Birds, Traditional Coffee Plantations and Spatial complexity: The Diversity Puzzle

Eurídice Leyequién Abarca

Proefschrift
ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van Wageningen Universiteit,
Prof. Dr. M.J. Kropff
in het openbaar te verdedigen
op vrijdag 21 april 2006
des namiddags te 16:00 uur in de Aula

Leyequién Abarca, E. (2006)
Birds, Traditional Coffee Plantations and Spatial Complexity: The Diversity Puzzle

Ph.D.-thesis, Department of Environmental Sciences, Sub-department of Nature Conservation, Resource Ecology Group, Wageningen University, the Netherlands, with summaries in English, Spanish and Dutch.

Keywords: Avian diversity, Double-observer approach, Habitat loss, Habitat fragmentation, Low montane rain forest, Lower montane rain forest, Metacommunity, Mexico, Remote sensing, Species competition.

ISBN 90-8504-416-2

Contents

Page 227 TSP

Training and Supervision Plan of the Graduate School Production Ecology and Resource Conservation (PE&RC)

Chapter 1

General introduction

Eurídice Leyequién Abarca

General introduction

Conserving the biological diversity on this planet is increasingly becoming a challenge due to the accelerated and increasingly loss of biodiversity amongst the contemporary conservationists. If we want to avoid a mass extinction we cannot rely only on remnant patches of natural areas to preserve biodiversity (Rosenzweig 2005, Toledo 2005). The previous protectionist paradigm where the isolation and protection of "natural areas" was placed above any social, economic, cultural or political consideration (Janzen 1986, Terborgh 199, Sanderson 2000) has led to the paradox of increasing loss of biodiversity.

Hence, conservation should also turn its efforts into the management and diversification of the *anthropogenic* matrix in which natural areas are embedded (Rosenzweig 2001, 2005). For example, in the case of tropical bird species, such linkages could be maintained by using the man-modified landscapes (e.g.; traditional shade coffee plantations) as these areas also harbour an ecological value as habitat for wildlife species. To understand how humans can share the landscapes with other species we need to understand which abiotic and biotic factors control species richness, and how these factors operate at multiple spatial scales, ultimately driving species persistence and coexistence.

Much arguments has been given about that independently of the scale in which the mechanism(s) that influence species richness patterns are measured, the results can be scaled up or down. However, several studies had proven that different processes are likely to determine species diversity at different spatial scales (Clarke and Lidgard 2000, Crawley and Harral 2001, Lennon *et al.* 2001, Rahbek and Graves 2001). It is becoming increasingly apparent that the factors best accounting for patterns of species diversity seems to be delimited by scale (Loreau 2000, Mouquet *et al.* 2003, Kneitel and Chase 2004, Borcard *et al.* 2004) where variables that best account for species richness on a local spatial scale may not be the same as those accounting for richness at regional spatial scales (Willis and Whittaker 2002). A hierarchical approach appears to be more appropriate for accurately modelling species richness where processes can be nested according to the scales (Willis and Wittaker 2002). Thus, the integration of scaling effects in studies of species-environment interactions and community composition is a prerequisite for aiming at proper conservation strategies.

Besides, one of the major problems for species conservation is the loss of habitat, and landscape fragmentation. In Latin America natural ecosystems are suffering from an accelerated deforestation, and there is a high rate of conversion to monocultures and grazing lands that has direct effects on Neotropical avian communities (i.e.; resident and migrants). The ecological impacts of both habitat loss (i.e.; reduction of total habitat area) and landscape fragmentation (i.e.; configuration changes in the landscape) on patterns and dynamics are the disruption of important ecological processes for species persistence (e.g.; mortality, re-colonisation, or reproductive rates) (Bender *et al.* 1998, Fahrig 1997, 2001, Fahrig and Merriam 1994, Stephens *et al.* 2003, Villard *et al.* 1995, Wiegand *et al.* 2005). Specifically, habitat loss affects (among others) the breeding and dispersal success (Belisle *et al.* 2001, Kurki *et al.* 2000, With and King 1999), trophic chain length (Komonen *et al.* 2000), species interactions (Taylor and Merrian 1995), species-specific extinction thresholds (With and Crist 1995), and has often been described as only having negative effects on species diversity.

In addition, habitat fragmentation, which leads to an increasing number and isolation of patches while decreasing patch sizes, changes the spatial structure of landscapes. The effects of fragmentation had been accounted as either positive or negative in a number of studies (e.g.; McGarigal and McComb 1995, Bender *et al.* 1998, Kremsater and Bunnell 1999, Trzcinski *et al.* 1999). Besides, both positive and negative effects of fragmentations may be species-dependent, or landscape configuration characteristics such as patch edge which could have positive effects on abundance or distribution of species (Kremsater and Bunnell 1999). Despite the important effects that habitat loss and fragmentation may cause to species survival and maintenance, a considerable amount of research had lead to small room for generalisations and often show ambiguous results (for a review see Fahrig 2003). Most researchers lump both the loss of habitat and the breaking apart of habitat into the single concept of habitat fragmentation, producing unclear results about the magnitude and direction of its individual effects on species diversity (Fahrig 2003). We argue that generalisation is possible only for the separate components of loss and breaking apart of habitat, and that the relative influence of each process should be accounted separately if we are to design proper conservation strategies.

Moreover, local communities are often connected by dispersal at the landscape or regional scale (Wilson 1992, Holt 1993, Hubbell 2001, Mouquet and Loreau 2002). Local extinctions and colonisations can be influenced by interspecific interactions such as competition. Understanding what determines interspecific competition and its strength will give us insight into the forces shaping the community patterns. Body mass is an easily determined characteristic of a species that probably influences competition interactions (Bowers and Brown 1982, Brown and Maurer 1986, French and Smith 2005, Gotelli and Ellison 2002) and could provide a reasonable simple variable to assess competition strength.

Another important issue in conservation biology is the monitoring of community trends to provide reliable information of species diversity and their status, for fast and efficient identification of conservation priorities. Species richness lists of bird communities are crucial to ecological research, conservation plans and environmental impact assessments. The problem arises when using different techniques to acquire the species information as this may lead to dissimilitude in the assessment of species richness, and therefore producing unreliable data about bird communities. Moreover, the costs i.e.; time and money related to the implementation of different techniques is in most of the cases a strong criterion in the decision of which technique to use. This decision may have important consequences in the reliability and completeness of the species richness assessments, thus it is relevant to monitoring programs to consider the biases, costs and efficiency of the potential methods to be used. Besides the field monitoring of species, a constantly developing technology, i.e.; remote sensing had brought the possibility to acquire data about the Earth's surface with high spectral, spatial and temporal resolution, providing a fast and efficient way of obtaining species data over time, with spatially continuous coverage. The potential of this remotely sensed information opens vast possibilities for conservation planning and monitoring of faunal species (Leyequien *et al.* accepted).

Why birds and traditional shade coffee plantations?

Neotropical avifauna comprises a high diversity and is worldwide recognised as threatened by habitat loss and fragmentation due to human activities (Winker 1998). In comparison to Neartic birds, there is still a gap in the knowledge about Neotropical birds, and this a serious concern in conservation biology. Several studies found that a number of resident and migratory birds in the Neotropics are dependent on agroecosystems (e.g.; traditional shade coffee plantations) for food and shelter resources as well as for connecting corridors (Calvo and Blake 1998, Wunderle 1999, Moguel and Toledo 1999, Van der Voort and Greenberg 1999). Thus, traditional shade coffee plantations may function as important areas for a number of Neotropical resident and migratory bird species (Pimentel *et al.*1992, Perfecto *et al.*1996, Mehta and Leuschner 1997, Moguel and Toledo 1999).

However, the current trend in northern Latin America (Colombia, Panama, Costa Rica, El Salvador, Guatemala, Nicaragua, Honduras and Mexico) is to reduce shade cover plantations and convert them into reduced or non-shaded coffee plantations. It has been reported for northern Latin America, that about 41% of the 2.7 million ha devoted to coffee production have been converted to reduced or non-shade coffee plantations (Rice and Ward 1996). This trend could have astounding implications for the loss of biodiversity including bird species; in addition to the ecological services that these agroecosystems provide at local, regional and global level such as maintaining the hydrological balance, improving the soil quality, increasing the forest cover, or improving the CO_2 balance (Moguel and Toledo 1999). However, despite the importance of agroecosystems for biodiversity conservation (Liung *et al.* 2001), there has been more attention on biological diversity in undisturbed ecosystems.

Aim of this study

What controls species richness? The issue of scale complicates the quest for finding the answers of this pivotal question for ecologists and other scientists. Processes and patterns that influence species persistence and coexistence are dependent on the spatial scale that we choose to study (Rosenzweig 1999). Moreover, how these spatial patterns are approached in ecological studies could have significant consequences for conservation planning. In addition to the issue of scale, finding optimal solutions for the design of large-scale monitoring is essential for biodiversity conservation.

The aim of this thesis is to give insight into the forces shaping ecological communities, addressing the issue of scale, to put forward effective monitoring techniques for Neotropical avifauna, and to give insight into the conservation implications of traditional shade coffee plantations for the conservation of biological diversity, in this case the Neotropical avifauna.

Site description

Mexico supports about 1,060 bird species, i.e.; 11% of the total of world's bird species, and ranks fifth in the world for the number of endemic bird areas, with 10% of the bird species endemic to the country. Because of its strategic position at the Nearctic and Neotropical biogeographic boundary, Mexico plays a crucial role in the conservation of migratory birds. The study area is located in the North Eastern mountain range of Puebla, within the Cuetzalan region, Mexico, and covers an area of ~ 151,368 ha Puebla is situated on the east migratory paths of Neartic-Neotropical birds that winter or refuel in this region (Figure 1).

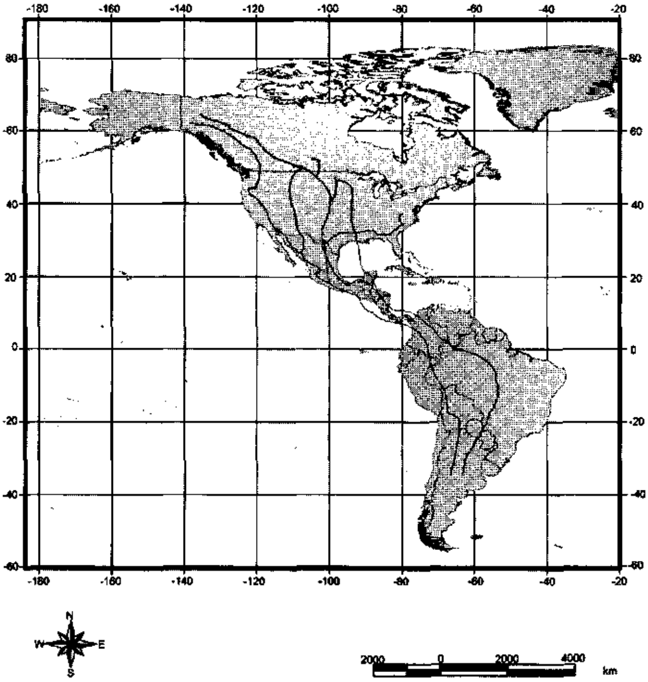

Figure 1. Neotropical-Neartic bird migration routes, passing from Canada and North America to the neotropics (Mexico to South America).

Moreover, the Cuetzalan region is predominantly a coffee agro-ecological zone, which covers an altitudinal range between 300 to 1200 m. The major agricultural system is traditional polyculture (traditional shade coffee plantation), while other land covers, such as seasonal crops (i.e.; maize and beans) and grazing lands are also present in the area. Forested areas are typically remnants of tropical evergreen forest with low montane rain forest in the higher areas (between 700 and 2500 m) and lowland rain forest in the lower areas (200-700 m) (Figure 2). The mean annual rainfall is 3,500 mm without a defined dry season; and the mean annual temperature is 22-26°C.

Gezellig Summary

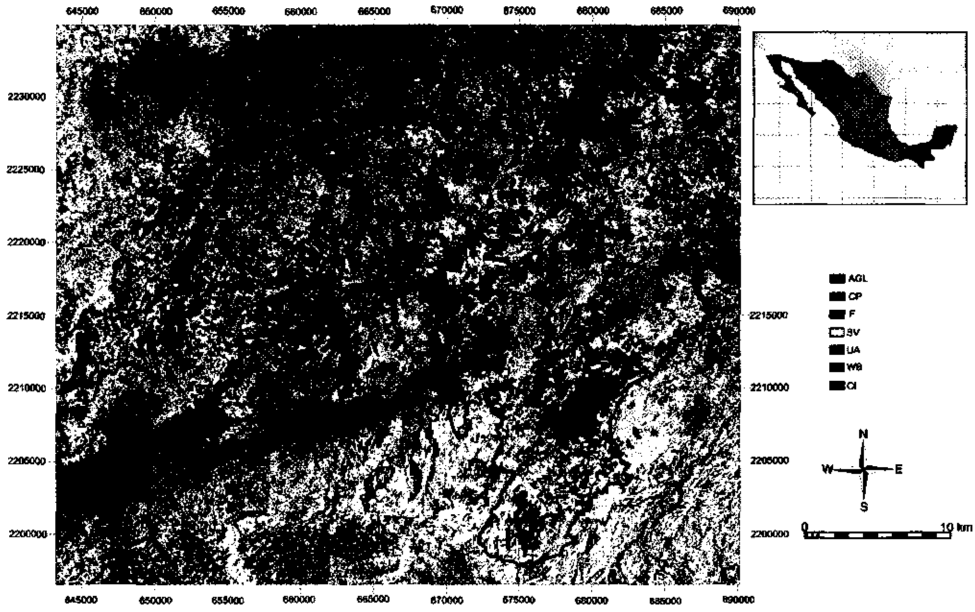

Figure 2. Location of the research area and land covers AGL = Agricultural lands, CP = Coffee plantations, F = Lower tropical evergreen forest, SV = Secondary vegetation, UA = Urban areas, WB = Water bodies, Cl = Clouds; the thick black line is the area of influence of the Cooperative Tosepan Titataniske where all the research samples occur. We performed a supervised classification using the maximum likelihood classifier method, including prior probabilities to generate the land cover map.

The studies described in this thesis were conducted within traditional shade coffee agroecosystem, and enclosed eight localities (i.e.; Acaxiloco, Yohualichan, Pinahuistan, Reyeshogpan, Limonco, Atalpan, Monte Alto and Tozan) situated in the municipalities of Cuetzalan del Progreso and Jonotla.

Coffee plantations in Mexico

There are five main coffee agricultural systems in Mexico, differentiated according to management level, vegetation composition and structural complexity (Fuentes-Flores 1979, Nolasco 1985) (Figure 3).

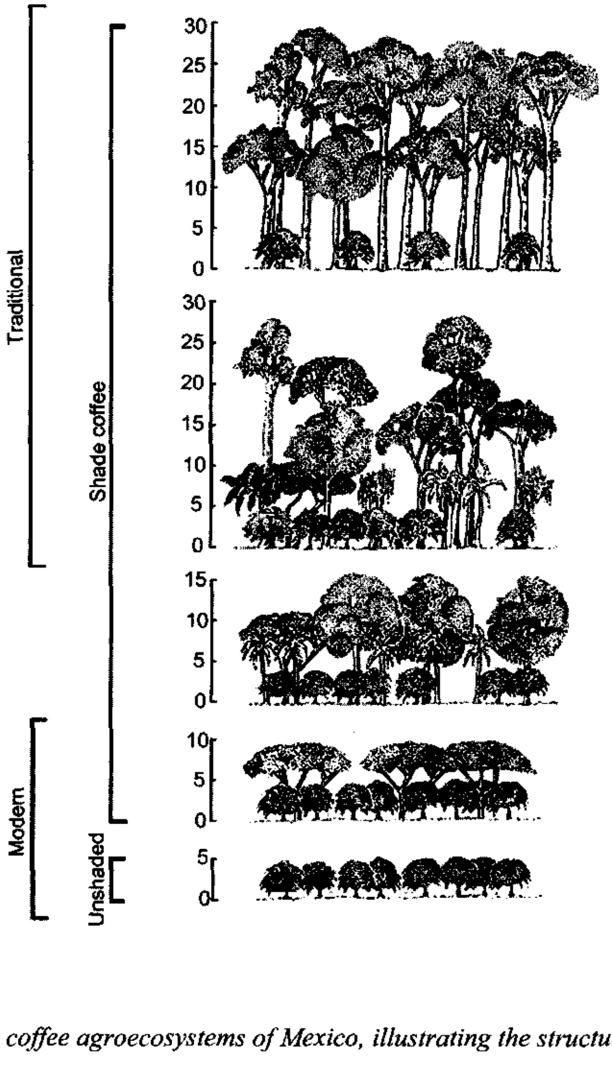

Figure 3. The five coffee agroecosystems of Mexico, illustrating the structural and floristic complexity of vegetation and height of canopy (source: Gobbi 2000).

Traditional rustic or "mountain". In this agro-ecosystem, the herbaceous stratum is removed from the original vegetation cover and replaced by coffee plants, while the shrub and arboreal strata remain. This type of agro-ecosystem has the lowest impact on the original vegetation cover and requires low labour-material inputs; however also produces generally low yields. In Mexico, this type of agro-ecosystem is located in relatively isolated areas managed by indigenous communities, which introduced coffee plants in their native forest (Moguel and Toledo 1999).

Traditional shade coffee plantations (polyculture). This agro-ecosystem, as in the traditional rustic, coffee plants are introduced below the canopy. However, certain original canopy species are removed, others maintained, or domesticated species introduced (e.g.; *Inga sp., Pimenta dioica, Cedrela odorata, Swietenia macrophylla*) as sources for shade, food, medicine or raw materials for market or local subsistence. While these species provide arboreal cover, coffee and other cash crops (citrus fruits, bananas, and other fruit trees), they grow in the shadow provided by the arboreal stratum.

This type of management increases the structural complexity of the vegetation and the species richness, as both wild and domesticated species co-exist. It has been estimated that this agro-ecosystem covers almost 50% of the Mexican coffee lands. Only low labour and material inputs (although some use agrochemicals), yet yields can be comparable to those of commercial "modern" systems (Moguel and Toledo 1999).

