversity. Ecology Letters 15:267–277

Conord C, Gurevitch J, Fady B (2012) Large-scale longitudinal gradients of genetic diversity: a meta-analysis across six phyla in the mediterranean basin. Ecology and Evolution 2:2600–2614

Corbelli JM, Zurita GA, Filloy J, et al (2015) Integrating taxonomic, functional and phylogenetic beta diversities: interactive effects with the biome and land use across taxa. PLoS ONE 10:1–17

Cornell H V, Lawton JH (1992) Species interactions , local and regional processes , and limits to the richness of ecological communities: a theoretical perspective. Journal of Animal Ecology 61:1–12

Cote J, Bestion E, Jacob S, et al (2017) Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. Ecography 40:56–73

Cracraft J (1981) Toward a phylogenetic classification of the recent birds of the world (Class Aves). The Auk 98:681–714

Currie DJ, Mittelbach GG, Cornell H V., et al (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7:1121–1134

Dawideit BA, Phillimore AB, Laube I, et al (2009) Ecomorphological predictors of natal dispersal distances in birds. Journal of Animal Ecology 78:388–395

Dehling DM, Fritz SA, Töpfer T, et al (2014) Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. Ecography 37:1047–1055

Dénes F V., Silveira LF, Beissinger SR (2015) Estimating abundance of unmarked animal populations: accounting for imperfect detection and other sources of zero inflation. Methods in Ecology and Evolution 6:543–556

Díaz S, Lavorel S, Chapin III FS, et al (2007) Functional diversity - at the crossroads between ecosystem functioning and environmental filters. In: Canadell J, Pataki D, Pitelka L (eds) Terrestrial ecosystems in a changing world. Springer-Verlag Berlin Heidelberg, pp 81–91

Dornelas M, Magurran AE, Buckland ST, et al (2013) Quantifying temporal change in biodiversity: challenges and opportunities. Proceedings Biological sciences / The Royal Society 280:20121931

Dulle HI, Ferger SW, Cordeiro NJ, et al (2016) Changes in abundances of forest understorey birds on Africa's highest mountain suggest subtle effects of climate change. Diversity and Distributions 22:288–299

Emck P (2007) A climatology of south Ecuador. Universität Erlangen-Nürnberg

Emer C, Galetti M, Pizo MA, et al (2018) Seed-dispersal interactions in fragmented landscapes – a metanetwork approach. Ecology Letters 21:484–493

Evans KL, Warren PH, Gaston KJ (2005) Species-energy relationships at the macroecological scale: a review of the mechanisms. Biological Reviews of the Cambridge Philosophical Society 80:1–25

Feinsinger P (2001) Species diversity: easy to quantify, but what does means. In: Feinsinger P (ed) Designing field studies for biodiversity conservation, 1st edn. Island Press, Washington DC, p 212

Feinsinger P (1976) Organization of a tropical guild of nectarivorous birds. Ecological Monographs 46:257–291

Ferger SW, Schleuning M, Hemp A, et al (2014) Food resources and vegetation structure mediate climatic effects on species richness of birds. Global Ecology and Biogeography 23:541–549

Fiedler K, Brehm G, Hilt N, et al (2008) Variation of diversity patterns across moth families along a tropical altitudinal gradient. In: Beck E, Bendix J, Kottke I, et al.

(eds) Gradients in a tropical mountain ecosystem of Ecuador. Springer, Berlin, pp 167–180

Flynn DFB, Gogol-Prokurat M, Nogeire T, et al (2009) Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters 12:22–33

Forrest JRK, Thorp RW, Kremen C, Williams NM (2015) Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. Journal of Applied Ecology 52:706–715

Francis AP, Currie DJ (2003) A globally consistent richness□climate relationship for angiosperms. The American Naturalist 161:523–536

Freeman BG (2015) Competitive interactions upon secondary contact drive elevational divergence in tropical birds. The American Naturalist 186:470–479

Fries A, Rollenbeck R, Nauß T, et al (2012) Near surface air humidity in a megadiverse Andean mountain ecosystem of southern Ecuador and its regionalization. Agricultural and Forest Meteorology 152:17–30

Frishkoff LO, Karp DS, Flanders JR, et al (2016) Climate change and habitat conversion favour the same species. Ecology letters 19:1081–1090

Gámez-Virués S, Perović DJ, Gossner MM, et al (2015) Landscape simplification filters species traits and drives biotic homogenization. Nature Communications 6:1–8

Gaston KJ (2000) Global patterns in biodiversity. Nature 405:220–227

Gaston KJ, Williams PH (1993) Mapping the world's species-the higher taxon approach. Biodiversity Letters 1:2–8

Gilman SE, Urban MC, Tewksbury J, et al (2010) A framework for community interactions under climate change. Trends in Ecology and Evolution 25:325–331

Gotelli NJ, Colwell RK (2001) Quantifyinf biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391

Gray MA, Baldauf SL, Mayhew PJ, Hill JK (2007) The response of avian feeding guilds to tropical forest disturbance. Conservation Biology 21:133–141

Greenberg R (1981) The abundance and seasonality of forest canopy birds on Barro Colorado Island, Panama. Biotropica 13:241–251

Greffard MH, Saulnier-Talbot É, Gregory-Eaves I (2011) A comparative analysis of fine versus coarse taxonomic resolution in benthic chironomid community analyses. Ecological Indicators 11:1541–1551

Grenyer R, Orme CDL, Jackson SF, et al (2006) Global distribution and conservation of rare and threatened vertebrates. Nature 444:93–96

Grindal SD., Collard TS., Brigham R. M, Barclay RM. R. (1992) The influence of precipitation on reproduction by Myotis bats in British Columbia. The American Midland Naturalist 128:339–344

Grøtan V, Lande R, Engen S, et al (2012) Seasonal cycles of species diversity and similarity in a tropical butterfly community. Journal of Animal Ecology 81:714–723

Guillera-Arroita G (2017) Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. Ecography 40:281–295

Harris JBC, Dwi Putra D, Gregory SD, et al (2014) Rapid deforestation threatens mid-elevational endemic birds but climate change is most important at higher elevations. Diversity and Distributions 20:1–13

Harris LD (1988) Edge effects and conservation of Biotic diversity. Conservation Biology 2:330–332

Hau M (2001) Timing of breeding in variable environments: tropical birds as model systems. Hormones and Behavior 40:281–290

Hawkins BA, Diniz-filho JA, Jaramillo CA, Soeller SA (2006) Post-eocene climate change, niche conservatism, and the latitudinal diversity gradient of new world birds. Journal of Biogeography 33:770–780

Hawkins BA, Diniz□Filho JAF, Jaramillo CA, Soeller SA (2007) Climate, niche conservatism, and the global bird diversity gradient. The American Naturalist 170:S16–S27

Hawkins BA, Field R, Cornell H V., et al (2003a) Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117

Hawkins BA, Mccain CM, Davies TJ, et al (2012) Different evolutionary histories underlie congruent species richness gradients of birds and mammals. Journal of Biogeography 39:825–841

Hawkins BA, Porter EE, Diniz-Filho JAF (2003b) Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. Ecology 84:1608–1623

Hawkins CP, MacMahon JA (1989) Guilds: the Multiple Meanings of a Concept. Annual Review of Entomology 34:423–451

Helmus MR, Keller W, Paterson MJ, et al (2010) Communities contain closely related species during ecosystem disturbance. Ecology Letters 13:162–174

Herzog SK, Kessler M, Bach K (2005) The elevational gradient in andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. Ecography 28:209–222

Hill MO (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54:427–432

Homeier J, Werner FA, Gradstein SR, Richter M (2008) Potential vegetation and floristic composition of Andean forests in south Ecuador, with a focus on the RBSF. In: Beck E, Bendix J, Kottke I, et al. (eds) Gradients in a tropical mountain ecosystem of Ecuador. Springer, Berlin, pp 87–100

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography, 1st edn. Princenton University Press, New Jersey

Hurlbert SH. (1971) The nonconcept of species diversity : a critique and alternative parameters. Ecology 52:577–586

Huston MA (1999) Local processes and regional patterns : appropriate scales for understanding variation in the diversity of plants and animals. Oikos 86:393–401

Jankowski JE, Merkord CL, Rios WF, et al (2013) The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. Journal of Biogeography 40:950–962

Janzen DH (1967) Why mountain passes are higher in the tropics. The American Naturalist 101:233–249

Jarvis A, Touval JL, Schmitz MC, et al (2010) Assessment of threats to ecosystems in South America. Journal for Nature Conservation 18:180–188

Jarzyna MA, Jetz W (2016) Detecting the multiple facets of biodiversity. Trends in Ecology and Evolution 31:527–538

Jordano P (2016) Chasing Ecological Interactions. PLoS Biology 14:2–5

Kallimanis AS, Mazaris AD, Tsakanikas D, et al (2012) Efficient biodiversity monitoring: which taxonomic level to study? Ecological Indicators 15:100–104

Keith SA, Webb TJ, Böhning-Gaese K, et al (2012) What is macroecology? Biology Letters 8:904–906

Khaliq I, Böhning-Gaese K, Prinzinger R, et al (2017) The influence of thermal tolerances on geographical ranges of endotherms. Global Ecology and Biogeography 26:650–668

Khaliq I, Hof C, Prinzinger R, et al (2014) Global variation in thermal tolerances and vulnerability of endotherms to climate change. Proceedings of the Royal Society B: Biological Sciences 281:20141097

Kissling WD, Field R, Böhning-Gaese K (2008) Spatial patterns of woody plant and bird diversity: functional relationships or environmental effects? Global Ecology and Biogeography 17:327–339

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

Kissling WD, Sekercioglu CH, Jetz W (2012) Bird dietary guild richness across latitudes, environments and biogeographic regions. Global Ecology and Biogeography 21:328–340

Kot M, Schaffer WM (1984) The effects of seasonality on discrete models of population-growth. Theoretical Population Biology 26:340–360

Kottek M, Grieser J, Beck C, et al (2006) World map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift 15:259–263

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305

Larsen FW, Rahbek C (2005) The influence of spatial grain size on the suitability of the higher-taxon approach in continental priority-setting. Animal Conservation 8:389–396

Larsen TH, Brehm G, Navarette H, et al (2011) Range shifts and extinctions diven by climate change in the tropical Andes: synthesis and directions. In: Herzog S, Matínez R, Jørgensen P, Tiessen H (eds) Climate change and biodiversity in the tropical Andes. Inter-American Institute for Global Change Research, pp 47–67

Laurance WF, Camargo JLC, Luizão RCC, et al (2011) The fate of Amazonian forest fragments: A 32-year investigation. Biological Conservation 144:56–67

Lawton JH, Bignell DE, Bolton B, et al (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391:72–76

Legrand D, Cote J, Fronhofer EA, et al (2017) Eco-evolutionary dynamics in fragmented landscapes. Ecography 40:9–25

Lehouck V, Spanhove T, Vangestel C, et al (2009) Does landscape structure affect resource tracking by avian frugivores in a fragmented Afrotropical forest? Ecography 32:789–799

Leigh EG (2008) Tropical forest ecology: sterile or virgin for theoreticians? In: Carson WP, Schnitzer SA (eds) Tropical forest community ecology, 1st edn. Blackwell Publishing Ltd., Oxford, pp 121–142

Loiselle BA (1988) Bird abundance and seasonality in a Costa Rican lowland forest canopy. The Condor 90:761–772

Loiselle BA, Blake JG (1991) Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology 72:180–193

Louthan AM, Doak DF, Angert AL (2015) Where and when do species interactions set range limits? Trends in Ecology and Evolution 30:780–792

Mac Nally R (2007) Use of the abundance spectrum and relative-abundance distributions to analyze assemblage change in massively altered landscapes. The American Naturalist 170:319–330

MacArthur RH, MacArthur JW (1961) On bird species diversity. Ecology 42:594–598

MacNally RC. (1983) On assessing the significance of interspecific competition to guild structure. Ecology 64:1646–1652

Magurran AE (2007) Species abundance distributions over time. Ecology Letters 10:347–354

Magurran AE (2004) Measuring biological biversity, First. Blackwell Publications, Oxford

Mason NWH, De Bello F, Mouillot D, et al (2013) A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. Journal of Vegetation Science 24:794–806

Mason NWH, Mouillot D, Lee WG, et al (2005) Functional richness , functional evenness and functional divergence: the primary components of functional diversity. Oikos 111:112–118

Mayfield MM., Boni MF., Daily GC., Ackerly D (2005) Species and functional diversity of native and human-dominated plant communities. Ecology 86:2365–2372

Mayfield MM, Bosner SP, Morgan JW, et al (2010) What does species richness tell us about function trait diversity? Predictions and evidence of species and function trait diversity to land-use change. Global Ecology and Biogeography 19:423–431

McCain CM (2009a) Vertebrate range sizes indicate that mountains may be “higher” in the tropics. Ecology Letters 12:550–560

McCain CM (2009b) Global analysis of bird elevational diversity. Global Ecology and Biogeography 18:346–360

McCain CM, Colwell RK (2011) Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. Ecology Letters 14:1236–1245

McCain CM, Grytnes J-A (2010) Elevational gradients in species richness. Encyclopedia of Life Sciences (ELS) 1–10

Meynard CN, Devictor V, Mouillot D, et al (2011) Beyond taxonomic diversity patterns: how do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? Global Ecology and Biogeography 20:893–903

Ministerio de Ambiente del Ecuador (2012) Sistema de clasificación de los ecosistemas del Ecuador continental, 1st edn. Subsecretaría de Patrimonio Natural, Quito

Mittelbach GG, Schemske DW, Cornell H V., et al (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecology Letters 10:315–331

Montaño-Centellas FA, Garitano-Zavala Á (2015) Andean bird responses to human disturbances along an elevational gradient. Acta Oecologica 65–66:51–60

Mori AS, Furukawa T, Sasaki T (2013) Response diversity determines the resilience of ecosystems to environmental change. Biological Reviews 88:349–364

Mulwa RK, Böhning-Gaese K, Schleuning M (2012) High bird species diversity in structurally heterogeneous farmland in western Kenya. Biotropica 44:801–809

Mulwa RK, Neuschulz EL, Böhning-Gaese K, Schleuning M (2013) Seasonal fluctuations of resource abundance and avian feeding guilds across forest-farmland boundaries in tropical Africa. Oikos 122:524–532

Myers N, Mittermeier RA, Mittermeier CG, et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Naoki K (2007) Arthropod resource partitioning among omnivorous tanagers (Tangara spp.) in western Ecuador. The Auk 124:197–209

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

Newbold T, Hudson LN, Hill SLL, et al (2015) Global effects of land use on local terrestrial biodiversity. Nature 520:45–50

Niu K, Choler P, de Bello F, et al (2014) Fertilization decreases species diversity but increases functional diversity: a three-year experiment in a Tibetan alpine meadow. Agriculture, Ecosystems and Environment 182:106–112

Nogués-Bravo D, Araújo MB, Romdal T, Rahbek C (2008) Scale effects and human impact on the elevational species richness gradients. Nature 453:216–219

Noss RF (1990) Indicators for monitoring biodiversity: a hierarchical approach. Coservation Biology 4:355–364

O'Brien EM (1998) Water-energy dynamics , climate, and prediction of woody plant species richness: an interim general model. Journal of Biogeography 25:379–398

O'Brien EM, Field R, Whittaker RJ (2000) Climatic gradients in woody plant (tree and shrub) diversity: water-energy dynamics, residual variation, and topography. Oecologia 89:588–600

Opdam P, Wascher D (2004) Climate change meets habitat fragmentation: Linking landscape and biogeographical scale levels in research and conservation. Biological Conservation 117:285–297

Orme CDL, Davies RG, Burgess M, et al (2005) Global hotspots of species richness are not congruent with endemism or threat. Nature 436:1016–1019

Ortega-Jimenez VM, Dudley R (2012) Flying in the rain: hovering performance of Anna's hummingbirds under varied precipitation. Proceedings of the Royal Society B: Biological Sciences 279:3996–4002

Pakeman RJ (2014) Functional trait metrics are sensitive to the completeness of the species' trait data? Methods in Ecology and Evolution 5:9–15

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annual of Ecology, Evolution and Systematics 37:637–669

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

Paulsch A, Piechowski D, Müller-Hohenstein K (2008) Forest vegetation structure along an altitudinal gradient in southern Ecuador. In: Beck E, Bendix J, Kottke I, et al. (eds) Gradients in a tropical mountain ecosystem of Ecuador. Ecological studies, vol 198. Springer-Verlag Berlin Heidelberg, Berlin, pp 113–121

Pawar S, Koo MS, Kelley C, et al (2007) Conservation assessment and prioritization of areas in Northeast India: priorities for amphibians and reptiles. Biological Conservation 136:346–361

Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecology Letters 9:741–758

Petit DR (2015) Papers lands evaluating the importance of human-modified for conservation. Conservation Biology 17:687–694

Pigot AL, Trisos CH, Tobias JA (2016) Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. Proceedings of the Royal Society B: Biological Sciences 283:1–9

Pohle P (2008) The people settled around Podocarpus National Park. In: Beck E, Bendix J, Kottke I, et al. (eds) Gradients in a tropical mountain ecosystem of Ecaudor. Ecological studies 198. Springer-Verlag Berlin Heidelberg, Berlin, pp 25–36

Pohle P, Gerique A, López MF, Spohner R (2013) Current provisioning ecosystem services for the local population: landscape transformation, land use, and plant use. In: Bendix J, Beck E, Bräuning A, et al. (eds) Ecosystem services, biodiversity and environmental change in a tropical mountain ecosystem of south Ecuador. Ecological studies 221. Springer-Verlag Berlin Heidelberg, Berlin, pp 219–234

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

Quintero I, Jetz W (2018) Global elevational diversity and diversification of birds. Nature 555:246–250

Quitián M, Santillán V, Espinosa CI, et al (2017) Elevation-dependent effects of forest fragmentation on plant-bird interaction networks in the tropical Andes. Ecography 40:1–10

Rahbek C (1997) The relationship among area, elevation, and regional species richness in neotropical birds. The American Naturalist 149:875–902

Rahbek C (1995) The elevational gradient of species richness: a uniform pattern? Oikos 18:200–205

Richter M, Beck E, Rollenbeck R, Bendix J (2013) The study area. In: Bendix J, Beck E, Bräuning A, et al. (eds) Ecosystem services, biodiversity and environmental change in a tropical mountain ecosystem of south Ecuador, First. Springer-Verlag Berlin Heidelberg, Berlin, pp 3–17

Ricklefs RE (2008) Disintegration of the Ecological Community. The American Naturalist 172:741–750

Ricklefs RE, Miller GL (2000) Ecology, 4th edn. Freeman, W. H, New York

Rohde K (1992) Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65:514–527

Rollenbeck R, Bendix J (2011) Rainfall distribution in the Andes of southern Ecuador derived from blending weather radar data and meteorological field observations. Atmospheric Research 99:277–289

Rosenzweig ML (1995) Species diversity in space and time, 1st edn. Cambridge University Press, Cambridge

Ruggiero A, Hawkins BA (2008) Why do mountains suport so many species of birds? Ecography 31:306–315

*Santillán V, Quitián M, Tinoco BA, et al (2018) Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient. PLoS ONE 13:1–15

*Santillán V, Quitián M, Tinoco BA, et al (2019) Different responses of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient.

Oecologia 189:863-873

*Santillán V, Quitián M, Tinoco BA, et al (submited) Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient. Submited to Acta Oecologica.

Schulze CH, Waltert M, Kessler PJA, et al (2004) Biodiversity Indicator Groups of Tropical Land-Use Systems: comparing Plants , Birds , and Insects. Ecological Applications 14:1321–1333

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

Seymour CL, Simmons RE, Joseph GS, Slingsby JA (2015) On bird functional diversity: species richness and functional differentiation show contrasting responses to rainfall and vegetation structure in an arid landscape. Ecosystems 18:971–984

Shimadzu H, Dornelas M, Henderson PA, Magurran AE (2013) Diversity is maintained by seasonal variation in species abundance. BMC Biology 11:1–9

Shimadzu H, Dornelas M, Magurran AE (2015) Measuring temporal turnover in ecological communities. Methods in Ecology and Evolution 6:1384–1394

Simberloff D, Dayan T (1991) The guild concept and the structure of ecological communities. Annual Review of Ecology and Systematics 22:115–143

Sitters H, Di Stefano J, Christie F, et al (2016) Bird functional diversity decreases with time since disturbance: does patchy prescribed fire enhance ecosystem function? Ecological Applications 26:115–127

Slik JWF, Franklin J, Arroyo-Rodríguez V, et al (2018) Phylogenetic classification of the world's tropical forests. Proceedings of the National Academy of Sciences 115:1837–1842

Smith B, Wilson JB (1996) A consumer's guide to evenness indices. Oikos 76:70–82

Soberón J, Peterson AT (2005) Short- and long-term effects of United Nations peace operations. Biodiversity Informatics 2:1–10

Soh MCK, Sodhi NS, Lim SLH (2006) High sensitivity of montane bird communities to habitat disturbance in Peninsular Malaysia. Biological Conservation 129:149–166

Stewart JR, Lister AM, Barnes I, Dalén L (2010) Refugia revisited: individualistic responses of species in space and time. Proceedings of the Royal Society B: Biological Sciences 277:661–671

Stotz DF, Fitzpatrick JW, Parker TA, Moskovits DK (1996) Neotropical birds: ecology and conservation, 1st edn. University of Chicago Press, Chicago

Suárez CF, Naranjo LG, Espinosa JC, Sabogal J (2011) Land use changes and their synergies with climate change. In: Herzog S, Matínez R, Jørgensen P, Tiessen H (eds) Climate change and biodiversity in the tropical Andes. Inter-American Institute for Global Change Research, pp 141–151

Tapia-Armijos MF, Homeier J, Espinosa CI, et al (2015) Deforestation and forest fragmentation in south Ecuador since the 1970s - losing a hotspot of biodiversity. PLoS ONE 10:1–18

Terborgh J (1977) Bird species diversity on an Andean elevational gradient. Ecology 58:1007–1019

Terborgh J (1985) The role of ecotones in the distribution of Andean birds. Ecology 66:1237–1246

Tews J, Brose U, Grimm V, et al (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31:79–92

Tilman D (1994) Competition and biodiversity in spatially structured habitats. Ecology 75:2–16

Tilman D (2001) Functional Diversity. Encyclopedia of Biodiversity 587–596

Tingley MW, Beissinger SR (2009) Detecting range shifts from historical species occurrences: new perspectives on old data. Trends in Ecology and Evolution 24:625–633

Tingley MW, Koo MS, Moritz C, et al (2012) The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. Global Change Biology 18:3279–3290

Tinoco BA, Santillán V, Graham CH (2018) Land use change has stronger effects on functional diversity than taxonomic diversity in tropical Andean hummingbirds. Ecology and Evolution 8:3478–3490

Tscharntke T, Sekercioglu CH, Dietsch T V., et al (2008) Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. Ecology 89:944–951

Verner J (1984) The guild concept applied to management of bird populations. Environmental Management 8:1–13

Villaseñor JL, Ibarra-manríquez G, Meave JA, Ortíz E (2005) Higher taxa as surrogates of plant biodiversity in a megadiverse country. Conservation Biology 19:232–238

Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301

Waide RB, Willig MR, Steiner CF, et al (1999) The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30:257–300

Wainwright PC (1994) Functional morphology as a tool in ecological research. In: Wainwright PC, Reilly S. . (eds) Ecological morphology, 1st edn. The University of Chicago Press, Chicago, pp 42–59

Walker BH, Steffen WL (1999) The nature of global change. In: Walker B, Steffen W, Canadell J, Ingram J (eds) The terrestrial biosphere and global change, 1st edn. Cambridge University Press, Cambridge, UK, p 439

Waltert M, Bobo KS, Sainge NM, et al (2005) From forest to farmland: habitat effects on afrotropical forest bird diversity. Ecological Applications 15:1351–1366

Walther G-R, Post E, Convey P, et al (2002) Ecological responses to recent climate change. Nature 416:389–395

Weir JT (2006) Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. Evolution 60:842–855

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:213–251

Wiens JJ (2011) The niche, biogeography and species interactions. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2336–2350

Wikelski M, Hau M, Douglas Robinson W, Wingfield JC (2003) Reproductive seasonality of seven neotropical passerine species. The Condor 105:683–695

Williams PH, Gaston KJ (1994) Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? Biological Conservation 67:211–217

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

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution, and Systematics 34:273–309

Willig MR, Presley SJ (2015) Biodiversity and metacommunity structure of animals along altitudinal gradients in tropical montane forests. Journal of Tropical Ecology 32:421–436

Willson MF (1974) Avian community organization and habitat structure. Ecology 55:1017–1029

Wilman H, Belmaker J, Jennifer S, et al (2014) EltonTraits 1.0: species-level foraging attributes of the world’s birds and mammals. Ecology 95:2027

Winfree R, Fox JW, Williams NM, et al (2015) Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. Ecology Letters 18:626–635

Wisz MS, Pottier J, Kissling WD, et al (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biological Reviews 88:15–30

Wright DH (1983) Species-energy theory: an extension of species-area theory. Oikos 41:496–506

10. Acknowledgements

I am grateful to Katrin Böhning-Gaese for giving me the opportunity to be part of her working group. She motivated me with her enthusiasm and her valuable advice in an atmosphere of cordiality and excellence.

I thank Roland Brandl for kindly reviewing my thesis and for being a member of the defence committee.

I am very grateful to Eike Lena Neuschulz for supervising and mentoring me during the lengthy process of my project. She always helped me out to get back on track and focus on the core of my PhD. I am most grateful for her advice, patience and hard work in dealing with my learning process.

I am grateful to Matthias Schleuning who gave me indispensable advice on all kind of ecological and statistical questions. I could always contact him for support in data analyses and the interpretation of the results with his great expertise on biodiversity and ecosystem functioning.

I am very grateful to Marta Quitián for her help and support in every step of this project and for her sincere friendship. How many things we have lived through during all these years...

I thank Maximilian Vollstädt for his help in statistical models, proof reading the thesis draft and for the German summary. I am also very grateful for the long talks, beers, football, excursions and honest friendship.

I am grateful to Agustín Carrasco and Patricio Estrella for their hard work during the fieldwork of this project, and to Dagmar Hanz and Nina Gunselmann for their help in the field.

I am grateful to Edwin Zárate and Boris Tinoco for their support in Ecuador and for their valuable comments on the chapters of this thesis.

I thank the entire Böhning-Gaese working group. I am very grateful to Mathias Templin, Anke Hempel, Sabine Heinrichsohn and Shari Rothvoss for their help with SBiK-F administrative tasks. I am also grateful to Jörg, Diana, Susanne and Thomas for giving me input with the manuscripts. I thank Larissa, Alison, Nandia, Theresa, Maree, Chloe, Ugo, Anna, Joel and Isa for all talks, concerts, football, parties and coffee breaks.

I am also grateful to Pedro, Marcia, Melissa, Francisco for their help and affection. I am very grateful to Dominik and Till for the good time in Germany and the good time in Ecuador.

I thank the staff of the San Francisco research station for their support and kindness during the hard, but beautiful fieldwork days (muchas gracias Felix, Jörg, María, Robert, Manaba, Tati, Rocio, Fidel y toda la gente linda que conocí).

I thank the Nature and Culture International staff for their support and kindness.

I thank Catherine Vits for her support and for sharing with me her love for birds.

I thank the Environmental Ministry of Ecuador for research permits.

I thank Dagmar Hanz, Larissa Nowak and Anna Phillips for contributing bird trait measurements.

I thank the Universidad del Azuay for support and cooperation.

I am very grateful to Veronica Torres for her love, support, patience and comprehension, and for always believing in me…”cuanto no puede curar el amor, cuando renace de tu Mirada”.

I thank my sisters, brothers-in-law, nieces and nephews, and all my family for their endless love. I thank my close friends for their time and connection.

Finally, I thank the German Research Foundation (DFG) for funding our projects in the framework of the Research Bundle 823–825 “Platform for Biodiversity and Ecosystem Monitoring and Research in South Ecuador” (PAK 825/1) and the Research Unit FOR2730 “Environmental changes in biodiversity hotspot ecosystems of South Ecuador: RESPonse and feedback effECTs”.

11. Appendices

Appendix 1: Direct and indirect effects of elevation, climate and vegetation structure on bird communities on a tropical mountain

Appendix 2: Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient

Appendix 3: Different responses of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient

Appendix 4: Curriculum Vitae

Appendix 1. Direct and indirect effects of elevation, climate and vegetation structure on bird communities on a tropical mountain

Authors:

Vinicio Santillán, Marta Quitián, Boris A. Tinoco, Edwin Zárate, Matthias Schleuning, Katrin Böhning-Gaese and Eike Lena Neuschulz

Title:

Direct and indirect effects of elevation, climate and vegetation structure on bird communities on a tropical mountain

Status:

Submitted to Acta Oecologica on May 15th 2019

Author Contributions:

1. Development and planning:

VS 80%, MS, KBG and ELN in total 20%

2. Field work/data collection:

VS collected bird data and data on vegetation structure and resource availability (75%) with support by MQ (25%).

3. Compilation of data sets and figures/tables:

VS assembled the data sets and prepared the figures (100%).

4. Data analyses and interpretation:

VS performed the statistical analyses (90%) with input from MS and ELN (10%). **VS** interpreted the results (85%), MS, KBG and ELN contributed with the interpretation of the results (15%).

5. Preparation of manuscript:

VS (80%) MQ, BAT and EZ (5%), MS, KBG and ELN (15%).

Direct and indirect effects of elevation, climate and vegetation structure on bird communities on a tropical mountain

Vinicio Santillán[1,2,3,], Marta Quitián[1,2], Boris A. Tinoco[3], Edwin Zárate[3], Matthias Schleuning[1], Katrin Böhning-Gaese[1,2], Eike Lena Neuschulz[1]

[1]Senckenberg Biodiversity and Climate Research Centre Frankfurt (SBiK-F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany

[2]Department of Biological Sciences, Goethe-Universität Frankfurt, Max-von-Laue-Straße 9, 60438 Frankfurt am Main, Germany

[3]Escuela de Biología, Ecología y Gestión, Universidad del Azuay, Av. 24 de Mayo 7-77 y Hernán Malo, 01.01.981, Cuenca, Ecuador

Correspondence author: vinicioestuardosantillan@gmail.com

Appendix 1. Direct and indirect effects of elevation, climate and vegetation structure on bird communities on a tropical mountain

---

Abstract

Climate and vegetation structure are important predictors of biodiversity along mountain slopes. The drivers of elevational biodiversity gradients are not yet fully resolved. For instance, there is little understanding of how direct and indirect effects of elevation shape species communities along mountain slopes. In this study, we identify the main drivers of bird diversity along an elevational gradient spanning 2000 m in the Ecuadorian Andes. We simultaneously tested the direct and indirect effects of elevation, temperature, precipitation and vegetation structure on overall bird diversity and on frugivorous and insectivorous birds, using structural equation models (SEMs). We found that elevation was mostly indirectly associated with bird diversity, mediated via abiotic (i.e., temperature, precipitation) and biotic (i.e., vegetation structure) factors. We found consistent positive effects of temperature and vegetation structure and negative effects of precipitation on overall bird diversity and on frugivorous and insectivorous birds. In addition, elevation was directly, positively associated with insectivore richness and abundance, but not with that of frugivores. Our results show that climatic factors and vegetation structure jointly shape the richness of bird communities on tropical mountains. However, other factors, such as biotic interactions or different evolutionary histories of lowland and highland communities, may additionally contribute to elevational patterns in bird diversity. Thus, species communities across tropical mountain slopes are shaped by a multitude of abiotic and biotic factors that need to be studied simultaneously for a mechanistic understanding of patterns in biodiversity.