Commercial polycultures. There is a complete removal of the original canopy trees in this agricultural system. Introduced tree species shade the coffee shrubs. These shade trees provide some economic utility and/or add nitrogen to the soil. Some of the most common species are rubber trees (*Castilla elastica*), old spice (*Pimenta dioica*), cedar (*Cedrela odorata*), jiniquil (*Inga* spp.), and colorin (*Erythrina* spp.) (Moguel and Toledo 1999). Other cash crops are grown under the canopy such as citrus, banana or other fruit trees.

This system is market-oriented, has high labour and material inputs (agrochemicals are regularly used) and is characterised by a higher coffee yield. Species diversity is however considerably lower than in the traditional rustic or traditional polyculture systems (Moguel and Toledo 1999).

Shaded monoculture. This is a "modern" cultivation where leguminous trees (*Inga* spp) almost exclusively provide shade to coffee shrubs. The result is an almost a mono-species canopy. The use of agrochemical products is compulsory, and it is exclusively market-oriented (Moguel and Toledo 1999).

Unshaded monoculture. This agricultural system has no tree stratum and the coffee shrubs are exposed to direct sunlight. Its management has lost the agroforestry character present in the other systems mentioned before. This specialised plantation requires high labour and material inputs (e.g.; chemical fertilizers and pesticides). The highest yields are reported under this system (Moguel and Toledo 1999).

Economic importance of coffee plantations

Worldwide, one of the most traded commodities is coffee, producing important economic benefits for developing countries. The International Coffee Council (2001) estimated that over 125 million of people are dependent on coffee for their income. Only in northern Latin America 3.1 million hectares are coffee lands generating 34% of the worldwide production (Perfecto and Ambrecht 2002).

Coffee production in Mexico. Mexico is ranked worldwide as number eight in coffee volume production, after Brazil, Vietnam, Colombia, Indonesia, Peru, India, and Papua Guinea (Table1), and seventh in yield performance (ICO 2005). Coffee production, in Mexico, is situated in 12 states from which five are the major coffee producers (i.e.; Chiapas, Oaxaca, Veracruz, Puebla and Guerrero). Coffee lands cover approximately 806,000 hectares (based on statistics of November 2005, SAGARPA 2005) distributed among 250,000 small-scale producers from which 185,000 belong to indigenous groups from the states of Chiapas, Oaxaca, Puebla or Guerrero (Pérez-Grovas *et al.* 2001). In Mexico, coffee represents one of the most important agricultural sources of foreign exchange (18% of total export) generating annually 500,000 direct and 3,000,000 indirect jobs. In addition, Mexico is the world's largest producer of organic coffee, accounting for about 20% of the global market (Pérez-Grovas *et al.* 2001).

*Table 1. Coffee exported by the top ten coffee-producing countries, both Arabica and/or Robusta in percentage of thousand of bags of 60 kg. *Thousands of bags of 60 kg. A = Arabica and R = Robusta. Modified from ICO (2005).*

Country	Coffee type	Oct-2005	Nov2004-Oct2005	Oct-2004	Nov2003-Oct2004
Brazil	A/R	34.8	30.4	36.9	28.6
Vietnam	R	15.3	15.6	15.9	16.7
Colombia	A	12.2	12.3	12.8	11.3
Indonesia	R/A	7.4	6.8	6.5	5.9
Peru	A	7.3	3.2	6.9	3.1
India	A/R	3.2	3.1	2.6	4.2
Papua New Guinea	A/R	2.5	1.3	1.3	1.2
Mexico	A	2.1	2.1	1.4	2.7
Worldwide Total		6164390	88451808	6880365	89143636

Social background

The Regional Agricultural Cooperation "Tosepan Titataniske" is an indigenous organisation that groups 5,800 coffee farmers (i.e.; Nahuats and Totonacos) from the north eastern mountain range of Puebla, Mexico. The cooperation is engaged with the social and economic welfare of the coffee farmers and their families, and has a high interest in the conservation of their natural resources. Their membership is oriented to small producers, labourers, house landladies and craftsmen. The cooperative produce organic coffee, and there is a growing number of coffee plantations converting to organic production. Moreover, the implementation of a floristic diversification program (native trees and plants) on their coffee plantations is currently carried out by the coffee farmers to avoid erosion and nutrient enrichment, to provide suitable habitat for wildlife species and to supply with alternative agricultural products for self consumption and local and global markets

(Tosepan Titataniske 2005). The Tosepan Titataniske area of influence encloses a large area of out the study region. Therefore this research was jointly developed with the Tosepan Titataniske to provide ecological information of the avifauna present in their coffee lands, as well as guidelines for biodiversity conservation and ecotourism programmes.

The importance of management actions carried out by indigenous groups, especially small farmers, has been pointed out by the United Nations University (UNU). The UNU recommended studies to examine the relationships between population and environmental change, and stimulated the participation of small farmers in the conservation and sustainable use of natural resources, especially, biodiversity. Hence, there is a need to analyze, model, and assess the ecological implications of these coffee agroecosystems.

Ecological importance of coffee plantations: bird responses

Mexico comprises more than 12% of the worldwide biota and is placed among the seven biologically most diverse countries in the world (Ramamoorthy *et al.* 1993). The10% of its biodiversity is located in areas managed by peasants that in many cases belong to an indigenous group (Ramamoorthy *et al.* 1993, Challenger 1998). Coffee plantations represent one of the most important land covers among indigenous communities (Pérez-Grovas *et al.* 2001). Approximately 806,000 hectares are under coffee plantations, and it has been estimated that 60-70% of the coffee areas are managed under traditional shade plantations. Moreover, 9% of these coffee areas overlap (or are near) regions with high biological diversity and endemicity, which are regarded as crucial to biodiversity conservation in Mexico (Moguel and Toledo 1999) (Figure 4).

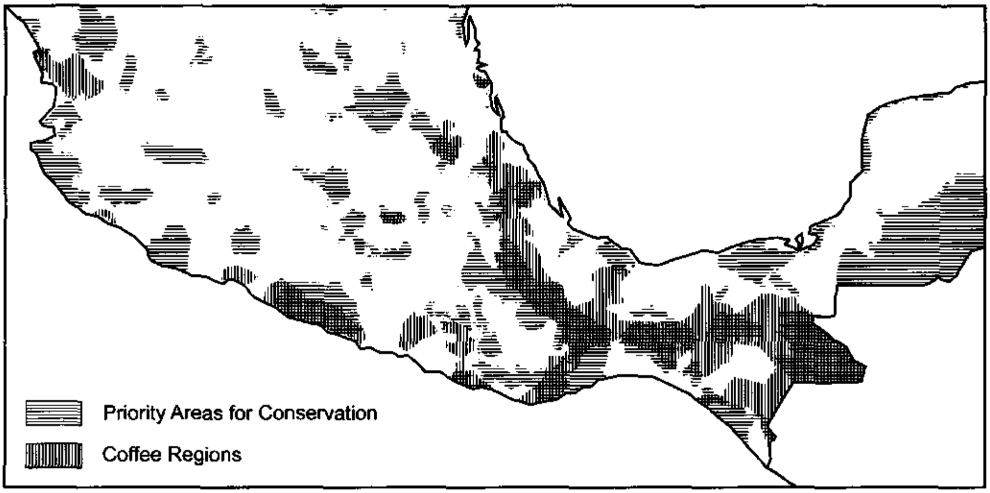

Figure 4. Priority areas for conservation in Mexico (based on CONABIO 2005) and coffee regions.

Shade coffee systems have been recognised in Latin America as important and potential areas for biodiversity conservation (Pimentel *et al.* 1992, Perfecto *et al.* 1996, Mehta and Leuschner 1997, Moguel and Toledo 1999, Gobbi 2000). Several studies have found that shade coffee plantations, especially the traditional rustic and the traditional polyculture, represent an important habitat for wildlife (Calvo and Blake 1998, Moguel 1996, Van der Voort and Greenberg 1999, Wunderle 1999). Studies of biological diversity in different types of coffee plantations have been conducted for diverse taxa, e.g.; arthropods (Torres 1984, Lopez-Mendez 1985, Moron 1985, Ibarra-Nunez 1990, Stork and Brendell 1990, Nestel *et al.*1993, Perfecto and Snelling 1995, Llorente-Bousquets *et al.* 1996, Perfecto *et al.* 1997, Estrada *et al.* 1998, Ibarra-Nunez and Garcia-Ballinas 1998, Mas 1999, Johnson 2000, Molina 2000, Sadeghian 2000, Perfecto *et al.* 2003, Pineda *et al.* 2005), mammals (Estrada *et al.*1993, 1994, Gallina *et al.* 1996, Estrada *et al.* 1998, Pineda *et al.* 2005), amphibians and reptiles (Rendon-Rojas 1994, Lenart *et al.* 1997, Pineda *et al.* 2005), macrofauna (Fragoso *et al.* 1993), and birds (Terborgh and Weske 1969, Aguilar-Ortiz 1982, Borrero 1986, Robbins *et al.* 1992, Wunderle and Wide1993, Vennini 1994, Thiollay 1995, Greenberg 1996, Perfecto *et al.* 1996, Wunderle and Latta 1994, 1996, Greenberg *et* *al.* 1997, Calvo and Blake 1998, Petit *et al.* 1999, Van der Voort and Greenberg 1999, Dietsch 2000, Johnson 2000, Tejeda-Cruz and Sutherland 2004). The general findings of the mentioned studies have shown that traditional shade coffee plantations hold high species richness for broad taxa compared to non-shade coffee plantations and other agricultural systems. In general, though the species composition differs from that of natural forests, many forest-dependent species or species that depend on dense high canopy are still found in traditional shade coffee plantations. Moreover, the species richness in these agroecosystems, in some cases, is nearly equal or even higher to the species richness of natural forests.

Avifauna

Avian studies in Latin America demonstrated a high species diversity and elevated bird densities in traditional shade coffee plantations, and found similar levels of bird species richness compared to natural forest (Aguilar-Ortiz 1982, Robbins *et al.* 1992, Wunderle and Wide 1993, Vennini 1994, Wunderle and Latta 1994, 1996, Greenberg *et al.* 1997, Van der Voort and Greenberg 1999, Dietsch 2000, Johnson 2000). Species composition in traditional shade coffee plantations may vary from natural forest, because forest-edge and second-growth species contribute significantly to the high diversity of birds in coffee plantations (Greenberg *et al.* 1997). It has been found in several studies that a large percentage of the birds in shade coffee plantations are omnivorous and partial nectarivorous (Wunderle and Latta 1996, Greenberg *et al.* 1997, Tejeda-Cruz and Sutherland 2004). Traditional shade coffee plantations have been recognised as an important habitat for migratory birds, which can be found even in higher densities than in natural forests (Borrero 1986, Greenberg *et al.* 1997). Moreover, most affected by habitat modifications are large frugivorous and insectivorous species of the canopy and low understory, or terrestrial interior forest specialists (Thiollay 1995). In addition, it has been suggested that traditional shade coffee plantations are an important refuge area for birds during the dry season when energetic demands are high and when food is scarce in other habitat types (Wunderle and Latta, 1994, Johnson, 2000). Wunderle and Latta (1998), Greenberg *et al.*

(1997) and Johnson (2000) stated that the tree canopy species in traditional shade coffee plantations could provide important food sources for nectarivorous and insectivorous birds.

The role of the avifauna in the ecosystem functioning of this agroecosystem (i.e.; traditional shade coffee plantation) had received significant attention (for a review see Perfecto and Armbrecht 2003). It has been suggested that the structural complexity and floristic diversity in traditional shade coffee plantations support a high density and diversity of predators, which are responsible for a reduced number of pests (arthropods) in plantations (Ibarra-Nunez 1990, Perfecto and Castineiras 1998). Many bird species registered in shade coffee plantations are either insectivorous or omnivorous, with arthropods as the majority of their diet. Additionally, experimental enclosure studies have demonstrated that birds often remove a great portion of the arthropod populations, in particular large herbivorous arthropods (Holmes *et al.* 1979, Gradwohl and Greenberg 1982, Moore and Yong 1991, Bock *et al.* 1992, Marquis and Whelan 1994, Perfecto *et al.* 2004), suggesting that the effect of birds is quite equally distributed across the ecological and taxonomic arthropod groups (Greenberg *et al.* 2000). Based on the latter information, Perfecto and Armbrecht (2003) suggested that diversely shaded coffee plantations could be more resistant to pest outbreaks than unshaded monocultures because of the higher diversity and density of insectivorous birds in these plantations.

Outline of this thesis

Chapter 2 examines methodological aspects of avifauna diversity assessments and evaluates the relative biases, costs and efficiency of field monitoring techniques for avifauna. Chapter 3 examines the influence of habitat loss and landscape fragmentation on the species richness of resident birds. The analysis focuses on the unimodal and linear response of species richness to habitat loss and fragmentation, respectively. Chapter 4 investigates the relative influence of body mass on the strength of interspecific competition between birds from similar food guild. Chapter 5 of this study deals with how bird species-environmental relationships operate at multiple spatial scales. The relative importance of each scale and the confounding effects between the scales on bird species richness and bird abundance was analysed. Chapter 6 gives an overview of studies in which remote sensing was used to assess faunal biological diversity, considering the current state of the art with regard to the development of proxies and methodologies for estimating the diversity in animals, and explores its challenges for contributing to conservation and sustainable use of biodiversity. In Chapter 7 finally, I synthesise the findings of these studies, and illustrate the conservation and management implications for Neotropical birds in shade coffee plantations.

References

Aguilar-Ortiz, F. 1982. Estudio ecológico de las aves del cafetal, in Estudios Ecológicos en el Agroecosistema Cafetalero, Jiménez-Ávila, E and Gómez-Pompa, A. (eds.) INIREB, Xalapa, Veracruz, México.

Bélisle, M., Desrochers, A. and Fortin, M.J. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. Ecology 82: 1893-1904.

Bender, D.J., Tischendorf, L. and Fahrig, L.1998. Evaluation of patch isolation metrics for predicting animal movement in binary landscapes. Landscape Ecology 15: 131-143.

Bock, C.E., Bock, J.H., and. Grant, M.C. 1992. Effects of bird predation on grasshopper densities in Arizona grasslands. Ecology, 73: 1706-1717.

Borrero, H. 1986. La substitución de cafetales de sombrío por caturrales y su efecto negativo sobre la fauna de vertebrados. Caldasia 15: 725-7326.

Borcard, D., Legendere, P., Avois-Jacquet C., Tuomisto, H. 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology 85(7):1826-1832.

Bowers, M.A. and Brown, J.H. 1982. Body size and coexistence in desert rodents: chance or community structure? Ecology 63(2): 391-400.

Brown, J.H. and Maurer, B.A. 1986. Body size, ecological dominance and Cope's rule. Nature 324: 248-250.

Calvo, L. and Blake, J. 1998. Bird diversity and abundance on two different shade coffee plantations in Guatemala. Birds Conservation International 8: 297–308.

Challenger, A. 1998. Utilización y conservación de los ecosistemas terrestres en México. Pasado, presente y futuro. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. Universidad Nacional Autónoma de México, Agrupación Sierra Madre, S.C., México, D.F.

Dietsch, T.V. 2000. Assessing the conservation value of shade-grown coffee: a biological perspective using Neotropical birds. Endangered Species Update 1750-72 [Electronic version]. Retrieved January 2, 2006, from http://www.umich.edu/-esupdatel

Estrada, A. 1994. Non-flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas. Ecography 17: 229-241.

Estrada, A., Coates-Estrada, R. and Memt, D. 1993. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats in Los Tuxtlas, Mexico. Ecography, 16: 309-318.

Estrada, A., Coates-Estrada, R., Dadda, A.A., Cammarano, P.1998. Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxlas, Mexico. Journal of Tropical Ecology 14: 577-593.

Fahrig, L. and Merriam, G. 1994. Conservation of fragmented populations. Conservation Biology 8: 50-59.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. Journal of Wildlife Management 61: 603-610.

Fahrig, L. 2001. How much habitat is enough? Biological Conservation. 100: 65-74.

French, A.R. and Smith, T.B. 2005. Importance of body size in determining dominance hierarchies among diverse tropical frugivores. Biotropica 37(1): 96-101.

Fragoso, C., Brown, G.G., Patron, J.C., Blanchart, E., Lavelle, P., Pashanasi, B., Senapati, B. and Kumar, T. 1997. Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of earthworms. Applied Soil Ecology 6: 17–35.

Fuentes-Flores, R. 1979. Coffee production systems in Mexico. In: De las Salas, F. (ed.) Workshop on agroforestry systems in Latin America. Centro Agronomico Tropical de Investigación y Enseñanza, Turrialba, Costa Rica.

Gradwohl, J. and Greenberg, R. 1982. The effect of a single species of avian predator on the arthropods of aerial leaf litter. Ecology, 63: 581-583.

Gallina, S.E., Mandujano, S. and González-Romero, A. 1996. Conservation of mammalian biodiversity in coffee plantations of Central Veracruz, Mexico. Agroforestry Systems 33: 13-27.

Gobbi, J.A. 2000. Is biodiversity-friendly coffee financially viable? An analysis of five different coffee production systems in western El Salvador. Ecological Economics 33: 267-281.

Gotelli, N.J. and Ellison, A.M. 2002. Assembly rules for New England ant assemblages. Oikos 99: 591-599.

Greenberg, R. 1996. Bird populations in forest patches in Southern Mexico. In: Schelhas, J. and Greenberg, R. (eds.). Forest Patches in Tropical Landscapes. Island Press, Washington, DC.

Greenberg, R., Bichier P. and Sterling J. 1997. Bird populations in rustic and planted shade coffee plantations of Eastern Chiapas, México. Biotropica 29: 501–514.

Greenberg, R., Bichier, P. and CruzAngon, A. 2000. The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations. Ecology 81: 1750-1755.

Holmes, R.T., Schultz, J.C. and Nothnagle, P. 1979. Bird predation on forest insects: an exclosure experiment. Science 206: 462463.

Holt, R. D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. In: Ricklefs, R. E. and Schluter, D. (eds.). Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, N.J.

Ibarra- Núñez, G. 1990. Los artropodos asociados a cafetos en un cafetal mixto del Soconusco, Chiapas, México, Variedad y abundancia. Folia Entomologica Mexicana 79: 207-231.

Ibarra-Núñez G. and García-Ballinas J.A. 1998. Diversidad de tres familias de arañas tejedoras (Araneae: Araneidae, Tetragnathidae, Theridiiae) en cafetales del soconusco, Chiapas, México. Folia Entomologica Mexicana 102: 11–20.

International Coffee Organization. 2005. Exports by exporting countries to all destinations [Electronic version]. Retrieved January 2, 2006, from http://www.ico.org/prices/m1.htm

Johnson, M.D. 2000. Effects of shade-tree species and crop structure on the winter arthropod and bird communities in a Jamaican shade coffee plantation. Biotropica 32: 133–145.

Kneitel, J.M. and Chase, J.M. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecological Letters 7: 69-80.

Komonen, A., Penttilae, R., Lindgren, M. and Hanski, I. 2000. Forest fragmentation truncates a food chain base don an old-growth forest bracket fungus. Oikos 90: 119-126.

Kremsater, L., and Bunnell, F. L. 1999. Edge effects: theory, evidence and implications to management of western North American forests. In: Rochelle, J. A., Lehmann, L. A. and Wisniewski, J. (eds.) Forest fragmentation: wildlife and management implications. Brill, Boston, Massachusetts, USA.

Kurki, S., Nikula, A., Helle, P. and Linden, H. 2000. Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. Ecology 81: 1985–1997.

Lenart, L.A., Powell, R., Parmerlee, J.S. Jr., Lathrop, A. and Smith, D.D. 1997. Anoline diversity in three differently altered habitats in the Sierra de Barouco, Republica Dominicana. Hispaniola Biotropica 29: 117-123.

Leyequien, E., Verrelst, J., Slot, M., Schaepman-Strub, G., Heitkönig, I.M.A. and Skidmore, A. (*accepted in JAG*). Capturing the fugitive: applying remote sensing to terrestrial animal distribution and diversity. A review.

Liang, L., Stocking, M., Brookfield, H. and Jansky, L. 2001. Biodiversity conservation through agrodiversity. Global Environmental Change. 11: 97-101.

Llorente-Bousquets, J.A., Martinez, I., Vargas-Fernandez, I. and Soberon-Mainero, J. 1996. Papilionoidea (Lepidoptera). In: Lorente-Bousquets, J., García-Aldrete, A. and Gonzalez-Soriano, E. (eds.). Biodiversidad, taxonomia y biogeografía de artrópodos en México, México, D.F.

López-Méndez, J.A. 1989. La Actividad y la Depredación de Artrópodos Asociados al Cultivo del Café-Cacao por dos Hormigas Ponerinas (Hymenoptera: Formicidae) en el municipio de Tuxtla Chico, Chiapas, B.Sc. thesis, Universidad Autónoma de Chiapas, México.

Loreau, M. 2000. Are communities saturated? On the relationship between α, β and γ diversity. Ecological Letters 3: 73-76.

McGarigal, K. and McComb,W.C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecological Monographs 65: 235–260.

Marquis, R.J. and Whelan, J.C. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology, 75: 2007-2014.

Mas, A.H. 1999. Butterfly diversity and the certification of shade coffee in Chiapas, Mexico, M.Sc. Thesis, University of Michigan, Ann Arbor, Michigan.

Mehta, N.G. and Leuschner, W.A. 1997. Financial and economic analyses of agroforestry systems and a commercial timber plantation in the La Amistad Biosphere Reserve, Costa Rica. Agroforestry Systems 37: 175-185.

Moguel, P. 1996. Biodiversidad y cultivos agroindustriales: el caso del café. Technical report. Instituto de Ecología, Universidad Nacional Autónoma de México, México, D.F.

Moguer, P. and Toledo, V.M. 1998. Biodiversity conservation in traditional coffee systems of Mexico. Conservation Biology13(1): 11-21.

Molina, J. 2000. Diversidad de escarabajos coprófagos (Scarabaeidae: Scarabaeinae) en matrices de la zona cafetera (Quindio-Colombia), in Memorias Foro Internacional Café y Biodiversidad, Federación Nacional de Cafeteros de Colombia (ed.), Chinchinil, Colombia.

Moore, F.R. and Yong, W. 1991. Evidence of food-based competition among passerine migrants during stopover. Behavioral Ecology and Sociobiology 28: 85-90.

Morón, M.A. and López-Méndez, J.A. 1985. Análisis de la entomofauna necrofila de un cafetal en el Soconusco, Chiapas, México. Folia Entomologica Mexicana 63: 47-59.

Mouquet, N. and Loreau, M. 2002. Coexistence in metacommunities: the regional similarity hypothesis. American Naturalist 159: 420-426.

Mouquet, N., Munguia, P., Kneitel, J.M. and Miller T.E. 2003. Community assembly time and the relationship between local and regional species richness. Oikos 103: 618-626.

Nestel, D., Dickschen, F. and Altieri, M.A. 1993. Diversity patterns of soil macro-coleopterans in Mexican shaded and unshaded coffee agroecosystems: an indication of habitat perturbation. Biodiversity and Conservation 2: 7-78.

Nolasco, M. 1985. Café y Sociedad en México, Centro de ecodesarro, Mexico City. In: Oxfam, 2002. Bitter Coffee: How the Poor are Paying for the Slump in Coffee Prices.

Pérez-Grovas, V., Trejo, C. and Burstein, J. 2001. Case Study of the Coffee Sector in Mexico (Research Paper for Oxfam Coffee Report "Mugged").

Perfecto, I. and Castineiras, A. 1998. Deployment of the predaceous ants and their conservation in agroecosystems. In: Barbosa, P. (ed.) 1998. Conservation Biological Control. Academic Press, Washington, D.C.

Perfecto I. and Snelling R. 1995. Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. Ecological Applications 5: 1084–1097.

Perfecto, I., Rice, R.A., Greenberg, R. and Van der Voort, M.E. 1996. Shade coffee: a disappearing refuge for biodiversity. BioScience 46: 598–608.

Perfecto, I., Vandermeer, J.H., Hanson, P. and Cartín, V. 1997. Arthropod biodiversity loss and the transformation of a tropical agro-ecosystem. Biodiversity and Conservation 6: 935–945.

Perfecto, I. and Ambrecht, I. 2002. The coffee agroecosystems in the Neotropics: Combining ecological and economic goals. In: Vandermeer, J.H. (ed.). Tropical agroecosystems. CRC Press, New York.

Perfecto, I., Mas, A., Diestch, T. and Vandermeer, J. 2003. Conservation of biodiversity in coffee agroecosystems: a tri taxa comparison in southern Mexico. Biodiversity and Conservation 12: 1239-1252.

Perfecto, I., Vandermeer, J.H., Lopez-Bautista, G., Ibarra-Nunez, G., Greenberg, R., Bichier, P. and Langridge, S. 2004. Greater predation in shaded coffee faros: the role of resident Neotropical birds. Ecology 85(10): 2677-2681.

Petit, L.J., Petit, D.R., Christian, D.G. and Powell, H.D.W. 1999. Bird communities of natural and modified habitats in panama. Ecography 22: 292-304.

Pimentel, D., Stachow, U., Takacs, D.A. and Brubaker, H.W. 1992. Conserving biological diversity in agricultural/forestry systems. Bioscience 42: 354-362.

Pineda, E., Moreno, C., Escobar, F. and Halffte, G. 2005. Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz, Mexico. Conservation Biology 19: 400-410.

Ramamoorthy, T.P., Bye, R., Lot, A. and Fa, J. (ed.). 1993. Biological biodiversity of Mexico: Origins and distribution. Oxford University Press, New York.

Rendón-Rojas, M.G. 1994. Estudio de la Herpetofauna de la Zona Cafetalera de Santiago Jalahui, Oaxaca, B.Sc. thesis, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico, Nacional, Mexico City.

Rice, R. and Ward, J. 1996. Coffee, Conservation and Commerce in the Western Hemisphere: How Individuals and Institutions Can Promote Ecologically Sound Farming and Forest Management in Northern Latin America, Smithsonian Migratory Bird Center and Natural Resources Defense Council, Washington, D.C.

Robbins, C.S. Dowell, B. A., Dawson, D. K., Colon, J. A., Estrada, R., Sutton, A., Sutton, R. and Weyer, D. 1992. Comparison of Neotropical migrant landbird populations wintering in tropical forests, isolated forest fragments, and agricultural habitats. In: Ecology and Conservation of Neotropical Migrant Landbirds, Hagan, J.M. and Johnson, D.W., Eds., Smithsonian Institution Press, Washington, D.C.

Rosenzweig, M.L.1999. Species diversity. In: McGlade, J. (ed.). Advanced theoretical ecology: principles and applications. Blackwell Science, Oxford, UK.

Rosenzweig, M.L. 2001. Loss of speciation rate will impoverish future diversity. PNAS 98: 5404-5410.

Rosenzweig, M.L. 2005. Avoiding mass extinction: Basic and applied challenges. 24th Annual Midwest Ecology and evolution Conference. Dept. of ecology and Evolutionary Biology, University of Arizona, Tucson.

Sadeghian, S. 2000. Diversidad de mesoorganismos del suelo en la zona cafetera, paper presented in Memorias Foro Internacional Café y Biodiversidad, Federación Nacional de Cafeteros de Colombia, Ed., Chinchinil, Colombia.

SAGARPA. 2005. Avance de siembras y cosechas perennes 2005. [Electronic version]. Retrieved January 2, 2006, from http://www.siap.sagarpa.gob.mx/ar_comagr2c.html

Stephens, S.E., Koons, D.N., Rotella, J.J. and Willey, D.W. 2003. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biological Conservation 115: 101-110.

Stork, N.E. and Brendell, M.J.D. 1990. Variation in the insect fauna of Sulawesi trees with season, altitude and forest type. In: Knight, W.J. and Holloway, J.D. (eds.). Insects and the Rain Forests of South East Asia (Wallacea). Royal Entomological Society, London, UK.

Taylor, P.D. and Merrian, G. 1995. Habitat fragmentation and parasitism of a forest damselfly. Landscape Ecology 11: 181-189.

Tejeda-Cruz, C. and Sutherland, W.J. 2004. Bird responses to shade coffee production. Animal Conservation 7: 169-179.

Terborgh, J. and Weske, J.S. 1969. Colonization of secondary habitats by Peruvian birds. Ecology 50: 765-782.

Thiollay, J.M. 1995. The role of traditional agroforests in the conservation of rain forest bird diversity in Sumatra. Coservation Biology 9: 335-353.

Toledo, V.M. 2005. Repensar la conservación: ¿áreas naturales protegidas o estrategia bioregional? Gaceta Ecológica 77: 67-82.

Torres, J.A. 1984. Diversity and distribution of ant communities in Puerto Rico. Biotropica 16: 296-303.

Tosepan Titataniske. 2005. Agricultura sustentable. [Electronic version]. Retrieved January 2, 2006, from http://www.tosepan.com/index.htm

Trzcinski, K.K., Fahrig, L. and Merriam, G. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecological Applications 9: 586-151.

Van de Voort, M. and Greenberg, R. 1999. Por qué a las aves migratorias les fascina el café? El Jarocho Verde 11: 52-54.

Vennini, J.P. 1994. Neartic avian migrants in coffee plantations and forest fragments of southwestern Guatemala, Birds Conservation International 4: 209-232.

Villard, M.A., Merriam, G. and Maurer, B.A. 1995. Dynamics in subdivided populations of Neotropical migratory birds in a temperate fragmented forest. Ecology 76: 27-40.

Wiegand, T., Revilla, E. and Moloney, K.A. 2005. Effects of habitat loss and fragmentation on population dynamics. Conserv. Biol.19(1): 108-121.

Wilson, D.S. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology 73: 1984-2000.

Winker, K. 1998. Recent geographic trends in Neotropical avian research. Condor 100(4): 764-768.

With, K. A. and Crist, T.O. 1995. Critical thresholds in species' response to landscape structure. Ecology 76: 2446–2459.

With, K.A. and King, A.W. 1999. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. Landscape Ecology 14: 73-82.

Wunderle J. 1999. Avian distribution in Dominican shade coffee plantations: area and habitat relationships. Journal of Field Ornithology 70: 58–70.

Wunderle, J. and Latta, S. 1994. Overwinter turnover of Neartic migrants wintering in small coffee plantations in Dominican Republic, Journal of Ornithology 13: 54-77.

Wunderle, J. and Latta, S. 1996. Avian abundance in sun and shade coffee plantations and remnant pine forest in the Cordillera Central, Dominican Republic. Ornitologia Neotropical 7: 19–34.

Wunderle, J. M. and Latta, S. C. 1998. Avian resource use in Dominican shade coffee plantations. Wilson Bulletin 110: 271–281.

Wunderle, J. and Wide, R.B. 1993. Distribution of overwintering Neartic migrants in the Bahamas and Greater Antilles. Condor 95: 904-933.

Chapter 2

Monitoring Neotropical birds

Efficiency of a modified double-observer point counts approach versus mist-netting

Eurídice Leyequién, Willem F. de Boer, Garry Bakker, Reinoud Vermoolen, Samuel López de Aquino

Abstract

Monitoring bird community trends is central in conservation biology, providing information of species diversity and their status. However, the use of different sampling techniques for collecting information may result in disparities in assessing species richness. Point counts and mist netting are frequently used for assessing bird species richness. Point counts and mist netting have been compared in previous studies; however the emphasis has been on breeding or wintering grounds whereas little on migration. Bird monitoring during migration could produce valuable information about long-term community changes. Assessing relative biases, costs and efficiency of both techniques would enable the optimisation in the design of large-scale monitoring. Moreover, Neotropical avifauna with a high diversity is worldwide recognised as threatened by habitat loss and fragmentation. In our study we compare the efficiency, limitations, and biases of a modified double-observer point count approach versus mist netting in estimating species richness and detecting understory and migrant species. We evaluated cost-efficiency aspects to optimise sampling protocols. We found that the point count technique was the most effective in total species richness completeness and presented lower total effort in comparison to mist netting. Point counts outperformed mist netting in the detection of new bird species, even after a large sampling effort. Mist netting significantly detected a higher proportion of understory species in comparison to point counts, though we found opposite results for migrant species. Finally, the cost-efficiency analysis showed that the modified double-observer point counts required less total effort thus decreasing total monetary costs compared to mist netting.

Introduction

Monitoring community trends is central in conservation biology, aimed at providing reliable information of species diversity and their status, for fast and efficient identification of conservation priorities. Quantifying the species richness of bird communities has a crucial role in ecological research (Huston 1994, Rosenzweig 1995), conservation planning (Bibby *et al.* 1992, Stotz *et al.* 1996), and environmental impact assessments (e.g.; Fjeldså 1999). Species lists are a basis for conservation efforts to identify areas with high species richness or high level of endemism (Peterson *et al.* 1998, Myers *et al.* 2000, Rojas-Soto *et al.* 2002). However, the use of different techniques to obtain this information may result in considerable disparities in assessing species richness (Thomas 1996, Poulin *et al.* 2000, Godoy-Bergallo *et al.* 2003), and therefore may result in strong biases in describing local and regional species patterns. Moreover, the economic costs associated with the different sampling techniques for assessing species richness represent an important factor influencing the final assessment.

Neotropical avifauna comprises a high diversity and is worldwide recognised as threatened by habitat loss and fragmentation due to human activities (Winker 1998). Despite the enormous effort of ornithologists and natural resource managers in counting terrestrial birds, knowledge about Neotropical birds is scanty compared for example with Neartic birds, which is in itself a major concern if long-term conservation goals are to be accomplished. However, this data is crucial in order to quantify species' distribution, bird-habitat relationships, or population and community trends. Point counts and mist net techniques are some of the most frequently used for assessing bird species richness. However, both techniques have inherent biases for bird detection (e.g.; neglecting secretive species, those with infrequent vocalisations, such as understory or high canopy species) (Bibby *et al.* 1992) which complicate a reliable comparison between e.g.; local and regional scale. Despite a number of studies comparing point counts and mist netting techniques, most of the emphasis has been centred on breeding or wintering grounds (Rappole *et al.* 1998, Ralph and Fancy 1995) whereas little attention was paid during migration (Wang and

Finch 2002). Bird monitoring during migration could produce invaluable information about the long-term community changes of resident and migratory Neotropical birds, improving effective conservation-oriented research and management. In addition, a cost-benefit analysis for the implementing of these techniques can assist in providing guidelines for cost effective monitoring and research. In this paper we compare the efficiency, limitations, and biases of a modified double-observer point count approach versus mist netting in estimating species richness during the period of migration. We also evaluated some economic aspects of either using one technique or a combination of both. These analyses allow us to optimise sampling protocols for monitoring Neotropical bird communities and estimate species richness. Even though our analyses were mainly exploratory, we made a number of *a priori* predictions based upon earlier findings: (1) point counts yields higher total species richness at lower sampling effort; (2) detectability of understory and migrant species is higher using mist nets.

Materials and Methods

Study area

The avian communities were sampled in the North Eastern mountain range of Puebla, within the Cuetzalan region, Mexico, which covers an area of ~ 151,368 ha. The North Eastern mountain ranges of Puebla is situated on the east migratory paths of Neartic-Neotropical birds that winter or refuel in this region. The region is predominantly a traditional shade coffee agro-ecological zone, which covers an altitudinal range between 300 to 1200 m. The major agricultural system is traditional polyculture (traditional shade coffee plantation), while other land covers, such as seasonal crops (i.e.; maize and beans) and grazing lands are also present in the area. Forested areas are typically remnants of tropical evergreen forest with low montane rain forest in the higher areas (between 7000 and 2500 m) and lowland rain forest in the lower areas (200-700 m). The mean annual rainfall is 3,500 mm without a defined dry season; and the mean annual temperature is 22-26°C.

Bird survey

We performed a bird survey during the migratory season from September to November 2003 (Leyequien *et al. submitted*). The period comprised sequential rounds, visiting six different locations within the overall area, which were selected using a stratified sampling technique, that minimised heterogeneity among plots (~ 1 ha). All bird surveys were conducted within traditional coffee plantations. Because all birds were sampled in a single habitat type (traditional coffee plantations), variation in species composition among different plots is assumed to represent natural fluctuations and is not created by habitat differences.