Keywords: Andes, avian diversity patterns, Ecuador, mountain biodiversity, structural equation modelling.

Introduction

Tropical mountains are hotspots of global biodiversity (Orme et al. 2005; Quintero and Jetz 2018). Due to rapid changes of environmental conditions across small spatial distance, they offer a great opportunity to understand how environmental factors shape species diversity (McCain and Grytnes 2010; Rahbek 1995). Although a plethora of factors related to climate, evolutionary history, biotic factors or area effects have been proposed (e.g., reviewed in McCain and Grytnes 2010), the underlying drivers that shape patterns of biodiversity across tropical mountain slopes are still under debate (Colwell et al. 2004; Willig and Presley 2015). Climatic factors, such as changes in temperature and precipitation across tropical mountain slopes, are most frequently related to patterns of montane biodiversity (McCain and Colwell 2011). Further, distinct climates in the evolutionary history of tropical mountains have likely contributed to current biodiversity patterns, due to different speciation rates in lowland and highland communities (Hawkins et al. 2007; Weir 2006). Biotic factors, such as vegetation structure (Ferger et al. 2014), resource availability (Ferger et al. 2014; Kissling et al. 2012) or competition (Freeman 2015), are other important drivers of biodiversity on tropical mountains that can explain variation in species diversity across elevational gradients (Jankowski et al. 2013). Species-area relationships suggest that those regions along elevational gradients that cover most area, such as the mountain base, should harbour highest species diversity (Rahbek 1997). The mid-domain effect, although highly debated, assumes that species ranges may occur randomly on a bounded environment (e.g., an elevational gradient) and thus, species richness peaks, *by chance,* in the centre (e.g., at mid elevations) where most ranges overlap (e.g., Colwell et al. 2004; Hawkins et al. 2005; Brehm et al. 2007).

Despite the importance of the inter-related effects of elevation, climate and vegetation on species communities, there is so far little understanding of how direct and indirect effects of these factors shape elevational patterns of biodiversity. Many previous studies have demonstrated that species communities, such as tropical lowland and highland bird communities, can strongly differ in their composition and structure (Patterson et al. 1998; Herzog et al. 2005). Only few empirical studies have, however, investigated the underlying mechanisms, showing for instance that the effects of elevation on bird diversity can be mediated via effects of climate (Kissling et al. 2007, 2008; Ruggiero and Hawkins 2008) or that effects of climate on bird diversity can be mediated via vegetation structure (Ferger et al. 2014; Zhang et al. 2013).

The direct and indirect effects of elevation, climate, and vegetation structure may also differ among different taxonomic groups of species (McCain and Grytnes 2010; Willig and Presley 2015) or among different functional guilds within species groups (Ferger et al. 2014; Pigot et al. 2016). For instance, Jankowski et al. (2013) found stronger effects of elevation and vegetation structure on insectivorous birds than on frugivorous birds along a tropical elevational gradient. Insectivorous birds have been shown to depend on diverse vegetation structure, due to their specialized foraging techniques in specific microhabitats (Naoki 2007; Pigot et al. 2016; Willson 1974). In contrast, frugivorous birds are often associated with plant species richness and fruit availability rather than with vegetation structure *per se* (Kissling et al. 2007; Loiselle and Blake 1991). Nevertheless, comprehensive studies that test the simultaneous direct and indirect effects of this multitude of factors on bird diversity are rare (but see Ferger et al. 2014).

In this study, we used structural equation models (SEMs) to simultaneously test the direct and indirect effects of elevation, temperature, precipitation and vegetation structure on bird diversity across an elevational gradient in the tropical Andes in Ecuador. First, we studied the effects of elevation, climate factors and vegetation structure on overall bird species richness and abundance. Then, we separately tested the effects of elevation, climate factors and vegetation structure on the richness and abundance of two distinct avian feeding guilds, i.e., frugivores and insectivores. We expected that direct effects of elevation are important for species richness and abundance of the overall bird community across the elevational gradient, for instance due to the different evolutionary history of lowland and highland communities (Weir 2006). In contrast, we expected that indirect effects of elevation mediated via climate and vegetation structure might be more important for the specific feeding guilds. For instance, we expected that vegetation structure is more associated with insectivorous bird richness than with frugivorous bird richness (Ferger et al. 2014; Jankowski et al. 2013).

Methods

Study area

The study was conducted on a total of 18 1-ha plots across three elevations (1000 m asl, 4° 6′ S, 78° 58′ W; 2000 m asl, 3° 58′ S, 79° 4′ W; 3000 m asl, 4° 6′ S, 79° 10′ W), covering two habitat types (natural and fragmented forest) within and around Podocarpus National Park (PNP) and San Francisco reserve (BRSF) at the southeastern slope of the Andes in Ecuador (Figure S1). The area is characterized by humid tropical montane climate (Kottek et al., 2006) with a bimodal rain regime (most humid season: May to June; least humid season: October to November; Emck 2007). At low elevations mean annual temperature is 20 °C and mean annual precipitation is 2432 mm. At mid elevations mean annual temperature is 15.5 °C and mean annual precipitation 2079 mm. At high elevations mean annual temperature is 10 °C and mean annual precipitation is

4522 mm (Emck 2007). The study plots cover three different vegetation types: evergreen premontane forest at low elevations, evergreen lower montane forest at mid elevations and upper montane forest at high elevations (Homeier et al. 2008). Vegetation at low elevations is dominated by emergent trees, climber plants and lianas; at mid elevations by the presence of few emergent trees, vascular epiphytes and climbers plants; and at high elevation by a high percentage of *Weinmannia* shrubs and vascular epiphytes as well as epiphytic mosses (Paulsch et al. 2008).

Climatic factors and vegetation structure

Temperature and precipitation data were collected for each 1-ha plot. The average monthly within-forest temperatures (i.e., monthly mean of daily mean temperatures) was obtained through an air temperature regionalization tool developed for the study region (Figure S2, Fries et al. 2012). Monthly mean precipitation (i.e., average of the sum of monthly precipitation) was obtained through remote sensing techniques (local area weather radar and satellite imagery) and meteorological data (Figure S2, Rollenbeck and Bendix 2011).

To obtain vegetation structure, we determined the vertical vegetation heterogeneity on nine point locations at each 1-ha plot, eight at the borders and one in the centre. At each point we estimated vegetation cover on different layers at 0, 1, 2, 4, 8, 16 and 32 m above ground and then calculated the Shannon–Wiener diversity index across these strata (Figure S2, Bibby et al. 2000).

Bird community and feeding guilds

To measure bird richness and abundance, we used nine point locations at each 1-ha plot. For 10 minutes, we recorded and identified all birds heard or seen to species level within a 20-metre radius of each point count. The sampling was repeated eight times per plot over two years (216 sampling hours in total, 144 spatio-temporal replicates across all 18 plots). We quantified the overall number of bird species (species richness) and the overall number of bird individuals (abundance) by summing the records of all point counts per plot and temporal replicate. We classified bird species as frugivores if their diet is more than or equal to 40% of fruit, and as insectivores if their diet is more than or equal to 40% of insects (Wilman et al. 2014).

Statistical analysis

Appendix 1. Direct and indirect effects of elevation, climate and vegetation structure on bird communities on a tropical mountain

---

To disentangle the effects of elevation, climate and vegetation structure on the overall bird communities and on the different bird feeding guilds, we used piecewise SEMs based on linear mixed effects models (LMMs), which are able to account for both direct and indirect relationships among variables in complex systems (Grace et al. 2012; Shipley 2016). We defined an a priori structure of the SEM including all biologically plausible links (Figure 1a). To account for the spatial sampling structure, we included the study plot as a random effect in all models. Prior to the analyses, we log-transformed the diversity variables (species richness and abundance of the overall community, and of frugivores and insectivores) to obtain a normal distribution. Then, all variables were standardized (mean = 0, SD = 0.5) to obtain standardized parameter estimates and ensure comparability among models including the overall community, frugivores or insectivores (Fan et al. 2016). We ran SEMs with all combinations of predictor variables on the respective response variables. Due to the unimodal distribution of precipitation across the three elevations (Figure S2), we included a linear and a quadratic term of elevation in the models including precipitation as a response. We evaluated the goodness of fit of the resulting SEMs through Chi-square tests ($p[\chi^2]$) and the comparative fit index (CFI). Chi-square tests indicate good model fit if $p > 0.05$; CFI ranges from 0 to 1, with larger values indicating a better model fit (Hooper et al. 2008; Hu and Bentler 1999). All statistical analyses were performed with R version 3.3.0 (R Development Core Team 2016) and the packages "lme4" (Bates et al. 2017), "piecewiseSEM" (Lefcheck 2016), and "lavaan" (Rosseel 2014).

Results

We recorded 238 bird species and 4318 bird individuals across all plots (see Figure S3a for species richness and abundance at each elevation). SEMs of overall bird richness and abundance explained 23 and 28% of the variation respectively and yielded a very good fit to the data ($p[\chi^2] > 0.1$, CFI > 0.9 for both models). Elevation directly and indirectly influenced overall bird richness and abundance (Figures 1b - S3a; Table 1). The indirect effects of elevation were jointly mediated via temperature, precipitation and vegetation structure (Figures 1b - S3a; Table 1). Elevation had a negative effect on temperature and vegetation heterogeneity, which were positively associated with bird richness and abundance. We also found a significant association of the quadratic term of elevation on precipitation, which was negatively related to overall species richness and abundance. We did not find significant associations between temperature and precipitation and bird richness or abundance mediated via vegetation cover.

We recorded 62 species and 1027 individuals of frugivores, and 143 species and 2985 individuals of insectivores (see Figure S3b-d for species richness and abundance of each feeding guild at each elevation). SEMs for species richness and abundance of frugivores and insectivores yielded a very good fit to the data (p[χ^2] > 0.1, CFI > 0.9 for all four models). In frugivores, 50 % of variance was explained in the species richness and abundance model (Figures 2 - S3). In insectivores, 18% of variance was explained in the species richness model and 22% in the abundance model (Figures 2 - S3). Elevation was directly, positively associated with insectivore richness and abundance, but not with the richness and abundance of frugivores (Figures 2 - S3). Indirect effects of elevation on frugivore and insectivore richness were jointly mediated via temperature, precipitation and vegetation structure (Figure 2, Table 2). Elevation had significant positive effects on temperature and vegetation heterogeneity, which had a positive effect on the richness of both feeding guilds (Figure 2, Table 2). The quadratic term of elevation was significantly negatively associated with precipitation, which was negatively associated with both frugivore and insectivore richness. SEMs of the abundance of both feeding guilds showed quantitatively similar results, apart from a significant direct link between vegetation structure and insectivore abundance that was not significant in the frugivore abundance model (Figure S4).

Discussion

In the present study, we examined the direct and indirect effects of elevation, climate and vegetation structure on bird communities along a tropical mountain slope. We found that elevation was mostly indirectly associated with bird diversity, jointly mediated via abiotic (i.e., temperature, precipitation) and biotic (i.e., vegetation structure) factors. In addition, elevation was directly, positively associated with insectivore richness and abundance, but not with that of frugivores. Our results show that climate and vegetation are important predictors of bird diversity across this tropical elevational gradient. However, our results also suggest that other elevation-related factors contribute to explaining diversity patterns in birds.

We found a positive direct effect of elevation on overall bird diversity. These findings indicate that, while accounting for the negative indirect effects of elevation (i.e., a reduction of bird diversity due to climatic factors and vegetation structure with increasing elevation), bird diversity was higher than expected at high elevations. Several explanations for this pattern are possible:

1) Edge- or spill-over effects: The surplus of bird diversity at high elevations could be due to a spill over from neighbouring habitat types, such as insectivorous birds from Paramo vegetation (Santillán et al. 2019). In fact, species richness and abundance of frugivores declined with increasing elevation, while that of insectivores remained constant (Figure S3), suggesting spill-over of insectivorous species from neighbouring Paramo habitats. Previous studies have shown that spill over effects across habitat boundaries may indeed strongly influence local species diversity (Cook et al. 2002).

2) Resource availability: biotic factors, such as resource availability and competition for resources, could have contributed to explaining the pattern in bird diversity. Although previous studies have shown that resource availability is often closely associated with climate and vegetation structure (Kissling et al. 2008), a study by Ferger et al. (2014) could demonstrate that resource availability (e.g., fruit and invertebrate biomass) is a better predictor of the richness of avian frugivores than vegetation (Ferger et al. 2014). Estimates of resource availability, however, are often are difficult to obtain in particular across large spatial gradients (Ferger et al. 2014). Moreover, the relevance of resource competition for shaping lowland and highland bird communities is contentious (Dehling et al. 2014).

3) Evolutionary history: previous empirical studies have shown different structures of bird communities at different elevations (Patterson et al. 1998; Herzog et al. 2005; Graham et al. 2009; Dehling et al. 2014), potentially related to a different evolutionary history of lowland and highland bird communities (Weir 2006; Hawkins et al. 2007). However, the impact of evolutionary history on shaping patterns of biodiversity is difficult to assess with data on current diversity patterns only (Wiens et al. 2007). While (macro)evolutionary models could be helpful, they tend to predict static diversity optima across mountain slopes, neglecting differences in local species diversity, environmental conditions and the biogeographic history of mountains (McCain 2010). It is likely that these factors play an important role for diversity pattern across mountain slopes, but quantifications of their actual contribution remain challenging.

4) Area effects: Area-related drivers of species diversity, such as species-area relationships or mid-domain effects, have often been additionally suggested as predictors of species diversity, mostly in concert with climate or biotic factors (Brehm et al. 2007; McCain 2009; McCain and Grytnes 2010). Although we did not formerly test for area effects in our study, they could have contributed to differences in diversity between lowland and highland communities.

We found a significant positive effect of temperature on the bird community. The positive relationship between temperature and bird diversity has been previously demonstrated to shape bird diversity across elevational and latitudinal gradients (Hawkins et al. 2003; Evans et al. 2005; Ruggiero and Hawkins 2008; McCain 2009), and is likely related to a higher productivity under high temperatures (Allen et al. 2002). Several previous studies have shown that temperature is not the only climatic factor explaining bird diversity patterns (McCain 2009; McCain and Grytnes 2010). In fact, precipitation has been considered as one of the main climate factors that shape biodiversity in tropical ecosystems (Hawkins et al. 2003). The negative effect of precipitation that we found in our study is in concordance with previous studies that have shown that heavy rain events can negatively affect insects (Aizen 2003), bats (Grindal et al. 1992), and birds (Santillán et al. 2018), potentially driven by a reduction in flight performance (Ortega-Jimenez and Dudley 2012) and associated foraging restrictions (Boyle et al. 2010).

In our study, we did not find an effect of climatic factors on vegetation structure, different to previous studies from tropical mountains (Suárez et al. 2011; Ferger et al. 2014). However, the positive effect of vegetation structure on the bird community indicates that it is an important predictor of bird diversity in our study system. Vegetation structure has been shown to be highly correlated with global bird diversity patterns (Kissling et al. 2012), as vegetation structure provides crucial structural element for refuge, nesting and foraging of birds (MacArthur and MacArthur 1961; Tews et al. 2004; Mulwa et al. 2012). The effect size of vegetation structure was twice as large for the richness of insectivorous birds as for frugivores (Table 2) and there was no significant association between vegetation structure and frugivore abundance (Figure S3). These results are in concordance with previous studies where vegetation structure had stronger effects on insectivorous birds than on frugivorous birds (Waltert et al. 2005; Jankowski et al. 2013; Ferger et al. 2014). Insectivorous birds often have specialized foraging techniques (Willson 1974; Jankowski et al. 2013; Pigot et al. 2016) and rely on specific microhabitats (Naoki 2007), often characterized by a complex vegetation structure. In contrast, frugivorous birds have rather been associated with plant species richness (Kissling et al. 2007) and fruit abundance (Loiselle and Blake 1991), which can be independent from overall vegetation structure (Kissling et al. 2007, 2008).

Conclusion

In this study, we show that both direct and indirect effects of elevation contribute to explaining patters of bird diversity along tropical mountain slopes. Indirect effects of elevation on patterns of biodiversity, mediated by changes in temperature, precipitation and vegetation structure, simultaneously shape patterns in bird diversity. Nevertheless, other factors that are associated with elevational gradients, such as edge or area effects, evolutionary history or biotic interactions, may also play an important role, especially for insectivorous birds. Our study emphasises that we need to consider the interplay of several drivers for a holistic understanding of the mechanisms that shape patterns of biodiversity across tropical mountain slopes.

Acknowledgements

We are grateful to Agustín Carrasco and Patricio Estrella for their help in fieldwork, and Jörg Albrecht and Maximilian Vollstädt for their help with fitting SEMs. We thank Nature and Culture International (NCI), Felix Matt, Jörg Zeilinger, Mathias Templin and Catherine Vits for logistic support. The Ecuadorian Ministry of the Environment (MAE) kindly provided permission to conduct research. We thank the German Research Foundation (DFG) for funding our projects in the framework of the Research Bundle 823–825 “Platform for Biodiversity and Ecosystem Monitoring and Research in South Ecuador” (PAK 825/1) and the Research Unit FOR2730 “Environmental changes in biodiversity hotspot ecosystems of South Ecuador: RESPonse and feedback e ECTs”.

References

Aizen MA (2003) Down-facing flowers, hummingbirds and rain. Taxon 52:675–680

Allen AP, Brown JH, Gillooly JF (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Science 297:1545–1548

Bates D, Maechler M, Bolker B, et al (2017) Linear mixed-effects models using "Eigen" and S4. R Help 67:1–113

Bibby C, Burgess N, Hill D, Mustoe S (2000) Bird census techniques, 2nd edn. Academic Press, Cambridge, UK

Boyle WA, Norris DR, Guglielmo CG (2010) Storms drive altitudinal migration in a tropical bird. Proceedings of the Royal Society B: Biological Sciences 277:2511–2519

Brehm G, Colwell RK, Kluge J (2007) The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. Global Ecology and Biogeography 16:205–219

Colwell RK, Rahbek C, Gotelli NJ (2004) The mid-domain effect and species richness patterns : what have we learned so far? The American Naturalist 163:1–23

Cook WM, Lane KT, Holt D (2002) Island theory , matrix effects and species richness patterns in habitat fragments. Ecology letters 5:619–623

Dehling DM, Fritz SA, Töpfer T, et al (2014) Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. Ecography 37:1047–1055

Emck P (2007) A climatology of south Ecuador. Universität Erlangen-Nürnberg

Evans KL, Warren PH, Gaston KJ (2005) Species-energy relationships at the macroecological scale: a review of the mechanisms. Biological Reviews of the Cambridge Philosophical Society 80:1–25

Fan Y, Chen J, Shirkey G, et al (2016) Applications of structural equation modeling (SEM) in ecological studies: an updated review. Ecological Processes 5:1–12

Ferger SW, Schleuning M, Hemp A, et al (2014) Food resources and vegetation structure mediate climatic effects on species richness of birds. Global Ecology and Biogeography 23:541–549

Freeman BG (2015) Competitive interactions upon secondary contact drive elevational divergence in tropical birds. The American Naturalist 186:470–479

Fries A, Rollenbeck R, Nauß T, et al (2012) Near surface air humidity in a megadiverse Andean mountain ecosystem of southern Ecuador and its regionalization. Agricultural and Forest Meteorology 152:17–30

Grace JB, Schoolmaster DR, Guntenspergen GR, et al (2012) Guidelines for a graph-theoretic implementation of structural equation modeling. Ecosphere 3:art73

Graham CH, Parra JL, Rahbek C, Mcguire JA (2009) Phylogenetic structure in tropical hummingbird communities. Proceedings of the National Academy of Sciences 107:513–513

Grindal SD., Collard TS., Brigham R. M, Barclay RM. R. (1992) The influence of precipitation on reproduction by Myotis bats in British Columbia. The American Midland Naturalist 128:339–344

Hawkins BA, Alexandre J, Diniz F, Weis AE (2005) The mid-domain effect and diversity gradients: is there anything to learn? The American Naturalist 166:E140–E143

Hawkins BA, Diniz□Filho JAF, Jaramillo CA, Soeller SA (2007) Climate, Niche Conservatism, and the Global Bird Diversity Gradient. The American Naturalist 170:S16–S27

Hawkins BA, Field R, Cornell H V., et al (2003) Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117

Herzog SK, Kessler M, Bach K (2005) Elevational gradient in andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. Ecography 28:209–222

Homeier J, Werner FA, Gradstein SR, Richter M (2008) Potential vegetation and floristic composition of Andean forests in south Ecuador, with a focus on the RBSF. In: Beck E, Bendix J, Kottke I, et al. (eds) Gradients in a tropical mountain ecosystem of Ecuador. Springer, Berlin, pp 87–100

Hooper D, Coughlan J, Mullen M (2008) Structural equation modelling: guidelines for determining model fit structural equation modelling. Electronic Journal of Business Research Methods 6:53–60

Hu LT, Bentler PM (1999) Cutoff criteria for fit indexes in covariance structure analysis: conventional criteria versus new alternatives. Structural Equation Modeling 6:1–55

Jankowski JE, Merkord CL, Rios WF, et al (2013) The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. Journal of Biogeography 40:950–962

Kissling WD, Field R, Böhning-Gaese K (2008) Spatial patterns of woody plant and bird diversity: functional relationships or environmental effects? Global Ecology and Biogeography 17:327–339

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

Kissling WD, Sekercioglu CH, Jetz W (2012) Bird dietary guild richness across latitudes, environments and biogeographic regions. Global Ecology and Biogeography 21:328–340

Kottek M, Grieser J, Beck C, et al (2006) World map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift 15:259–263

Lefcheck J (2016) piecewiseSEM: piecewise structural equation modeling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution 7:573–579

Loiselle BA, Blake JG (1991) Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology 72:180–193

MacArthur RH, MacArthur JW (1961) On bird species diversity. Ecology 42:594–598

McCain CM (2009) Global analysis of bird elevational diversity. Global Ecology and Biogeography 18:346–360

McCain CM (2010) Global analysis of reptile elevational diversity. Global Ecology and Biogeography 19:541–553

McCain CM, Colwell RK (2011) Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. Ecology

Letters 14:1236–1245

McCain CM, Grytnes J-A (2010) Elevational gradients in species richness. Encyclopedia of Life Sciences (ELS) 1–10

Mulwa RK, Böhning-Gaese K, Schleuning M (2012) High bird species diversity in structurally heterogeneous farmland in western Kenya. Biotropica 44:801–809

Naoki K (2007) Arthropod resource partitioning among omnivorous tanagers (Tangara spp.) in western Ecuador. The Auk 124:197–209

Orme CDL, Davies RG, Burgess M, et al (2005) Global hotspots of species richness are not congruent with endemism or threat. Nature 436:1016–1019

Ortega-Jimenez VM, Dudley R (2012) Flying in the rain: hovering performance of Anna’s hummingbirds under varied precipitation. Proceedings of the Royal Society B: Biological Sciences 279:3996–4002

Patterson BD, Stotz DF, Solarit S, et al (1998) Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. Journal of Biogeography 25:593–607

Paulsch A, Piechowski D, Müller-Hohenstein K (2008) Forest vegetation structure along an altitudinal gradient in southern Ecuador. In: Beck E, Bendix J, Kottke I, et al. (eds) Gradients in a tropical mountain ecosystem of Ecuador. Ecological studies, vol 198. Springer-Verlag Berlin Heidelberg, Berlin, pp 113–121

Pigot AL, Trisos CH, Tobias JA (2016) Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. Proceedings of the Royal Society B: Biological Sciences 283:1–9

Quintero I, Jetz W (2018) Global elevational diversity and diversification of birds. Nature 555:246–250

R Development Core Team (2016) A language and environment for statistical computing

Rahbek C (1997) The relationship among area, elevation, and regional species richness in neotropical birds. The American Naturalist 149:875–902

Rahbek C (1995) The elevational gradient of species richness: a uniform pattern? Oikos 18:200–205

Rollenbeck R, Bendix J (2011) Rainfall distribution in the Andes of southern Ecuador derived from blending weather radar data and meteorological field observations. Atmospheric Research 99:277–289

Rosseel Y (2014) The lavaan tutorial. R Help 37

Ruggiero A, Hawkins BA (2008) Why do mountains suport so many species of birds? Ecography 31:306–315

Santillán V, Quitián M, Tinoco BA, et al (2018) Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient. PLoS ONE 13:1–15

Santillán V, Quitián M, Tinoco BA, et al (2019) Different responses of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient. Oecologia 189:863-873

Shipley B (2016) Cause and correlation in biology, 2nd edn. Cambridge University Press

Suárez CF, Naranjo LG, Espinosa JC, Sabogal J (2011) Land use changes and their synergies with climate change. In: Herzog S, Matínez R, Jørgensen P, Tiessen H (eds) Climate change and biodiversity in the tropical Andes. Inter-American Institute for Global Change Research, pp 141–151

Tews J, Brose U, Grimm V, et al (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31:79–92

Waltert M, Bobo KS, Sainge NM, et al (2005) From forest to farmland: habitat effects on afrotropical forest bird diversity. Ecological Applications 15:1351–1366

Weir JT (2006) Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. Evolution 60:842

Wiens JJ, Parra-olea G, Garcı M, Wake DB (2007) Phylogenetic history underlies elevational biodiversity patterns in tropical salamanders. Proceedings of the Royal Society B: Biological Sciences 274:919–928

Willig MR, Presley SJ (2015) Biodiversity and metacommunity structure of animals along altitudinal gradients in tropical montane forests. Journal of Tropical Ecology 32:421–436

Willson MF (1974) Avian community organization and habitat structure. Ecology 55:1017–1029

Wilman H, Belmaker J, Jennifer S, et al (2014) EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. Ecology 95:2027

Zhang J, Kissling WD, He F (2013) Local forest structure, climate and human disturbance determine regional distribution of boreal bird species richness in Alberta, Canada. Journal of Biogeography 40:1131–1142

Appendix 1. Direct and indirect effects of elevation, climate and vegetation structure on bird communities on a tropical mountain

---

Table 1. Standardized direct and indirect effects of predictor variables on species richness. Effects are given for elevation (Elev) plus quadratic elevation (Elev^2), temperature (Temp), precipitation (Prec) and vegetation structure (VegHet), as derived from the model shown in Figure 1b.

	Bird richness	
Predictor	*Direct*	*Indirect*
Elev	1.09	-1.44
Elev^2*	n.a.	0.70
Tem	0.96	n.s.
Prec	-0.28	n.s.
VegHet	0.43	n.a.

* only included in the precipitation model;

n.s., not significant; n.a., not applicable.

Table 2. Standardized direct and indirect effects of predictor variables on frugivores and insectivores richness. Effects are given for elevation (Elev) plus quadratic elevation (Elev^2), temperature (Temp), precipitation (Prec) and vegetation structure (VegHet), as derived from model shown in Figure 2a-b.

	Frugivore richness		Insectivore richness	
Predictor	*Direct*	*Indirect*	*Direct*	*Indirect*
Elev	n.s.	-1.06	1.40	-1.48
Elev^2*	n.a.	0.35	n.a.	0.67
Tem	0.81	n.s.	0.93	n.s.
Prec	-0.14	n.s.	-0.27	n.s.
VegHet	0.24	n.a.	0.50	n.a.

* only included in the precipitation model;

n.s., not significant; n.a., not applicable.

Appendix 1. Direct and indirect effects of elevation, climate and vegetation structure on bird communities on a tropical mountain

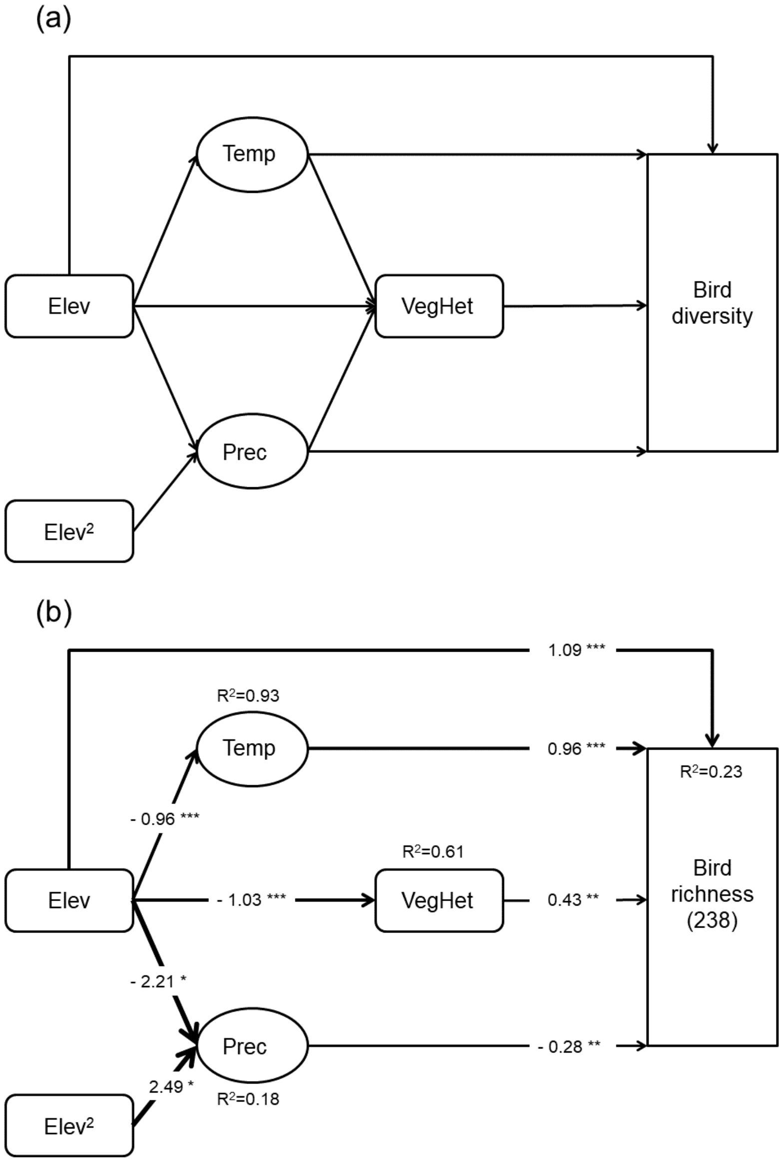


Figure 1. a) Hypothesized causal relationships of structural equation model, with all possible direct and indirect links between elevation (linear and quadratic term, Elev+Elev^2), temperature (Temp), precipitation (Prec) and vegetation structure (VegHet) on bird richness. b) Relationship between elevation (linear and quadratic term), temperature, precipitation and vegetation structure showing the best-fitting structural equation models for bird species richness across an Andean mountain slope. Given are the standardized path coefficients and their respective statistical significance (*p<0.05, **p<0.01, ***p<0.001) and the marginal coefficients of determination for each response variable (R^2). Number of recorded bird species are given in brackets.