Point counts. We used a modified double-observer approach (Nichols *et al.* 2000), i.e.; at each single point count two observers were registering all visual and acoustic detections, each covering a range of 180° (a total of 360°) with a fixed-radius of 25 m. in a ten minute period for each single count (Dawson *et al.* 1997, Vielliard 2000). Communication between observers was performed to avoid double record, and individual field notes were recorded. In addition, to avoid counting bias in the sampling, the order of the point counts was alternated in every visit. A distance of 100 m between point counts was used to avoid dependency between points' data. A number of 10-12 point counts were carried out in each location per day. The total effective sampling effort per plot per day was ~12 hours.

Mist net. We used five 12-m mist nets (2.5 X 12 m) with 30 mm mesh in each plot. As a standard, five mist nets (60 m) were used at each location. Nets were open from approximately sunrise till noon. The nets within a plot were placed using a random setting. The total effective sampling effort per plot was 170.5 hours.

Statistical analysis

Species accumulation curves and S_{max}. The species accumulation curves for point counts and mist nets were calculated using a predictive approach by taking the number of survey days as sampling effort. To eliminate the influence of the order in which days were added to the total, the sample order was randomised 1000 times using EstimateS software (Colwell 2004). This produces smoothed accumulation curves by repeated random reordering of the samples (Longino and Colwell 1997). Thereafter, these accumulation curves were used to fit predicted curves derived from the species collection of each method. The Pearsons correlation squared between the fitted curve and species accumulation curve was calculated. The values of the fitted curve were used to predict the S_{max} for each method, using an exponential function, with halt after 100 tries with < 0.0001.

Total species richness. In order to evaluate both sampling methods we established an estimate of actual richness of bird species occurring in the overall area, which could provide a standard for comparison of the two sampling methods (as recommended by Verner 1985, Watson 2004). We used predictive equations to estimate the total richness of the overall area, i.e.; the theoretical value for the maximum number of species that exist (S_{max}), based on a finite number of samples (Colwell and Coddington 1994, Herzog *et al.* 2002). The S_{max} was calculated using an exponential function with halt after 100 tries with < 0.0001; the total number of species recorded for the area (i.e.; the species collection derived from both methods) was used for further comparison.

Species richness percentage of completeness. The performance of the methods was estimated by dividing the species richness estimates (S_{max} derived from the two methods) by the total richness (S_{max}) of the overall area, resulting in percentages of completeness and associated coefficients of variation.

Predicted effort and sampling optimisation. We determined the effort (i.e.; number of sample days) required to obtain the total predicted species richness (S_{max}) using the software Effort Predictor V1.0 (Colwell 2004). In addition, in order to find an optimisation of the bird sampling, we calculated the added value of the sampling techniques. We compared the added value of mist netting days versus point counts days, calculating the effect of swapping a certain number of point counts sampling days against the same number of mist net samples, by calculating total species richness from 100 random combinations for each extra mist net sample.

Understory and migrant species. The proportion of understory species (including migrants and residents) and migrants detected by each technique were calculated. Shared and unique understory and migrant species for both techniques were derived. To test if there was a significant difference of percentage (arcsine transformed) of understory species between point counts and mist netting an analysis of variance (ANOVA) was performed. The same procedure was carried out for the migrant species.

Cost-efficiency analysis. The costs of the monitoring schemes were calculated using indicative recurrent monitoring costs, i.e.; USD/total sampling effort to detect 90% of the total species richness. Costs by day are based on locally-based monitoring by professional staff for the year 2003. Other day-costs such as field material and transportation were included in the analyses. In addition, the predicted effort to obtain the total species richness (S_{max}) was included in the comparison.

The benefits of using each technique were based on the total number of species, the number of unique species, proportion of understory species, number of unique understory species, proportion of migrant species, and number of unique migrant species that were detected by each technique.

Results

The total species richness (S_{max}) estimated for the area is 136.7 (k: 0.08, Pearsons Correlation squared: 0.982), while the estimated species richness (S_{max}) for the point count was 108.1 (k: 0.09, Pearsons Correlation squared: 0.994) and for the mist net was 70.1 (k: 0.03, Pearsons Correlation squared: 0.987) (Table 1).

Table 1. Cost-efficiency analysis of monitoring schemes: (a) point counts, (b) mist nets.

Monitoring scheme	Point counts	Mist nets
Number of sampling days	23	23
Number of detected birds	2555	354
Predicted species richness (S_{max})	108.1	70.1
Recorded species richness	115	79
Indicative recurrent costs of monitoring (USD/day to detect 90% of S_{max})	1207	3297
Sampling effort in days (detecting 90% of S_{max})	26	71
Unique species	59	23
Understory species (%) including double counting (*N*=30)	63	90
Unique understory species	3	11
Migrant species (%) including double counting (*N*=51)	75	61
Unique migrant species	20	13

Species richness percentage of completeness. The comparison of the different methods using the percentage of completeness showed that the point count technique yielded the most complete species richness estimates with the highest consistency (83%, V = 3.3, n = 23), whereas the mist net technique had a lower completeness (53%, V = 4.2, n = 23).

Predicted effort and sampling optimisation. We found that for point counts, the sampling effort required to detect 90% of the total species richness required 26 sample days, whereas mist netting required 71 sample days (Figure 1).

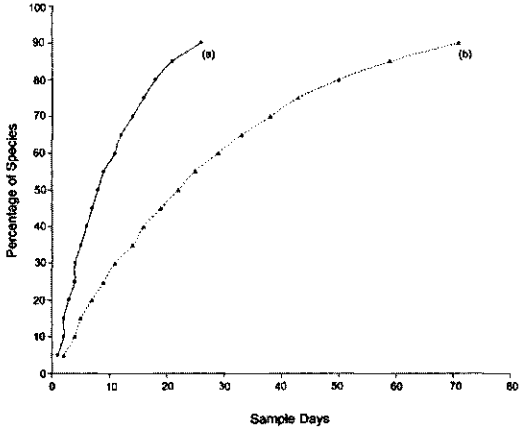

Figure 1. Predicted sampling effort for detecting 90% of the calculated total species richness (S_{max} 130.7) for (a) point count and (b) mist net techniques.

In addition, mist nets samples did not show a significant added value compared to point counts when point counts were swapped by mist nets (Figure 2). The analysis of variance showed that the percentage of understory species in the two survey techniques was significantly different ($F_{1,44} = 19, P < 0.001$) (Figure 3). The number of understory species detected by the point counts was 19 (63 %), whereas 27 (90%) understory species were detected using mist netting. From the 19 understory species recorded by the point counts only 3 were unique to this technique, whereas from the 27 understory species detected by mist nets, 11 were unique.

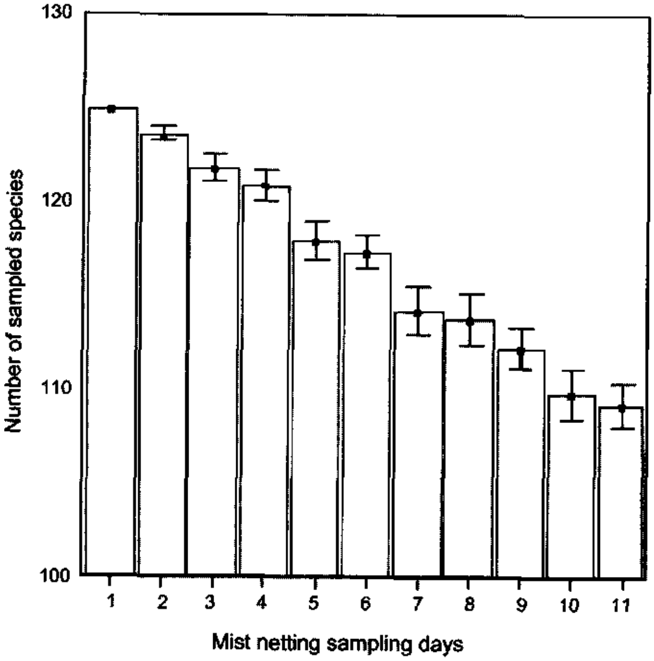

Figure 2. Added value, i.e. number of detected species, of mist net sampling days when substituting a certain number of point counts sampling days by mist net samples (e.g. 1-10 mist net sampling days as shown in the bar chart). Error bars show 95.0% CI of Mean. Understory and migrant species.

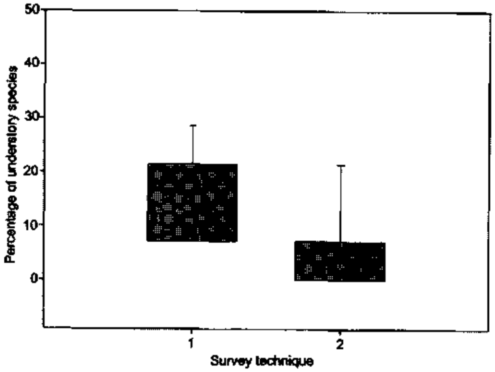

Figure 3. Significant differences in the mean number of understory species for the two survey techniques. 1 = Point counts, 2 = Mist netting.

Moreover, for migrant species, the analysis demonstrated that the percentage of migrants was significantly different between the two survey techniques ($F_{1,44} = 33$, $P < 0.001$) (Figure 4). The number of migrant species detected by the point counts was 38 (75 %), whereas 31 (61%) migrant species by mist netting. From the 38 migrant species recorded by the point counts 20 were unique to this technique, whereas from the 31 migrant species detected by mist nets, only 13 were unique.

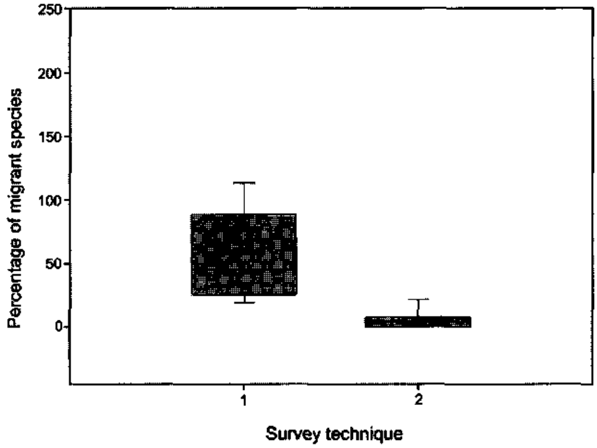

Figure 4. Significant differences in the mean number of migrant species for the two survey techniques. 1 = Point counts, 2 = Mist netting.

Cost-efficiency analysis. The cost for detecting 90% of the total species richness was 1207 USD/total sampling effort using point counts, whereas with the use of mist netting the total costs for the same percentage would increase to 3297 USD/total sampling effort. Mist netting required an additional effort of 45 sampling days than the point counts, with an additional cost of 2090 USD/total sampling effort.

We found that 59 species were detected only by the point counts, whereas 23 species were reported only from mist netting, both methods shared 56 species. Point count sampling detected a higher number of unique species, while detecting a lower proportion of understory species and unique number of understory species in comparison to mist netting. In addition, point counts sampling detected a higher proportion of migrant species and number of unique species of migrants (Table 2).

Table 2. Total number of species detected by point counts and mistnetting. Understory and migrant species.

Order	Family	Species	Understory[1]	Status	PC	MN
Ciconiiformes	Ardeidae	*Bubulcus ibis*	0	0	X	
	Cathartidae	*Cathartes aura*	0	0	X	
Falconiformes	Accipitridae	*Accipiter striatus*	0	1	X	
		Buteo platypterus	0	1	X	
	Columbidae	*Columba flavirostris*	0	0	X	
		Columbina inca	1	0	X	
		Columbina talpacoti	0	0	X	
		Leptotila verreauxi	1	0	X	
		Zenaida asiatica	0	0	X	
Psittaciformes	Psittacidae	*Amazona autumnalis*	0	0	X	
		Pionus senilis	0	0	X	
Cuculiformes	Cuculidae	*Crotophaga sulcirostris*	0	0	X	X
		Piaya cayana	0	0	X	
Strigiformes	Strigidae	*Glaucidium brasilianum*	0	0	X	X
Apodiformes	Apodidae	*Chaetura vauxi*	0	0	X	
	Trochilidae	*Amazilia candida*	0	0	X	X
		Amazilia cyanocephala	0	0		X
		Amazilia yucatanensis	0	0	X	X
		Archilochus colubris	0	1	X	
		Campylopterus curvipennis	0	0	X	X
		Eugenes fulgens	0	0	X	
		Hylochoris leucotis	0	0		X
		Lampornis amethystinus	0	0	X	
		Selasphorus platycercus	0	1		X
Trogoniformes	Trogonidae	*Trogon elegans*	0	0	X	
Coraciiformes	Momotidae	*Momotus momota*	0	0	X	
Piciformes	Picidae	*Dryocopus lineatus*	0	0	X	
		Melanerpes aurifrons	0	0	X	X
		Melanerpes formicivorus	0	0	X	
		Piculus aeruginosus	0	0	X	X
		Piculus rubiginosus	0	0	X	
		Sphyrapicus varius	0	1		X
Passeriformes	Dendrocolaptidae	*Lepidocolaptes affinis*	0	0		X
		Sittasomus griseicapillus	0	0	X	X
	Tyrannidae	*Camptostoma imberbe*	0	0	X	
		Contopus borealis	0	1	X	
		Contopus cooperi	0	1		X
		Contopus pertinax	0	0	X	
		Contopus sordidulus	0	1	X	X
		Contopus virens	0	1	X	
		Empidonax alnorum	0	1	X	
		Empidonax flaviventris	1	1	X	X
		Empidonax hammondii	0	1		X

Order	Family	Species	Understory[1]	Status	PC	MN
		Empidonax occidentalis	1	0	X	X
		Empidonax traillii	0	1	X	
		Empidonax wrightii	0	1	X	
		Megarynchus pitangua	0	0	X	X
		Mionectes oleagineus	1	0		X
		Mitrephanes phaeocercus	0	0	X	X
		Myiarchus crinitus	0	1	X	X
		Myiarchus tuberculifer	0	0	X	X
		Myiarchus tyrannulus	0	0	X	
		Myiodynastes luteiventris	0	0	X	
		Myiozetetes similis	0	0	X	X
		Pitangus sulphuratus	0	0	X	
		Tityra semifasciata	0	0	X	
		Tyrannus couchii	0	0	X	
		Tyrannus melancholicus	0	0	X	
	Hirundinidae	*Streptoprocne zonaris*	0	0	X	
	Corvidae	*Cyanocorax morio*	0	0	X	
		Cyanocorax yncas	0	0	X	X
	Troglodytidae	*Campylorhynchus zonatus*	0	0	X	X
		Henicorhina leucophrys	1	0	X	X
		Henicorhina leucosticta	1	0	X	X
		Thryothorus maculipectus	1	0	X	X
		Troglodytes aedon	1	1	X	X
		Troglodytes brunneicollis	0	0	X	
	Sylviidae	*Polioptila caerulea*	0	1	X	X
	Regulidae	*Regulus calendula*	0	1	X	X
	Turdidae	*Catharus mexicanus*	1	0		X
		Catharus ustutatus	0	1		X
		Chatarus aurantiirostris	1	0		X
		Hylocichla mustelina	0	1		X
		Myadestes occidentalis	0	0		X
		Sialia sialis	0	0	X	
		Turdus assimilis	0	0	X	X
		Turdus grayi	0	0	X	X
	Mimidae	*Dumetella carolinensis*	1	1	X	X
		Melanotis caerulescens	1	0	X	X
	Vireonidae	*Cyclarhis gujanensis*	0	0	X	
		Vireo gilvus	0	1	X	
		Vireo griseus	0	1	X	X
		Vireo huttoni	0	0	X	
		Vireo leucophrys	0	0	X	X
		Vireo olivaceus	0	1	X	X
		Vireo philadelphicus	0	1	X	
		Vireo solitarius	0	1	X	X
	Parulidae	*Basileuterus belli*	1	0		X
		Basileuterus culicivorus	1	0	X	X
		Basileuterus rufifrons	1	0	X	X
		Dendroica coronata	0	1	X	
		Dendroica occidentalis	0	1	X	
		Dendroica magnoliae	0	1		X
		Dendroica townsendi	0	1	X	
		Dendroica virens	0	1	X	X
		Geothlypis trichas	0	1	X	
		Helmitheros vermivorus	1	1		X
		Icteria virens	1	1	X	
		Mniotilta varia	0	1	X	X

Order	Family	Species	Understory[1]	Status	PC	MN
		Myioborus miniatus	0	0		X
		Oporornis formosus	1	1		X
		Parula americana	0	1	X	
		Parula pitiayumi	0	0	X	
		Seiurus aurocapillus	1	0	X	X
		Seiurus motacilla	1	1		X
		Setophaga ruticilla	0	1	X	
		Vermivora celata	0	1	X	
		Vermivora pinus	0	1	X	X
		Vermivora ruficapilla	0	1	X	X
		Wilsonia canadensis	0	1	X	X
		Wilsonia citrina	1	1	X	X
		Wilsonia pusilla	0	1	X	X
	Thraupidae	*Chlorospingus ophthalmicus*	0	0	X	X
		Cyanerpes cyaneus	0	0	X	X
		Euphonia hirundinacea	0	0	X	X
		Piranga leucoptera	0	0	X	
		Piranga rubra	0	1	X	
		Thraupis abbas	0	0	X	X
	Cardinalidae	*Cyanocompsa parellina*	1	0		X
		Passerina ciris	1	1		X
		Passerina cyanea	1	1		X
		Pheucticus ludovicianus	0	0	X	X
		Saltator atriceps	0	0	X	X
	Emberizidae	*Arremonops rufivirgatus*	1	0	X	X
		Atlapetes brunneinucha	1	0	X	X
		Melospiza lincolnii	1	1		X
		Sporophila torqueola	1	0	X	X
		Tiaris olivacea	1	0	X	X
		Volatinia jacarina	0	0	X	
	Icteridae	*Dives dives*	0	0	X	X
		Icterus galbula	0	1	X	X
		Icterus graduacauda	0	0	X	X
		Icterus gularis	0	0	X	X
		Icterus spurius	0	1	X	
		Psarocolius montezuma	0	0	X	
		Quiscalus mexicanus	0	0	X	
	Fringillidae	*Carduelis psaltria*	0	0	X	
		Coccothraustes abeillei	0	0	X	

Discussion

In accordance with our first prediction, the point count was clearly the most effective survey technique in terms of total species richness completeness. The point count technique was the most consistent of both techniques showing the smallest internal variation (V= 3.3). Whitman *et al.* (1997) found similar results in which the species detection rate was higher for point counts (60%) than for mist netting (25%). Similarly, Wang and Finch (2002) found that point counts detected 82% of the species, whereas mist netting only 74%. Contrasting results showed that mist netting was more effective for detecting species (92%) than point counts (68%) (Rappole *et al.* 1998), or as twice as many species as point counts detected (Gram and Faaborg 1997). Differences between the techniques could be habitat and species dependent. Variation in the vertical structure of vegetation could affect the capture rate of specific species (e.g.; canopy species). However, for some species it has been found that detectability could not be attributed only to vegetation structure but also by species behaviour (Wang and Finch 2002). Species behaviour plays an important role in the detection performance of both techniques, for example the food searching behaviour of *Cathartes aura* or the complete aerial activities of *Streptoprocne zonaris*, makes them easy to detect but difficult to capture regardless of habitat type.