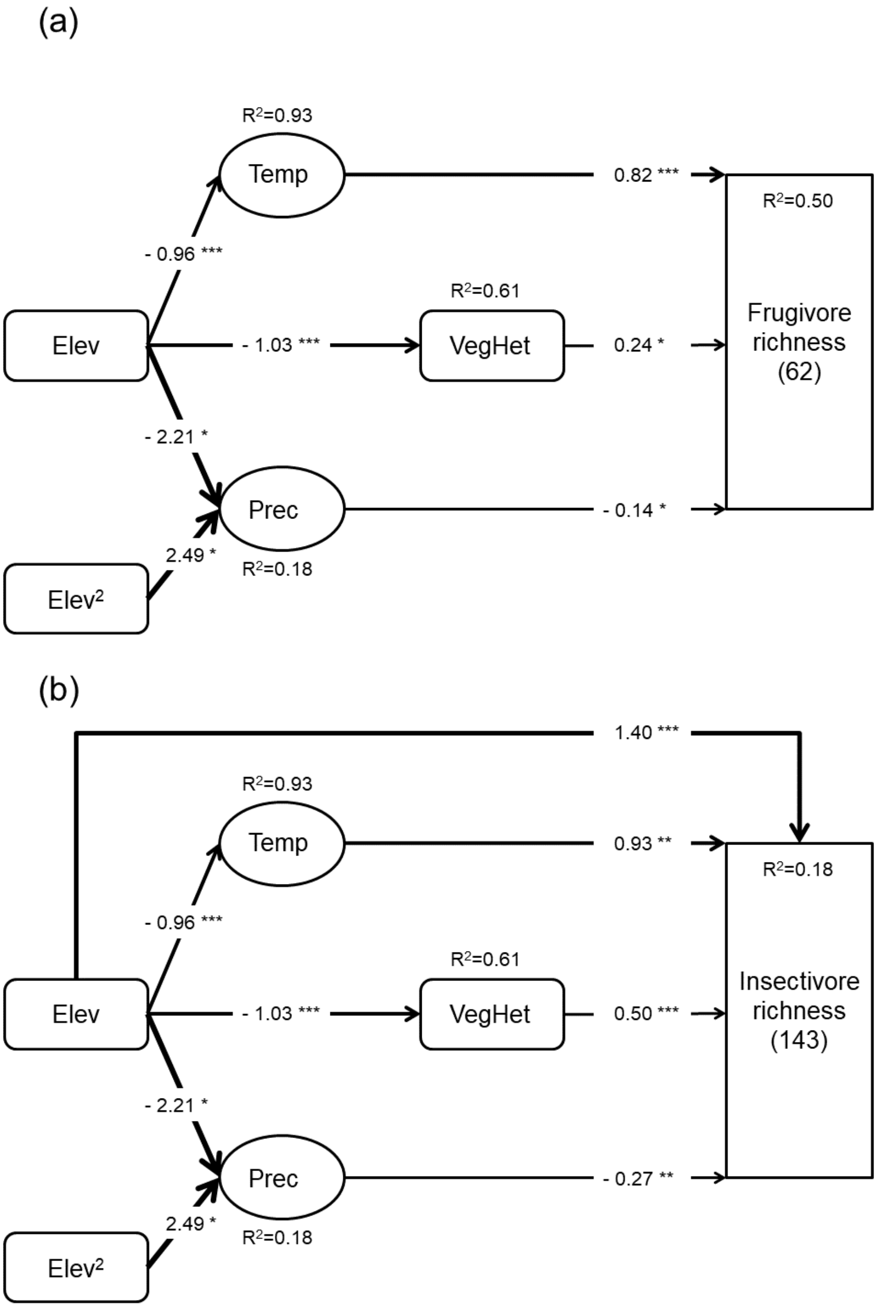


Figure 2. Relationships of structural equation model, with all possible direct and indirect links between elevation (Elev+Elev^2), temperature (Temp), precipitation (Prec) and vegetation structure (VegHet) on a) frugivore richness and b) insectivore richness. Given are the standardized path coefficients and their respective statistical significance (*p<0.05, **p<0.01, ***p<0.001) and the marginal coefficients of determination for each response variable (R^2). Numbers of recorded bird species are given in brackets.

Supplementary material

Direct and indirect effects of elevation, climate and vegetation structure on bird communities on a tropical mountain

Vinicio Santillán, Marta Quitián, Boris A. Tinoco, Edwin Zárate, Matthias Schleuning, Katrin Böhning-Gaese and Eike Lena Neuschulz

Corresponding author: Vinicio Santillán: vinicioestuardosantillan@gmail.com

Appendix S1. Study area.

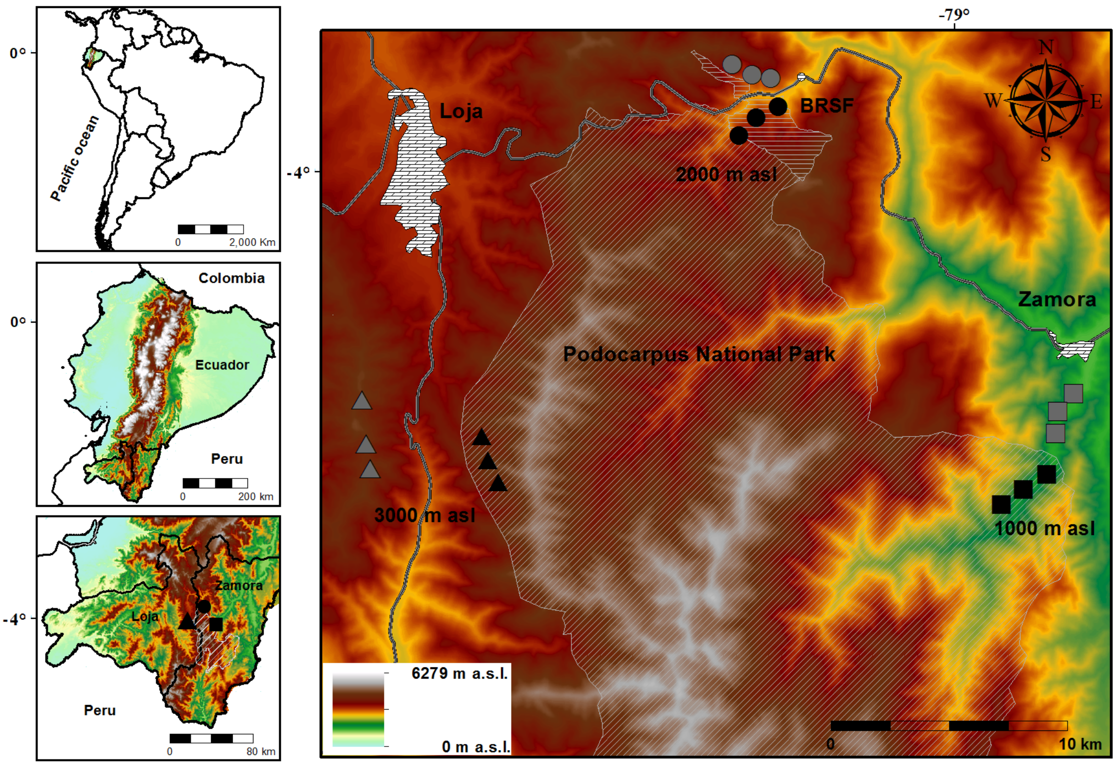


Figure S1. Map of the study area within and around Podocarpus National Park (PNP) and San Francisco reserve (BRSF), southeast slope of the Andes in Ecuador. Locations of 1-ha plots across the elevational gradient (squares at low elevations, circles at mid elevations, and triangles at high elevations), plots in natural forests are in black and plots in fragmented forests are in grey.

Appendix S2. Climate data and vertical vegetation heterogeneity of the study region.

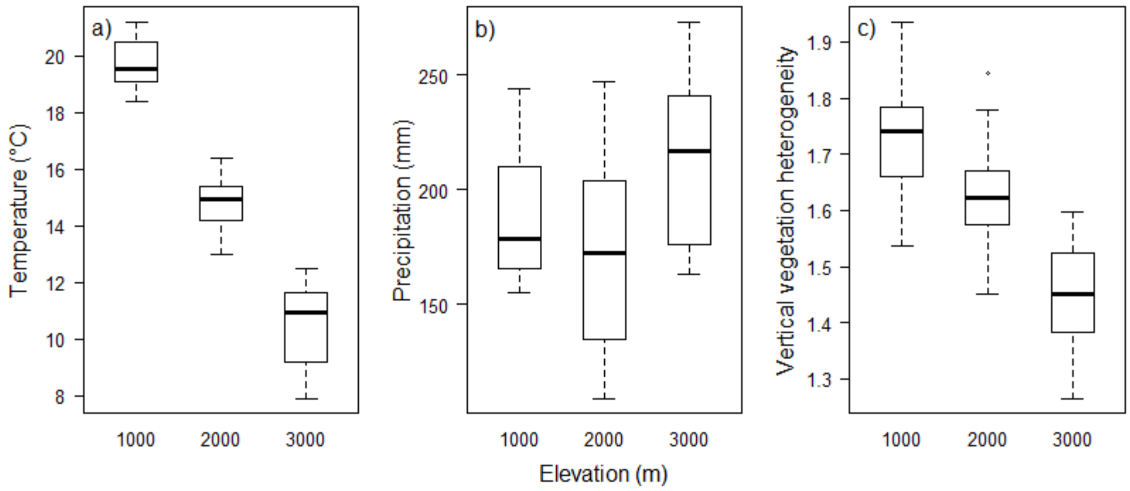


Figure S2. Monthly mean temperature a), monthly mean precipitation b), and vegetation structure c) averaged over the sampling months in 2014 and 2015 at three elevations in Podocarpus National Park.

Appendix S3. Bird richness and abundance of overall community and feeding guilds.

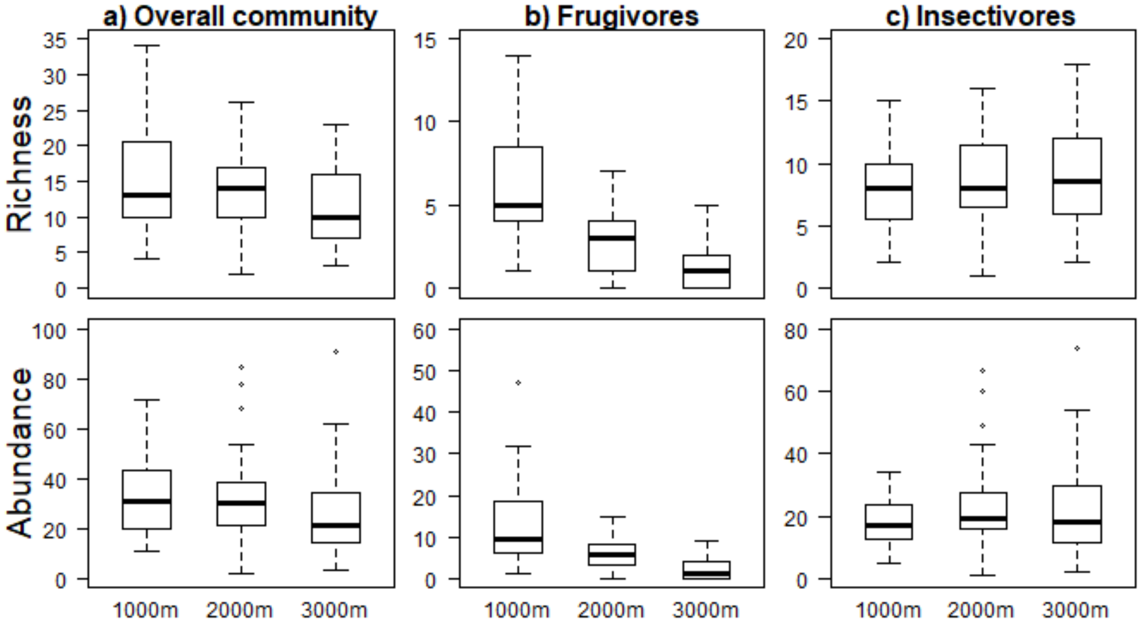


Figure S3. Species richness and abundance of a) the overall bird community, and three different feeding guilds: b) frugivores and c) insectivores per plot and temporal replicate (n = 144) at three elevations in Podocarpus National Park.

Appendix S4. Structural equation models of bird abundance.

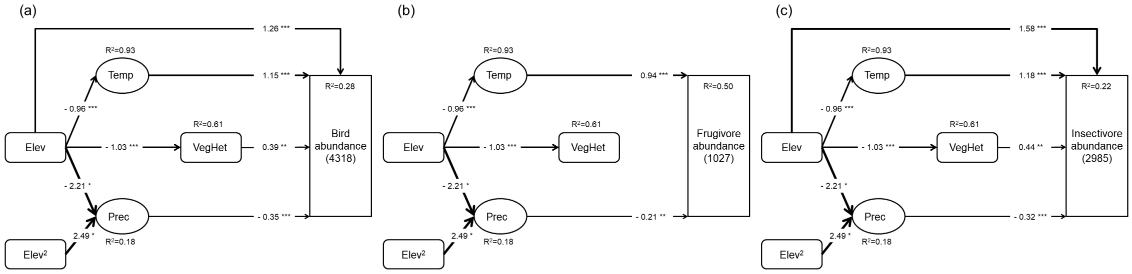


Figure S4. Relationships of structural equation model, with all possible direct and indirect links between elevation (Elev+Elev^2), temperature (Temp), precipitation (Prec) and vegetation structure (VegHet) on a) overall bird abundance, b) frugivore abundance and b) insectivore abundance. Given are the standardized path coefficients and their respective statistical significance (*p<0.05, **p<0.01, ***p<0.001) and the marginal coefficients of determination for each response variable (R^2). Numbers of recorded bird individuals are given in brackets.

Appendix 2. Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient

Authors:

Vinicio Santillán, Marta Quitián, Boris A. Tinoco, Edwin Zárate, Matthias Schleuning, Katrin Böhning-Gaese and Eike Lena Neuschulz

Title:

Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient

Status:

Published in PLoS ONE on May 10th 2018

Author Contributions:

1. Development and planning:

VS 80%, MS, KBG and ELN in total 20%

2. Field work/data collection:

VS collected bird data and data on resource availability (80%) with support by MQ (20%).

3. Compilation of data sets and figures/tables:

VS assembled the data sets and prepared the figures (100%).

4. Data analyses and interpretation:

VS performed the statistical analyses (80%) with input from MS, KBG and ELN (20%). **VS** interpreted the results (75%), BAT, KBG, MS and ELN contributed with the interpretation of the results (25%).

5. Preparation of manuscript:

VS (75%) MQ and EZ (5%), BAT, MS, KBG and ELN (20%).

Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient

Vinicio Santillán[1,2,3], Marta Quitián[1,2], Boris A. Tinoco[3], Edwin Zárate[3], Matthias Schleuning[1], Katrin Böhning-Gaese[1,2], Eike Lena Neuschulz[1]

[1]Senckenberg Biodiversity and Climate Research Centre Frankfurt (SBiK-F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany

[2]Department of Biological Sciences, Goethe-Universität Frankfurt, Max-von-Laue-Straße 9, 60438 Frankfurt am Main, Germany

[3]Escuela de Biología, Ecología y Gestión, Universidad del Azuay, Av. 24 de Mayo 7-77 y Hernán Malo, 01.01.981, Cuenca, Ecuador

Correspondence author: vinicioestuardosantillan@gmail.com

Appendix 2. Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient

Abstract

Understanding the spatial and temporal dynamics of species assemblages is a main challenge in ecology. The mechanisms that shape species assemblages and their temporal fluctuations along tropical elevational gradients are particularly poorly understood. Here, we examined the spatio-temporal dynamics of bird assemblages along an elevational gradient in Ecuador. We conducted bird point counts at three elevations (1000, 2000 and 3000 m) on 18 1-ha plots and repeated the sampling eight times over two years (216 hours in total). For each plot, we obtained data of monthly temperatures and precipitation and recorded the overall resource availability (i.e., the sum of flower, fruit, and invertebrate resources). As expected, bird richness decreased from low to high elevations. Moreover, we found a significant decrease in bird abundance and richness and an increase in evenness between the most and least humid season at each of the three elevations. Climatic factors were more closely related to these temporal fluctuations than local resource availability. While temperature had significant positive effects on the abundance of birds at mid and high elevations, precipitation negatively affected bird abundance at low and mid elevations. Our study highlights that bird assemblages along tropical elevational gradients can show pronounced seasonal fluctuations. In particular, low temperatures and high precipitation seem to impose important constraints on birds. We conclude that potential changes in climate, due to global warming, are likely to affect the spatio-temporal dynamics of bird assemblages along tropical elevational gradients.

Key words: Abundance; Climatic gradient, Ecuador; Seasonality; Species richness.

Introduction

Understanding the spatial and temporal patterns in species' abundance and richness along environmental gradients is a fundamental challenge in ecology (Gaston 2000). Many studies have shown that climate (Hawkins et al. 2003a; Rahbek et al. 2007) and productivity (Waide et al. 1999; Hawkins et al. 2003b) determine the structure of species assemblages across large spatial scales. However, the mechanisms that drive spatio-temporal dynamics of species assemblages have received little attention so far (Jetz et al. 2005; Dornelas et al. 2013; Ferger et al. 2014).

Appendix 2. Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient

Elevational gradients present a great opportunity to study the spatial patterns of species assemblages because they comprise a variety of environmental conditions across relatively small spatial extents (McCain and Grytnes 2010). Many previous studies have, for instance, examined the spatial pattern in bird species richness along elevational gradients and showed that bird diversity generally declines with increasing elevation (Terborgh 1977; Herzog et al. 2005; Merkord 2010; Dehling et al. 2014). Climate has been identified as the main factor influencing bird assemblages along these gradients (McCain 2009b), in particular at high elevations where climatic conditions are harsh (Louthan et al. 2015). Climatic factors, such as temperature and precipitation, may affect birds directly via physiological constraints (Root 1988), for instance by restricting the activity, mobility and foraging time of birds (Boyle et al. 2010). Additionally, temperature and precipitation may also have indirect effects on birds via net primary productivity (Currie et al. 2004), which determines the amount of resources available to birds (O'Brien 1998). However, the degree to which primary productivity translates into a high diversity of birds strongly depends on the capacity of birds to obtain the available resources (Rosenzweig 1993, 1995). A previous study has shown that guild-specific resources, such as invertebrate biomass, can be more important determinants of the spatial richness patterns of avian feeding guilds than climatic factors (Ferger et al. 2014). The extent to which abiotic and biotic factors shape the spatial patterns of bird assemblages may vary across environmental gradients (McCain 2009b; McCain and Grytnes 2010) and among spatial scales (Field et al. 2009; Wisz et al. 2013). Under harsh environmental conditions, such as at high elevations, abiotic factors often determine the structure of bird assemblages (Hawkins et al. 2003a; Louthan et al. 2015). Under benign environmental conditions (e.g., at low elevations), biotic factors, such as the competition for resources, may play a critical role in shaping bird assemblages (Brown et al. 1996b; Louthan et al. 2015). Biotic factors are also expected to be more important, and better detectable, at small than at large spatial scales (Wisz et al. 2013; Zhang et al. 2013).

While the spatial pattern of bird species richness have been relatively well studied, temporal dynamics of bird assemblages are less known, specifically in tropical ecosystems (Brown 2014) that are characterized by relatively constant climatic conditions throughout the year (Barry 2008). However, many tropical ecosystems are, in fact, characterized by seasonality, for instance by seasonal variation in precipitation

(Emck 2007; Rollenbeck and Bendix 2011). Temporal changes in climatic conditions can occur locally, resulting in climatic variability (Williams and Middleton 2008) and in fluctuations in resource availability (Mulwa et al. 2013) on relatively small spatial scales. Only few studies so far have examined the temporal dynamics of tropical bird assemblages. These studies have shown pronounced temporal fluctuations of bird assemblages (Loiselle and Blake 1991) and suggest that both changes in temperature and precipitation (Boyle 2011), as well as in resource availability (Mulwa et al. 2013) can cause local fluctuations of bird assemblages. However, none of these studies has simultaneously tested how climate factors and resource availability affect the spatial and temporal dynamics of bird assemblages across environmental gradients.

In this study, we examined the spatio-temporal dynamics of bird assemblages along an elevational gradient within and around Podocarpus National Park in Southern Ecuador. First, we tested the effects of elevation (i.e., 1000, 2000, and 3000 m) and season (most humid and least humid season) on bird abundance, evenness and richness. Second, we examined whether climate (i.e., temperature and precipitation) and/or resource availability (i.e., the sum of flower, fruit and invertebrate resources) explained the temporal fluctuations in bird abundance, evenness and richness along the elevational gradient. We hypothesized that 1) bird abundance, evenness and richness would decrease with increasing elevation (McCain 2009b; Willig and Presley 2015) and 2) that the effect of seasonal variation in climate and resources on bird assemblages may vary across the three elevations (Loiselle and Blake 1991), due to different constraints at high and low elevations. We expected that fluctuations of bird assemblages relate to both climatic factors and resource availability. While we expected that temperature and precipitation limit bird abundance, evenness and richness mostly at high elevations, likely due to physiological constraints (Hawkins et al. 2003a; McCain 2009b), we expected resource availability to affect bird abundance, evenness and richness in particular at low elevations, due to high competition for resources (Brown et al. 1996b).

Material and methods

Study area

We carried out this study within and around Podocarpus National Park and San Francisco reserve in southern Ecuador (Figure 1). The region is characterized by three vegetation types, evergreen premontane forest at low elevations (1000 m), evergreen lower montane forest at mid elevations (2000 m) and upper montane forest at high elevations (3000 m) (Homeier et al. 2008). The climate is tropical humid with a mean annual temperature of 20°C at low elevations, 15.5°C at mid elevations and 10°C at high elevations (Emck 2007). Mean annual precipitation is 2432 mm at low elevations, 2079 mm at mid elevations and 4522 mm at high elevations (Emck 2007). At each of three elevations, we selected two study sites. At each study site, we established three one-hectare plots, resulting in a total of 18 plots (Figure 1). Plot selection was conducted within the framework of the “Platform for Biodiversity and Ecosystem Monitoring and Research in South Ecuador”; the selected plots are representative for local site conditions.

Bird point counts and surveys of resource availability

We conducted point counts in each of the 18 plots. Bird assemblages were sampled twice in the most humid season (May-July) and twice in the least humid season (September-November) in 2014 and 2015, resulting in eight temporal replicates per plot. At each plot, we placed nine point count locations, eight at the borders of the 1-ha plots and one in the centre. For 10 minutes, we recorded and identified all birds heard or seen to species level (Ridgely and Greenfield 2001) within a 20-m radius around the centre of each point count location. The 20-metre sampling radius was chosen because of the low visibility in the dense tropical forest beyond that radius (Bibby et al. 2000; Ferger et al. 2014). Sampling started at sunrise and ended before 09:00 h and was conducted by three observers. Plots were randomized among observers to minimize sampling bias. We quantified bird abundance, evenness and species richness by summing the records of all point counts per plot and temporal replicate (sampled area for each plot approx. 1.1 ha). Abundance was measured as the overall number of bird individuals per plot and temporal replicate. Evenness measures the relative abundance of each species in the community and was calculated as $e^{(H)} / S$, where H is the Shannon diversity index and S the species richness per plot and temporal replicate (Kindt 2016). Species richness was measured as the overall number of bird species recorded per plot and temporal replicate. We computed species accumulation curves on the relationship between the proportion of recorded species and the number of point counts conducted on each plot in each season (i.e., 18 point counts over both years). Similar slopes and saturating trends of the accumulation curves for the most humid and least humid season indicated that communities were similarly well sampled in both seasons (S1 Fig). On average, over 90% of the bird species were recorded after 13 point counts (S1 Fig). To further test whether bird detectability differed among elevations and between seasons, we recorded the distance of each bird from the centre of the point count location in all counts conducted in 2015. We found that the median distance of birds to the observer did not differ significantly among elevations (Generalized linear mixed effects model, low elevation compared to mid elevation: $\beta = -0.18$, $z = -1.45$, $p = 0.15$; low elevation compared to high elevation: $\beta = -0.15$, $z = -1.25$, $p = 0.21$) and between season ($\beta = -0.16$, $z = -1.56$, $p = 0.12$), indicating that the detectability of birds was similar across elevations and seasons.

We recorded the overall resource availability for each plot, comprising flower, fruit and invertebrate resources. To estimate flower and fruit availability, we recorded all plants with open flowers and ripe fruits within a 20-metre radius around each point count location. For each plant, we choose several randomly-picked branches, counted the number of flowers and fruits per branch and estimated the overall abundance of flowers and fruits per plant. Flower and fruit abundances of each of the nine point count locations were summed to obtain the overall abundance per plot (Mulwa et al. 2013). To obtain a relative comparison of invertebrate resources among all plots, we assessed understory invertebrate biomass by using a standardized sweep-netting design (Mulwa et al. 2013). We made a total of 100 sweeps along one of the 100-metre borders of each plot and subsequently weighted the cumulative invertebrate fresh biomass. Flowers, fruits and insect biomass were scaled to zero mean and unit variance and then summed to calculate the overall resource availability per plot.

Data analyses

We used R v. 3.3.0 (R Development Core Team 2016) for all statistical analyses. We obtained average monthly climate data for each study plot (S2 Fig). Average monthly within-forest temperatures (i.e., monthly mean of daily maximum temperatures) were obtained through an air temperature regionalization tool developed for the study region (Fries et al. 2009). Monthly mean precipitation (i.e., average of the sum of monthly precipitation) was obtained through remote sensing techniques (local area weather radar and satellite imagery) and meteorological data (Rollenbeck and Bendix 2011). Combining remote sensing techniques with meteorological data using geostatistical tools is most suitable to derive local climate information of high spatial and temporal resolution for the eastern slope of the southern Andes in Ecuador (Rollenbeck 2006; Fries et al. 2009).

First, we tested the effect of elevation (three levels: 1000, 2000, 3000 m) and season (two levels: most humid and least humid season) on bird abundance, evenness and richness using generalized linear mixed effects models (GLMMs) assuming a Poisson error distribution for abundance and richness and a Gaussian error distribution for evenness. To account for the spatio-temporal sampling structure, we included the study plot nested in site and the sampling month in each respective year (i.e., in total eight sampling months over two years) as random effects in all models. We fitted all models with and without the interaction term between elevation and season and selected the best model based on the lowest Akaike's information criterion (Burnham and Anderson 2002). We retained the simple model without interaction term in all cases (see S1 Table). To test whether patterns in bird richness were driven by patterns in abundance, we built a model of richness and included abundance as a predictor in addition to elevation and season.

Second, we tested whether temperature, precipitation and/or resource availability (i.e., the sum of flower, fruit, and invertebrate resources) explained temporal fluctuations in bird abundance, evenness and richness over the eight temporal point count replicates using GLMMs assuming a Poisson error distribution. We built separate models for each predictor variable and for each elevation (i.e., nine models in total). All predictor variables were scaled prior to the analyses to achieve comparability among models. We included the respective predictor variable as fixed effect and random intercept and slope effects of the study plot in all models allowing for potential differences in intercept and slopes among study plots. All models were fitted with a restricted maximum likelihood approach assuming a Poisson error distribution for abundance and richness and a Gaussian error distribution for evenness. To account for multiple testing across the nine models, we used a Bonferroni correction. To maintain a critical error rate of $\alpha = 0.05$, we considered an effect significant if $p < 0.005$ (Rice 1989).

To test whether different bird feeding guilds respond differently to their respective resource type, we classified the birds recorded per plot according their diet into nectarivores, frugivores, insectivores, and omnivores. We assigned birds consuming

60% or more of a food type (e.g. fruits) to the respective feeding guild (e.g. frugivores, see also Pigot et al. (2016), S2 Table) based on the Elton trait database (Wilman et al. 2014). We then repeated the analyses and tested whether temperature, precipitation and/or the availability of the resource type (i.e., flowers, fruits, *or* invertebrates, respectively) explained temporal fluctuations in bird abundance separately for each of the feeding guilds.

Results

We recorded 4323 individuals of 241 species across all elevations and seasons. Among these, 1589 individuals of 127 species were recorded at low elevations, 1494 individuals of 100 species at mid elevations and 1240 individuals of 70 species at high elevations. While 1694 individuals of 185 species were recorded in the most humid season, 2629 individuals of 208 species were recorded in the least humid season (see Table 1 for an overview of abundance and species richness of bird feeding guilds across all elevations and seasons).

Bird abundance and richness were positively correlated ($r = 0.73$, $p < 0.01$), whereas abundance and richness were negatively related with evenness ($r = -0.5$, $p < 0.001$; r 0 -0.13, $p = 0.11$, respectively). Bird abundance per plot was significantly lower in the most humid compared to the least humid season (most humid season: mean = 24, SD = 13.2, n = 72; least humid season: mean = 37, SD = 17, n = 72), but did not significantly differ among elevations (low elevation: mean = 33, SD = 14.9, n = 48; mid elevation: mean = 31, SD = 16.4, n = 48; high elevation: mean = 26, SD = 17.6, n = 48; Tables 2a - S3; Figure 2a). Bird evenness was significantly higher in the most humid compared to the least humid season (most humid season: mean =0.844, SD =0.093, n =72; least humid season: mean =0.797, SD =0.086, n = 72), and increased significantly at the highest elevation (low elevation: mean =0.794, SD =0.095, n = 48; mid elevation: mean =0.818, SD =0.088, n = 48; high elevation: mean = 0.849, SD =0.087, n = 48; Tables 2b - S3; Figure 2b). Bird species richness was significantly lower in the most humid than in the least humid season (most humid season: mean = 12, SD = 5.8, n = 72; least humid season: mean = 15, SD = 5.7, n = 72), and decreased significantly at the highest elevation (low elevation: mean = 15, SD = 6.5, n = 48; mid elevation: mean = 14, SD = 5.5, n = 48; high elevation: mean = 12, SD = 5.6, n = 48; Tables 2c - S3; Figure 2c). In the bird richness model that additionally included bird abundance as a predictor, bird richness was significantly positively related to bird abundance and decreased at the highest elevation, but was unaffected by season (Tables 2d - S3).

Climate factors were more important than resource availability for explaining the temporal fluctuations of birds along the elevational gradient (Tables 3 - S4; Figure 3). This pattern was only significant for bird abundance, albeit the patterns were similar for evenness and richness (Tables 3 - S4; Figures 3 - S3). Maximum temperature was positively related to bird abundance over the two study years and was significantly positively associated with bird abundance at mid and high elevations (Tables 3a - S4; Figures 3 - S3). In contrast, precipitation was negatively related to bird abundance over the two study years and was significantly negatively associated with bird abundance at low and mid elevations (Tables 3a - S4; Figures 3 - S3). Overall resource availability had no significant effect on the temporal variation in bird abundance, evenness and richness (Tables 3 - S4, Figures 3 - S3). Separate analyses for the different feeding guilds (nectarivores, frugivores, insectivores and omnivores) supported the pattern that climatic factors were generally more important in explaining temporal variation in these groups than their respective resource type (i.e., flowers, fruits, insects and all resources combined, S4 Fig).

Discussion

We show that bird species richness decreased significantly at high elevations and that bird abundance, evenness and richness varied significantly between the most humid and least humid season across all elevations. The pronounced temporal fluctuations in bird abundances were mainly related to climatic factors (i.e., temperature and precipitation) rather than by resource availability. Our findings suggest that the temporal fluctuations in tropical bird assemblages in our study region likely occur due to temporary constraints related to climatic conditions rather than due to resource limitations.

We found a significant decline of bird richness at the highest elevation, which even persisted when accounting for declines in bird abundance. Our results are in line with previous studies showing a decline of species richness along elevational gradients (McCain 2009b), which has been attributed to limiting abiotic and biotic factors, such as harsh climatic conditions or reduced resource availability at high elevations (Currie et al. 2004). In contrast, we found no significant changes in overall bird abundance across the elevational gradient. In species-poor assemblages, such as at high elevations, the relative abundance of individual species is often higher compared to species-rich assemblages (Willig and Presley 2015), which is consistent with the slight increase in species evenness at the highest elevations. Such effects of density compensation of the persisting species may explain similar overall bird abundance at all elevations.

While we did not find spatial patterns in bird abundances, we found pronounced temporal fluctuations. At all three elevations, bird abundances increased in the least humid season. This increase in abundance corresponded to a consistent decline of bird evenness in the least humid season, indicating a more skewed abundance distribution during that time, likely due to an increase in abundance of the dominant species in the assemblage. We also encountered changes in species richness between seasons, but these changes were largely driven by changes in bird abundance, as abundance changes accounted for the seasonal variation in bird richness (Table 2d). One explanation for seasonal fluctuations in bird abundances might be the narrow thermal tolerance of tropical species (Brown 2014) that may force birds to leave their habitat if climatic conditions become temporarily unsuitable (Hau 2001). The consistent increase in bird abundances in the least humid season across all three elevations suggests medium- to long-distance seasonal movements of birds (Terborgh 1985) rather than to short-distance elevational migrations among the low, mid and high elevation sites (Boyle 2011). Another explanation could be differences in the detectability of birds across the course of the year. For instance, are vocally more active and visible during the breeding season (Boyle 2011). However, breeding cycles of tropical birds are known to lack a pronounced seasonality and may differ between species of a local assemblage (Hau 2001). Moreover, both species accumulation curves and distance-sampling revealed no significant differences in bird detectability between seasons, suggesting that bird abundances and evenness indeed fluctuated strongly between seasons independent of bird activity.

In our study, temperature and precipitation had contrasting effects on the temporal fluctuation of bird abundance along the elevational gradient. Temperature had a significant positive effect on bird abundance at mid and high elevations, while precipitation had a significant negative effect at mid and low elevations. Our results are supported by previous studies showing that bird assemblages of low and high elevations may be affected by different climatic factors (Ruggiero and Hawkins 2008; McCain 2009b), probably due to specific physiological constrains under the respective climate conditions (Wingfield et al. 1992; Boyle et al. 2010). In fact, temperature and precipitation covered distinct extremes along the elevational gradient. For example, monthly maximum temperatures were much lower and more variable at high compared to low elevations (3000 m: mean = 13.1 °C, SD = 1.7; 1000 m: mean = 23.1 °C, SD = 1.2). While mean monthly precipitation was low at low elevations (mean = 188 mm, SD = 29), precipitation increased towards high elevations (mean = 213 mm, SD = 36). Further, high elevation forests in the study area are characterized by persistent cloud cover and fog all year long, resulting in additional moisture bound to aerosols (Bendix et al. 2006; Emck 2007). While bird abundances were clearly affected by the low temperatures at high elevations, the high amount of rainfall did not seem to affect bird abundance. This pattern suggests that bird assemblages at high elevations are limited by temperature, but might be adapted to the persisting rainy conditions at these sites. In contrast, lowland bird assemblages are not limited by extreme temperatures, but rainfall may pose limitations to birds forcing them to leave the area (Williams and Middleton 2008; Boyle et al. 2010). The significant negative effect of precipitation on bird assemblages at low elevations conflicts our initial expectation that abiotic factors are the main constraints of bird assemblages only at high elevations (Hawkins et al. 2003a; McCain 2009b). In fact, most studies that have identified precipitation as a main predictor of bird assemblages demonstrate that high precipitation at upper elevations may cause down-slope movements of birds (Williams and Middleton 2008; Boyle et al. 2010; Tingley et al. 2012). Interestingly, in our study, the overall amount of rainfall was comparatively moderate at low, compared to high elevations, but still significantly affected lowland bird assemblages. Other studies, mostly from water-limited ecosystems, have in turn shown positive effects of precipitation on bird assemblages (McCain 2009b). Our results highlight that beside the well-studied negative effects of low temperatures (McCain 2009b; McCain and Grytnes 2010), an excess of precipitation can lead to reduced abundances in bird assemblages.

In contrast to the significant effects of climatic factors, food resource availability did not contribute to explaining the temporal fluctuations in bird assemblages. Our findings are different to those of previous studies where resource availability influenced temporal variation of bird assemblages (Loiselle and Blake 1991; Poulin et al. 1992; Borghesio and Laiolo 2004; Mulwa et al. 2013). One explanation for this difference could be that most of these previous studies focused on particular species or feeding guilds rather than on the response of the entire bird assemblage to resource availability (Waide et al. 1999). Separate analyses of different feeding guilds and their respective food resources, however, supported the pattern that climate rather than the availability of resources was more closely associated with temporal variation in bird guilds (S4 Fig). Another explanation for the low importance of resources for the spatio-temporal dynamics of bird assemblages could be the overall high productivity of the studied ecosystem (Fiedler et al. 2008; Homeier et al. 2008). In systems that provide a surplus of resources to animal consumers, such as birds, this could result in a decoupling of resource availability and consumer diversity (Feinsinger 1976). However, resource effects on bird assemblages may generally be difficult to detect because the sampling of resources in tropical forests can never be exhaustive. In our study, we did, for instance, not account for invertebrates occurring in higher forest strata or the amount of nectar produced by flowers. Moreover, the local heterogeneity of resources was probably higher than that of temperature and precipitation, which could have contributed to the stronger relationship of bird abundance with climatic conditions than with resource availability. We therefore concede that resource effects on temporal fluctuations in bird abundance could be underestimated due to methodological constraints.

Conclusions

In our study we showed that bird assemblages along an elevational gradient in the tropical Andes experienced strong seasonal variation that was governed by changes in temperature and precipitation. In particular, low temperature and high precipitation caused decreases in bird abundances. Although climatic factors are expected to increase in importance, relative to biotic factors, at large spatial scales (Wisz et al. 2013), we show here that climatic constraints can overrule biotic effects at small spatial scales. The high importance of climatic factors in shaping the spatio-temporal dynamics of bird assemblages highlights the sensitivity of tropical birds towards projected climate change (Blake and Loiselle 2015). Climate change projections for the tropical Andes predict an increase of temperature, especially at high elevations, and an increase of extreme rainfall events, in particular at low elevations (Anderson et al. 2011). While bird species at high elevations might benefit from warmer temperatures, extreme drought events could also negatively affect high-elevation assemblages (Larsen et al. 2011). In the lowlands, projected increases in rainfall and in the temporal variation in precipitation will likely have negative effects on bird assemblages and could trigger an increase in spatio-temporal movements of lowland species in the future (Larsen et al. 2011). We conclude that understanding the spatio-temporal dynamics of species assemblages in response to shifts in temperature and precipitation are essential for projecting potential responses of species to future climatic conditions.

Acknowledgements

We thank the German Research Foundation (DFG) for funding our project in the framework of the Research bundle 823-825 “Platform for Biodiversity and Ecosystem Monitoring and Research in South Ecuador” (PAK 825/1; BO 1221/20-1). The Ecuadorian Ministry of the Environment (MAE) kindly provided permission to conduct research. We are grateful to Agustín Carrasco and Patricio Estrella, for their help in fieldwork. Jörg Bendix, Rütger Rollenbeck and Katja Trachte provided climate data. We thank Nature and Culture International (NCI), Felix Matt, Jörg Zeilinger, Mathias Templin and Catherine Vits for logistic support and David Siddons for English proofreading. We thank two anonymous reviewers for previous comments on an earlier version of this manuscript.

Author Contributions

Conceptualization: VS, MQ, MS, KBG, ELN. Data curation: VS, MQ, MS, KBG, ELN. Formal analysis: VS, MS, ELN. Funding acquisition: MS, KBG, ELN. Investigation: VS, MQ, MS, ELN. Methodology: VS, MQ, MS, KBG, ELN. Project administration: KBG, ELN. Resources: KBG. Supervision: MS, KBG, ELN. Validation: VS, BAT, EZ, MS, ELN. Visualization: VS. Writing – original draft: VS, ELN. Writing – review & editing: VS, MQ, BAT, EZ, MS, KBG, ELN.

References

Anderson P, Marengo J, Villalba R, et al (2011) Consequences of Climate Change for ecosystems and ecosystem services in the Tropical Andes. In: Herzog S, Matínez R, Jørgensen P, Tiessen H (eds) Climate change and biodiversity in the tropical Andes. Inter-American Institute for Global Change Research, pp 1–18

Barry RG (2008) Mountain weather and climate, 3rd edn. Cambridge University Press, Boulder

Bendix J, Rollenbeck R, Göttlicher D, Cermak J (2006) Cloud occurrence and cloud properties in Ecuador. Climate Research 30:133–147

Bibby C, Burgess N, Hill D, Mustoe S (2000) Bird census techniques, 2nd edn. Academic Press, Cambridge, UK

Blake JG, Loiselle BA (2015) Enigmatic declines in bird numbers in lowland forest of eastern Ecuador may be a consequence of climate change. PeerJ 3:e1177

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

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

Boyle WA, Norris DR, Guglielmo CG (2010) Storms drive altitudinal migration in a tropical bird. Proceedings of the Royal Society B: Biological Sciences 277:2511–2519

Brown JH (2014) Why are there so many species in the tropics? Journal of Biogeography 41:8–22

Brown JH, Stevens GC, Kaufman DM (1996) The geographic range: size, shape, boundaries, and internal structure. Annual Review of Ecology and Systematics 27:597–623

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York

Currie DJ, Mittelbach GG, Cornell H V., et al (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7:1121–1134

Dehling DM, Fritz SA, Töpfer T, et al (2014) Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. Ecography 37:1047–1055

Dornelas M, Magurran AE, Buckland ST, et al (2013) Quantifying temporal change in biodiversity: challenges and opportunities. Proceedings Biological sciences / The Royal Society 280:20121931

Emck P (2007) A climatology of south Ecuador. Universität Erlangen-Nürnberg

Feinsinger P (1976) Organization of a tropical guild of nectarivorous birds. Ecological Monographs 46:257–291

Ferger SW, Schleuning M, Hemp A, et al (2014) Food resources and vegetation structure mediate climatic effects on species richness of birds. Global Ecology and Biogeography 23:541–549

Fiedler K, Brehm G, Hilt N, et al (2008) Variation of diversity patterns across moth families along a tropical altitudinal gradient. In: Beck E, Bendix J, Kottke I, et al. (eds) Gradients in a tropical mountain ecosystem of Ecuador. Springer, Berlin, pp 167–180

Field R, Hawkins BA, Cornell H V., et al (2009) Spatial species-richness gradients across scales: A meta-analysis. Journal of Biogeography 36:132–147

Fries A, Rollenbeck R, Göttlicher D, et al (2009) Thermal structure of a megadiverse Andean mountain ecosystem in southern Ecuador and its regionalization. Erdkunde 63:321–335

Gaston KJ (2000) Global patterns in biodiversity. Nature 405:220–227

Hau M (2001) Timing of breeding in variable environments: Tropical birds as model systems. Hormones and Behavior 40:281–290

Hawkins BA, Field R, Cornell H V., et al (2003a) Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117

Hawkins BA, Porter EE, Diniz-Filho JAF (2003b) Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. Ecology 84:1608–1623

Herzog SK, Kessler M, Bach K (2005) The elevational gradient in andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. Ecography 28:209–222

Homeier J, Werner FA, Gradstein SR, Richter M (2008) Potential vegetation and floristic composition of Andean forests in south Ecuador, with a focus on the RBSF. In: Beck E, Bendix J, Kottke I, et al. (eds) Gradients in a tropical mountain ecosystem of Ecuador. Springer, Berlin, pp 87–100

Jetz W, Rahbek C, Lichstein JW (2005) Local and global approaches to spatial data analysis in ecology. Global Ecology and Biogeography 14:97–98

Kindt R (2016) BiodiversityR: package for community ecology and suitability analysis. 133

Larsen TH, Brehm G, Navarette H, et al (2011) Range shifts and extinctions diven by climate change in the tropical Andes: synthesis and directions. In: Herzog S, Matínez R, Jørgensen P, Tiessen H (eds) Climate change and biodiversity in the tropical Andes. Inter-American Institute for Global Change Research, pp 47–67

Loiselle BA, Blake JG (1991) Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology 72:180–193

Louthan AM, Doak DF, Angert AL (2015) Where and when do species interactions set range limits? Trends in Ecology and Evolution 30:780–792

McCain CM (2009) Global analysis of bird elevational diversity. Global Ecology and Biogeography 18:346–360

McCain CM, Grytnes J-A (2010) Elevational gradients in species richness. Encyclopedia of Life Sciences (ELS) 1–10

Merkord CL (2010) Seasonality and elevational migration in an Andean bird community

Mulwa RK, Neuschulz EL, Böhning-Gaese K, Schleuning M (2013) Seasonal fluctuations of resource abundance and avian feeding guilds across forest-farmland boundaries in tropical Africa. Oikos 122:524–532

O’Brien EM (1998) Water-energy dynamics , climate, and prediction of woody plant species richness: An interim general model. Journal of Biogeography 25:379–398

Pigot AL, Trisos CH, Tobias JA (2016) Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. Proceedings of the Royal Society B: Biological Sciences 283:1–9

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

R Development Core Team (2016) A language and environment for statistical computing

Rahbek C, Gotelli NJ, Colwell RK, et al (2007) Predicting continental-scale patterns of bird species richness with spatially explicit models. Proceedings of the Royal Society B: Biological Sciences 274:165–174

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223–225

Ridgely RS, Greenfield PJ (2001) The birds of Ecuador volume II. Cornell University Press, New York

Rollenbeck R (2006) Variability of precipitation in the reserva biólogica San Francisco / southern Ecuador. Lyonia 9:43–51

Rollenbeck R, Bendix J (2011) Rainfall distribution in the Andes of southern Ecuador derived from blending weather radar data and meteorological field observations. Atmospheric Research 99:277–289

Root T (1988) Energy constraints on avian distributions and abundances. Ecology 69:330–339

Rosenzweig ML (1993) How are diversity and productivity related? In: Press TU of C (ed) Species diversity in ecological communities, 1st edn. Chicago, pp 67–74

Rosenzweig ML (1995) Species diversity in space and time, 1st edn. Cambridge University Press, Cambridge

Ruggiero A, Hawkins BA (2008) Why do mountains suport so many species of birds? Ecography 31:306–315

Terborgh J (1977) Bird species diversity on an Andean elevational gradient. Ecology 58:1007–1019

Terborgh J (1985) The role of ecotones in the distribution of Andean birds. Ecology 66:1237–1246

Tingley MW, Koo MS, Moritz C, et al (2012) The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. Global Change Biology 18:3279–3290

Waide RB, Willig MR, Steiner CF, et al (1999) The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30:257–300

Williams SE, Middleton J (2008) Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: Implications for global climate change. Diversity and Distributions 14:69–77

Willig MR, Presley SJ (2015) Biodiversity and metacommunity structure of animals along altitudinal gradients in tropical montane forests. Journal of Tropical Ecology 32:421–436

Wilman H, Belmaker J, Jennifer S, et al (2014) EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. Ecology 95:2027

Wingfield JC, Hahn TP, Levin R, Honey P (1992) Environmental predictability and control of gonadal cycles in birds. Journal of Experimental Zoology 261:214–231

Wisz MS, Pottier J, Kissling WD, et al (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. Biological Reviews 88:15–30

Zhang J, Kissling WD, He F (2013) Local forest structure, climate and human disturbance determine regional distribution of boreal bird species richness in Alberta, Canada. Journal of Biogeography 40:1131–1142

Appendix 2. Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient

Table 1. Overview of bird abundances and species richness belonging to different feeding guilds across all elevations in both study seasons. MHS = most humid season, LHS = least humid season, Ind = number of individuals, Spp = number of species.

	1000 m				2000 m				3000 m			
	MHS		LHS		MHS		LHS		MHS		LHS	
	Ind	Spp	Ind	Spp	Ind	Spp	Ind	Spp	Ind	Spp	Ind	Spp
Nectarivores	31	11	49	13	43	11	84	11	44	11	57	8
Frugivores	237	27	371	31	78	12	154	16	38	8	64	7
Insectivores	209	34	321	42	317	36	425	36	301	25	528	28
Omnivores	179	19	192	22	136	15	257	19	81	12	127	16
TOTAL	656	91	933	108	574	74	920	82	464	56	776	59

Appendix 2. Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient

Table 2. Generalized linear mixed effects models testing a) bird abundance, b) evenness, c) species richness as a function of elevation (1000, 2000, 3000 m) and season (most humid and least humid), and d) species richness as a function of abundance, elevation and season. Study plot nested in site and sampling months of each year were included as random effects in all models. All models assume a Poisson error distribution. Significant effects ($p < 0.05$) are printed in bold.

	Predictor variable	β	SE	p
a) Bird abundance	Most humid season	-0.45	0.12	**<0.001**
	Mid elevation	-0.06	0.21	0.776
	High elevation	-0.31	0.21	0.141
b) Bird evenness	Most humid season	0.05	0.01	**0.001**
	Mid elevation	0.02	0.02	0.265
	High elevation	0.06	0.02	**0.018**
c) Bird richness	Most humid season	-0.28	0.09	**<0.001**
	Mid elevation	-0.11	0.13	0.411
	High elevation	-0.3	0.13	**0.024**
d) Bird richness	Abundance	0.27	0.02	**<0.001**
	Most humid season	-0.05	0.05	0.348
	Mid elevation	-0.08	0.08	0.283
	High elevation	-0.18	0.08	**0.024**

Appendix 2. Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient

Table 3. Generalized linear mixed effects models testing the effects of temperature, precipitation and resource availability on eight temporal replicate counts in a) bird abundance b) species evenness and c) species richness at three elevations. Estimates for each predictor variable and elevation result from separate models and assume a Poisson error distribution; all predictors were scaled to zero mean and unit variance prior to model fitting. All models include the respective predictor variable as fixed effect and random intercept and slope effects of the study plot. Significant effects after Bonferroni correction ($p < 0.005$) are printed in bold.

	Predictor variable	Elevation (m)	β	SE	p
a) Bird abundance	Temperature	3000	0.53	0.16	**0.001**
		2000	0.86	0.27	**0.002**
		1000	0.42	0.22	0.052
	Precipitation	3000	0.24	0.09	0.005
		2000	-0.28	0.05	**<0.001**
		1000	-0.24	0.05	**<0.001**
	Resources	3000	0.03	0.04	0.391
		2000	0.02	0.07	0.753
		1000	-0.06	0.03	0.079
b) Bird evenness	Temperature	3000	-0.06	0.03	0.072
		2000	-0.01	0.08	0.882
		1000	-0.13	0.05	0.013
	Precipitation	3000	0.004	0.02	0.861
		2000	0.01	0.01	0.542
		1000	0.04	0.02	0.104
	Resources	3000	-0.01	0.01	0.351
		2000	0.001	0.01	0.932
		1000	-0.02	0.01	0.288
c) Bird richness	Temperature	3000	0.38	0.21	0.078
		2000	0.61	0.39	0.116
		1000	0.15	0.2	0.464
	Precipitation	3000	0.12	0.09	0.21
		2000	-0.17	0.08	0.034
		1000	-0.14	0.08	0.073
	Resources	3000	-0.02	0.04	0.604
		2000	-0.09	0.03	0.005
		1000	-0.07	0.03	0.036

Appendix 2. Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient

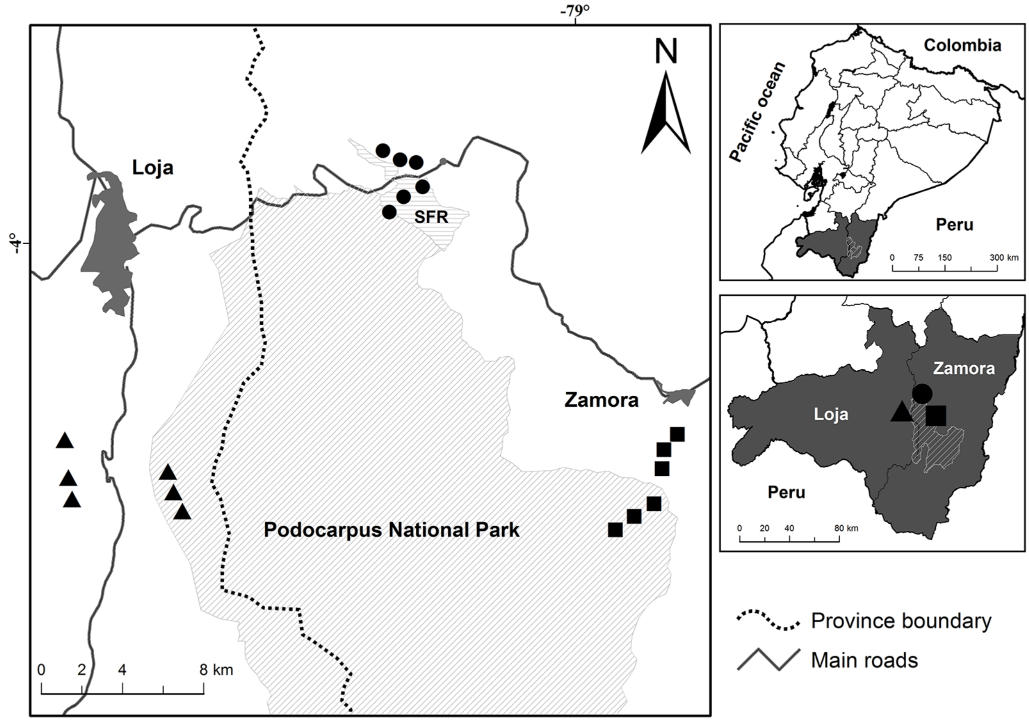


Figure 1. Study area within and around Podocarpus National Park and San Francisco reserve (SFR) in southern Ecuador. Squares represent study plots at 1000 m, circles those at 2000 m and triangles those at 3000 m.

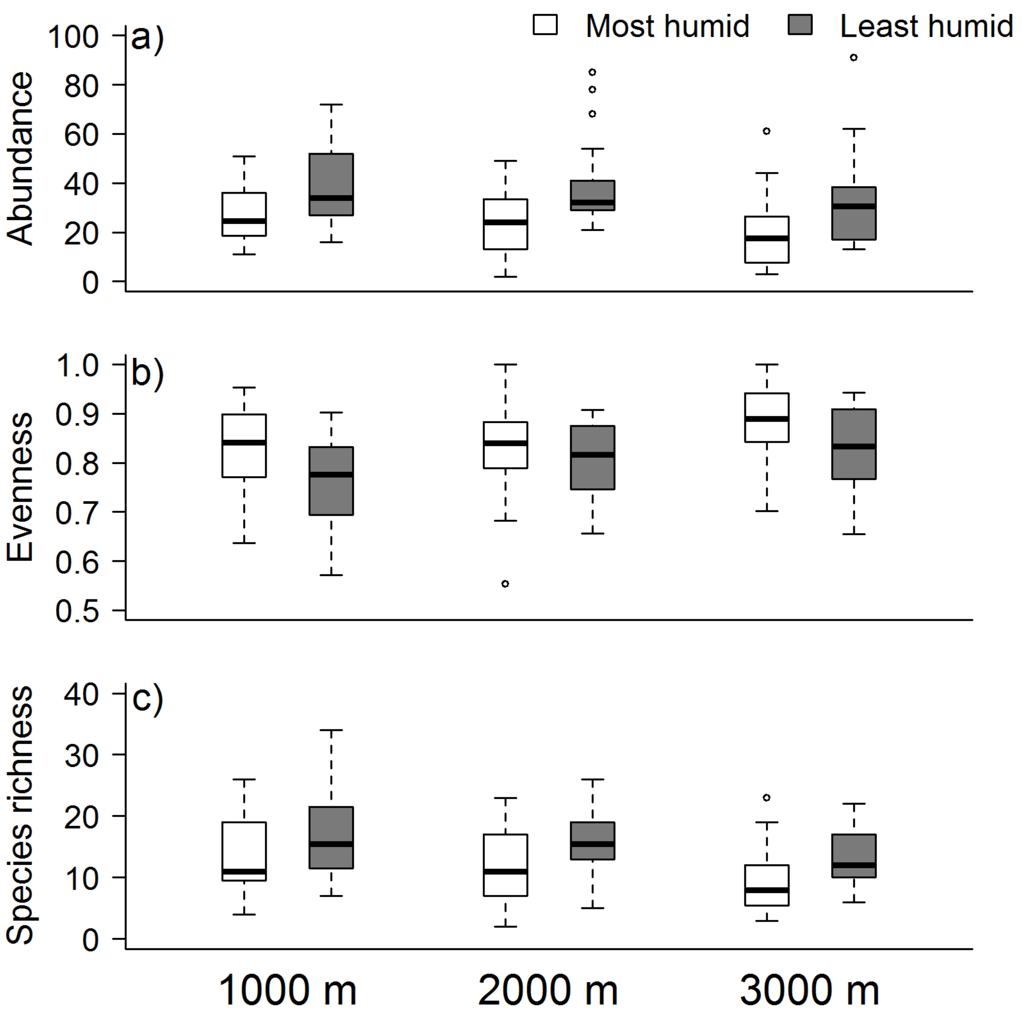


Figure 2. Spatio-temporal fluctuations of a) bird abundance, b) evenness and c) species richness across three elevations (1000, 2000, 3000 m) and in the most humid (white) and least humid (grey) season. Each box depicts the median, and 25th and 75th percentiles of bird records of six plots replicated four times within the respective season. Whiskers indicate the normal data range, circles represent outliers.

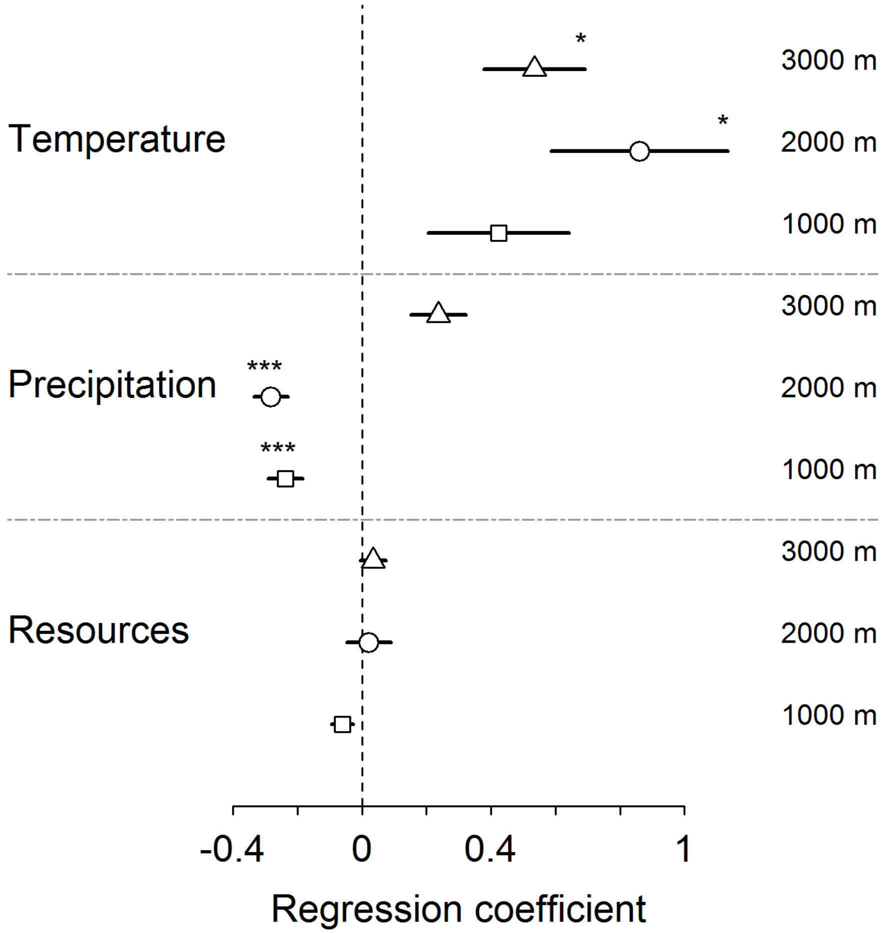


Figure 3. Effects on bird abundance of temperature, precipitation and resource availability on the temporal fluctuations along the elevational gradient. Squares represent sites at 1000 m, circles those at 2000 m, and triangles those at 3000 m. Shown are regression coefficients from generalized linear mixed effects models of eight temporal replicates including the respective predictor variable as fixed effect and random intercept and slope effects of the study plot in all models. Horizontal lines refer to standard error (SE). P-values after Bonferroni correction: *p<0.005, ***p<0.0001.