In addition, our results showed that point count technique requires a lower total effort in comparison to the mist netting. In our study the sampling effort required by the point counts to detect 90% of the total species richness was 2.7 times lower than the required effort by the mist net technique, giving a higher overall efficiency. Identifying differences in sampling effort is critical in the assessments of species richness and composition; omitting these differences could produce erroneous assessments of diversity.

Our second prediction was partially supported also by our results; we found that even though the overall efficiency of the mist netting is lower, this technique significantly detected a higher proportion of understory species in comparison to point counts. The number of unique understory species detected by mist netting was almost three times higher than detected by point counts. For example, secretive species, such as *Catharus mexicanus*, *Catharus aurantiirostris*, *Mionectes oleagineus*, *Oporornis formosus* and *Seiurus motacilla*, were only detected by mist netting. For specific cases like the migrant *Seiurus motacilla* (with low overall density), that are difficult to monitor accurately in its breeding and wintering grounds, mist netting is relevant. It has been suggested by Remsen and Good (1996) that any bird survey must be accompanied by intensive mist net sampling to avoid under representation of secretive and understory species. However, the use of mist nets alone must be considered with caution; other studies showed that mist nets are not a replacement for overall community sampling, detecting only 41% (57% in our study) of the total species richness recorded in the area (Bierregaard 1990). In addition, pros and cons of mist netting should be taken into consideration for successful monitoring, i.e.; the advantage of mist netting in reducing biases created by variability in observer experience and qualification, should be compared to biases created by net avoidance, habitat structure and behavioural differences between species (Herzog *et al.* 2002).

However, for migrant species, point counts significantly detected more species than mist netting. Point counts detected a higher number of migrant species and more unique species. In the case of the species detected only by point counts, the failure of mist netting in detecting the species could be partly explained by its inherent bias to miss canopy species such as raptors, e.g.; *Accipiter striatus* or *Buteo platypterus*. Other notable species detected only by point counts are *Empidonax* species (i.e.; *Empidonax alnorum*, *Empidonax flaviventris*, *Empidonax traillii*, *Empidonax wrightii*) and the majority of warbler species (e.g.; *Dendroica coronata*, *Dendroica occidentalis*, *Dendroica townsendi*, *Dendroica virens*, *Icteria virens*, *Mniotilta varia*). Rappole *et al.* (1998) found that point counts performed better than mist netting for detecting migrating *Wilsonia pusilla* warbler across habitats in Mexico. However, other migrants that forage in the understory were detected only by mist netting (e.g.; *Passerina ciris*, *Passerina cyanea*, *Melospiza lincolnii*). It has been suggested that during migration mist netting is a more suitable technique because many migrants are actively foraging during stopovers and therefore easier to catch, while they are less vocal and territorial (Wang and Finch 2002). However, we did not find evidence in our study that supports this suggestion.

Finally, the cost-efficiency analysis showed that point counts require less total labour and therefore decreases monetary costs compared to mist netting. The performance of point counts in terms of species detections including migrants is greater than mist netting. Despite the evident profits derived from point counts, the use of mist netting should not be disregarded when designing a monitoring programme as this technique showed a higher detection of understory and secretive birds. For a successful design of monitoring, the relative costs and biases of both techniques must be considered. Besides, whenever time and resources are available, point counts and mist netting should both be part of the monitoring scheme (Rappole *et al.* 1998).

Acknowledgments

We thank Dr. Adolfo Navarro Sigüensa and Laura E. Villasenor Gomez for providing the mist nets, and Gabriela Garcia Deras for field assistance. This research was supported by the CONACYT grant 149557 to E. Leyequién.

References

Bibby, C.J., Burgess N.D. Hill D.A. 1992. Bird census techniques. Academic Press, California.

Bierregaard, JR., O. 1990. Species composition and trophic organization of the understory bird community in a central Amazonian terra firme forest. In: Four Neotropical forests (A. H. Gentry, ed.)Yale Univ. Press, New Haven, Connecticut.

Colwell, R.K. 2004 . EstimateS: Statistical estimation of species richness and shared species from samples. Version 7. User's Guide and application published at: http://purl.oclc.org/estimates.

Colwell, R.K. and Coddington, J.A. 1994. Estimating terrestrial biodiversity through extrapolation. Phil. Tran. Royal Soc.Lon. 345: 101–118.

Dawson, D.K., Smith D.R., Robbins C.S. 1997. Point count length and detection of forest Neotropical migrant birds. In: Ralph C.J., Sauer J.R. and Droege S. (eds) Monitoring Bird populations by point counts. General technical Report PSW-GTR-149. Albany, California, pp 35-43.

Fjeldså, J. 1999. The impact of human forest disturbance on the endemic avifauna of the Udzungwa Mountains, Tanzania. Bird Conservation International 9:47–62.

Godoy-Bergallo, H., Esberard, C.E.L., Riberiro-Mello, M.A., Lins, V., Mangolin, R., Melo, G.G.S. and Baptista, M. 2003. Bat species richness in atlantic forest: What is the minimum sampling effort? Biotropica 35 (2): 278-288.

Gram, W.R. and Faaborg, J.1997. The distribution of Neotropical migrant birds wintering in the El Cielo Biosphere Reserve, Tamaulipas, Mexico. Condor 99: 658–670.

Herzog, S.K., Kessler, M. and Cahill, T.M. 2002. Estimating species richness of tropical bird communities from rapid assessment data. Auk 119 (3): 749–769.

Huston, M.A. 1994. Biological Diversity. CambridgeUniversity Press, Cambridge, United Kingdom.

Longino, J. and Colwell, R.K. 1997. Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. Ecol. Applications 7: 1263-1277.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853-858.

Nichols, J.D., Hines, J.E., Sauer, J.R., fallon, F.W., Fallon, J.E. and Heglund, P.J. 2000. A double-observer approach for estimating detection probability and abundance from point counts. Auk 117 (2): 393–408.

Peterson, A. T., A. G. Navarro & H. Benítez. 1998. The need for continued scientific collections: A geographic analysis of Mexican birds specimens. Ibis 140: 288-294.

Poulin, B., Lafebvre, G. and Pilard, P. 2000. Quantifying the breeding assemblage of reedbed passerines with mist-net and point-count surveys. J. Field Ornithol. 71 (3): 443–454.

Ralph, C. J. and Fancy, S.G. 1995. Demography and movements of Apapane and Iiwi in Hawaii. Condor 97: 729–742.

Rappole, J.H., Winker, K. and Powell, G.V.N. 1998. Migratory bird habitat use in southern Mexico: mist nets versus point counts. Journal of Field Ornithology 69: 635–643.

Remsen, J.V., and Good, D.A. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. Auk 113: 381–398.

Rojas-Soto, O., S. López de Aquino, L. Sánchez-González & B. Hernández-Baños. 2002. La colecta científica en el Neotrópico: el caso de las aves de México. Ornitología Neotropical 13: 209-214.

Rosenzweig, M.L. 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, United Kingdom.

Stotz, D.F., Fitzpatrick, J.W., Parker III, T.A. and Moskovits, D.K. (eds.) 1996. Neotropical Birds: Ecology and Conservation. University of Chicago Press, Chicago.

Thomas, L. 1996. Monitoring long-term population change: Why are there so many analysis methods? Ecology 1: 49-58.

Verner, J. 1985. Assessment of counting techniques. Current Ornithology 2: 247–302.

Vielliard, J.M. 2000. Bird community as an indicator of biodiversity: results from quantitative surveys. Brazil. A. Acad. Bras. Ci. 72 (3): 323-330.

Wang, Y. and Finch, D.M. 2002. Consistency of mist netting and point counts in assessing landbird species richness and relative abundance during migration. Condor 104: 59–72.

Watson, D.M. 2004. Comparative evaluation of new approaches to survey birds. Wildlife Research 31: 1-11.

Winker, K. 1998. Recent geographic trends in Neotropical avian research. Condor 100(4): 764-768.

Whitman, A. A., Hagan Iii, J. M. and Brokaw, N.V.L. 1997. A comparison of two bird survey techniques used in a subtropical forest. Condor 99: 955–965.

Chapter 3

Fragmentation and habitat loss: species richness responses in an avian metacommunity in Mexico.

Eurídice Leyequién, Willem F. de Boer, Víctor M. Toledo

Abstract

In this paper we argue that fragmentation and habitat loss is of central importance in understanding the effects of spatial structure on species richness. We consider that an approach which separates and quantifies the effects of fragmentation and habitat loss on species richness will be more adequate to understand the influence of each process in the community structure. However, many studies do not separate the individual relative effects of fragmentation and habitat loss, leading small room for generalisations on patterns of species richness influenced by fragmentation and habitat loss. We examined the relative individual and combined influence of these two factors on species richness in an avian metacommunity. The first hypotheses in our study was (1) species richness will show a hump-shaped relationship (unimodal response) as a result of habitat fragmentation at landscape level, (2) as the amount of habitat in the landscape declines, extinction thresholds will be exceeded, creating a linear negative effect on species richness. Moreover, difference in explanatory power of individual and combined influence of both factors was compared. The results indicate that the response of species richness to habitat fragmentation shows a unimodal response at landscape level, and a negative response to habitat loss. The combined influence of fragmentation and habitat loss did not offer a better approximation of species richness response. This suggests that there is no interaction between the effects of fragmentation and habitat loss. Due to growing human perturbation in the landscape, crucial decisions for conservation and landscape management have to be made. We argue that influencing fragmentation levels will mitigate the negative effects of habitat loss on species richness.

Introduction

The role of spatial dynamics in understanding differences in species diversity, mainly through fragmentation and habitat loss, is increasingly becoming an important subject in ecology (Fahrig 2003, Rosenzweig 1995). The metacommunity theory has recently emerged as a common framework for scientists to understand the effects of fragmented systems in community ecology (Leibold *et al.* 2004). In a metacomunity, a set of local communities is linked by dispersal of species (Gilpin and Hanski 1991, Wilson 1992). Landscape fragmentation and habitat loss strongly influence these (meta)community patterns and dynamics, disrupting important ecological processes for species persistence (e.g.; mortality, re-colonisation, or reproductive rates) (Bender *et al.* 1998, Fahrig 1997, 2001, Fahrig and Merriam 1994, Stephens *et al.* 2003, Villard *et al.* 1995, Wiegand *et al.* 2005).

Habitat fragmentation leads to configuration changes in the landscape, increasing the number and isolation of patches, and decreasing patch sizes. Changes in the spatial structure of landscapes through fragmentation or aggregation of natural habitats can alter the abundance of single species, the species diversity patterns, and thereby the community assemblage (Johnson *et al.* 1992, Robinson and Wilcove 1994). Additionally, when high fragmentation levels occur dispersal probabilities decrease, so that species with low dispersal capacities can no longer colonize these isolated patches, consequently leading to a parallel reduction of local diversity (Leibold *et al.* 2004). Moreover, at low fragmentation levels species richness will decline as a dominant competitor will invade each local community as one large community is created (Mouquet and Loreau 2002). At intermediate fragmentation levels, species are believed to be able to colonize isolated patches, but fragmentation levels are still not so low that a dominant competitor can invade all patches and control local diversity. Therefore we would expect a unimodal response of species richness in response to an increase in fragmentation.

Habitat loss, described here as the reduction of total habitat area, has a consistently negative effects on species diversity. The destruction of habitat affects, among others, breeding and dispersal success (Belisle *et al.* 2001, Kurki *et al.* 2000, With and King 1999), trophic chain length (Komonen *et al.* 2000) and species interactions (Taylor and Merrian 1995). An increase in habitat loss gradually exceeds species-specific extinction thresholds (With and Crist 1995).

Many studies, describing the relative effects of fragmentation and habitat loss, resulted in varying or even conflicting conclusions. Generally, negative linear trends have been predicted by theoretical models as well as by field studies, however also positive effects on species richness have been found in landscapes with a large number of smaller patches. The dissimilarities among these conclusions are partially due to differences in defining habitat fragmentation, where many researches do not separate the effects of habitat loss from the configuration effects of fragmentation (Fahrig 2003) producing unclear results leaving small basis for generalisations. An approach which quantifies both the effects of the degree of fragmentation and habitat loss on species richness will be more adequate.

We argue that the impact of habitat fragmentation on species richness in a metacommunity can not be adequately explained by linear trends; non-linear relationships would perform better. We assume that species richness will decrease at high and low fragmentation levels because first at high levels dispersal probabilities decrease leading to a reduction of local diversity, and at low levels a dominant competitor will invade each local community. In addition, we assume that at intermediate levels, species colonise isolated patches where a dominant competitor can invade all patches and control local diversity. Moreover, we expect a negative trend in species richness as a result of habitat loss, we assume that an increase of habitat loss gradually exceeds species-specific extinction thresholds. The predictive power of both habitat fragmentation and habitat loss in explaining species richness at metacommunity level will be greater than the individual influence.

We examined the relative individual and the combined influence of fragmentation and habitat loss on species richness in an avian metacommunity in a Mexican coffee agro-ecological area. The aims of our study were to test the hypotheses that (1) species richness will show a hump-shaped relationship (unimodal response) as a result of habitat fragmentation at landscape level, and (2) as the amount of habitat in the landscape declines, extinction thresholds will be exceeded, creating a linear negative effect on species richness. Moreover, the difference in explanatory power of the individual and combined influence of both habitat fragmentation and habitat loss will be compared, and we expect that the combined model performs significantly better than each of the individual models.

Material and methods

Study site

The avian communities were sampled in the North Eastern mountain range of Puebla, within the Cuetzalan region, Mexico, which covers an area of ~ 151,368 ha. The region is predominantly a traditional shade coffee agro-ecological zone, which covers an altitudinal range between 300 to 1200 m. The major agricultural system is traditional polyculture (traditional shade coffee plantation), while other land covers, such as seasonal crops (i.e.; maize and beans) and grazing lands are also present in the area. Forested areas are typically remnants of tropical evergreen forest with low montane rain forest in the higher areas (between 700 and 2500 m) and lowland rain forest in the lower areas (200-700 m). The mean annual rainfall is 3,500 mm without a defined dry season; and the mean annual temperature is 22-26°C. We selected eight landscape frames of 10 x 10 km for the study, for the characterisation of the metacommunity. All landscapes were selected using a stratified sampling design to minimise heterogeneity among the landscapes using a supervised classification image derived from an ETM satellite image (2003). All landscapes were selected within traditional shade coffee plantation areas where altitude, exposition and age of plantation were homogenised as much as field conditions allowed.

Bird survey and species richness

We performed a bird survey during the migratory and breeding seasons from November 2002 to November 2003 (Leyequien *et al. submitted*). The period of sampling consisted of weekly sequential rounds visiting all of the eight landscapes in each round. For bird detection we used standard point count techniques (Bibby *et al.* 1992) with a modified double-observer approach, combining visual and acoustic bird detections (Parker 1991). Bird observations were recorded over 360° with a fixed-radius of 25 m, and we used a ten minute period for each single count (Dawson *et al.* 1997, Vielliard 2000). A distance of 100 m between point counts was used to avoid dependency between points' data. We restricted our bird species data set to only year-round resident birds. The total number of registered species in all the landscapes consisted of 112 resident birds, representing 12 orders, 28 families and 82 genera (Annex 1).

Species richness estimators for the nine bird communities were calculated using the software EstimateS V7.0 (Colwell 2004) and Effort Predictor V1.0. We estimated the S_{max} richness estimator using an exponential model with 100 iterations after which improvements were < 0.0001; we also estimated the first-order Jacknife richness estimator, using mean among runs (Burnham and Overton 1978, 1979, Heltshe and Forrester 1983, Smith and van Belle 1984), and the Chao 1 richness estimator, also using mean among runs (Chao 1984), as response variables. For the calculations we used the randomization protocol for estimators' prediction using sampling without replacement and the bias-corrected formula for Chao 1, with an upper abundance limit for rare or infrequent species of 10.

Landscape fragmentation and habitat loss

We used Fragstats 3.3 to compute the landscape metrics used to quantify landscape configuration (fragmentation) and habitat loss. The fragmentation explanatory variable set consisted of: contiguity index distribution for each land cover class (i.e.; coefficient of variation parameter), percentage of like-adjacencies involving the corresponding land cover class, landscape fractal index distribution, landscape shape index, landscape contagion index, landscape percentage of like adjacencies, connectance index, and landscape Shannon's diversity index. The habitat loss explanatory variable set consisted of total class area, percentage of landscape comprised of the corresponding class, and number of patches of the corresponding class.

We used multivariate statistics to test for the effects of habitat fragmentation and habitat loss variables' sets on the avian species composition and relative abundances. We utilised a redundancy analysis (RDA) (Jongman *et al.* 1987) to quantify the strength of the variables that best explained the variation in the species data. We used a log transformation of species data, and stepwise forward selection of explanatory variables with Monte Carlo permutation tests (9999 number of unrestricted permutations) where the residuals of the reduced model were permuted (the reduced-model method was selected to reduce a type I error). After selecting the canonical axis that best explained the variation in species data, we used the variance partitioning procedure (Borcard *et al.* 1992) to quantify the marginal and conditional effects of the significant explanatory variables ($\alpha = 0.05$) and the unexplained variation accounted for by either fragmentation or habitat loss explanatory sets.