Supplementary material

Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient

Vinicio Santillán, Marta Quitián, Boris A. Tinoco, Edwin Zárate, Matthias Schleuning, Katrin Böhning-Gaese and Eike Lena Neuschulz

Corresponding author: Vinicio Santillán: vinicioestuardosantillan@gmail.com

Appendix S1. Species accumulation curves.

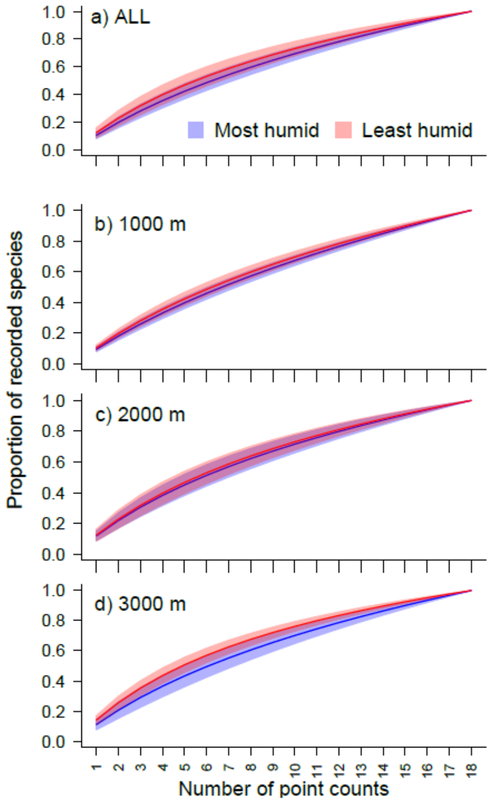


Figure S1. Species accumulation curves showing the relationship between the proportion of recorded species and the number of point counts conducted on each plot in each season (i.e., 18 point counts in total over both years**).** Curves were calculated for each plot and were averaged for (a) all study sites and (b, c, d) for each elevation separately. Blue lines represent mean species accumulation for the most humid season, red lines represent mean species accumulation for the least humid season. Blue and red areas show standard deviation for most humid and least humid seasons, respectively.

Appendix S2. Climate data of the study region.

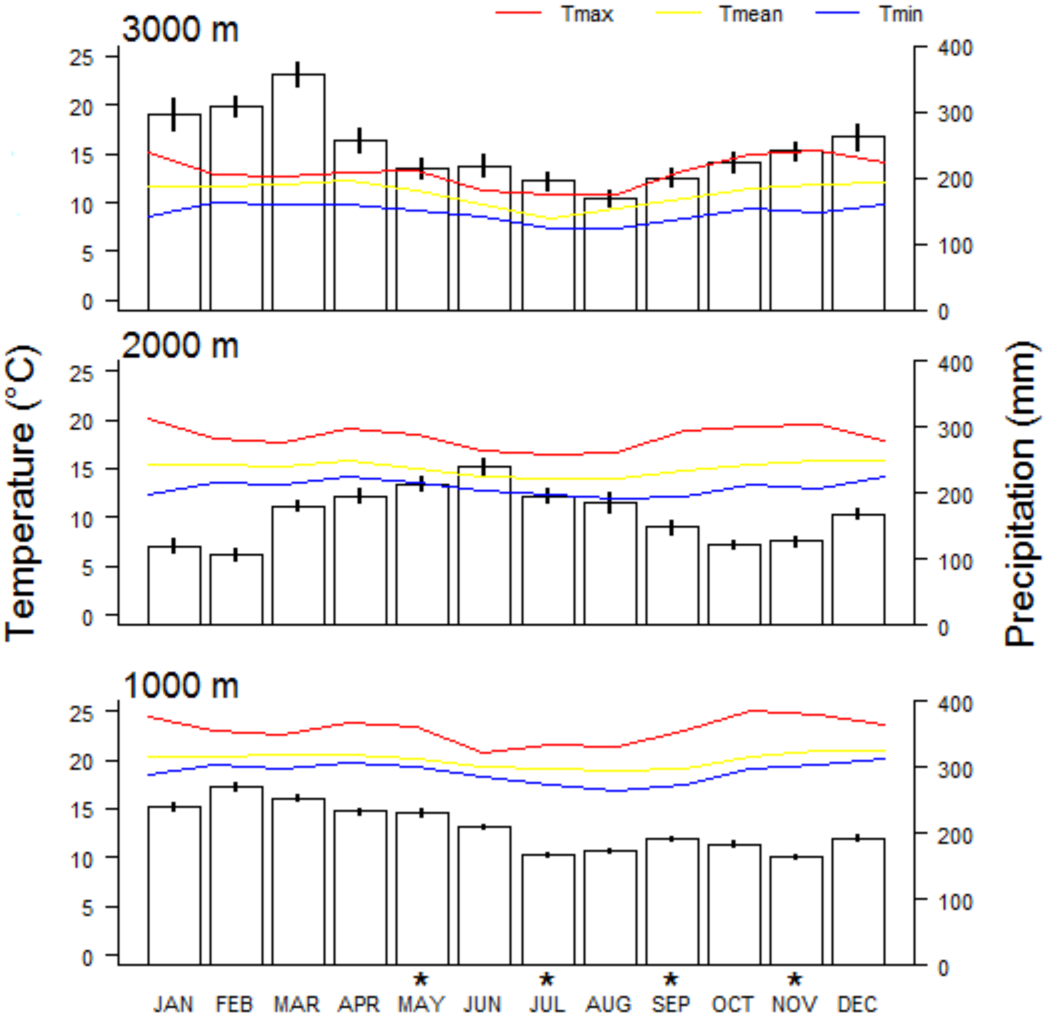


Figure S2. Mean monthly temperature (i.e., monthly mean of daily minimum [blue], mean [yellow] and maximum [maximum] temperatures) and precipitation (i.e., average of the sum of monthly precipitation) over all six study plots located at 1000, 2000 and 3000 m a.s.l. Sampling months are indicated by an asterisk.

Appendix S3. Effects of temperature, precipitation and resource availability on the temporal fluctuations in bird evenness and bird species richness.

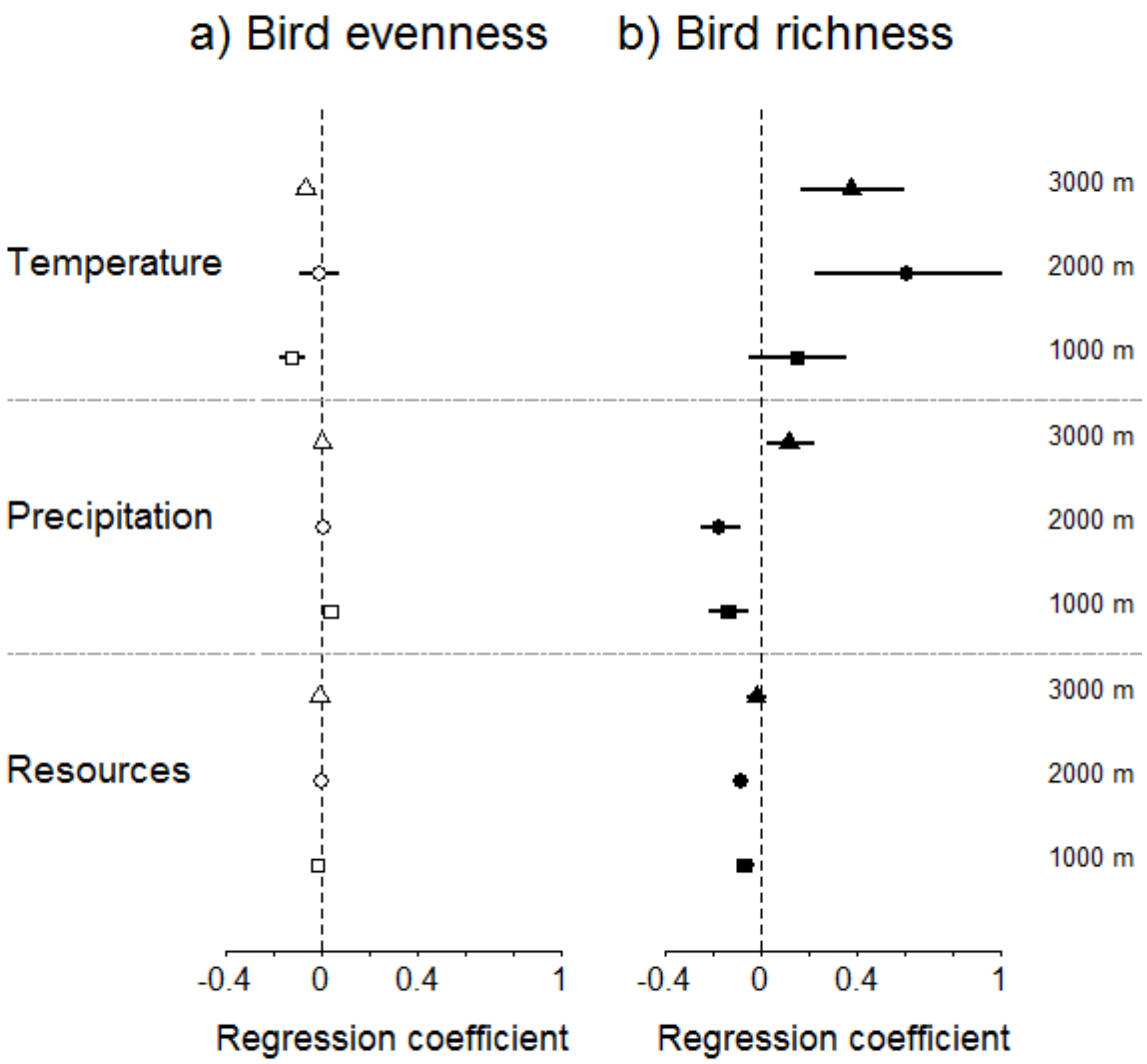


Figure S3. Effects of temperature, precipitation and resource availability on the temporal fluctuations in a) bird evenness (white) and bird species richness (black) along the elevational gradient. Squares represent sites at 1000 m, circles those at 2000 m, and triangles those at 3000 m. Shown are regression coefficients from generalized linear mixed effects models of eight temporal replicates including the respective predictor variable as fixed effect and random intercept and slope effects of the study plot in all models. Horizontal lines refer to standard error (SE).

Apendix S4. Effects of temperature, precipitation and resource type on the temporal fluctuations in abundance of feeding guilds.

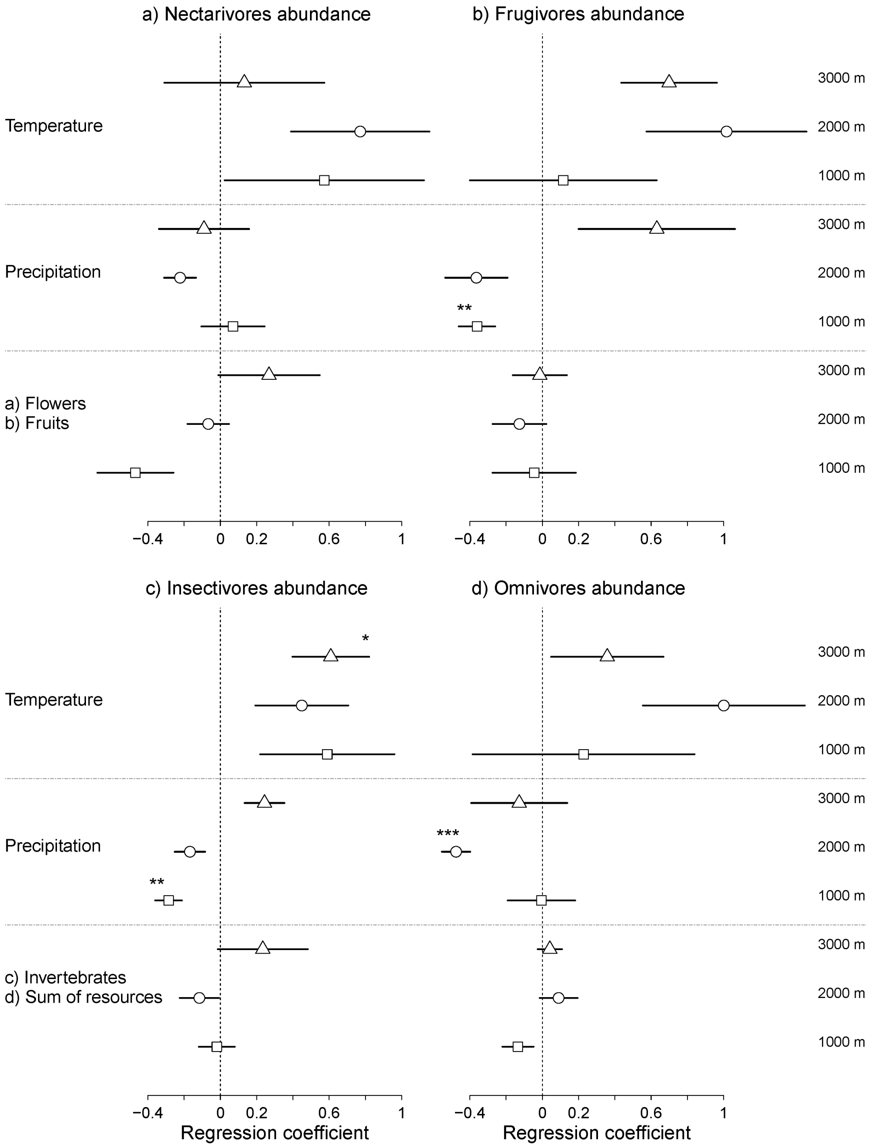


Figure S4. Effects of temperature, precipitation and resource type [i.e., a) flowers, b) fruit, c) insects, d) sum of all resources] on the temporal fluctuations in abundance of a) nectarivores, b) frugivores, c) insectivores and d) omnivores along the elevational gradient. Squares represent sites at 1000 m, circles those at 2000 m, and triangles those at 3000 m. Shown are regression coefficients from generalized linear mixed effects models of eight temporal replicates including the respective predictor variable as fixed effect and random intercept and slope effects of the study plot in all models. Horizontal lines refer to standard error (SE). P-values after Bonferroni correction: *p<0.005, ***p<0.0001.

Appendix S5. Akaike's information criterion ofmodels testing main and interaction effects of elevation and season on bird abundance, evenness and richness.

Table S1. Akaike's information criterion (AIC) of generalized linear mixed effect models testing main and interaction effects of elevation and season on bird a) abundance, b) evenness, c) species richness. Species richness model in d) also includes abundance as a fixed effect. Study plot nested in site and sampling month of each year were included as random effects in all models. All models assume a Poisson error distribution.

	Predictor variables	**AIC**	**ΔAIC**
a) Bird abundance	Season + elevation	1391	1
	Season x elevation	1390	
b) Bird evenness	Season + elevation	-283	4
	Season x elevation	-279	
c) Bird richness	Season + elevation	927	3
	Season x elevation	930	
d) Bird richness	Abundance + season + elevation	833	4
	Abundance + season x elevation	837	

Appendix S6. List of bird species recorded and their feeding guilds.

Table S2. List of 241 bird species recorded and their feeding guilds (60% or more of a food type) based on the Elton trait database, at three elevations (1000, 2000 and 3000 m) in and around Podocarpus National Park and San Francisco reserve in southern Ecuador.

	Nectarivores	**Frugivores**	**Insectivores**	**Omnivores**
1000				
Tinamiformes				
Crypturellus soui				X
Tinamus tao				X
Galliformes				
Aburria aburri		X		
Chamaepetes goudotii		X		
Odontophorus speciosus				X
Ortalis guttata		X		
Columbiformes				
Columba plumbea				X
Columba subvinacea		X		
Geotrygon frenata				X
Leptotila rufaxilla		X		
Psittaciformes				
Pyrrhura albipectus		X		
Cuculiformes				
Crotophaga ani				X
Piaya cayana			X	
Apodiformes				
Aglaiocercus kingi	X			
Amazilia fimbriata	X			
Chrysuronia oenone	X			
Colibri coruscans	X			
Doryfera ludovicae	X			
Eutoxeres aquila	X			
Heliodoxa leadbeateri	X			
Heliothryx aurita	X			
Klais guimeti	X			
Ocreatus underwoodii	X			
Phaethornis griseogularis	X			
Phaethornis guy	X			
Phaethornis syrmatophorus	X			
Thalurania furcata	X			
Trogoniformes				
Trogon collaris			X	

Coraciiformes				
Momotus aequatorialis			X	
Piciformes				
Aulacorhynchus derbianus				X
Dryocopus lineatus			X	
Eubucco bourcierii		X		
Galbula pastazae			X	
Malacoptila fulvogularis			X	
Piculus rubiginosus			X	
Picumus lafresnayi			X	
Veniliornis passerinus			X	
Passeriformes				
Ammodramus aurifrons		X		
Ampelioides tschudii				X
Anabacerthia striaticollis			X	
Arremon aurantiirostris				X
Basileuterus fulvicauda			X	
Cacicus uropygialis			X	
Campylorhamphus pusillus			X	
Catharus ustulatus			X	
Cephalopterus ornatus				X
Cercomacra nigrescens			X	
Chamaeza campanisona			X	
Chlorochrysa calliparaea		X		
Chlorophanes spiza		X		
Chlorospingus canigularis				X
Chlorospingus flavigularis		X		
Cissopis leveriana		X		
Coereba flaveola	X			
Colonia colonus			X	
Conopias cinchoneti				X
Coryphospingus cucullatus				X
Cyanocorax violaceus				X
Cyanocorax yncas				X
Dacnis cayana				X
Dacnis lineata		X		
Dendrocincla fuliginosa			X	
Dixiphia pipra		X		
Dysithamnus mentalis			X	
Euphonia xanthogaster		X		
Glyphorynchus spirurus			X	
Grallaria haplonota			X	
Hemithraupis guira			X	
Henicorhina leucosticta			X	

Herpsilochmus axillaris		X	
Hylophilus olivaceus		X	
Hylophylax poecilinota		X	
Hypocnemis cantator		X	
Iridophanes pulcherrima	X		
Lepidothrix isidorei	X		
Leptopogon rufipectus		X	
Leptopogon superciliaris		X	
Lochmias nematura		X	
Machaeropterus striolatus	X		
Mionectes oleagineus	X		
Mionectes olivaceus	X		
Mionectes striaticollis			X
Myadestes ralloides			X
Myiarchus cephalotes		X	
Myiarchus ferox			X
Myioborus miniatus		X	
Myiotriccus ornatus		X	
Myiozetetes similis			X
Odontorchilus branickii		X	
Parula pitiayumi		X	
Phyllomyias plumbeiceps			X
Pipra erythrocephala	X		
Pipreola chlorolepidota	X		
Piranga leucoptera			X
Platycichla leucops	X		
Platyrinchus mystaceus		X	
Pogonotriccus ophthalmicus		X	
Pogonotriccus poecilotis		X	
Psarocolius angustifrons			X
Psarocolius decumanus			X
Rupicola peruviana	X		
Saltator grossus		X	
Saltator maximus		X	
Sittasomus griseicapillus		X	
Syndactyla subalaris		X	
Tachyphonus cristatus			X
Tangara arthus	X		
Tangara chilensis	X		
Tangara chrysotis	X		
Tangara cyanicollis	X		
Tangara gyrola	X		
Tangara nigrocincta	X		
Tangara punctata	X		

Tangara schrankii		X		
Tangara xanthogastra				X
Thraupis episcopus				X
Thraupis palmarum		X		
Todirostrum cinereum			X	
Tolmomyias viridiceps			X	
Troglodytes aedon			X	
Turdus albicollis			X	
Turdus fulviventris		X		
Turdus nigriceps		X		
Tyrannus melancholicus			X	
Wilsonia canadensis			X	
Xenops minutus			X	
Xiphorhynchus triangularis			X	
2000				
Tinamiformes				
Nothocercus bonapartei				X
Galliformes				
Chamaepetes goudotii		X		
Odontophorus speciosus				X
Penelope barbata		X		
Columbiformes				
Columba fasciata		X		
Geotrygon frenata				X
Coraciiformes				
Momotus aequatorialis			X	
Psittaciformes				
Amazona mercenaria		X		
Touit stictoptera				X
Apodiformes				
Adelomyia melanogenys	X			
Aglaiocercus kingi	X			
Chalcostigma ruficeps	X			
Coeligena coeligena	X			
Coeligena torquata	X			
Colibri coruscans	X			
Colibri thalassinus	X			
Doryfera johannae	X			
Doryfera ludovicae	X			
Heliangelus amethysticollis	X			
Heliodoxa leadbeateri	X			
Heliodoxa rubinoides	X			
Metallura tyrianthina	X			
Ocreatus underwoodii	X			

Phaethornis syrmatophorus	X			
Trogoniformes				
Pharomachrus auriceps		X		
Trogon personatus				X
Piciformes				
Aulacorhynchus prasinus				X
Campephilus pollens			X	
Piculus rivolii			X	
Passeriformes				
Anairetes parulus			X	
Anisognathus lacrymosus		X		
Anisognathus somptuosus				X
Atlapetes latinuchus				X
Basileuterus coronatus			X	
Basileuterus nigrocristatus			X	
Basileuterus tristriatus			X	
Buarremon brunneinuchus				X
Buarremon torquatus				X
Cacicus uropygialis			X	
Chlorospingus canigularis				X
Chlorospingus flavigularis		X		
Chlorospingus ophthalmicus			X	
Contopus fumigatus			X	
Creurgops verticalis			X	
Cyanocorax yncas				X
Cyclarhis gujanensis			X	
Dendroica fusca			X	
Diglossa albilatera				X
Diglossa humeralis				X
Diglossopis cyanea			X	
Drymophila caudata			X	
Elaenia albiceps				X
Elaenia pallatangae				X
Grallaria ruficapilla			X	
Grallaricula flavirostris			X	
Hemispingus frontalis			X	
Henicorhina leucophrys			X	
Iridosornis analis				X
Lepidocolaptes lacrymiger			X	
Leptopogon rufipectus			X	
Lochmias nematura			X	
Mecocerculus calopterus			X	
Mionectes olivaceus		X		
Mionectes striaticollis				X

Myadestes ralloides				X
Myiarchus cephalotes			X	
Myiarchus tuberculifer			X	
Myioborus miniatus			X	
Ochthoeca cinnamomeiventris			X	
Phyllomyias nigrocapillus			X	
Pipraeidea melanonota				X
Pipreola riefferii		X		
Poecilotriccus ruficeps			X	
Pogonotriccus ophthalmicus			X	
Pogonotriccus poecilotis			X	
Pyrrhomyias cinnamomea			X	
Rupicola peruviana		X		
Scytalopus latrans			X	
Scytalopus micropterus			X	
Sericossypha albocristata			X	
Synallaxis azarae			X	
Tangara cyanicollis		X		
Tangara labradorides			X	
Tangara nigroviridis			X	
Tangara parzudakii		X		
Tangara vassorii		X		
Tangara xanthocephala		X		
Thamnophilus unicolor			X	
Thraupis cyanocephala		X		
Thraupis palmarum		X		
Thryothorus euophrys			X	
Troglodytes solstitialis			X	
Turdus fuscater				X
Turdus serranus		X		
Vireo leucophrys			X	
Wilsonia canadensis			X	
Xiphocolaptes promeropirhynchus			X	
Xiphorhynchus triangularis			X	
Zimmerius chrysops			X	
Zonotrichia capensis				X
3000				
Galliformes				
Penelope barbata		X		
Columbiformes				
Columba fasciata		X		
Apodiformes				
Adelomyia melanogenys	X			
Aglaeactis cupripennis	X			

Boissonneaua matthewsii	X			
Chalcostigma herrani	X			
Coeligena iris	X			
Coeligena lutetiae	X			
Coeligena torquata	X			
Eriocnemis vestitus	X			
Heliangelus viola	X			
Lafresnaya lafresnayi	X			
Metallura odomae	X			
Metallura tyrianthina	X			
Pterophanes cyanopterus	X			
Piciformes				
Aulacorhynchus prasinus				X
Piculus rivolii			X	
Passeriformes				
Amblycercus holosericeus			X	
Ampelion rubrocristatus		X		
Anairetes parulus			X	
Anisognathus igniventris				X
Anisognathus lacrymosus		X		
Atlapetes latinuchus				X
Atlapetes pallidinucha				X
Basileuterus coronatus			X	
Basileuterus nigrocristatus			X	
Buarremon torquatus				X
Buthraupis montana		X		
Catamblyrhynchus diadema			X	
Catamenia homochroa				X
Chlorornis riefferii				X
Cinnycerthia unirufa			X	
Cnemoscopus rubrirostris			X	
Conirostrum albifrons			X	
Conirostrum cinereum				X
Conirostrum sitticolor				X
Cyanolyca turcosa			X	
Diglossa albilatera				X
Diglossa humeralis				X
Diglossa lafresnayii				X
Diglossopis cyanea			X	
Dubusia taeniata				X
Elaenia albiceps				X
Elaenia pallatangae				X
Grallaria nuchalis			X	
Grallaria ruficapilla			X	

Grallaria rufula		X	
Grallaria squamigera		X	
Grallaricula nana		X	
Hellmayrea gularis		X	
Hemispingus superciliaris		X	
Hemispingus verticalis		X	
Iridosornis rufivertex			X
Margarornis squamiger		X	
Mecocerculus stictopterus		X	
Myioborus melanocephalus		X	
Ochthoeca rufipectoralis		X	
Pheucticus chrysogaster			X
Phyllomyias nigrocapillus		X	
Pipreola arcuata	X		
Pseudocolaptes boissonneautii		X	
Scytalopus latrans		X	
Scytalopus parkeri		X	
Synallaxis azarae		X	
Tangara vassorii	X		
Thraupis cyanocephala	X		
Thryothorus euophrys		X	
Troglodytes solstitialis		X	
Turdus fuscater			X
Zonotrichia capensis			X

Appendix S7. Estimates of random effects for models testing the effects of elevation and season on bird communities.

Table S3. Variance and standard deviation (SD) of the random effects in the models testing the effect of elevation and season on bird a) abundance, b) evenness and c) species richness. Species richness model in d) also includes abundance as a fixed effect. See Table 2 in the main manuscript for model estimates of fixed effects.

	Random effect	Variance	SD
a) Abundance	Plot:site	0.08	0.27
	Site	0.02	0.14
	Sampling month	0.03	0.17
b) Evenness	Plot:site	<0.01	0.02
	Site	0.00	0.00
	Sampling month	0.00	0.00
c) Richness	Plot:site	0.03	0.18
	Site	<0.01	0.05
	Sampling month	0.01	0.11
d) Richness*	Plot:site	0.01	0.09
	Site	0.00	0.00
	Sampling month	0.00	0.00

Appendix S8. Estimates of random effects for models testing the effects of temperature, precipitation and resource availability on the temporal fluctuations in bird communities.

Table S4. Variance and standard deviation (SD) of the random effects in the models testing the effects of temperature, precipitation and resource availability on eight temporal replicate counts in a) bird abundance b) evenness and c) species richness at three elevations. See Table 3 in the main manuscript for model estimates of fixed effects.

a) Bird abundance	Random effect		Variance	SD
Temperature 3000 m	Plot: temperature	Intercept	0.34	0.58
		Temperature	0.10	0.32
Temperature 2000 m	Plot: temperature	Intercept	0.07	0.26
		Temperature	0.33	0.58
Temperature 1000 m	Plot: temperature	Intercept	0.17	0.41
		Temperature	0.22	0.47
Precipitation 3000 m	Plot: temperature	Intercept	0.25	0.50
		Precipitation	0.02	0.14
Precipitation 2000 m	Plot: temperature	Intercept	0.04	0.20
		Precipitation	0.01	0.11
Precipitation 1000 m	Plot: temperature	Intercept	0.03	0.17
		Precipitation	0.01	0.09
Resources 3000 m	Plot: temperature	Intercept	0.26	0.51
		Resources	0.01	0.08
Resources 2000 m	Plot: temperature	Intercept	0.04	0.20
		Resources	0.02	0.16
Resources 1000 m	Plot: temperature	Intercept	0.05	0.23
		Resources	<0.01	0.06
b) Bird evenness				
Temperature 3000 m	Plot: temperature	Intercept	<0.01	0.01
		Temperature	<0.01	0.04
Temperature 2000 m	Plot: temperature	Intercept	<0.01	0.01
		Temperature	0.03	0.16
Temperature 1000 m	Plot: temperature	Intercept	<0.01	0.01
		Temperature	<0.01	<0.01
Precipitation 3000 m	Plot: temperature	Intercept	<0.01	0.04
		Precipitation	<0.01	0.03
Precipitation 2000 m	Plot: temperature	Intercept	<0.01	0.01
		Precipitation	<0.01	0.01
Precipitation 1000 m	Plot: temperature	Intercept	<0.01	0.02
		Precipitation	<0.01	0.02
Resources 3000 m	Plot: temperature	Intercept	<0.01	0.03
		Resources	<0.01	0.01

Resources 2000 m	Plot: temperature	Intercept	<0.01	0.01
		Resources	<0.01	<0.01
Resources 1000 m	Plot: temperature	Intercept	<0.01	0.02
		Resources	<0.01	0.02
c) Bird richness				
Temperature 3000 m	Plot: temperature	Intercept	0.27	0.52
		Temperature	0.18	0.43
Temperature 2000 m	Plot: temperature	Intercept	0.05	0.22
		Temperature	0.71	0.84
Temperature 1000 m	Plot: temperature	Intercept	0.08	0.28
		Temperature	0.11	0.34
Precipitation 3000 m	Plot: temperature	Intercept	0.10	0.31
		Precipitation	<0.01	0.05
Precipitation 2000 m	Plot: temperature	Intercept	0.02	0.13
		Precipitation	0.03	0.17
Precipitation 1000 m	Plot: temperature	Intercept	0.01	0.09
		Precipitation	0.02	0.13
Resources 3000 m	Plot: temperature	Intercept	0.06	0.25
		Resources	<0.01	0.06
Resources 2000 m	Plot: temperature	Intercept	0.03	0.18
		Resources	<0.01	0.03
Resources 1000 m	Plot: temperature	Intercept	0.02	0.14
		Resources	<0.01	0.01

Appendix 3. Different responses of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient

Authors:

Vinicio Santillán, Marta Quitián, Boris A. Tinoco, Edwin Zárate, Matthias Schleuning, Katrin Böhning-Gaese and Eike Lena Neuschulz

Title:

Different responses of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient

Status:

Published in Oecologia on April 29th 2019

Author Contributions:

1. Development and planning:

VS 80%, MS, KBG and ELN in total 20%

2. Field work/data collection:

VS collected bird data (75%) with support by MQ (25%).