The models

To test the fragmentation-dispersal and habitat loss hypotheses, we used non-linear regression models for curve fitting, using GraphPad Prism V4.0. For comparison of fit we used three different models as follows: Polynomial First Order (straight line), Polynomial Second Order and a Gaussian distribution. To discriminate among models we used the extra sum-of-squares F test for nested models with $p = 0.05$ (Pesaran and Deaton 1978), or the Akaike's Information Criterion (AIC) for non-nested models (Bozdogan 2000).

For testing our third hypothesis we developed a combined model using both fragmentation and habitat loss explanatory sets using a multiple non-linear regression ($P = 0.05$) with iterative estimation algorithms (SPSS V12.0.1.). The F value was estimated using the sum of squares for the regression and the residual, and the p value referred to the corresponding F-statistics ($p = 0.05$).

Results

From the eight selected landscape fragmentation variables, the contiguity index for the class secondary vegetation ($p = 0.0060$), and the class forest ($p = 0.0200$), significantly explained 0.526 of the variance in the species data according to the RDA. The marginal effect explained by the fragmentation explanatory variable was 23.7 % accounted for by the contiguity index for the class secondary vegetation, and 17.4 % accounted for by the contiguity index for the class forest. Both variables explained 11.5 % of variance by their conditional effect, and ultimately the unexplained fraction of variance was 58.9 %.

For the habitat loss explanatory variables, total area for the class secondary vegetation ($p = 0.008$) and the number of patches for the class coffee plantations ($p = 0.05$) explained 0.478 of the variance in species data. Moreover, the total area for the class secondary vegetation explained 15.4 % of the community composition by its marginal effect, whereas this was 25.9 % for the number of patches for the class coffee plantations. Both variables explained 6.5 % of variance by their conditional effect, whereby the unexplained fraction of variance was 58.7 % (Fig. 1).

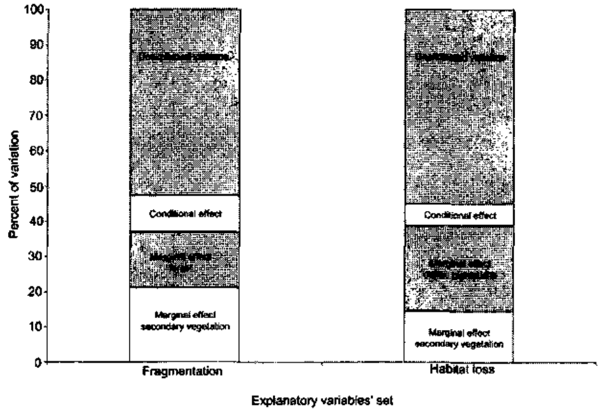

Figure 1. The variance partitioning of the species data, showing the percentage of variance explained by the marginal effect of the variables contiguity for the class secondary vegetation and the variable contiguity for the class forest (fragmentation explanatory set); and the variables total area for the class secondary vegetation and the variable number of patches for the class coffee plantations (habitat loss explanatory set). In addition, the conditional effects for the variables of both fragmentation and habitat loss explanatory sets, and the unexplained variance are depicted.

The models

For the fragmentation explanatory set, results demonstrated that for the variable contiguity for the class secondary vegetation, the Gaussian distribution model had the best fit in explaining the species richness (Jacknife estimator). The AIC test showed that based on the comparison of fits, the Gaussian distribution model had the highest (62.05 %) probability in describing the observed response patterns in species richness ($p = <0.0001$; $R^2 = 0.1848$), with a probability ratio of 1.7. For the second variable, contiguity for the forest class, based on the AIC test, the Gaussian distribution model was also the most likely to be correct in explaining the species richness (Chao 1 estimator). It had a 54.8 % probability of being correct, with a probability ratio of 1.5 ($p = <0.0001$; $R^2 = 0.4888$) (Table 1; Fig. 2).

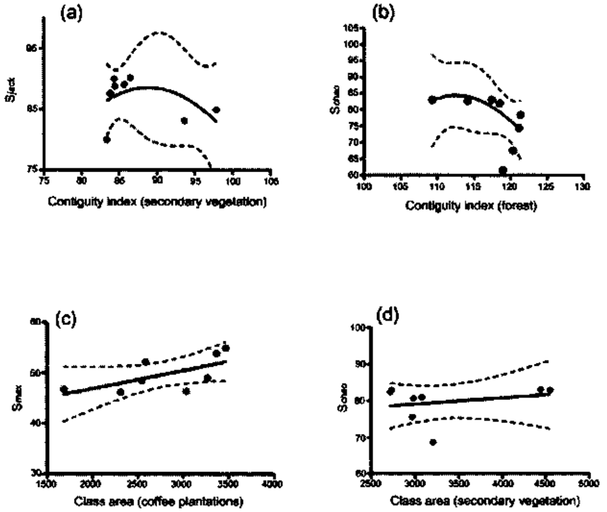

Figure 2. Predicted models for fragmentation and habitat loss (CI 95%) describing the observed response in bird species richness (closed dots). A humped-shaped relationship between fragmentation and species richness (contiguity index for secondary vegetation, P = <0.0001, R^2 = 0.1848; contiguity index for forest, P = <0.0001, R^2 = 0.4888). A positive linear relationship between habitat loss and species richness (total class area for coffee plantation, P = <0.0001, R^2 = 0.4648; total class area for secondary vegetation, (P = <0.0001, R^2 = 0.060). Habitat loss increases from left to right on the x-axis.

*Table 1. Comparison of model fitting for fragmentation explanatory variables, best fit (*) was selected based on the probability to be correct (%) and the R^2. * Probability of correctness.*

Fragmentation explanatory variables					
Explanatory variable	*Species richness estimator*	*Model*	*AIC*		
			Probability* (%)	R^2	*P*-value
Contiguity Index (secondary vegetation)	Jacknife	Polynomial 2nd order	37.95	0.1810	<0.0001
		Gaussian	62.05*	0.1848	
Contiguity Index (forest)	Chao1	Polynomial 2nd order	45.25	0.4866	
		Gaussian	54.8*	0.4888	<0.0001

As expected, for the habitat loss explanatory set, results showed that there is a negative linear relationship between the amount of habitat and species richness. For the explanatory variable class area for the class coffee plantation, we found that the first order polynomial had the best fit (p = <0.001; R^2 = 0.4648) in explaining species richness (Smax estimator). Additionally, for the explanatory variable class area for the secondary vegetation, the first order polynomial also had the best fit. The extra sum-of-squares F-test showed that, based on the comparison of fits, the first order polynomial described the observed response patterns in species richness best (Chao 1 estimator; p = <0.0001, R^2 = 0.060; Table 2; Fig. 2).

Table 2. Comparison of model fitting for habitat loss explanatory variables, models with P = 0.05 were selected (*) that explained most variance of the species richness data (R^2). S, Species richness.

Habitat loss explanatory variables					
Explanatory variable	*S estimator*	*Model*	*Extra sum-of-squares F test*		
			Hypothesis	R^2	P-value
Total Class Area (coffee plantation)	Smax	Polynomial 1st order	H_0 : accepted*	0.4648	<0.0001
		Polynomial 2nd order	H_1 : rejected	0.4064	
Total Class Area	Chao 1	Polynomial 1st order	H_0 : accepted*	0.060	
(secondary vegetation)		Polynomial 2nd order	H_1 : rejected	0.5811	<0.0001

The combined model that explained the species richness response best (Chao 1 estimator) had an R^2 = 0.54 with p = <0.0001. The AIC test showed that the combined model has a low probability of being correct in comparison to any of the individual models. The probability that the combined model was correct was 36.5 % against 63.5 % for all the individual models with a probability ratio of 1.8.

Discussion

Firstly, our results indicate that the bird species richness show a unimodal response to habitat fragmentation at landscape level. This suggests that landscape configuration patterns (such as fragmentation levels) determine species richness, indicating that landscape patterns are central in understanding ecological processes (Bascompte and Rodriguez 2001, Turner 1989). In landscapes with intermediate levels of habitat fragmentation species richness was higher. Hence, there is an optimum spatial structure at which species richness is highest, due to a balance between important ecological processes occurring at landscape scale, such as species competition and dispersal frequency. On the other hand, when one large community is created, at lowest fragmentation levels, a regionally dominant competitor can invade each local community, reducing the local diversity. (Amarasekare and Nisbet 2001, Caswell 1978, Forbes and Chase 2002, Mouquet and Loreau 2002, Taylor 1988). At high fragmentation levels species richness in local communities will decrease and become homogenised, by gradually exceeding species-specific extinction thresholds (Leibold *et al.* 2004). Another determinant explaining this unimodal response is the reduction of fragments isolation (i.e.; higher connectedness) of suitable habitat (i.e.; forest, secondary vegetation) that increases the dispersal frequency. Consequently, dispersal-limited species and some rare species (which are typically driven to extinction quickly) can be maintained in local communities as transient fugitives or by a rescue effect (Brown and Kodric-Brown 1977, Loreau and Mouquet 1999, Mouquet and Loreau 2002, Pulliam 1988, Shmida and Wilson 1985). These results coincide with those obtained by other authors: highly isolated habitat fragments present lower species richness, whereas fragments with higher connectedness had higher species richness (Baur and Erhardt 1995, van Dorp and Opdam 1987. Furthermore, smaller patches with intermediate connectedness that are not separated by an inhospitable matrix may support higher species richness. Additionally, in our study, the significant effect of connectedness of the forest and secondary vegetation classes could indicate that some forest specialists as well as generalists can coexist locally in these intermediate fragmented landscapes.

Secondly, the effect of habitat loss that we found was consistent with previous studies. Similar to our results, several studies found a negative effect of habitat loss on species richness (Collinge 1995, Fahrig 1997, Holt *et al.* 1995a, 1995b, Olff and Ritchie 2000, Robinson *et al.* 1992, Verboom and Apeldoorn 1990). We found that as the amount of suitable habitat (i.e.; coffee plantations, secondary vegetation) in the landscape declined, species richness responses showed a negative linear relationship. However, in the case of the variable area for the secondary vegetation class there is a low percentage of variance explained. This might be explained by the fact that connectedness in this land cover class is more important than the area availability itself, and that the degree of habitat loss does not reach an extinction threshold (Andrén 1994, Farina 1997, Santos and Tellería 1997).

Some studies found a threshold for habitat cover from which habitat fragmentation had no significant influence on species richness (Andrén 1994, Fahrig 1997, McGarigal and McComb 1995). However, these latter findings considered forested areas, which may be significantly more accessible for bird dispersal than agricultural areas (Villard *et al.* 1999), as is the case in our study in which fragments of forest were embedded in an agricultural matrix. A matrix with agricultural areas as predominant cover may influence not only the species composition but also the dispersal threshold of species. Interestingly, the combined influence of both fragmentation and habitat loss did not offer a better approximation of the species richness response of the bird metacommunity than the individual effect. This suggests that the effects of a single process (fragmentation or habitat loss) do not show any interaction. We believe that by understanding the impact of both fragmentation and habitat loss on species richness separately, generalisations can be made regarding species richness responses in metacommunity at landscape level.

Conclusion

Our results address fundamental issues in ecology, such as the relationship between species richness and habitat fragmentation and habitat loss. Our univariate models at the landscape scale explain significantly the species richness unimodal response to habitat fragmentation and the negative linear response to habitat loss. Moreover, the conservation of species or assemblages in a region requires knowledge of the relevant indicators for conservation and the underlying structuring forces. We have shown that species richness responses to habitat fragmentation follow a hump-shaped pattern, and that there is a clear negative linear relationship between species richness and habitat loss, which obviously has major implications for conservation strategies. Fragmentation does not always have a negative effect on species richness, but there seems to be an optimal level of fragmentation at which species richness is highest. In the context of the growing perturbation in the landscape by human activities, crucial decisions for conservation and landscape management will have to be made. It seems that by influencing fragmentation levels, the negative effects of habitat loss could be mitigated.

Acknowledgements

Thanks to Dr. Ir. Andre Schaffers of the Nature Conservation and Plant Ecology Group and Drs. Nicole Heuermann of the Resource Ecology Group at Wageningen University for statistical consultation. We thank the "Society for the advancement of research in the tropics" for the grant bestowed to E. Leyequién. This research was supported by the CONACYT grant 149557 to E. Leyequién.

References

Andrén, H. 1994. Effects of fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355-366.

Amarasekare, P. and Nisbet, R. 2001. Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. American Naturalist 158: 572-584.

Bascompte, J. and Rodríguez, M.A. 2001. Habitat patchiness and plant species richness. Ecology Letters 4: 417-420.

Baur, B. and Erhardt, A. 1995. Habitat fragmentation and habitat alterations: principal threats to most animal and plant species. GAIA 4: 221-226.

Bélisle, M., Desrochers, A. and Fortin, M.J. 2001. Influence of forest cover on the movements of forest bords: a homing experiment. Ecology 82: 1893-1904.

Bender, D.J., Tischendorf, L. and Fahrig, L.1998. Evaluation of patch isolation metrics for predicting animal movement in binary landscapes. Landscape Ecology 15: 131-143.

Bibby, C.J., Burgess, N.D. and Hill, D.A. 1992. Bird census techniques, 1st edn. Academic Press, California.

Borcard, D., Legendere, P. and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology 73(3), 1045-1055.

Bowman, J., Cappuccino, N. and Fahrig, L.2002. Patch size and population density: the effect of immigration behavior. Conservation Ecology 6:9.

Bozdogan, H. 2000. Akaike's Information Criterion and Recent Developments in Information Complexity. Journal of Mathematical Psychology 44(1), 62-91(30).

Brown, J.H. and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration or extinction. Ecology 58: 445-449.

Burnham, K.P. and Overton, E.W. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. Biometrika 65: 623-633.

Burnham, K.P. and Overton, E.W. 1979. Robust estimation of population size when capture probabilities vary among animals. Ecology 60: 927-936.

Caswell, H. 1978. Predator mediated co-existence: a non-equilibrium model. American Naturalist 112: 127-154.

Collinge, S.K. 1995. Spatial arrangements of patches and corridors in the landscape: consequences for biological diversity and implications for landscape architecture. Ph.D. dissertation. Harvard University, Cambridge, Massachutes.

Colwell, R.K. 2004 . EstimateS: Statistical estimation of species richness and shared species from samples. Version 7. User's Guide and application published at: http://purl.oclc.org/estimates.

Chao, A. 1984. Non-parametric estimation of the number of classes in a population. Scandinavian Journal of Statistics 11: 265-270.

Dawson, D.K., Smith, D.R. and Robbins, C.S.. 1997. Point count length and detection of forest Neotropical migrant birds. Pp. 181. In: Ralph, C.J., Sauer, J.R. and Droege, S. (eds.) Monitoring Bird populations by point counts. General technical Report PSW-GTR-149. Albany, California.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. Journal of Wildlife Management 61: 603-610.

Fahrig, L.1998. When does fragmentation of breeding habitat affect population survival? Ecological Modelling 105: 273-292.

Fahrig, L. 2001. How much habitat is enough? Biological Conservation. 100: 65-74.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34: 487-515.

Fahrig, L. and Merriam, G. 1994. Conservation of fragmented populations. Conservation Biology 8: 50-59.

Farina, A. 1997. Landscape structure aNd breeding bird distribution in a sub-Mediterranean agro-ecosystem. Landscape Ecology 12: 365-378.

Forbes, A.E. and Chase, J.M. 2002. The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. Oikos 96: 433-440.

Gilpin, M.E. and Hanski, I.A. 1991. Metapopulation dynamics: Empirical and theoretical investigations. Academic press, London.

Heltshe, J. and Forrester, N.E. 1983. Estimating species richness using jacknife procedure. Biometrics 39: 1-11.

Holt, R.D., Debinski, D.M., Diffendorfer, Gaines, M., Martinko, E., Robinson, G., and Ward, G. 1995a. Perspectives from an experimental study of habitat fragmentation in an agroecosystem. Pp.147-175 in Glen, D.M., Greaves, M.P., and Anderson, H.M., editors. Ecology and integrated farming systems. Wiley, New York.

Holt, R.D., Robinson, G.R. and Gaines, M.S. 1995b. Vegetation dynamics in an experimentally fragmented landscape. Ecology 76: 1610-1624.

Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilma, D., Loreau, M. and Gonzalez, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7: 601-613.

Johnson, A.R., Wiens, J.A., Milne, B.T. and Crist, T.O. 1992. Animal movements and population dynamics in heterogeneous landscapes. Landscape Ecology 7: 63-75.

Jongman, R.H.G., Ter Braak, C.J.F. and Van Tongeren, O.F.R. 1987. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge.

Keitt, T.H., D.L. Urban, and B.T. Milne. 1997. Detecting critical scales in fragmented landscapes. Conservation Ecology (online) 1(1): 4. http://www.consecol.org/vol1/iss1/art4/

Komonen, A., Penttilae, R., Lindgren, M. and Hanski, I. 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. Oikos 90: 119-126.

Kurki, S., Nikula, A., Helle, P. and Linden, H.. 2000. Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. Ecology 81: 1985–1997.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreao, M. and Gonzalez, A. 2004. The metacomunity concept: a fraMework for multiscale community ecology. Ecology Letters 7: 601-613.

Leyequien, E., De Boer, W.F. and Skidmore, A.K. (submitted) Linking species-environment relationships and multiple spatial scales in community ecology.

Loreau, M. and Mouquet, N. 1999. Immigration and the maintenance of local species diversity. American Naturalist 154: 427-440.

Mcgarigal, K. and Mccomb, W.C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecol. Monogr. 65: 235-260.

Mouquet, N. and Loreau, M. 2002. Coexistence in metacommunities: the regional similarity hypothesis. American Naturalist 159: 420-426.

Olff, H. and Ritchie, M.E. 2000. Fragmented nature: Consequences for biodiversity. 3rd International Workshop on Sustainable Land Use Planning, Wageningen.

Parker, T.A. 1991. On the use of tape recorders in avifaunal surveys. AUK 108(2), 443-444.

Pesaran, M. H. and Deaton, A. S. 1978. Testing Non-nested Nonlinear Regression Models. Econometrica 46, 677–694.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. American Naturalist 132: 652-661.

Robinson, G.R., Holt, R.D., Gaines, M.S., Hamburg, S.P., Johnson, M.L., Fitch, H.S. and Martinko, E.A. 1992. Diverse and contrasting effects of habitat fragmentation. Science 257: 524-526.

Robinson, S.K. and Wilcove, D.S. 1994. Forest fragmentation in the temperate zone and its effects on migratory song birds. Bird Conservation International 4: 223-249.

Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, united Kingdom.

Santos, T. and Telleria, J.L. 1997. Efectos de la fragmentación sobre las aves insectívoras forestales de dos localidades europeas. Ardeola 44: 113-117.

Shmida, A. and Wilson, M.V. 1985. Biological determinants of species diversity. Journal of Biogeography 12: 1-20.

Smith, E.P. and Van Belle, G. 1984. Nonparametric estimation of species richness. Biometrics 40: 119-129.

Steffan-Dewenter, I. Munzenberg, U., Burger, C., Thies, T. and Tscharntke, T. 2002. Scale-dependent effects of landscape structure on three pollinator guilds. Ecology 38: 1421-1432.

Stephens, S.E., Koons, D.N., Rotella, J.J. and Willey, D.W. 2003. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biological Conservation 115: 101-110.

Taylor, A.D. 1988. Large-scale spatial structure and population dynamics in arthropod predator-prey systems. Annale Zoologici Fennici 25:63–74.

Taylor, P.D. and Merrian, G. 1995. Habitat fragmentation and parasitism of a forest damselfly. Landscape Ecology 11: 181-189.

Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. Annu. Rev. Ecol. Syst. 29:171-197.

Van Dorp, D. and Opdam, P.F.M. 1987. Effects of patch size, isolation and regional abundance on forest bird communities. Landscape Ecology (1)1: 59-73.

Verboom, B. and Van Apeldoorn, R. 1990. Effects of habitat fragmentation on the squirrel, *Sciurus vulgaris* L. Landscape Ecology 4(2/3): 171-176.

Vielliard, J.M.E. 2000. Bird community as an indicator of biodiversity: results from quantitative surveys. Brazil. A. Acad. Bras. Ci. 72(3), 323-330.

Villard, M.A., Merriam, G. and Maurer, B.A. 1995. Dynamics in subdivided populations of Neotropical migratory birds in a temperate fragmented forest. Ecology 76: 27-40.

Villard, M.A., Trzcinki, M.K, and Merriam, G. 1999. Fragmentation effects of forest birds: Relative influence of woodland cover and configuration on landscape occupancy. Conservation Biology 13(4): 774-783.

Wiegand, T., Revilla, E. and Moloney, K.A. 2005. Effects of habitat loss and fragmentation on population dynamics. Conservation Biology 19(1): 108-121.

Wilson, D.S. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology 73: 1984-2000.

With, K.A. and Crist, O.C. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76(8): 2446-2459.

With, K.A. and King, A.W. 1999. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. Landscape Ecology 14: 73-82.

Annex

Order	Family	Species	E	PC	FG	FD
Galliformes	Cracidae	*Ortalis vetula*	NA	NA	F	NA
Ciconiiformes	Ardeidae	*Bubulcus ibis*	NA	NA	C/I	NA
	Cathartidae	*Coragyps atratus*	NA	NA	C	NA
		Cathartes aura	NA	NA	C	NA
Falconiformes	Accipitridae	*Buteo magnirostris*	NA	NA	C	NA
Columbiformes	Columbidae	*Patagioenas flavirostris*	NA	NA	G/F	NA
		Zenaida asiatica	NA	NA	G/F	NA
		Columbina inca	NA	NA	G	NA
		Columbina talpacoti	NA	NA	G	NA
		Leptotila verreauxi	NA	NA	G/F	NA
Psittaciformes	Psittacidae	*Pionus senilis*	NA	E	F	NA
		Amazona autumnalis	NA	NA	G/F	NA
Cuculiformes	Cuculidae	*Piaya cayana*	NA	NA	I	NA
		Crotophaga sulcirostris	NA	NA	I	NA
Strigiformes	Strigidae	*Megascops guatemalae*	ND	NA	C	NA
		Glaucidium brasilianum	NA	NA	C	NA
		Ciccaba virgata	NA	NA	C	NA
Apodiformes	Apodidae	*Streptoprocne zonaris*	NA	NA	I	NA
		Chaetura vauxi	NA	NA	I	NA
	Trochilidae	*Campylopterus curvipennis*	NA	NA	N/I	NA
		Campylopterus hemileucurus	NA	NA	N	NA
		Anthracothorax prevostii	NA	NA	N/I	NA
		Hylochoris leucotis	NA	NA	N	NA
		Amazilia candida	NA	NA	N/I	NA
		Amazilia cyanocephala	NA	NA	N	NA
		Amazilia tzacatl	NA	NA	N/I	NA
		Amazilia yucatanensis	MX	NA	N	NA
		Lampornis amethystinus	NA	NA	N	NA
		Lampornis clemenciae	NA	NA	N	NA
		Eugenes fulgens	NA	NA	N	NA
		Atthis heloisa	MX	NA	N	NA

Order	Family	Species	E	PC	FG	FD
Trogoniformes	Trogonidae	*Trogon elegans*	NA	NA	O	FR
Coraciiformes	Momotidae	*Momotus momota*	NA	NA	O	NA
	Ramphastidae	*Aulacorhyncus prasinus*	NA	SSP	O	NA
Piciformes	Picidae	*Melanerpes formicivorus*	NA	NA	O	FR
		Melanerpes aurifrons	NA	NA	I	NA
		Veniliornis fumigatus	NA	NA	I	NA
		Piculus rubiginosus	NA	NA	I	NA
		Dryocopus lineatus	NA	NA	I	NA
		Campephilus guatemalensis	NA	SSP	I	NA
Passeriformes	Dendrocolaptidae	*Sittasomus griseicapillus*	NA	NA	F/I	FR
		Xiphorhynchus flavigaster	NA	NA	I	NA
		Lepidocolaptes affinis	NA	NA	I	FR
	Tyrannidae	*Camptostoma imberbe*	NA	NA	I	NA
		Mitrephanes phaeocercus	NA	NA	I	NA
		Contopus pertinax	NA	NA	I	NA
		Empidonax difficilis	NA	NA	I	NA
		Empidonax occidentalis	NA	NA	I	NA
		Sayornis nigricans	NA	NA	I	NA
		Myiarchus tuberculifer	NA	NA	I/F	NA
		Myiarchus tyrannulus	NA	NA	O	NA
		Pitangus sulphuratus	NA	NA	I/F	NA
		Megarynchus pitangua	NA	NA	O	NA
		Myiozetetes similis	NA	NA	I/F	NA
		Myiodynastes luteiventris	NA	NA	I	NA
		Tyrannus melancholicus	NA	NA	O	NA
		Tyrannus couchii	NA	NA	O	NA
		Tityra semifasciata	NA	NA	F	NA
	Vireonidae	*Vireo huttoni*	NA	NA	O	NA
		Vireo leucophrys	NA	NA	F/I	NA
		Hylophilus ochraceiceps	NA	SSP	I	NA
		Vireolanius melitophrys	NA	NA	I	NA
		Cyclarhis gujanensis	NA	NA	I	NA

Order	Family	Species	E	PC	FG	FD
	Corvidae	*Cyanocorax yncas*	NA	NA	O	NA
		Cyanocorax morio	NA	NA	O	NA
	Hirundinidae	*Stelgidopteryx serripenis*	NA	NA	I	NA
		Hirundo rustica	NA	NA	I	NA
	Troglodytidae	*Campylorhynchus zonatus*	NA	NA	I	NA
		Catherpes mexicanus	NA	NA	I	NA
		Thryothorus maculipectus	NA	NA	I	NA
		Henicorhina leucosticta	NA	NA	I	NA
		Henicorhina leucophrys	NA	NA	I	FR
	Turdidae	*Sialia sialis*	NA	NA	O	NA
		Myadestes occidentalis	NA	SSP	F	NA
		Myadestes unicolor	NA	E	F	NA
		Catharus mexicanus	NA	SSP	O	NA
		Turdus grayi	NA	NA	I/F	NA
		Turdus assimilis	NA	NA	I/F	NA
	Mimidae	*Toxostoma longirostre*	NA	NA	F	NA
		Melanotis caerulescens	MX	NA	F	NA
	Parulidae	*Parula pitiayumi*	NA	NA	I	NA
		Geothlypis poliocephala	NA	NA	O	NA
		Euthlypis lachrymosa	NA	NA	I	NA
		Basileuterus culicivorus	NA	NA	I	NA
		Basileuterus rufifrons	NA	NA	I	NA
	Thraupidae	*Chlorospingus ophthalmicus*	NA	NA	O	NA
		Piranga leucoptera	NA	NA	O	NA
		Thraupis abbas	NA	NA	F	NA
		Cyanerpes cyaneus	NA	NA	O	NA
	Emberizidae	*Volatinia jacarina*	NA	NA	G/I	NA
		Sporophila torqueola	NA	NA	G	NA
		Sporophila minuta	NA	NA	G	NA
		Tiaris olivaceus	NA	NA	O	NA
		Atlapetes albinucha	NA	NA	I	NA
		Buarremon brunneinucha	NA	NA	I	FR

Order	Family	Species	EN	PC	FG	FD
		Arremonops rufivirgatus	NA	NA	G	NA
		Aimophila rufescens	NA	NA	G	NA
		Spizella passerina	NA	NA	G/I	NA
	Cardinalidae	*Saltator atriceps*	NA	NA	O	NA
		Cyanocompsa parellina	NA	NA	G/I	NA
	Icteridae	*Dives dives*	NA	NA	O	NA
		Quiscalus mexicanus	NA	NA	O	NA
		Molothrus aeneus	NA	NA	O	NA
		Icterus gularis	NA	NA	I/N	NA
		Icterus graduacauda	MX	NA	I/N	NA
		Amblycercus holosericeus	NA	NA	I	NA
		Psarocolius montezuma	NA	SSP	F	NA
	Fringillidae	*Euphonia hirundinacea*	NA	NA	G/F	NA
		Euphonia elegantissima	NA	NA	F	NA
		Carduelis pinus	NA	NA	G	NA
		Carduelis psaltria	NA	NA	G	NA
		Coccothraustes abeillei	NA	NA	G	NA

Annex 1. Total list of observed, heard and/or captured birds in taxonomic order in all the landscapes (according to AOU 1998). Abbreviations: EN, Endemic; PC, Protection Category; FG, Foraging Guild; FD, Forest Dependent; MX, endemic to Mexico; R, resident; M, migratory; E, endangered; SSP, subject to special protection; F, frugivorous; I, insectivorous; G, granivorous, N, nectarivorous; O, omnivorous; C, carnivorous; FR, forest dependent (species that breed exclusively in the forest); NA, not applicable.

Chapter 4

Influence of body size on coexistence of bird species.

Eurídice Leyequién, Willem F. de Boer, Antoine M. Cleef

Abstract

Interspecific competition is thought to be an important ecological force structuring ecological communities. Despite almost three decades efforts, there is no unifying theory that predicts patterns and processes in ecological communities. Body mass is an easily determined characteristic of animals that probably influences competition strength. Our objective is to examine the effect of body size (mass) on competitive interactions between bird pairs, ranging from hummingbirds species with small body mass to oropendula species with higher body mass. We hypothesized that the competition strength between competing species will show a negative relationship with body mass ratio, with the largest level of competition between species with the lowest body size ratio. Moreover species that have a greater overlap in resource use tend to exhibit stronger competition than species that overlap less in their resource use. Our results demonstrate that there is a significant negative relationship between bird body mass ratio and the competition strength i.e.; the larger the body mass ratio, the lower the competition strength thereby suggesting that high variation in body sizes amongst sympatric species may promote coexistence in communities. In addition, we did not find significant influence of foraging strategy type in the relationship between body mass ratio and competition strength.

Introduction

Interspecific competition has long been recognised as a major ecological force shaping the community patterns (Ricklefs 1975, Giller 1984, Wiens 1989, Keddy 2001). However, the mechanisms of such competition have remained elusive. Specifically, one attribute that probably influences competition strength in communities is body size of sympatric species. Brown and Maurer (1986) demonstrated that large species dominated smaller species in competition for food. French and Smith (2005) found a significant linear positive correlation between the mass of each species and its dominance rank, which critically influences the resource competition among species. In addition, Gotelli and Ellison (2002) found that body size in ant communities has important consequences for resource utilisation and species interactions where co-existing species exhibit regular spacing of body sizes. It has been also suggested that species can evade competition by differing in body size, as species with dissimilar body masses have dissimilar energetic requirements and capacities in terms of food searching, harvesting, or processing (Bowers and Brown 1982). However, the functional significance of body mass in community ecology remains unclear, and the relationship between coexistence and body size differences amongst ecologically similar species is still debated.

In addition, it is presumed that species similar in morphology, physiology, and behaviour will experience more intense competition (Brown and Wilson 1956, Hutchinson 1959, Grant 1972, Martin and Martin 2001). Particularly, species that exploit the same food resource (i.e.; same foraging strategy) in a similar way will be expected to experience competition, which separates the species ecologically within the region of niche by a guild. (Wiens 1989).

Phase portraits

Species interactions are the foundation of community ecology. However the identification of species interactions (e.g.; competition) and the quantitative measure of its strength have proven difficult in natural communities. Recently, several studies have concentrated on developing methods that can differentiate among these different "signals", and are able to identify the interaction type and to quantify the interaction strength using time series. Seip (1997) developed and tested a method, called the Key Factor Method, for characterising species interactions from ecological data using time series, plotted in so-called phase portraits. This method extracts quantitative variables that characterise species interactions. Later an extension of the Key Factor Method, called the Angle Frequency Method was developed and tested in modelling studies (Seip and Pleym 2000, Sandvik *et al.* 2002) and observational studies (Sandvik *et al.* 2003, Sandvik *et al.* 2004).

Both methods are developed from the traditional graphical analysis of species interactions in ecology (Lotka 1925, Volterra 1926, Rosenzweig and MacArthur 1963, MacArthur 1972). The Key Factor Method and the Angle Frequency Method show that species interactions (i.e.; prey-predation, competition, mutualism and facilitator-gainer) could all be distinguished by their biomass trajectories, where different types of ecological interactions will show unique patterns in phase portraits. This simple approach avoids past difficulties where studies relied on simplifying assumptions which are often violated in ecological synoptic data, or the need of extensive information about the studied community (Sandvik *et al.* 2004).In an ideal competition interaction, an increase of species *a* will cause a proportional decrease of species *b*. The corresponding phase portrait (i.e.; where the biomass of both species are plotted on the *x* and *y* axis) will show a sequences of trajectories along a line through the centre point at a 135° angle to the *x* axis, clearly distinctive from other interaction types (i.e.; mutualism, prey-predator and facilitator-gainer) (Gilpin *et al.* 1982, Seip 1997).

Moreover, even though a diverse of theories predict the conditions in which species interactions ought to be strong (Sarnelle 1994, Thompson 1999), it has proven to be difficult to determine the actual strength in a quantitative approach. Despite these difficulties, the aforementioned methods showed to be successful in differentiating competition interactions and the strength of the interactions in natural communities. Our objective is to examine the effect of body size on competitive interactions between species pairs of ecologically similar birds. We hypothesized that the competition strength between competing species will show a negative relationship with body size ratio, with the largest level of competition between species with the lowest difference in body size. Moreover we will test whether species that share food resources (i.e.; belonging to the same foraging guild) will exhibit stronger competition than species that differ in their resource use.

Materials and Methods

The bird species data set was a compilation of presence-absence and abundance data obtained from point count observations from the Cuetzalan Region (~ 54,200 ha) in the north-eastern mountain range of Puebla, Mexico, from November 2002 to November 2003 (Leyequien *et al. submitted*). We used standard point count techniques for bird detection (Bibby *et al.* 1992), with ±10 point counts, replicates per site per month. A modified double-observer approach was used for visual and sound avian detection (Parker 1991). Bird observations were recorded over 360° with a fixed-radius of 25 m, and a counting period (single count) of ten minutes (Dawson *et al.* 1997; Vielliard 2000). A distance of 100 m between point counts was used to avoid dependency between points' data. From this species data set we calculated the average number of birds for each species for each of the 12 months.

Selection of species and construction of the competition prototype.

From the bird species data set we selected 20 competitive species pairs and six non-competitive (see Table 1 for species list). The competitive species pairs were selected based on body mass (ranging from 6.2 g to 324 g) and foraging strategy, i.e.; (a) diet specialists, (b) opportunistic feeders which depends on a primary food source other than the secondary food source, and (c) generalists taking a wider range of diet. For the non-competitive pairs, species were selected based on body mass but with unrelated foraging strategies. To compare and estimate the similarity of these observed pairs to a theoretically ideal competition interaction, we constructed a prototype case where the assumptions underlying the expected patterns for competition were fulfilled, i.e.; competing species replace each other consequently; an increase in the biomass of one species causes a proportional decrease in the biomass of the species (Seip, 1997). In addition, we constructed purely random interactions to identify stochasticity in the pairwise interactions. The random interaction was constructed using random numbers created by a random number generator with 10.000 permutations.

Table 1. Bird species selected for pair-wise comparison. Status (S) code: R, resident; M, migratory. Diet code: I, insectivore; F, frugivore; N, nectarivore; G, granivore; O, omnivore.