3. Compilation of data sets and figures/tables:

VS assembled the data sets and prepared the figures (100%).

4. Data analyses and interpretation:

VS performed the statistical analyses (80%) with input from MS and ELN (20%). **VS** interpreted the results (80%), KBG, MS and ELN contributed with the interpretation of the results (20%).

5. Preparation of manuscript:

VS (80%) MQ, BAT and EZ (5%), MS, KBG and ELN (15%).

Different responses of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient

Vinicio Santillán[1,2,3], Marta Quitián[1,2], Boris A. Tinoco[3], Edwin Zárate[3], Matthias Schleuning[1], Katrin Böhning-Gaese[1,2], Eike Lena Neuschulz[1]

[1]Senckenberg Biodiversity and Climate Research Centre Frankfurt (SBiK-F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany

[2]Department of Biological Sciences, Goethe-Universität Frankfurt, Max-von-Laue-Straße 9, 60438 Frankfurt am Main, Germany

[3]Escuela de Biología, Ecología y Gestión, Universidad del Azuay, Av. 24 de Mayo 7-77 y Hernán Malo, 01.01.981, Cuenca, Ecuador

Correspondence author: vinicioestuardosantillan@gmail.com

Appendix 3. Different responses of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient

Abstract

Many studies have investigated how habitat fragmentation affects the taxonomic and functional diversity of species assemblages. However, the joint effects of habitat fragmentation and environmental conditions on taxonomic and functional diversity, for instance across elevational gradients, have largely been neglected so far. In this study, we compare whether taxonomic and functional indicators show similar or distinct responses to forest fragmentation across an elevational gradient. We based our analysis on a comprehensive data set of species-rich bird assemblages from tropical montane forest in the Southern Andes of Ecuador. We monitored birds over two years in two habitat types (continuous and fragmented forest) at three elevations (i.e., 1000, 2000, 3000 m a.s.l) and measured nine morphological traits for each bird species on museum specimens. Bird species richness and abundance were significantly higher in fragmented compared to continuous forests and decreased towards high elevations. In contrast, functional diversity was significantly reduced in fragmented compared to continuous forests at low elevations, but fragmentation effects on functional diversity tended to be reversed at high elevations. Our results demonstrate that taxonomic and functional indicators can show decoupled responses to forest fragmentation and that these effects are highly variable across elevations. Our findings reveal that functional homogenization in bird communities in response to fragmentation can be masked by apparent increases in taxonomic diversity, particularly in diverse communities at low elevations.

Key words: Ecuador, monitoring, traits, richness, abundance, functional diversity.

Introduction

Human land-use change threatens biodiversity and associated ecosystem functions (Chapin et al. 2000). In order to assess changes in biodiversity, previous studies have used taxonomic indicators, such as species richness, abundance or evenness (e.g., Lawton et al. 1998). However, taxonomic indicators of diversity are often not sufficient to assess other aspects of biodiversity, such as the functional roles of species in ecosystems (Villéger et al. 2010). Functional diversity is an important component of biodiversity, which reflects the diversity and distribution of functional traits in species assemblages (Flynn et al. 2009; Meynard et al. 2011) and has been proposed to be related to important ecosystem functions, such as pollination, pest control or biomass production (Sekercioglu 2006, Díaz and Cabido 2001).

Habitat structure in combination with other environmental conditions (e.g., temperature or precipitation along environmental gradients) influence patterns of taxonomic and functional diversity (Ferger et al. 2014; Montaño-Centellas and Garitano-Zavala 2015). Thus, the responses of species to human disturbance often depend on the environmental conditions experienced by a community (Vollstädt et al. 2017). Species richness often declines with human disturbances, but detrimental effects often depend on the intensity of land use (Flynn et al. 2009; Mulwa et al. 2012) or taxonomic group (e.g., Lawton et al. 1998). Also, functional diversity has been demonstrated to decrease in response to a decrease in habitat structure (Tscharntke et al. 2008) or increasing land use intensity (Flynn et al. 2009; Sabatini et al. 2014), which may lead to a reduction in the ecosystem functions provided by the respective community (Gagic et al. 2015). Other studies have demonstrated only partial congruence between taxonomic and functional diversity (e.g., Devictor et al. 2010, Meynard et al. 2011, Schipper et al. 2016). These mismatches occur because species in a given community may respond differently to environmental conditions (Devictor et al. 2010) and a loss of functional diversity, i.e. a homogenization of functional traits is expected if correlated species' responses are mediated by traits (Suding et al. 2008). Considering these potentially different responses of taxonomic and functional diversity is of particular importance for monitoring the effects of human disturbance on biodiversity across environmental gradients, since a loss of functional diversity may be obscured by apparent increases in taxonomic indicators.

To quantify the effects of human disturbance and environmental conditions on taxonomic and functional diversity, elevational gradients represent suitable study systems, because they provide a rapid turnover of habitats and climatic conditions (Nogués-Bravo et al. 2008). Previous studies have demonstrated that changes in habitats and climate along elevational gradients strongly affect taxonomic diversity and species distributions (Chamberlain et al. 2012, Chamberlain et al. 2013, Chamberlain et al. 2016, Morueta-Holme et al. 2015), but often neglect interacting effects between elevation and land use. For instance, species-rich communities in the lowlands are often functionally over-dispersed (Dehling et al. 2014). One explanation for this pattern could be competition among species that cannot co-occur if they are functionally too similar (Fleming 1979). In contrast, species-poor communities at high elevations are often functionally clustered (Dehling et al. 2014), likely due to environmental filtering that allows only species with specific traits to persist under harsh environmental conditions (Webb 2002). These differences in community structure might make functional diversity in lowland communities particularly prone to fragmentation, because of the loss of functionally extreme species, whereas the functional diversity of highland communities might be less affected by fragmentation, as highland communities are functionally more redundant. Yet, the interacting effects between human disturbance and elevation on both taxonomic and functional diversity have, to the best of our knowledge, not been studied so far.

Here we compare taxonomic (i.e., species richness, abundance and evenness) and functional (i.e. functional richness, dispersion, evenness) indicators of bird diversity in response to human-induced forest fragmentation (i.e., continuous and fragmented forest) across an elevational gradient in the Andes of southern Ecuador. First, we hypothesised a consistent decrease of bird species richness in fragmented compared to continuous forests across the elevational gradient (Nogués-Bravo et al. 2008; Montaño-Centellas and Garitano-Zavala 2015). Second, we hypothesised an overall decrease of functional diversity in fragmented forests across the elevational gradient (Tscharntke et al. 2008; Sitters et al. 2016) in association with a decrease in taxonomic diversity (Flynn et al., 2009). Third, we expect that fragmentation effects on functional diversity might be stronger in species-rich (i.e., functionally over-dispersed) lowland communities compared to species-poor (i.e., functionally clustered) highland communities (Dehling et al. 2014).

Materials and methods

Study area

The study was conducted within and around Podocarpus National Park and San Francisco reserve at the Eastern Cordillera of the Andes in southern Ecuador (Figure 1). The climate in the region is humid tropical montane (Kottek et al. 2006), with a bimodal rain regime. Mean annual temperature at low elevations is 20 °C, at mid elevations 15.5 °C and at high elevations 10 °C (Emck 2007). Mean annual precipitation at low elevations is 2432 mm, at mid elevations 2079 mm and at high elevations 4522 mm (Emck 2007). The most humid season extends from March to June, the least humid season from October to November (Emck 2007). The region is characterized by different vegetation types: evergreen premontane forest (1000 m a.s.l., 4° 6′ S, 78° 58′

W), evergreen lower montane forest (2000 m a.s.l., 3° 58′ S, 79° 4′ W) and upper montane forest (3000 m a.s.l., 4° 6′ S, 79° 10′ W, Homeier et al. 2008).

Our study was conducted in two forest types (i.e., continuous and fragmented forest) at three elevations (i.e., 1000, 2000, and 3000 m a.s.l., Figure 1). Natural continuous forests within the protected reserves are mostly undisturbed by humans (Homeier et al. 2008). Fragmented forests surrounding the reserves are forest remnants embedded in a matrix of cattle pastures (Tapia-Armijos et al. 2015) and range from 3.2 – 6.73 ha in size (see Table S1 for details). To compare the similarity of vegetation structure between continuous and fragmented forests, we quantified the vertical vegetation heterogeneity according to Bibby et al. (2000) by estimating vegetation cover at eight layers (0, 1, 2, 4, 8, 16, 32 and 64 m above the ground) at nine locations (20 m radius) per plot. We then calculated the Shannon–Wiener diversity index across these eight strata for each plot (Bibby et al. 2000). We found no significant difference in vegetation structure between continuous and fragmented forest across all elevations ($F_{1,16} = 1.63$, $P = 0.219$; continuous forests: mean = 1.69, SD = 0.15, n = 9; fragmented forest = 1.61, SD = 0.11, n = 9).

Taxonomic indicators of bird diversity

A total of 18 one-hectare plots was established at six different sites (i.e., three in continuous forests and three in fragmented forests at each elevation, Figure 1 and Table S1). To monitor bird diversity, we placed nine point count stations, eight at the borders and one in the centre at each plot. We conducted 10-minutes bird point counts within a 20-metre radius around the centre of each point count location (total sampling area per plot ~ 1.1 ha), where we recorded and identified all birds heard or seen to species level. Taxonomy of birds follows Ridgely and Greenfield (2001). The 20-metre radius was chosen because it is suitable for bird counts in dense vegetation of tropical forests (Bibby et al. 2000). Sampling started at sunrise and ended before 09:00 h and was conducted by three trained ornithologists. Plots were randomized among the observers to minimize sampling bias. We pooled the nine point count records per plot to quantify bird species richness and abundance as the sum of all bird species and individuals recorded per plot at a given sampling time. We also calculated species evenness (Pielou's evenness; Smith and Wilson 1996) for each plot at a given time. Evenness ranges from zero to one with low values indicating more skewed abundance distributions (e.g., the presence of a few dominant species). We repeated the sampling of each plot eight times between 2014 and 2015 (216 hours in total), twice per year in the most humid season (May-July) and twice per year in the least humid season (September-November), resulting in a total of 144 spatio-temporal replicates across all 18 plots.

We computed species accumulation curves to estimate the relationship between the proportion of recorded species and the number of point counts conducted in continuous and fragmented forests (i.e., 18 point counts over both years). Accumulation curves showed similar slopes and saturating trends in both habitat types indicating that communities were similarly well sampled (Figure S1).

Functional indicators of bird diversity

To quantify the functional richness (FRic), functional dispersion (FDis) and functional evenness (FEve) of the bird assemblages, we measured nine continuous morphological traits for each of the recorded bird species on museum specimens (four specimens per species). The selection of traits for compiling functional indicators requires careful consideration, as it can influence the outcome of the study (Calba et al. 2014). Therefore, we explicitly selected traits that capture different functional roles of birds in ecosystems, reflecting flight performance, food intake and bipedal locomotion (Dawideit et al. 2009; Pigot et al. 2016). Flight performance is associated with foraging behaviour and flight patterns, which are strongly related to body size and wing and tail shape (Moermond and Denslow 1995; Norberg 1995; Lockwood et al. 1998). Food intake is associated with the type of resources used by birds, e.g. invertebrate vs. plant diet (Herrel et al. 2005), and relates to the morphology of the bill of a bird. Bipedal locomotion is associated with the habitat use and foraging mode of birds and relates to tarsus morphology (Zeffer et al. 2003). For flight performance, we measured wing length (distance from the bend of the wing to the tip of the longest primary feathers), Kipp´s distance (distance between tip of the first secondary and tip of the longest primary of the folded wing), and tail length (distance from the insertion point of the central rectrices on the body to the tip of the longest rectrix). For food intake, we measured the bird´s bill morphology through bill length, width and height. For bipedal locomotion, we measured tarsus length, and the lateral and sagittal width of the tarsus. From these traits, we computed six morphological trait indices (Table S2, see Table S3 for a pair-wise correlation matrix). Body mass was additionally obtained from Dunning (2007) to describe variation in bird size. Functional diversity analyses were conducted with these trait indices and body mass.

We calculated the three functional diversity indices for each plot and temporal replicate (n = 144) from a principal coordinate analyses (PCoA) that projected Euclidian distances among bird species into a multidimensional trait space (see Figure S2). This approach decomposes trait variation among species into orthogonal trait axes to illustrate relationships among multiple variables. We only retained the first two axes of the ordination, as these contained most of the biologically relevant information (70 %, Figure S2). FRic estimates the volume of the multidimensional convex hull spanned by the species of an assemblage in the vertices of the trait space (Villéger et al. 2008) with larger values indicating a high diversity of traits in the community. FRic does not take into account species abundance and is sensitive to outliers, because rare species with extreme trait values can inflate the trait space (Laliberté and Legendre 2010). FDis estimates the spread of species in the trait space calculated as the abundance weighted mean distance to the assemblage centroid across all species (Laliberté and Legendre 2010) with larger values indicating a higher potential for functional complementarity among species. FEve estimates the regularity of distances between species in the trait space along a minimum spanning tree (Villéger et al. 2008). FEve ranges from 0 to 1 with larger values indicating a regular abundance distribution along the minimum spanning tree. For all analyses, we used R 3.3.0 (Development Core Team 2016) and the package 'FD' (Laliberté et al. 2015).

Data analyses

In order to compare the responses of taxonomic and functional diversity indicators, we used linear mixed effects models (R package 'lme4', Bates et al. 2017) to test the effect of fragmentation (two levels: continuous and fragmented forest) and elevation (three levels: 1000, 2000, 3000 m a.s.l.) on bird richness, abundance, evenness, FRic, FDis, and FEve (see Table S4 for a correlation of all taxonomic and functional indices). We included the study plot nested in site, and the sampling season as another, crossed random effect in the model to account for the spatial and temporal sampling structure. We fitted the models of bird richness, abundance and evenness with a maximum likelihood approach assuming that bird richness and abundance followed a Poisson distribution. Models of FRic, FDis and FEve were fitted with a maximum likelihood approach assuming a Gaussian error distribution. We selected the best-fitting models with or without the interaction term between fragmentation and elevation based on the lowest Akaike's information criterion (Burnham and Anderson 2002). For bird richness, abundance, evenness and FEve, we retained the models without interaction term and for FRic and FDis we retained the models with interaction term (Table S5).

We illustrated how changes in functional diversity relate to the loss and gain of functional groups among habitat types and elevations and visualized changes in functional diversity between continuous and fragmented forests for each elevational belt. To this end, we grouped species into taxonomic orders that represent the main types of bird morphology (Cracraft 1981). As the order of Passeriformes comprises a high diversity of bird species with distinct morphologies, we grouped species belonging to this order at the family level. The gain and loss of bird functional groups in fragmented forests was obtained by calculating the normalized difference of each taxonomic group (order and family, respectively) between continuous and fragmented forest for each of the eight temporal replicates at each elevation. The normalized difference was calculated as the difference between the species number recorded in continuous and fragmented forest, divided by the sum of species of this order recorded in both forest types. In addition, we conducted a RLQ analysis (ade4 package, Chessel et al. 2004), which investigates the relationships between habitat type, elevation and specific functional traits. Three matrices are compared: R – environmental conditions (habitat type x elevation), L – species abundances at each plot, and Q – functional traits of each species (Dolédec et al. 1996). We ran correspondence and principal components analyses for each of the matrices according to Edwards et al. (2013). These ordinations were then combined to perform the RLQ analyses followed by Monte-Carlo permutations tests with 1000 repetitions for significance testing (Edwards et al. 2013).

Results

Taxonomic indicators of bird diversity

We recorded 4318 individuals of 238 bird species across all plots. Among these, 1790 individuals of 184 bird species were recorded in continuous forest, and 2528 individuals of 186 bird species were recorded in fragmented forest. While 1586 individuals of 125 species and 10 orders were recorded at low elevations, 1494 individuals of 100 species and nine orders were recorded at mid, and 1238 individuals of 69 species and five orders were recorded at high elevations (Table S6).

Bird species richness (predicted range: 7 to 21 species per temporal replicate of each plot) and abundance (predicted range: 11 to 51 individuals) were significantly higher in fragmented compared to continuous forests, and were significantly reduced at the highest elevation (Table 1; Figure 2a-b). We did not find significant differences in species evenness (predicted range: 2.5 to 2.5) between continuous and fragmented forests and among elevations (Table 1, Figure S3).

Functional indicators of bird diversity

Functional richness ranged from 0.9 to 2.7, functional dispersion from 1.6 to 2 and functional evenness from 0.6 to 0.7 across the spatio-temporal replicates of the plots. Fragmentation effects on FRic and FDis varied significantly between elevations. Both FRic and FDis were significantly reduced in fragmented compared to continuous forests, but only at low elevations (Table 1; Figure 2c-d). In contrast, both functional diversity measures were similar or higher in fragmented compared to continuous forests at mid and high elevations (Figure 2c-d). We did not find significant effects of fragmentation or elevation on FEve (Table S1, Figure S3).

The differential effects of fragmentation on functional diversity across the three elevations were corroborated when species were grouped into taxonomic orders and families representing the main types of bird morphology. We found a considerable gain of Coraciiformes, Furnariidae, Formicariidae, Cotingidae and Troglodytidae in continuous forests at low elevations, and of Trogoniformes, Coraciiformes, Cotingidae and Troglodytidae at mid elevations (Figures 3 - 4). In contrast, there was a gain of species in fragmented forests belonging to the order of Tinamiformes at low elevations, the orders and families of Galliformes and Columbiformes, Furnariidae, Tyrannidae, Turdidae and Emberizidae at mid elevations, and the orders and families of Galliformes, Apodiformes, Piciformes and Emberizidae at high elevations (Figures 3 - 4). Overall, the turnover of bird orders and families in response to fragmentation was distinct among the three elevations. These patterns were in concordance with the differential responses of functional diversity to fragmentation across the elevational gradient. RLQ analyses additionally revealed significant changes in functional traits across the elevational gradient ($p < 0.01$, permutation test), but not between habitat types ($p > 0.05$, Figure

S4). At low elevations, species with large tarsus indices (e.g., ground-dwelling birds) were more abundant than at high elevations (Figure S4), whereas changes in specific functional traits with fragmentation were less pronounced and not significant (Figure S4).

Discussion

We here compared the joint effects of forest fragmentation and environmental conditions along an elevational gradient on taxonomic (i.e., species richness, abundance and evenness) and functional (i.e., FRic, FDis and FEve) bird diversity. While species richness and abundance were higher in fragmented compared to continuous forests, FRic and FDis were negatively affected by fragmentation, but only at low elevations. Our results show that forest fragmentation can differently affect taxonomic and functional diversity across elevational gradients. Our findings also suggest that measures of taxonomic diversity can be uncoupled from measures of functional diversity, particularly in diverse communities at low elevations.

Bird species richness and abundance were higher in fragmented than in continuous forests and declined at high elevations. A decline of bird species richness and abundance with increasing elevation is widely reported (e.g., Nogués-Bravo et al. 2008; McCain 2009). In line with our expectation, many previous studies have also demonstrated a decline of bird diversity in response to human disturbance (Lehouck et al. 2009; Mulwa et al. 2013; Montaño-Centellas and Garitano-Zavala 2015). Other studies have shown an increase of bird species diversity in disturbed habitats (Blake and Loiselle 2001; Mulwa et al. 2012). Such an increase in diversity in disturbed habitats often stems from an increase of habitat generalists, such as open habitat species, which may compensate the loss of forest specialists (Neuschulz et al. 2011). Additionally, forest fragments in our study area appear to provide suitable habitat conditions for habitat specialists, such as the chestnut-naped antpitta (*Grallaria nuchali*s, Stotz et al. 1996). The close distance from forest fragments to the border of the nearest continuous forest (range: 4859 – 1059 m, Table S1), and similar vegetation structure between continuous and fragmented forests or edge effects could explain high species richness and abundance in fragmented forests.

In our study, bird functional richness and dispersion showed different responses to forest fragmentation at low compared to mid and high elevations, while fragmentation effects on individual traits were generally weak (Figure S4). The decline of FRic and

FDis in fragmented forests at low elevations was probably due to the loss of functionally distinct species, such as the highland motmot (*Momotus aequatorialis)* belonging to the order of Coraciiformes or species from the family of Formicariidae (e.g., short-tailed antthrush [*Chamaeza campanizona],* or Cotingidae (e.g., Amazonian umbrellabird [*Cephalopterus ornatus],* scaled fruiteater *[Ampeliodes tchudii]*)*,* all species with extreme morphological traits (Figures 3 - 4). The loss of functionally specialized species has been reported for other disturbed habitats in tropical ecosystems (Flynn et al. 2009; Bregman et al. 2016). In contrast to these findings, we found relatively weak effects of fragmentation on FRic, FDis and FEve at mid elevations, and a significant increase of FRic in fragmented forests at high elevations. These differential responses of functional diversity to fragmentation across the elevational gradient are likely related to the functional structure of the communities. Our findings demonstrate that the species-rich lowland communities were more prone to the loss of morphologically unique species in response to fragmentation, likely because lowland communities are usually functionally over-dispersed (Dehling et al. 2014). In turn, less diverse communities at mid and high elevations might be less likely to lose species with extreme morphologies, because high-elevation communities are generally more clustered and functionally similar due to environmental filtering (Graham et al. 2009, Dehling et al. 2014). These findings are in contrast to previous studies that have demonstrated that highland bird assemblages are more sensitive to forest fragmentation than lowland bird assemblages (Soh et al. 2006; Harris et al. 2014). Elevation-dependent factors, such as resource or habitat availability have been associated with the particular sensitivity of highland species to fragmentation (Chamberlain et al. 2012, Chamberlain et al. 2013). However, these studies have mostly focused on taxonomic diversity, or endemic or threatened species, but not on the functional diversity of bird assemblages. The increase of FRic in fragmented forests at high elevations that we observed in our study resulted from a gain of species belonging to different taxonomic orders and families (e.g., Galliformes, Columbiformes, Apodiformes, Emberizidae [Figures 3 – 4]; Stotz et al. 1996; Bregman et al. 2014). These changes in the functional composition in fragmented forests of the highlands might have originated from an addition of species primarily adapted to open habitats, such as sparrow species that inhabit the neighbouring paramo and grassland ecosystems. Yet, in particular forest specialist species might be of conservation concern at high elevations.

Taxonomic and functional diversity measures showed different responses to human disturbance along the elevational gradient. Theoretical evidence supports our findings by showing that an increase of species richness can be associated with a decrease of functional diversity (Petchey and Gaston 2006). Also empirical studies have demonstrated contrasting responses of taxonomic and functional trait diversity for different taxa, such as bees (Forrest et al. 2015), lichens (Bässler et al. 2016), plants (Niu et al. 2014) and birds (Seymour et al. 2015, Schipper et al. 2016, Jarzyna and Jetz 2017). For instance, Seymour et al. (2015) found that bird species richness and functional diversity showed opposite patterns along a gradient of precipitation and vegetation structure in an arid landscape. Our results suggest that decoupled responses of taxonomic and functional diversity might occur in particular in species-rich and functionally over-dispersed communities, such as in tropical lowlands, but are less likely to occur in functionally clustered communities at high elevations or latitudes.

Conclusions

Here we show that functional indicators that account for morphological differences among species can respond differently to forest fragmentation than taxonomic indicators of biodiversity. Our results highlight in particular that an increase in taxonomic diversity in response to fragmentation may be coupled with a functional homogenization of bird communities, especially in functionally diverse communities at low elevations or latitudes. Our study suggests that including additional information, such as data on morphological traits that are increasingly accessible for many taxa (Wilman et al. 2014; Ricklefs 2012), may help to refine predictions of responses of biodiversity *and* its associated ecosystem functions to human disturbance in different types of environments.

Acknowledgements

We thank the German Research Foundation (DFG) for funding our project in the framework of the Research Unit 823-825 “Platform for Biodiversity and Ecosystem Monitoring and Research in South Ecuador” (PAK 825/1; BO 1221/20-1). The Ecuadorian Ministry of the Environment (MAE) kindly provided permission to conduct research. We are grateful to Agustín Carrasco and Patricio Estrella, for their help in fieldwork. We thank Nature and Culture International (NCI), Felix Matt, Jörg Zeilinger, Mathias Templin and Catherine Vits for logistic support. Two anonymous reviewers provided helpful comments on an earlier version of this manuscript.

Author Contributions

ELN, MS, KBG, VS, MQ conceived and designed this study. VS and MQ conducted fieldwork. VS analysed the data. VS, ELN, MS wrote the manuscript. KBG, BT, EZ provided editorial advice.

References

Bässler C, Cadotte MW, Beudert B, et al (2016) Contrasting patterns of lichen functional diversity and species richness across an elevation gradient. Ecography 39:689–698

Bates D, Maechler M, Bolker B, Walker S (2017) Linear Mixed-Effects Models using 'Eigen' and S4 Contact. R package version 1.1-17. Available at: https://cran.r-project.org/web/packages/lme4

Bibby CJ, Burgess ND, Hill DA, Mustoe S (2000) Bird Census Techniques, 2nd edn. Academic Press, Cambridge, UK

Blake JG, Loiselle BA (2001) Bird assemblages in second-growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. Auk 118:304–326

Bregman TP, Lees AC, MacGregor HEA, et al (2016) Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. Proc R Soc B Biol Sci 283:20161289

Bregman TP, Sekercioglu CH, Tobias JA (2014) Global patterns and predictors of bird species responses to forest fragmentation: Implications for ecosystem function and conservation. Biol Conserv 169:372–383

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. Springer-Verlag, New York

Calba S, Maris V, Devictor V (2014) Measuring and explaining large-scale distribution of functional and phylogenetic diversity in birds: Separating ecological drivers from methodological choices. Glob Ecol Biogeogr 23:669–678

Chamberlain D, Arlettaz RL, Caprio E, Maggini R, Pedrini P, Rolando A, Zbinden N (2012) The altitudinal frontier in avian climate impact research. Ibis 154:205–209

Chamberlain D, Negro M, Caprio E, Rolando A (2013) Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. Biol Conserv 167:127–135

Chamberlain D, Brambilla M, Caprio E, Pedrini P, Rolando A (2016) Alpine bird distributions along elevation gradients: the consistency of climate and habitat effects across geographic regions, Oecologia DOI 10.1007/s00442-016-3637-y

Chapin FS, Zavaleta ES, Eviner VT, et al (2000) Consequences of changing biodiversity. Nature 405:234–242

Chessel D, Dufour AB, Thioulouse J (2004) The ade4 package - I: One-table methods. R News 4:5–10

Cracraft J (1981) Toward a phylogenetic classification of the recent birds of the world (Class Aves). Auk 98:681–714

Dawideit BA, Phillimore AB, Laube I, et al (2009) Ecomorphological predictors of natal dispersal distances in birds. J Anim Ecol 78:388–395

Dehling DM, Fritz SA, Töpfer T, et al (2014) Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. Ecography 37:1047–1055

Devictor V, Mouillot D, Meynard C, et al (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. Ecol Lett 13:1030–1040

Díaz S, Cabido M (2001) Vive la différence: Plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16:646–655

Dolédec S, Chessel D, Ter Braak CJF, Champely S (1996) Matching species traits to environmental variables: A new three-table ordination method. Environ Ecol Stat 3:143–166

Dunning JB (2007) CRC Handbook of avian body masses. Taylor and Francis, Boca Raton, Florida

Edwards FA, Edwards DP, Hamer KC, Davies RG (2013) Impacts of logging and conversion of rainforest to oil palm on the functional diversity of birds in Sundaland. Ibis 155:313–326

Emck P (2007) A climatology of south Ecuador. PhD disertation. Universität Erlangen-Nürnberg

Ferger SW, Schleuning M, Hemp A, et al (2014) Food resources and vegetation structure mediate climatic effects on species richness of birds. Glob Ecol Biogeogr 23:541–549

Fleming TH (1979) Do tropical frugivores compete for food? Integr Comp Biol 19:1157–1172

Flynn DFB, Gogol-Prokurat M, Nogeire T, et al (2009) Loss of functional diversity under land use intensification across multiple taxa. Ecol Lett 12:22–33

Forrest JRK, Thorp RW, Kremen C, Williams NM (2015) Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. J Appl Ecol 52:706–715

Gagic V, Bartomeus I, Jonsson T, et al (2015) Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proc R Soc B Biol Sci 282:20142620

Graham CH, Parra JL, Rahbek C, Mcguire JA (2010) Phylogenetic structure in tropical hummingbird communities. Proc Natl Acad Sci 107:513–513

Harris JBC, Dwi Putra D, Gregory SD, et al (2014) Rapid deforestation threatens mid-elevational endemic birds but climate change is most important at higher elevations. Divers Distrib 20:773–785

Herrel A, Podos J, Huber SK, Hendry AP (2005) Bite performance and morphology in a population of Darwin’s finches : implications for the evolution of beak shape. Funct Ecol 19:43–48

Homeier J, Werner FA, Gradstein SR, et al (2008) Potential vegetation and floristic composition of Andean forests in south Ecuador, with a focus on the RBSF. In: Beck E, Bendix J, Kottke I, et al. (eds) Gradients in a tropical mountain ecosystem of Ecuador. Ecological studies, vol 198. Springer, Berlin, pp 87–100

Jarzyna MA, Jetz W (2017) A near half-century of temporal change in different facets of avian diversity. Glob Chang Biol 23:2999–3011

Kottek M, Grieser J, Beck C, et al (2006) World map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift 15:259–263

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits A distance-based framework for measuring from multiple traits functional diversity. Ecology 91:299–305

Laliberté E, Legendre P, Bill Shipley (2015) Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package version 1.0-12. Available at: https://cran.r-project.org/web/packages/FD

Lawton JH, Bignell DE, Bolton B, et al (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391:72–76

Lehouck V, Spanhove T, Vangestel C, et al (2009) Does landscape structure affect resource tracking by avian frugivores in a fragmented Afrotropical forest? Ecography 32:789–799

Lockwood R, Swaddle JP, Rayner JM V (1998) Avian wingtip shape reconsidered : Wingtip shape indices and morphological adaptations to migration. J Avian Biol 29:273–292

Loiselle BA, Blake JG (1991) Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology 72:180–193

Martensen AC, Ribeiro MC, Banks-Leite C, et al (2012) Associations of forest cover, fragment area, and connectivity with neotropical understory bird species richness and abundance. Conserv Biol 26:1100–1111

McCain CM (2009) Global analysis of bird elevational diversity. Glob Ecol Biogeogr 18:346–360

Meynard CN, Devictor V, Mouillot D, et al (2011) Beyond taxonomic diversity patterns: How do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? Glob Ecol Biogeogr 20:893–903

Moermond TC, Denslow JS (1995) Neotropical avian frugivores : Patterns of behavior, morphology, and nutrition, with consequences for fruit selection. Ornithol Monogr 865–897

Montaño-Centellas FA, Garitano-Zavala Á (2015) Andean bird responses to human disturbances along an elevational gradient. Acta Oecologica 65-66:51–60

Morueta-Holme N, Engemann K, Sandoval-Acuña P, Jonas JD, Segnitz M, and Svenning JC (2015) Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. Proc Natl Acad Sci 112: 12741–12745

Mulwa RK, Böhning-Gaese K, Schleuning M (2012) High bird species diversity in structurally heterogeneous farmland in western Kenya. Biotropica 44:801–809

Mulwa RK, Neuschulz EL, Böhning-Gaese K, Schleuning M (2013) Seasonal fluctuations of resource abundance and avian feeding guilds across forest-farmland boundaries in tropical Africa. Oikos 122:524–532

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

Niu K, Choler P, de Bello F, et al (2014) Fertilization decreases species diversity but increases functional diversity: A three-year experiment in a Tibetan alpine meadow. Agric Ecosyst Environ 182:106–112

Nogués-Bravo D, Araujo MB, Romdal T, Rahbek C (2008) Scale effects and human impact on the elevational species richness gradients. Nature 453:216–219

Norberg U. M. (1995) How a long tail and changes in mass and wing shape affect the cost for flight in animals. Funct Ecol 9:48–54

Petchey OL, Gaston KJ (2006) Functional diversity: Back to basics and looking forward. Ecol Lett 9:741–758

Pigot AL, Trisos CH, Tobias JA (2016) Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. Proc R Soc B Biol Sci 283:20152013

R Development Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org

Ricklefs RE (2012) Species richness and morphological diversity of passerine birds. Proc Natl Acad Sci 109:14482–14487

Ridgely RS, Greenfield PJ (2001) The birds of Ecuador volume II., 1st edn. Christopher Helm, A & C Black Publishers, London

Sabatini FM, Burton JI, Scheller RM, et al (2014) Functional diversity of ground-layer plant communities in old-growth and managed northern hardwood forests. Appl Veg Sci 17:398–407

Schipper AM, Belmaker J, de Miranda MD, et al (2016) Contrasting changes in the abundance and diversity of North American bird assemblages from 1971 to 2010. Glob Chang Biol 22:3948–3959

Sekercioglu CH (2006) Increasing awareness of avian ecological function. Trends Ecol Evol 21:464–471

Seymour CL, Simmons RE, Joseph GS, Slingsby JA (2015) On bird functional diversity: Species richness and functional differentiation show contrasting responses to rainfall and vegetation structure in an arid landscape. Ecosystems 18:971–984

Sitters H, Di Stefano U, Christie F, et al (2016) Bird functional diversity decreases with time since disturbance: Does patchy prescribed fire enhance ecosystem function? Ecol Appl 26:115–127

Smith B, Wilson JB (1996) A consumer’s guide to evenness indices. Oikos 76:70–82

Soh MCK, Sodhi NS, Lim SLH (2006) High sensitivity of montane bird communities to habitat disturbance in Peninsular Malaysia. Biol Conserv 129:149–166

Stotz DF, Fitzpatrick JW, Parker TAI, Moskovits DK (1996) Neotropical birds: Ecology and Conservation. University of Chicago Press, Chicago, IL, USA

Suding KN, Lavorel S, Chapin FS, et al (2008) Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. Glob Chang Biol 14:1125–1140

Tapia-Armijos MF, Homeier J, Espinosa CI, et al (2015) Deforestation and forest fragmentation in south Ecuador since the 1970s - Losing a hotspot of biodiversity. PLoS ONE 10:1–18

Tscharntke T, Sekercioglu CH, Dietsch T V, et al (2008) Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. Ecology 89:944–951

Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301

Villéger S, Miranda JR, Hernández DF, Mouillot D (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecol Appl 20:1512–1522

Vollstädt MGR, Ferger SW, Hemp A, et al (2017) Direct and indirect effects of climate, human disturbance and plant traits on avian functional diversity. Glob Ecol Biogeogr 26:1–10

Webb, CO, Ackerly DD, McPeek MA, et al (2002) Phylogenies and community ecology. Annu Rev Ecol Syst 33:475–505

Wilman H, Belmaker J, Jennifer S, et al (2014) EltonTraits 1.0 : Species-level foraging attributes of the world’s birds and mammals. Ecology 95:2027

Zeffer A, Johansson LC, Marmebro Å (2003) Functional correlation between habitat use and leg morphology in birds (Aves). Biol J Linn Soc 79:461–484

Appendix 3. Different responses of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient

---

Table 1. Linear mixed effects models testing the effects of fragmentation (continuous forest and fragmented forest), elevation (1000, 2000, 3000 m a.s.l.) and their interaction on bird species richness, abundance, species evenness, functional richness (FRic), functional dispersion (FDis), and functional evenness (FEve). Sampling season and study plot nested in site are included as two random effects in all models to account for repeated measures of the same plot. Models of bird species richness and abundance assume a Poisson distribution. Models of species evenness, functional richness, functional dispersion and functional evenness assume a Gaussian distribution. Best model based on lowest AIC are shown. β = model estimate. SE = standard error. Significant effects ($p < 0.05$) are printed in bold.

	Predictor variable	β	SE	p
Species richness	Fragmented	0.22	0.09	**0.014**
	Elevation 2000	-0.1	0.11	0.325
	Elevation 3000	-0.29	0.11	**0.006**
Abundance	Fragmented	0.37	0.12	**0.002**
	Elevation 2000	-0.06	0.15	0.686
	Elevation 3000	-0.31	0.15	**0.034**
Species evenness	Fragmented	-0.01	0.01	0.41
	Elevation 2000	0.01	0.01	0.615
	Elevation 3000	0.02	0.01	0.082
FRic	Fragmented	-0.51	0.25	**0.041**
	Elevation 2000	0.11	0.25	0.664
	Elevation 3000	-0.85	0.25	**0.001**
	Fragmented: Elevation 2000	0.72	0.35	**0.044**
	Fragmented: Elevation 3000	1.33	0.35	**< 0.001**
FDis	Fragmented	-0.35	0.13	**0.006**
	Elevation 2000	-0.11	0.13	0.403
	Elevation 3000	-0.2	0.13	0.108
	Fragmented: Elevation 2000	0.48	0.18	**0.008**
	Fragmented: Elevation 3000	0.4	0.18	**0.027**
FEve	Fragmented	0.02	0.02	0.384
	Elevation 2000	0.02	0.02	0.365
	Elevation 3000	-0.02	0.02	0.446

Appendix 3. Different responses of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient

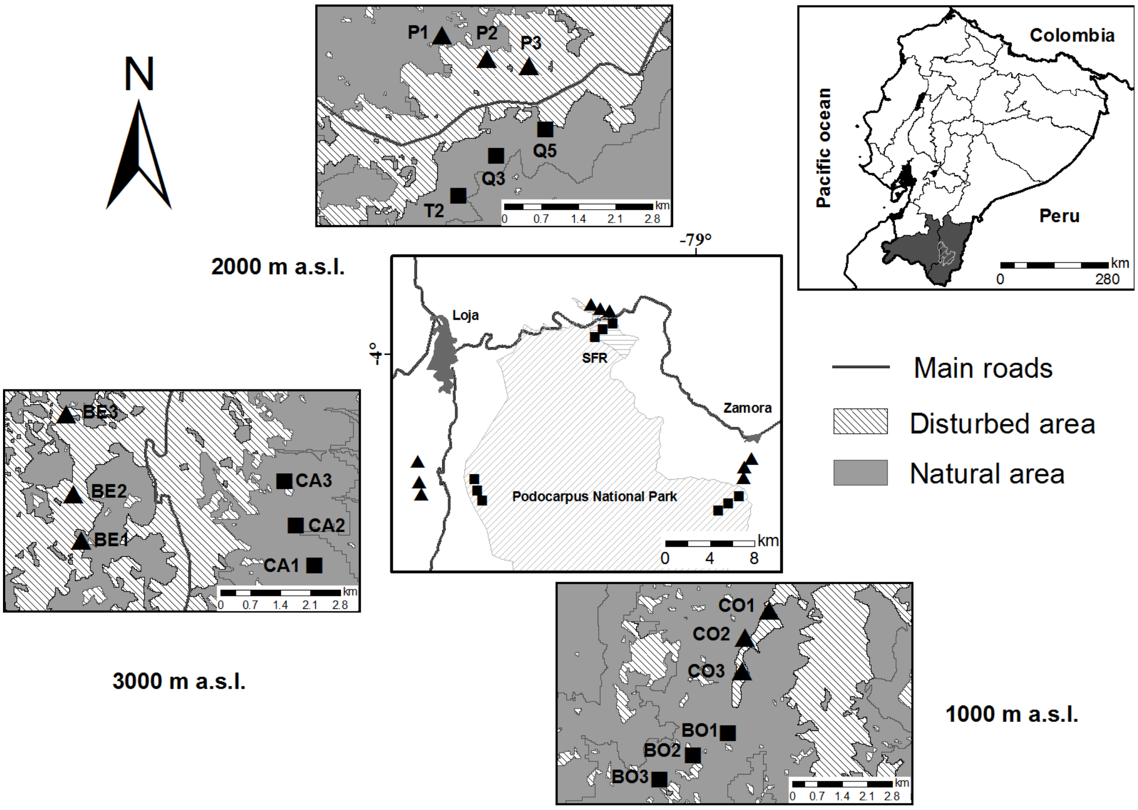


Figure 1. Study area located within and around Podocarpus National Park and San Francisco Reserve (SFR) at the Eastern Cordillera of the Andes in southern Ecuador. The figures show the location of plots at each elevation (i.e., 1000, 2000, and 3000 m a.s.l.). Squares represent plots in continuous forests and triangles plots in fragmented forests.

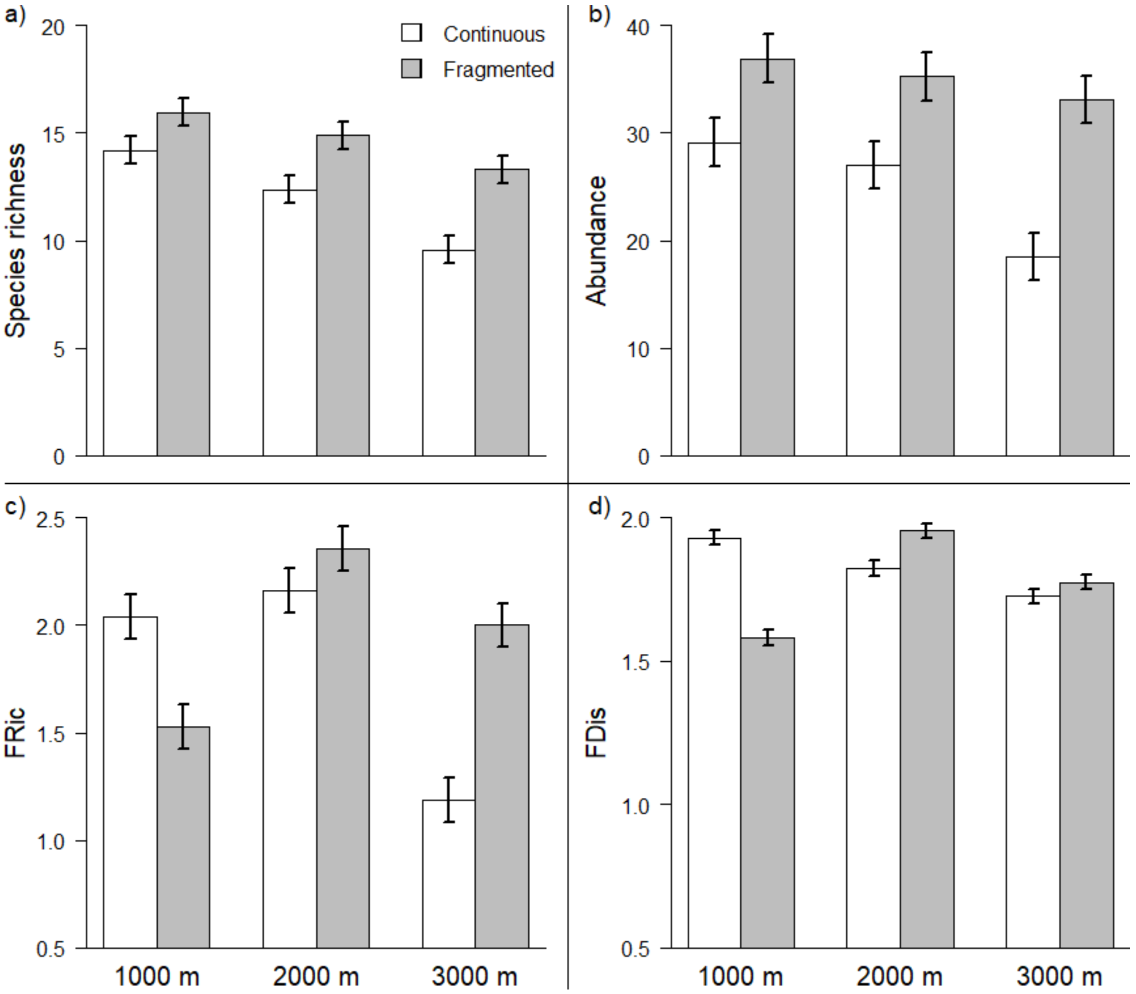


Figure 2. Predicted values of a) bird species richness, b) abundance, c) functional richness (FRic), and d) functional dispersion (FDis) in the continuous and fragmented forest at three elevations (1000 m a.s.l., 2000 m a.s.l., 3000 m a.s.l.). Models of bird species richness and abundance assume a Poisson error distribution. Functional richness and functional dispersion assume a Gaussian error distribution. Data are based on eight temporally replicated bird counts on each plot (see Figure 1). For predicted values of species evenness and functional evenness (FEve) see Figure S3.

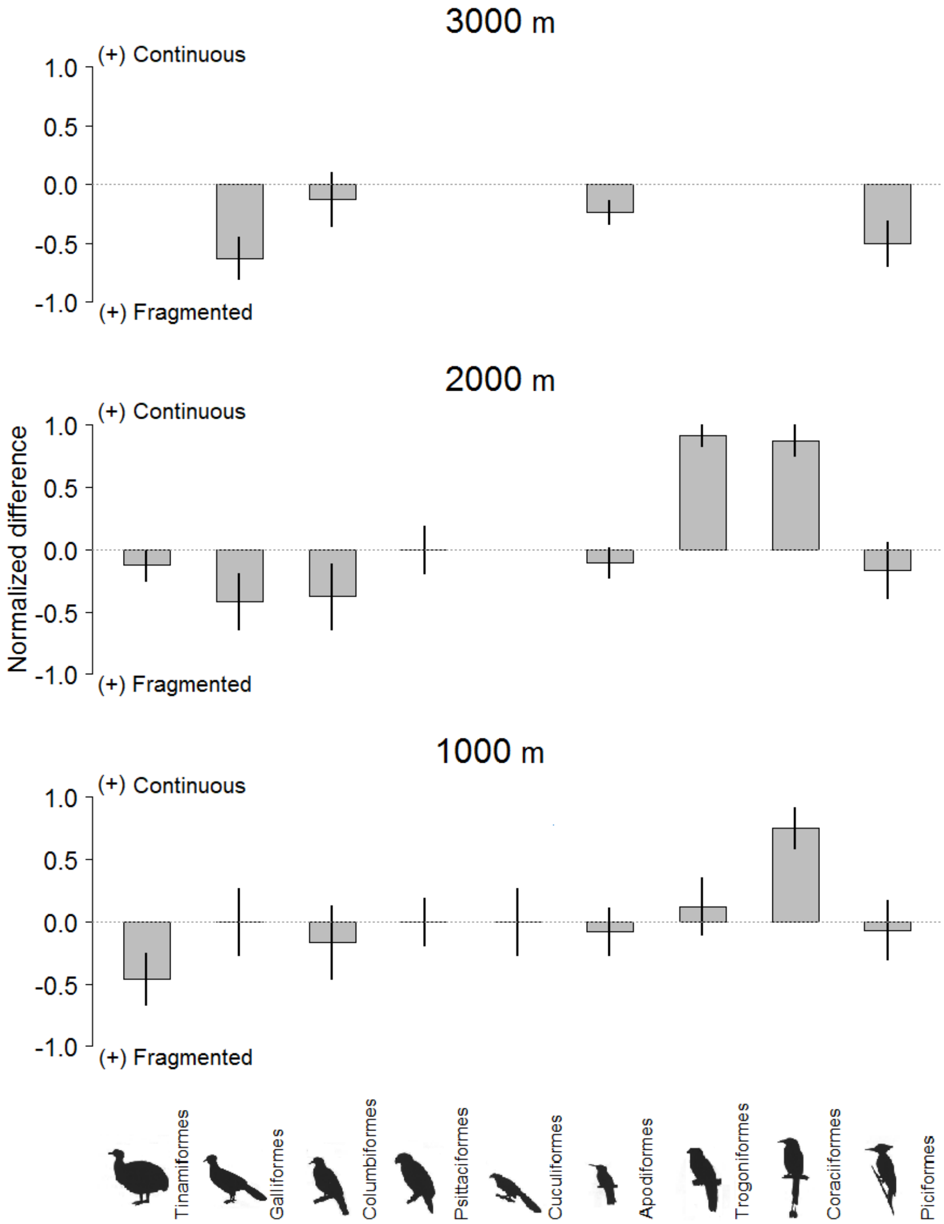


Figure 3. Gain and loss of bird functional groups representing the main types of bird morphology. Shown are normalized differences between species belonging to taxonomic orders present in continuous and fragmented forests at three elevations (i.e., 1000, 2000, 3000 m a.s.l). The normalized difference was calculated as the difference in species numbers between continuous and fragmented forest for each of the eight temporal replicates per plot at each elevation, divided by the sum of species of this order recorded in both forest types at the given elevation. The normalized difference ranges between -1 and 1. Positive bars represent a gain of species in a respective order in continuous forests, negative bars represent a gain of species in a respective order in fragmented forests. Please note that the order of Passeriformes is depicted separately in Figure 4.

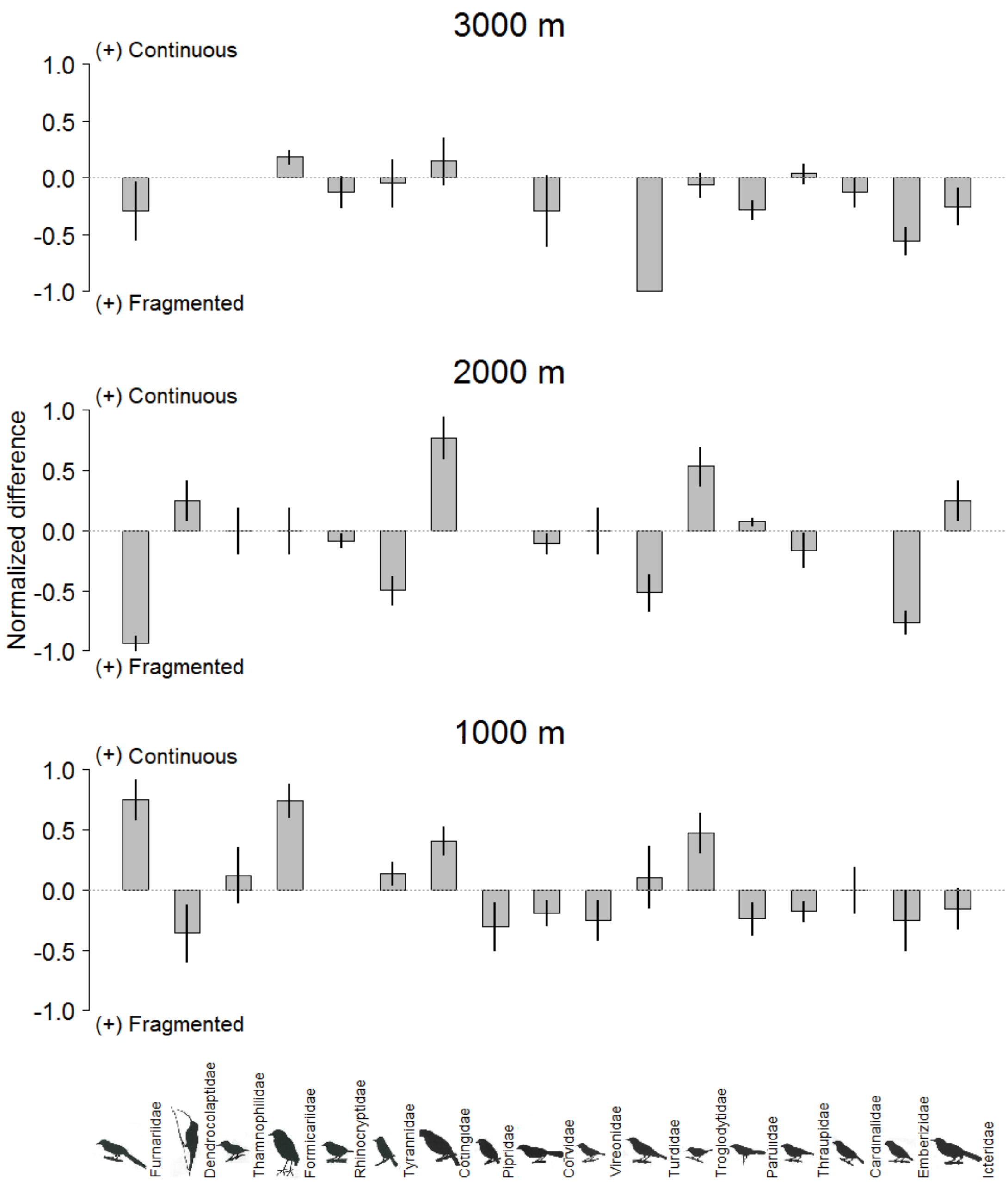


Figure 4. Gain and loss of bird functional groups representing the main types of bird morphology. Shown are normalized differences between species belonging to taxonomic families of the Passerifomes present in continuous and fragmented forests at three elevations (i.e., 1000, 2000, 3000 m a.s.l). The normalized difference was calculated as the difference in species numbers between continuous and fragmented forest for each of the eight temporal replicates per plot at each elevation, divided by the sum of species of this order recorded in both forest types at the given elevation. The normalized difference takes on values between -1 and 1. Positive bars represent a gain of species in a respective family in continuous forests, negative bars represent a gain of species in a respective family in fragmented forests.

Appendix 3. Different responses of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient

---

Supplementary material

Different response of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient

Vinicio Santillán, Marta Quitián, Boris A. Tinoco, Edwin Zárate, Matthias Schleuning, Katrin Böhning-Gaese and Eike Lena Neuschulz

Corresponding author: Vinicio Santillán: vinicioestuardosantillan@gmail.com

Appendix S1. Species accumulation curves.

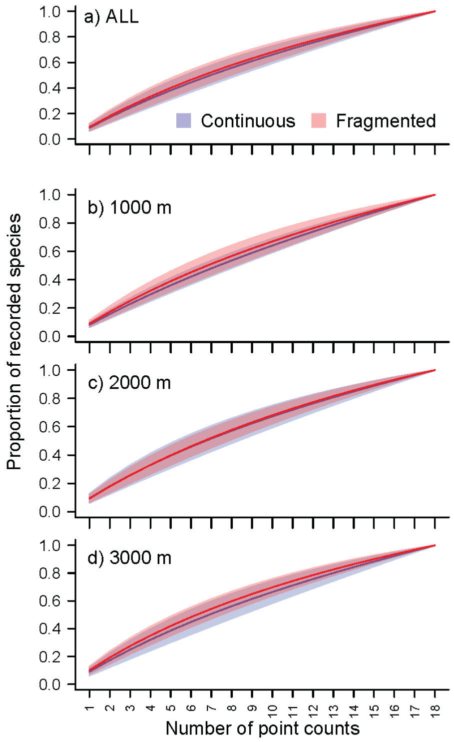


Figure S1. Species accumulation curves showing the relationship between the proportion of recorded species and the number of point counts conducted in continuous and fragmented forests at each elevation (i.e., 18 point counts in total over both years). Curves were calculated for each plot and were averaged for (a) all study sites and (b, c, d) for each elevation separately. Blue lines represent mean species accumulation for continuous forest, red lines represent mean species accumulation for fragmented forest. Blue and red areas show standard deviation for continuous and fragmented forests, respectively.

Appendix S2. Principal coordinate analysis of ecomorphological traits.

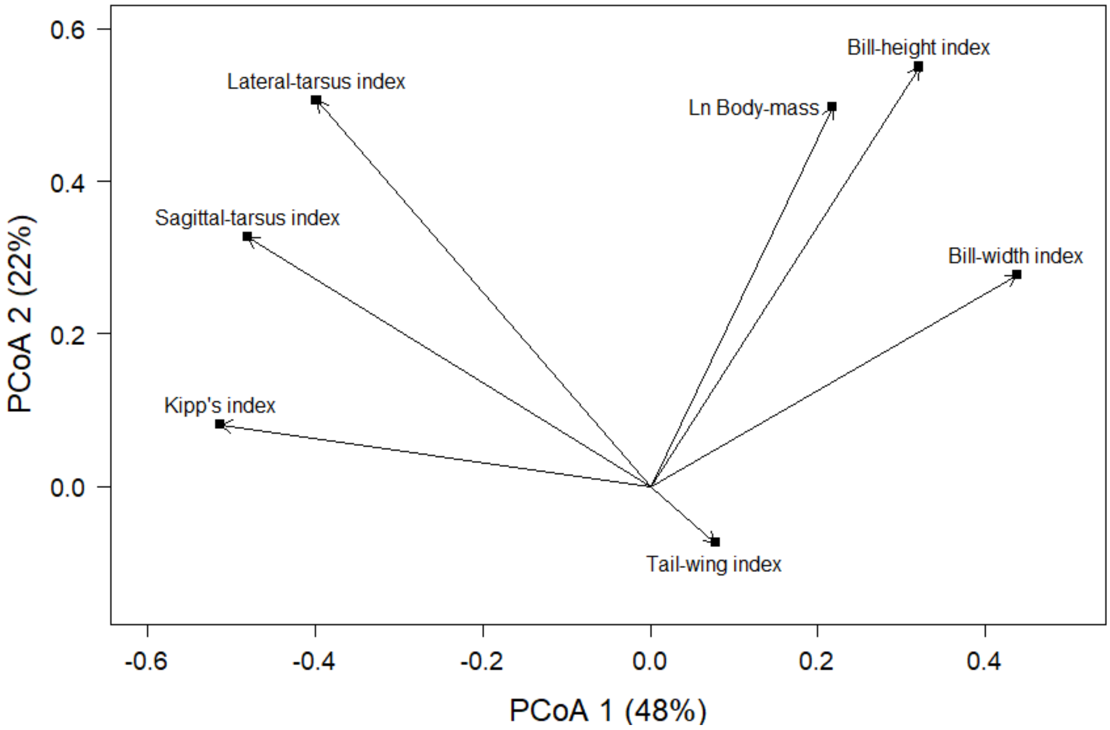


Figure S2. Projections of trait indices in the multidimensional trait space of the principal coordinate analysis (PCoA). PCoA axis 1 and PCoA axis 2 explain a total of 70 % of the variance. The first PCoA axis explained 48 % and separated birds mainly according to their foraging and flight patterns. The second axis (22 %) was associated to body mass, resource-and habitat use.

Appendix S3. Taxonomic and fuctional evenness.

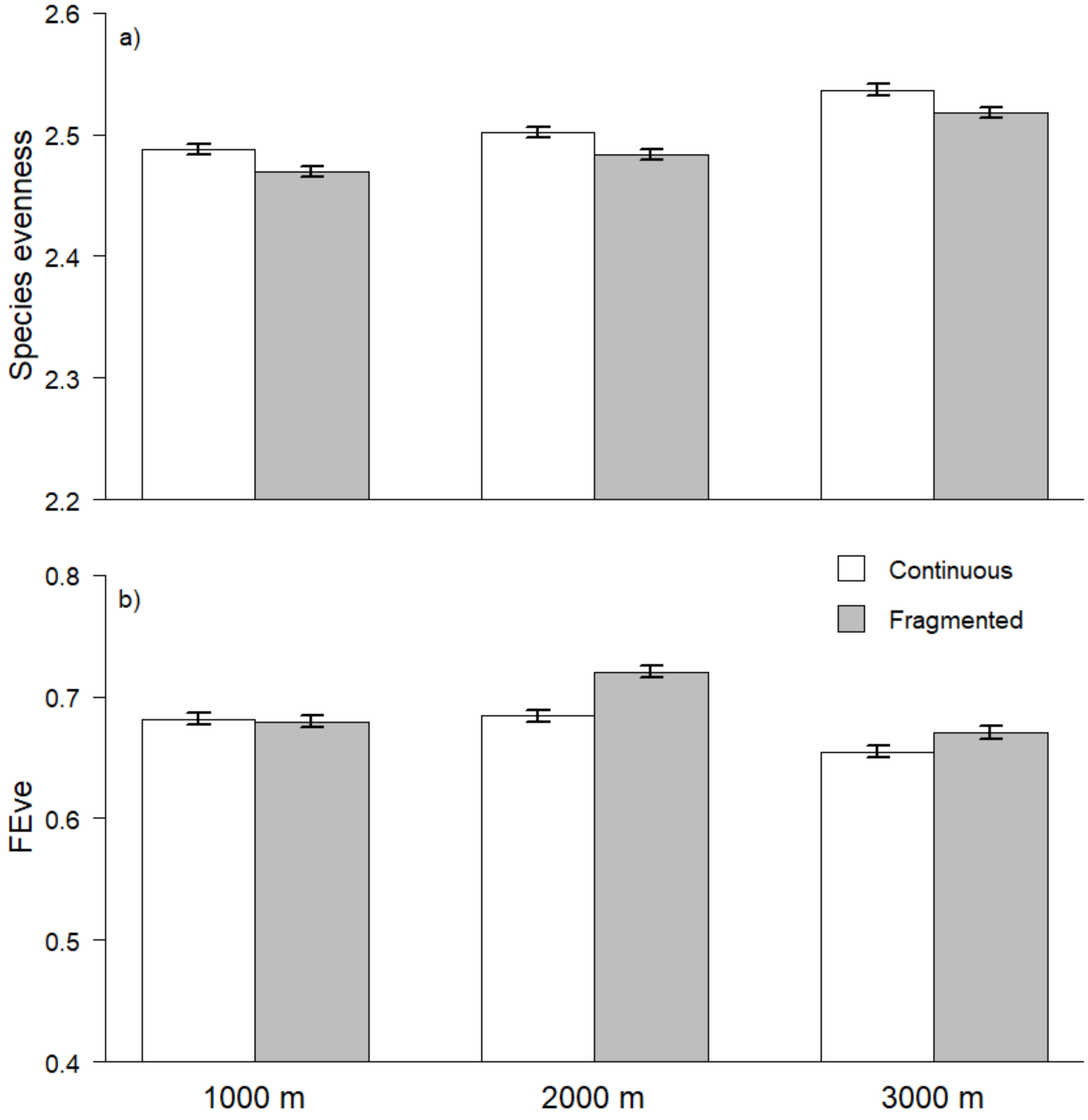


Figure S3. Predicted values of a) species evenness and b) functional evenness (FEve) in the continuous and fragmented forest at three elevations (1000 m a.s.l., 2000 m a.s.l., 3000 m a.s.l.). Both models assume a Gaussian error distribution. Please note different scales and breaks in the y-axis.

Appendix S4. RLQ analysis of morphological traits.

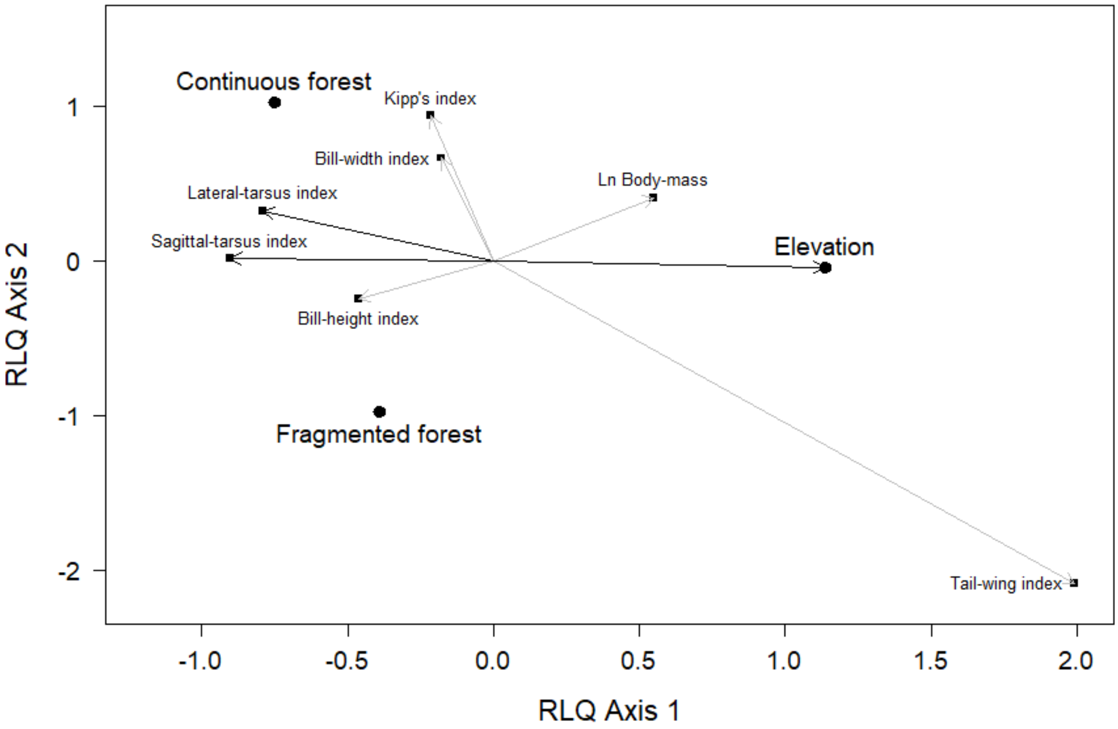


Figure S4. RLQ scores showing the relationship between functional trait indices, forest type (continuous and fragmented forest) and elevation. RLQ Axes 1 and 2 explain 91 % and 9 %, respectively. Black arrows show significant, grey arrows non-significant relationships. For a description of trait indices see Table S2.

Appendix S5. Plot distances and characteristics.

Table S1. Characteristics of all 18 study plots located at six study sites, including elevation, slope, fragment size, the minimum distance of the plot center to the closest continuous forest, and the minimum distance of the plot center to the closest forest edge.

Study site	Forest type	Elevation (m a.s.l.)	Slope (°)	Fragment size (ha)	Distance to continuous forest (m)	Distance to forest edge (m)
Bombuscaro	Continuous	1057	23.9	-	0	720
Bombuscaro	Continuous	1092	30.0	-	0	1400
Bombuscaro	Continuous	1008	37.1	-	0	1850
Copalinga	Fragmented	970	26.2	5.31	1845	70
Copalinga	Fragmented	980	28.9	6.62	2643	60
Copalinga	Fragmented	1001	28.4	3.49	2903	60
ECSF	Continuous	2045	21.1	-	0	450
ECSF	Continuous	2047	33.4	-	0	590
ECSF	Continuous	2025	26.9	-	0	460
Finca	Fragmented	2051	31.2	4.57	1267	75
Finca	Fragmented	2119	36.7	3.2	1191	50
Finca	Fragmented	2068	30.2	3.47	1059	50
Cajanuma	Continuous	2891	41.4	-	0	1570
Cajanuma	Continuous	2874	37.1	-	0	1020
Cajanuma	Continuous	2894	42.6	-	0	930
Bellavista	Fragmented	2898	27.5	6.73	3818	75
Bellavista	Fragmented	2966	27.3	4.29	3811	73
Bellavista	Fragmented	2884	23.1	4.61	4859	55

Appendix S6. Morphological traits description.

Table S2. Description of morphological trait indices used to measure functional richness and functional dispersion of the bird community.

Trait index	Role	Description	Definition
Kipp's index	Flight performance	Kipp's distance by wing length	Associated with foraging and flight patterns
Tail-wing index		Longest rectrix by wing length	
Bill-height index	Food intake	Bill height by bill length	Associated with type of resources used
Bill-width index		Bill width by bill length	
Lateral-tarsus index	Bipedal locomotion	Lateral tarsus diameter by tarsus length	Associated with habitat use and foraging mode
Sagittal-tarsus index		Sagittal tarsus diameter by tarsus length	

Appendix S7. Correlation of morphological traits.

Table S3. Pearson correlation coefficients of morphological trait indices and body mass.

	Kipp's index	Tail-wing index	Bill-height index	Bill-width index	Lateral-tarsus index	Sagittal-tarsus ind
Kipp's index						
Tail-wing index	-0.14					
Bill-height index	-0.45	0.04				
Bill-width index	-0.64	0.05	0.72			
Lateral-tarsus index	0.70	-0.10	-0.01	-0.37		
Sagittal-tarsus index	0.87	-0.07	-0.24	-0.53	0.87	
Ln Body-mass	-0.37	0.01	0.41	0.32	0.03	-0.14

Appendix S8. Correlation of taxonomic and functional indicators.

Table S4 Pearson correlation coefficients of taxonomic and functional indicators.

	Species richness	Abundance	Species evenness	FRic	FDis
Species richness					
Abundance	0.720				
Species evenness	0.199	-0.183			
FRic	0.627	0.461	0.110		
FDis	0.133	0.040	0.294	0.552	
FEve	0.031	-0.134	0.354	-0.063	0.165

Appendix S9. AIC and R^2 of linear models.

Table S5. Model selection of linear mixed effects models testing the effects of fragmentation (continuous forest and fragmented forest), elevation (1000, 2000, 3000 m a.s.l.) and their interaction on bird species richness, abundance, species evenness, functional richness (FRic), functional dispersion (FDis), and functional evenness (FEve). Best-fitting models with or without the interaction term between fragmentation and elevation were selected based on the lowest Akaike's information criterion (Burnham and Anderson 2002). If Δ AIC < 2, we retained the most parsimonious model. Marginal and conditional R^2 are shown as goodness of fit statistic for each of the models, indicating the amount of variance explained by fixed factors and fixed and random factors, respectively. Selected models are shown in bold. For model coefficients see Table 1 in the main manuscript.

	Predictor variables	AIC	R^2	
			Marginal	Conditional
Species richness	**Forest type + elevation**	**936.2**	**0.183**	**0.489**
	Forest type x elevation	937.7	0.220	0.492
Abundance	**Forest type + elevation**	**1475.7**	**0.270**	**0.832**
	Forest type x elevation	1477.2	0.316	0.832
Species evenness	**Forest type + elevation**	**-414.8**	**0.027**	**0.027**
	Forest type x elevation	-416.1	0.062	0.063
FRic	Forest type + elevation	395.0	0.083	0.248
	Forest type x elevation	**388.8**	**0.158**	**0.260**
FDis	Forest type + elevation	193.6	0.024	0.048
	Forest type x elevation	**189.8**	**0.078**	**0.078**
FEve	**Forest type + elevation**	**-272.5**	**0.040**	**0.122**
	Forest type x elevation	-273.0	0.083	0.124

Appendix 3. Different responses of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient

---

Appendix S10. List of bird species recorded.

Table S6. List of 238 bird species grouped in ten taxonomical orders in continuous (C) and fragmented forest (F), at three elevations (1000, 2000 and 3000 m a.s.l.) in and around Podocarpus National Park and San Francisco reserve in southern Ecuador.

	1000		**2000**		**3000**	
	C	**F**	**C**	**F**	**C**	**F**
Tinamiformes						
Tinamidae						
Crypturellus soui	X	X				
Nothocercus bonapartei				X		
Tinamus tao	X	X				
Galliformes						
Cracidae						
Aburria aburri	X					
Chamaepetes goudotii	X		X			
Ortalis guttata	X	X				
Penelope barbata			X	X		X
Odontophoridae						
Odontophorus speciosus	X		X			
Columbiformes						
Columbidae						
Columba fasciata				X	X	X
Columba plumbea	X	X				
Columba subvinacea		X				
Geotrygon frenata	X		X			
Leptotila rufaxilla		X				
Psittaciformes						
Psittacidae						

Amazona mercenaria			X			
Pyrrhura albipectus	X	X				
Touit stictoptera				X		
Cuculiformes						
Cuculidae						
Crotophaga ani		X				
Piaya cayana	X	X				
Apodiformes						
Trochilidae						
Adelomyia melanogenys			X	X	X	
Aglaeactis cupripennis						X
Aglaiocercus kingi		X	X	X		
Amazilia fimbriata		X				
Boissonneaua matthewsii					X	
Chalcostigma herrani						X
Chalcostigma ruficeps				X		
Chrysuronia oenone	X	X				
Coeligena coeligena			X			
Coeligena iris					X	X
Coeligena lutetiae					X	
Coeligena torquata			X	X	X	
Colibri coruscans		X	X	X		
Colibri thalassinus			X	X		
Doryfera johannae			X			
Doryfera ludovicae	X	X	X			
Eriocnemis vestitus					X	X
Eutoxeres aquila		X				
Heliangelus amethysticollis				X		
Heliangelus viola					X	X

Heliodoxa leadbeateri	X		X	X		
Heliodoxa rubinoides			X	X		
Heliothryx aurita		X				
Klais guimeti	X	X				
Lafresnaya lafresnayi						X
Metallura tyrianthina				X	X	X
Ocreatus underwoodii	X		X	X		
Phaethornis griseogularis	X	X				
Phaethornis guy	X	X				
Phaethornis syrmatophorus		X	X			
Pterophanes cyanopterus					X	
Thalurania furcata		X				
Trogoniformes						
Trogonidae						
Pharomachrus auriceps			X	X		
Trogon collaris	X	X				
Trogon personatus			X			
Coraciiformes						
Momotidae						
Momotus aequatorialis	X		X			
Piciformes						
Galbulidae						
Galbula pastazae	X	X				
Bucconidae						
Malacoptila fulvogularis	X					
Capitonidae						
Eubucco bourcierii	X					
Ramphastidae						
Aulacorhynchus derbianus	X					

Aulacorhynchus prasinus			X	X		X
Picidae						
Campephilus pollens				X		
Dryocopus lineatus		X				
Piculus rivolii			X	X	X	X
Piculus rubiginosus	X					
Picumus lafresnayi	X					
Veniliornis passerinus		X				
Passeriformes						
Furnariidae						
Anabacerthia striaticollis	X					
Hellmayrea gularis					X	
Lochmias nematura		X		X		
Margarornis squamiger					X	X
Pseudocolaptes boissonneautii					X	X
Synallaxis azarae			X	X		X
Syndactyla subalaris	X					
Xenops minutus	X					
Dendrocolaptidae						
Campylorhamphus pusillus	X					
Dendrocincla fuliginosa	X					
Glyphorynchus spirurus	X	X				
Lepidocolaptes lacrymiger			X	X		
Sittasomus griseicapillus	X	X				
Xiphocolaptes promeropirhynchus			X			
Xiphorhynchus triangularis	X		X			
Thamnophilidae						
Cercomacra nigrescens	X	X				
Drymophila caudata			X			

Dysithamnus mentalis		X				
Hylophylax poecilinota	X	X				
Hypocnemis cantator	X					
Thamnophilus unicolor				X		
Formicariidae						
Chamaeza campanisona	X					
Grallaria haplonota	X	X				
Grallaria nuchalis					X	X
Grallaria ruficapilla				X	X	X
Grallaria rufula					X	X
Grallaria squamigera					X	X
Grallaricula flavirostris			X			
Grallaricula nana					X	
Rhinocryptidae						
Scytalopus latrans			X	X	X	X
Scytalopus micropterus			X	X		
Scytalopus parkeri					X	X
Tyrannidae						
Anairetes parulus				X		X
Colonia colonus	X					
Conopias cinchoneti		X				
Contopus fumigatus			X	X		
Elaenia albiceps				X	X	X
Elaenia pallatangae			X	X		X
Leptopogon rufipectus		X	X			
Leptopogon superciliaris	X	X				
Mecocerculus calopterus				X		
Mecocerculus stictopterus					X	X
Mionectes oleagineus		X				

Mionectes olivaceus	X		X	X		
Mionectes striaticollis	X	X	X	X		
Myiarchus cephalotes	X		X	X		
Myiarchus ferox		X				
Myiarchus tuberculifer				X		
Myiotriccus ornatus	X	X				
Myiozetetes similis	X	X				
Ochthoeca cinnamomeiventris				X		
Ochthoeca rufipectoralis					X	X
Phyllomyias nigrocapillus				X	X	
Phyllomyias plumbeiceps	X	X				
Platyrinchus mystaceus	X					
Poecilotriccus ruficeps				X		
Pogonotriccus ophthalmicus	X	X		X		
Pogonotriccus poecilotis	X	X		X		
Pyrrhomyias cinnamomea			X	X		
Todirostrum cinereum	X	X				
Tolmomyias viridiceps		X				
Tyrannus melancholicus	X	X				
Zimmerius chrysops			X	X		
Cotingidae						
Ampelioides tschudii	X					
Ampelion rubrocristatus					X	X
Cephalopterus ornatus	X					
Pipreola arcuata					X	X
Pipreola chlorolepidota	X	X				
Pipreola riefferii			X	X		
Rupicola peruviana	X	X	X			
Pipridae						

Dixiphia pipra	X	X				
Lepidothrix isidorei	X	X				
Machaeropterus striolatus		X				
Pipra erythrocephala	X	X				
Corvidae						
Cyanocorax violaceus		X				
Cyanocorax yncas	X	X	X	X		
Cyanolyca turcosa					X	X
Vireonidae						
Cyclarhis gujanensis			X	X		
Hylophilus olivaceus		X				
Vireo leucophrys			X			
Turdidae						
Catharus ustulatus	X	X				
Myadestes ralloides	X	X	X	X		
Platycichla leucops	X					
Turdus albicollis	X	X				
Turdus fulviventris		X				
Turdus fuscater			X	X		X
Turdus nigriceps		X				
Turdus serranus			X			
Troglodytidae						
Cinnycerthia unirufa					X	
Henicorhina leucophrys			X	X		
Henicorhina leucosticta	X	X				
Thryothorus euophrys			X	X	X	X
Troglodytes aedon	X	X				
Troglodytes solstitialis			X	X	X	X
Parulidae						

Basileuterus coronatus			X	X	X	X
Basileuterus fulvicauda		X				
Basileuterus nigrocristatus			X	X	X	X
Basileuterus tristriatus			X			
Dendroica fusca			X	X		
Myioborus melanocephalus					X	X
Myioborus miniatus	X	X	X	X		
Parula pitiayumi	X	X				
Wilsonia canadensis	X	X	X			
Thraupidae						
Anisognathus igniventris					X	X
Anisognathus lacrymosus			X	X	X	X
Anisognathus somptuosus			X	X		
Buthraupis montana					X	
Catamblyrhynchus diadema						X
Chlorochrysa calliparaea	X	X				
Chlorophanes spiza		X				
Chlorornis riefferii					X	X
Chlorospingus canigularis	X			X		
Chlorospingus flavigularis	X	X	X	X		
Chlorospingus ophthalmicus			X	X		
Cissopis leveriana		X				
Cnemoscopus rubrirostris					X	
Coereba flaveola	X	X				
Conirostrum albifrons						X
Conirostrum cinereum						X
Conirostrum sitticolor					X	
Creurgops verticalis			X	X		
Dacnis cayana		X				

Dacnis lineata	X	X				
Diglossa albilatera			X	X	X	X
Diglossa humeralis			X	X	X	X
Diglossa lafresnayii					X	X
Diglossopis cyanea			X	X	X	X
Dubusia taeniata						X
Euphonia xanthogaster	X	X				
Hemispingus frontalis			X	X		
Hemispingus superciliaris					X	X
Hemispingus verticalis					X	
Hemithraupis guira		X				
Iridophanes pulcherrima		X				
Iridosornis analis			X			
Iridosornis rufivertex					X	
Pipraeidea melanonota			X			
Sericossypha albocristata				X		
Tachyphonus cristatus		X				
Tangara arthus	X	X				
Tangara chilensis	X	X				
Tangara chrysotis	X	X				
Tangara cyanicollis	X	X	X			
Tangara gyrola	X	X				
Tangara labradorides			X			
Tangara nigrocincta	X	X				
Tangara nigroviridis			X	X		
Tangara parzudakii			X	X		
Tangara punctata	X	X				
Tangara schrankii	X	X				
Tangara vassorii			X	X	X	X

Tangara xanthocephala			X	X		
Tangara xanthogastra		X				
Thraupis cyanocephala			X	X		X
Thraupis episcopus	X	X				
Thraupis palmarum	X	X		X		
Cardinalidae						
Pheucticus chrysogaster						X
Piranga leucoptera	X					
Saltator grossus	X					
Saltator maximus		X				
Emberizidae						
Ammodramus aurifrons		X				
Arremon aurantiirostris	X	X				
Atlapetes latinuchus			X	X	X	X
Atlapetes pallidinucha					X	
Buarremon brunneinuchus			X			
Buarremon torquatus				X		X
Catamenia homochroa					X	
Coryphospingus cucullatus		X				
Zonotrichia capensis				X		X
Icteridae						
Amblycercus holosericeus						X
Cacicus uropygialis	X	X	X			
Psarocolius angustifrons	X	X				
Psarocolius decumanus	X	X				

Appendix 4. Curriculum vitae

Vinicio Estuardo Santillán Rodríguez

Address: Andrés F. Córdova 1-78

010110, San Blas

Cuenca, Ecuador

Email: vinicioestuardosantillan@gmail.com

Phone: 593961413575

EDUCATION

PhD candidate, Senckenberg Biodiversity and Climate Research Centre (SBIK-F) and Goethe University Frankfurt, Frankfurt am Main, Germany. As part of the Project C3: “Development and validation of functional indicators for avian seed dispersal” of the DFG program: “Platform for Biodiversity and Ecosystem Monitoring and Research in South Ecuador” Dissertation title: Spatial and temporal pattern in bird communities along an elevational gradient in the tropical Andes.

M.Sc. Geomatics, Universidad del Azuay, 2013. Escuela de Posgrados. Dissertation title: Application of Geografical Information Systems (GIS) for the creation of Zoogeographical models: a case study. *(Aplicación de Sistemas de Información Geográfica (SIG) para la elaboración de modelos zoogeográficos: un estudio de caso).*

B.Sc. Biology, Universidad del Azuay, 2006. Escuela de biología del medio ambiente. Dissertation title: Evaluation of the importance of Quinua patches (*Polylepis spp.*) as refuges for non-flying small mammals in Cajas National Park (CNP). (*Evaluación de la importancia de los parches de quinua (Polylepis spp.) como refugio para especies de micromamíferos no voladores en el Parque Nacional Cajas (PNC)).*

PEER-REVIEWED PUBLICATIONS

Dugger, P.J., Blendinger, P.G., Böhning-Gaese, K., Chama, L., Correia, M., Dehling, D.M., Emer, C., Farwig, N., Fricke, E.C., Galetti, M., García, D., Grass, I., Heleno, R., Jacomassa, F.A.F., Moraes, S., Moran, C., Muñoz, M.C., Neuschulz, E.L., Nowak, L., Piratelli, A., Pizo, M.A., Quitián, M., Rogers, H.S., Ruggera, R.A., Saavedra, F., Sánchez, M.S., Sánchez, R., **Santillán, V.**, Schabo, D.G., Ribeiro, F., Timóteo, S., Traveset, A., Vollstädt, M.G.R., Schleuning, M., 2019. Seed-dispersal networks are more specialized in the Neotropics than in the Afrotropics. Global Ecology and Biogeography. doi: https ://doi.org/10.1111/geb.12833

Hanz, D.M., Böhning-gaese, K., Ferger, S.W., Fritz, S.A., Neuschulz, E.L., Quitián, M., **Santillán, V.**, Töpfer, T., Schleuning, M., 2019. Functional and phylogenetic diversity of bird assemblages are filtered by different biotic factors on tropical mountains. Journal of Biogeography. Doi: https://doi.org/10.1111/jbi.13489

Quitián, M., **Santillán, V.**, Bender, I.M.A., Homeier, J., Neuschulz, E.L., Espinosa, C.I., Schleuning, M., 2019. Functional responses of avian frugivores to variation in fruit resources between natural and fragmented forests. Functional Ecology. doi: https ://doi.org/10.1111/1365-2435.13255

Quitián, M., **Santillán, V.**, Espinosa, C.I., Homeier, J., Böhning-Gaese, K., Schleuning, M., Neuschulz, E.L., 2019. Direct and indirect effects of plant and frugivore diversity on structural and functional components of fruit removal by birds. Oecologia. doi: https://doi.org/10.1007/s00442-018-4324-y

Santillán, V., Quitián, M., Tinoco, B.A., Zárate, E., Schleuning, M., Gaese, K.B., Neuschulz, E.L., 2019. Different responses of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient. Oecologia 189:863-873

Bender, I.M.A., Kissling, W.D., Blendinger, P.G., Böhning-gaese, K., Hensen, I., Kühn, I., Muñoz, M.C., Neuschulz, E.L., Nowak, L., Quitián, M., Saavedra, F., **Santillán, V.**, Töpfer, T., Wiegand, T., Dehling, D.M., Schleuning, M., 2018. Morphological trait matching shapes plant–frugivore networks across the Andes. Ecography 41:1–10

Santillán, V., Quitián, M., Tinoco, B.A., Zárate, E., Schleuning, M., Böhning-Gaese, K., Neuschulz, E.L., 2018. Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient. PLoS ONE 13:1–15

Tinoco, B.A., **Santillán, V.**, Graham, C.H., 2018. Land use change has stronger effects on functional diversity than taxonomic diversity in tropical Andean hummingbirds. Ecology and Evolution, 8:3478–3490

Quitián, M., **Santillán, V.**, Espinosa, C.I., Homeier, J., Böhning-Gaese, K., Schleuning, M., Neuschulz, E.L., 2017. Elevation-dependent effects of forest fragmentation on plant-bird interaction networks in the tropical Andes. Ecography 40:1–10

Santillán, V., Segovia, E., 2013. Primer registro de la rata cangrejera de Tweedy Ichthyomys tweedii (SIGMODONTINAE: ICHTHYOMYINI) en la provincia del Azuay, Ecuador. Mastozoologia Neotropical 20:421–424

OTHER ARTICLES AND BOOK CHAPTERS

Santillán, V. 2012. Identificación de zonas de importancia ambiental y vulnerabilidad de ecosistemas mediante métodos de evaluación multicriterio (EMC) en el entorno de los Sistemas de Información Geográfica (SIG). Cuenca del río Paute (CRP), suroriente del Ecuador. Geografía y Sistemas de Información Geográfica. (GESIG-UNLU, Luján). Año 4, N° 4, Sección I:56-76

Santillán, V. 2012. Identificación de zonas de intervención en la cuenca del Río Paute, a partir de una Evaluación Multicriterio sobre factores: sociales, económico-productivos y ambientales. FONAPA, Instituto Ecuatoriano de Régimen Seccional (IERSE), Universidad del Azuay. 73 pp.

Zamora, J., **Santillán, V.** & Pacheco, X. 2008. Aves del Bosque Protector Cubilán. Fundación ECOHOMODE. EMAPAL. Azoguez, Ecuador. 118 pp.

CONFERENCE CONTRIBUTIONS

Vinicio Santillán, Marta Quitián, Boris A. Tinoco, Edwin Zárate, Matthias Schleuning, Katrin Böhning-Gaese and Eike Lena Neuschulz. 2014. Monitoring bird diversity across elevational and land-use gradients. Poster at the Symposium of the Joint Member Assembly of the DFG-PAK 823/4/5: Platform for biodiversity and ecosystem monitoring and research in South Ecuador, Cuenca, Ecuador.

Vinicio Santillán, Marta Quitián, Boris A. Tinoco, Edwin Zárate, Matthias Schleuning, Katrin Böhning-Gaese and Eike Lena Neuschulz. 2015. Monitoring bird diversity across elevational and land-use gradients. Poster at the Annual Conference of the

Society for Tropical Ecology (Gesellschaft für Tropenökologie, GTÖ), Zurich, Switzerland.

Vinicio Santillán, Marta Quitián, Boris A. Tinoco, Edwin Zárate, Matthias Schleuning, Katrin Böhning-Gaese and Eike Lena Neuschulz. 2015. Monitoring bird diversity across elevational and land-use gradients in Southern Ecuador. Talk at the Symposium of the Joint Member Assembly of the DFG-PAK 823/4/5: Platform for biodiversity and ecosystem monitoring and research in South Ecuador. Loja, Ecuador.

Vinicio Santillán, Marta Quitián, Boris A. Tinoco, Edwin Zárate, Matthias Schleuning, Katrin Böhning-Gaese and Eike Lena Neuschulz. 2016. Monitoring bird diversity across elevational and land-use gradients in Southern Ecuador. Talk at the Annual Conference of the Society for Tropical Ecology (Gesellschaft für Tropenökologie, GTÖ), Göttingen, Germany.

Vinicio Santillán, Marta Quitián, Boris A. Tinoco, Edwin Zárate, Matthias Schleuning, Katrin Böhning-Gaese and Eike Lena Neuschulz. 2016. Spatial and temporal variation in bird assemblages along elevational gradients in Southern Ecuador. Talk at the Symposium of the Joint Member Assembly of the DFG-PAK 823/4/5: Platform for biodiversity and ecosystem monitoring and research in South Ecuador. Loja, Ecuador.

Vinicio Santillán, Marta Quitián, Boris A. Tinoco, Edwin Zárate, Matthias Schleuning, Katrin Böhning-Gaese and Eike Lena Neuschulz. 2017. Structural and functional diversity of tropical bird assemblages along land-use gradients. Talk at the Annual Conference of Ecology (Ecology across borders, BES, GFÖ, NecoV, EEF), Ghent, Belgium.

Vinicio Santillán, Marta Quitián, Boris A. Tinoco, Edwin Zárate, Matthias Schleuning, Katrin Böhning-Gaese and Eike Lena Neuschulz. 2018. Different responses of bird diversity to forest fragmentation across an elevational gradient. Poster at the Symposium of the Joint Member Assembly of the DFG-PAK 823/4/5: Platform for biodiversity and ecosystem monitoring and research in South Ecuador, Cuenca, Ecuador.

ACADEMIC OR PROFESSIONAL POSITIONS

Lecturer (March 2012 to March 2014). Escuela de Biología, Ecología y Gestión, Universidad del Azuay.

Lecturer (March 2013 to March 2014). Escuela de Ingeniería en Minas, Universidad del Azuay.

Research Associate (January 2009 to March 2014). Escuela de Biología, Ecología y Gestión, Decanato General de Investigaciones, Universidad del Azuay.

Research Associate (2012). Eco-acoustic characteristics of pollinated flowers by bats, (Características Eco-acústicas de flores polinizadas por murciélagos). Collaboration between Universität Ulm and Universidad del Azuay.

Research Associate (January 2010 to 2012). Instituto Ecuatoriano de Régimen Seccional (IERSE), Decanato General de Investigaciones, Universidad del Azuay.

Project Researcher (2011). Identification of intervention zones in the Paute river basin based on a multicriterial evaluation of social, economic and environmental factors. (Identificación de zonas de intervención en la cuenca del río paute, a partir de una evaluación multicriterio sobre factores: sociales, económico – productivos y ambientales) FONAPA, Instituto Ecuatoriano de Régimen Seccional (IERSE), Universidad del Azuay.

Project Researcher (2008 to 2009). Relationship of the Andean Bear and Livestock in the Colepato Cooperative. (Estudio de la Relación Oso Andino-Ganado Vacuno en la Cooperativa Colepato) Cañar, Ecuador. Proyecto Don Oso. Fundación Cordillera Tropical.

Project Researcher (2008). Conserving the Andean Bear (*Tremarctos ornatus*) on Private Lands within Sangay National Park, Ecuador". University of Wisconsin. Conservation Biology and Sustainable Development Program.

Project Researcher (2008). Abundance and distribution of the Australian Black Widow (*Latrodectus hasselti*) in the Ucubamba Valley, Cuenca, Ecuador. (Distribución y abundancia de la Viuda Negra australiana (*Latrodectus hasselti*) en el valle de

Ucubamba, Cuenca, Ecuador) ETAPA. Planta de Tratamiento de Aguas Residuales (PTAR). Ucubamba. Ecuador.

Consultant Zoologist (2006 to 2011). In several baseline projects of national importance for Ecuador.

Project Researcher (2004). Seed dispersal by Frugivorous Birds and Bats, Resource Availability, and Habitat selection of three species of Bats (Chiroptera: Phyllostomidae) in the San Francisco Biological Reserve. Fundación Alemana para la Investigación (DFG).