Common Name	Scientific name	Order	Family	S	Diet
Red-billed Pigeon	*Columba flavirostris*	Columbiformes	Columbidae	R	G/F
White-tipped Dove	*Leptotila verreauxi*	Columbiformes	Columbidae	R	G/F
White-crowned Parrot	*Pionus senilis*	Psittaciformes	Psittacidae	R	F
Squirrel Cuckoo	*Piaya cayana*	Cuculiformes	Cuculidae	R	I
Wedge-tailed Sabrewing	*Campylopterus curvipennis*	Apodiformes	Trochilidae	R	N/I
White-bellied Emerald	*Amazilia candida*	Apodiformes	Trochilidae	R	N
Blue-crowned Motmot	*Momotus momota*	Coraciiformes	Momotidae	R	O
Golden-fronted Woodpecker	*Melanerpes aurifrons*	Piciformes	Picidae	R	I
Lineated Woodpecker	*Dryocopus lineatus*	Piciformes	Picidae	R	I
Dusky-capped Flycatcher	*Myiarchus tuberculifer*	Passeriformes	Tyrannidae	R	I/F
Great Kiskadee	*Pitangus sulphuratus*	Passeriformes	Tyrannidae	R	I/F
Social Flycatcher	*Myiozetetes similis*	Passeriformes	Tyrannidae	R	I/F
Sulphur-bellied Flycatcher	*Myiodynastes luteiventris*	Passeriformes	Tyrannidae	R	I
Masked Tityra	*Tityra semifasciata*	Passeriformes	Tyrannidae	R	F
Green Jay	*Cyanocorax yncas*	Passeriformes	Corvidae	R	O

Common Name	Scientific name	Order	Family	S	Diet
Brown Jay	*Cyanocorax morio*	Passeriformes	Corvidae	R	O
Band-backed Wren	*Campylorhynchus zonatus*	Passeriformes	Troglodytidae	R	I
Spot-breasted Wren	*Thryothorus maculipectus*	Passeriformes	Troglodytidae	R	I
White-breasted Wood-Wren	*Henicorhina leucosticta*	Passeriformes	Troglodytidae	R	I
Blue-gray Gnatcatcher	*Polioptila caerulea*	Passeriformes	Sylviidae	M	I
Clay-colored Robin	*Turdus grayi*	Passeriformes	Turdidae	R	I/F
White-throated Robin	*Turdus assimilis*	Passeriformes	Turdidae	R	I/F
Black-throated Green	*Dendroica virens*	Passeriformes	Parulidae	M	I
Wilson's Warbler	*Wilsonia pusilla*	Passeriformes	Parulidae	M	I
Golden-crowned Warbler	*Basileuterus culicivorus*	Passeriformes	Parulidae	R	I
Rufous-capped Warbler	*Basileuterus rufifrons*	Passeriformes	Parulidae	R	I
Yellow-throated Euphonia	*Euphonia hirundinacea*	Passeriformes	Thraupidae	R	G/F
Yellow-winged Tanager	*Thraupis abbas*	Passeriformes	Thraupidae	R	F
Green-backed Sparrow	*Arremonops rufivirgatus*	Passeriformes	Emberizidae	R	G
Dark-backed Goldfinch	*Carduelis psaltria*	Passeriformes	Fringillidae	R	G
Melodious Blackbird	*Dives dives*	Passeriformes	Icteridae	R	O
Great-tailed Grackle	*Quiscalus mexicanus*	Passeriformes	Icteridae	R	O
Altamira Oriole	*Icterus gularis*	Passeriformes	Icteridae	R	I/N
Black-headed Oriole	*Icterus graduacauda*	Passeriformes	Icteridae	R	I/N
Montezuma Oropendola	*Psarocolius montezuma*	Passeriformes	Icteridae	R	F

Form factors

We used the key factor method to characterise the species pairwise interactions (Seip, 1997). First, we constructed phase portraits for each species pair, including the random interaction and the ideal competitive pairs, where the average number of individuals for species x and y was plotted using the 12 synoptic samples. The phase portrait for the prototype competition interaction was plotted; the sequences of trajectories are depicted as a line through the centre point at a 135° angle to the x axis (Gilpin *et al.* 1982, Seip 1997, Seip and Pleym 2000). Thereafter, we extracted 13 form factors from each of the phase portraits of pairwise interactions. The form factors express attributes that characterise each phase portrait for competition (see Seip, 1997).

To calculate dissimilarity scores (distances) for each of the pairwise interactions with the prototype competition and random pairs we used clustering techniques based on principal component analysis (PCA) (Jongman *et al.* 1987). We constructed a matrix (27x13) that contained the independent form-factor variables, with 25 species pairs, one random interaction and one prototype competition interaction (rows), and 13 form factor parameters (columns). The scaling was done by inter-species correlations and the species scores were divided by standard deviations; data was not transformed, and centred by species. The resulting scatter plot shows points representing the interacting pairs in a coordinate system formed by the principal axes defined by the PCA. We used the scores of the first and second axis to calculate distance scores (D) from the interacting pairs to the prototype competition interaction. We used the Pythagorean Theorem to calculate the distance between each of the interacting pair (xy) and the reference competition point from their coordinates on the first and second principal component axis. These distance scores (D) were used as the dependent variable for hypothesis testing. To test if there were significant differences between the means of the random and potentially competitive pairs, we used a One-Way ANOVA procedure, with the dependent variable D, and the random/non-random pair interactions as independent factor. Next, we calculated the ratio in ln body mass (lnBM) for each of the interacting pairs body masses of the bird species were taken from Dunning (1993). Subsequently, we calculated the association between the lnBM ratio and the strength of competition (D) using a Pearson product-moment correlation coefficient (SPSS 12). Subsequently, we used a univariate general linear model (GLM with Type III sums of squares) for regression analysis, where the lnBM ratios were used as the covariate and the distance scores D as the dependent variable. We included two fixed factors to categorize the species pairs. The first fixed factor contained three groups, classifying the different foraging guilds into specialist-generalist classes. The second fixed factor was used to distinguish the classes for random/non-random pair interactions.

Results

Competition dissimilarity scores

The PCA scores for the assumed competitive and random interactions were dissimilar, forming distinct clusters, indicating signals of competition or stochasticity for the different species pairs (Figure 1). The first principal component axis explained 50% of the variability in the data, and the second axis explained 43%, totalling 93 % for the two axes.

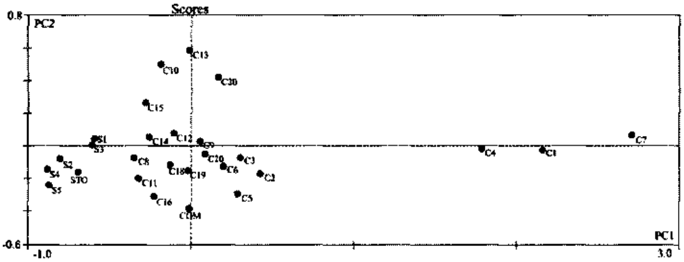

Figure 1. The score plot shows the first principal component in the x-axis, which explains 50% of the variance, and the second principal component in the y-axis, which explains 43% of the variance. It shows the position of the prototype interaction for competition (COM), the stochastic interaction (STO), the interacting pairs ($C_1 \ldots C_n$) and the random pairs ($R_1 \ldots R_n$).

The analysis of variance showed that the D scores of the random and competitive groups were significantly different ($F_{1,26} = 7.226$, $P = 0.015$) (Fig. 2), with a higher D score (i.e.; a larger distance from the competition reference point) for random pairs compared to potentially competing pairs.

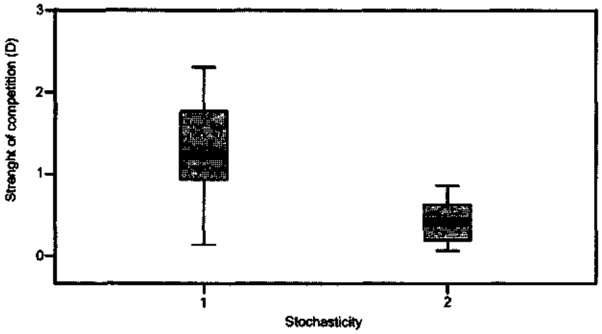

Figure 2. Significant differences in the mean D scores of the two random and competitive groups. 1 = Random, 0 = Competitive.

Effects of body mass on species competition

We found a significant negative correlation between the body mass ratio and the strength of competition (D) ($r = 0.536139$; $P = 0.02$, $R^2 = 0.446$) (Figure 3), note that the *y* axis ranges from strong to weak competition starting from the origin (0). In addition, the foraging guild included as a fixed factor in the model did not show a significant effect of foraging guild on competition strength (D).

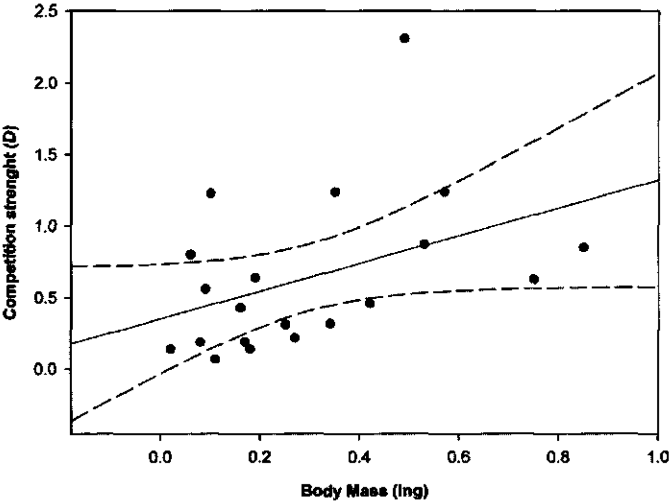

Figure 3. Positive correlation between the body mass ratio, i.e. |lnBMspecie1-lnBMspecies2|, and the strength of competition (D). Here the y axis ranges strong to weak competition starting from the origin (0).

Discussion

We have demonstrated a significant negative relationship between bird body mass and the competition strength; the larger the body mass difference between species pairs the lower the competition strength. This is no direct proof that species coexistence in communities is structured by difference in body masses, but evidence of size-related resource division sustains the conclusion that different size classes in the community may promote coexistence (Hutchinson 1959, Bowers and Brown 1982, Grant 1986, Ernest 2005). The encountered relationship may also result from restrictions imposed by size-dependent metabolic rates, biotic interactions, and energy availability to different size classes (Knouft 2002). Previous results have suggested that body size-mediated competition may be important for structuring energy use (Ernst 2005), and that energy is unequally available across body sizes. Therefore body sizes with the greatest access to resources would be favoured, resulting in species aggregations around specific masses (Holling 1992). Moreover, Brown and Bowers (1984) found that species of similar size (body mass) coexist less frequently in local communities suggesting that their co-occurrence is precluded by interspecific competition.

Our results indicate that similarity in body size (i.e.; a low body mass difference) increases competition, and thereby would promote character displacement. However, no data are available about the resource availability, so that it remains unclear whether the coexistence of species with relative similar body sizes is supported by unequal access to resources. In addition, morphological differences (i.e.; beak size and structure) in similar sized bird species that occupy the same habitat might promote coexistence by feeding niche differentiation (Grant 1966, 1968, 1999, Baldwin 1953, Freed *et al.* 1987, Conant 1988).

In addition, in accordance with our results, it has been suggested that body mass is the main factor influencing the dominance patterns of competitive species rather than diet specialisation (French and Smith 2005). In our results we did not find a significant influence of guild type in the relationship between body mass and competition strength. Alternative explanations are based on the theory of speciation and radiation where genetically variable traits in morphological differences (e.g.; beak size) may result in greater specialisation in obtaining some particular food, and therefore avoiding competition (Grant 2001). Besides, it has been suggested that allometric scaling partly determines coexistence through competition, thereby structuring species assemblages, especially between closely related species of similar size in the same guild (Brown and Bowers 1984).

Moreover, our results indicate that the body mass-competition strength relationship may be a valuable robust and powerful tool to identify patterns of community structure. However, further exploration of the body mass-competition relationship, considering different temporal and spatial scales, as well as different taxa should produce further insights into the forces shaping community structure and species coexistence. Moreover, correlativeexperiments that measure the competition intensity should be performed to corroborate existing gradient in competition intensity (i.e.; from diffuse competition to monopolistic competition) in the natural community.

Acknowledgments

We would like to acknowledge Knut L. Seip for his advice and comments, and Dr. Ir. Andre Schaffers for statistical consultation. Namgail Tsewang provided comments that improved this manuscript. This research was supported by the CONACYT grant 149557 to E. Leyequién

References

Baldwin, P.H. 1953. Annual cycle, environment and evolution in the Hawaiian honeycreepers (Aves: Drepaniidae). Univ. calif. Publ. Zool. 52: 285-398.

Bibby, C.J., Burgess, N.D. and Hill, D.A. 1992. Bird census techniques. Academic Press, California.

Bowers, M.A. and Brown, J.H. 1982. Body size and coexistence in desert rodents: chance or community structure? Ecology 63(2): 391-400.

Brown, J. H., and M. A. Bowers. 1984. Patterns and processes in three guilds of terrestrial vertebrates. Pages 282–296. In: Strong, Jr., D. R. , Simberloff, D., Abele, L. G. and Thistle, A. B. (eds.) Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, N.J.

Brown, J.H. and Maurer, B.A. 1986. Body size, ecological dominance and Cope's rule. Nature, 324: 248-250.

Brown, W.L. and Wilson, E.O. 1956. Character displacement. Systematic Zoology 5: 49-64.

Conant, S. 1988. Geographic variation in the Laysan Finch (Telespiza cantans). Evol. Ecol. 2: 270-282.

Dawson, D.K., Smith, D.R. and Robbins, C.S. 1997. Point count length and detection of forest Neotropical migrant birds. In: Ralph, C.J., Sauer, J.R. and Droege, S. Monitoring Bird populations by point counts. General technical Report PSW-GTR-149. Albany, California.

Dunning, J. B., Jr. 1993. CRC handbook of avian body masses. CRC Press, Boca Raton, Florida, USA.

Ernest, S.K.M. 2005. Body size, energy use, and community structure of small mammals. Ecology 86(6): 1407-1413.

Freed, L., Conant, S. and Fleischer, R.C. 1987. Evolutionary ecology and radiation of Hawaiian passerine birds. Trends ecol. Evol. 2: 196-203.

French, A.R. and Smith, T.B. 2005. Importance of body size in determining dominance hierarchies among diverse tropical frugivores. Biotropica 37(1): 96-101.

Giller, P.S. 1984. Community structure and the niche. Chapman and Hall, London.

Gilpin, M.E., Case, T.J. and Bender, E.A. 1982. Counterintuitive oscillations in systems of competition and mutualism. American Naturalist 119(4): 584-588.

Gotelli, N.J. and Ellison, A.M. 2002. Assembly rules for New England ant assemblages. Oikos 99: 591-599.

Grant, P.R. 1966. Ecological compatibility of bird species in islands. American Naturalist 100: 451-462.

Grant, P.R. 1968. Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. Syst. Zool. 17: 319-333.

Grant, P.R. 1972. Convergent and divergent character displacement. Biol. J. of the Linnean Soc.4: 39-68.

Grant, P.R. 1986. Interspecific competition, island biogeography and null hypotheses. Evolution 34: 332-341.

Grant, P.R. 1999. Ecology and evolution of Darwin's finches, 2nd ed., Princenton University Press.

Grant. P.R. 2001. Reconstructing the evolution of birds on islands: 100 years of research. Oikos 92: 385-403.

Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs 62: 447-502.

Hutchinson, G.E. 1959. Homeage to santa rosalia; or, why are there so many kinds of animals? American Naturalist 93: 145-159.

Jongman, R.H.G., Ter Braak, C.J.F. and Van Tongeren, O.F.R. 1987. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge.

Keddy, P.A. 2001. Competition. Kluwer Academic Publishers, Dordrecht.

Knouft, J.H. 2002. Regional analysis of body size and population density in stream fish assemblages: testing predictions of the energetic equivalence rule. Can. J. Fish. Aquat. Sci. 59: 1350-1360.

Leyequien, E., De Boer, W.F. and Skidmore, A.K. (*submitted*) Linking species-environment relationships and multiple spatial scales in community ecology.

Lotka, A. J. 1925. Elements of physical biology. Williams and Wilkins, Baltimore, Maryland, USA.

MacArthur, R.H. 1972. Geographical ecology. Harper and Row, New york, New York, USA.

Martin, P.R. and Martin, T.E. 2001. Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. Ecology 82(1): 189-206.

Owen-Smith, R.N. 1992. Megaherbivores. The influence of very large body size on ecology. Cambridge studies in ecology. Cambridge University Press, Cambridge.

Parker, T.A. 1991. On the use of tape recorders in avifaunal surveys. The AUK 108(2):443-444.

Ricklefs, R. 1975. Competition and the structure of bird communities. Evolution 29: 581-584.

Rosenzweig, M.L. and MacArthur, R.H. 1963. Graphical Representation and Stability Conditions of Predator-Prey Interactions. American Naturalist 97: 209–223.

Sandvik, G., Seip, K.L. and Pleym, H. 2002. An anatomy of interactions among species in a seasonal world. Oikos 99: 260-271.

Sandvik, G., Seip, K.L. and Pleym, H. 2003. Extracting signals of predation and competition from paired plankton time series. Arch. Hydrobiol. 157(4): 455-471.

Sandvik, G., Jessup, C.M., Seip, L.S. and Bohannan, B.J.M. 2004. Using the angle frequency method to detect signals of competition and predation in experimental time series. Ecology Letters 7: 640-652.

Sarnelle, O. 1994. Inferring process from pattern: trophic level abundances and imbedded interactions. Ecology 75: 1835-1841.

Seip, K.L. 1997. Defining and measuring species interactions in aquatic ecosystems. Can. J. Fish. Aquat. Sci. 54: 1513-1519.

Seip, K.L. and Pleym, H. 2000. Competition and predation in a seasonal world. Verh. Internat. Verein. Limnol. 27: 1-5.

Thompson, J.N. 1999. The evolution of species interactions. Science 284: 2116-2118.

Vielliard, J.M.E. 2000. Bird community as an indicator of biodiversity: results from quantitative surveys. Brazil. A. Acad. Bras. Ci. 72(3): 323-330.

Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. Nature 118:558–560.

Wiens, J.A. 1989b. The ecology of bird communities. Volume 2. Processes and variations. Cambridge University Press.

Chapter 5

Linking species-environment relationships and multiple spatial scales in community ecology

Eurídice Leyequién, Willem F. de Boer, Andrew K. Skidmore

Abstract

Biological communities are organised at multiple functional spatial scales and interactions between these scales determine both local and regional patterns of species richness. Despite the recognition that species-environment relationships are scale-dependent many ecologists have neglected the influence of scale on species richness patterns and processes. We analysed the influence of spatially explicit bio-physical variables on a bird community in a Mexican region denominated as an important area for bird conservation. Using a multiple scale approach with plot, patch and landscape level variables using abundance and presence-absence data, we demonstrated that landscape variables explained most of the variation in bird species in both abundance and presence-absence analyses in all explanatory sets. Interestingly, results demonstrated that variation in community structure was described best at family-level than at genera- or species-level. In addition, shade coffee plantations could provide habitat for neo-tropical migrants and forest-dependent birds (e.g.; endemic, protected species). Selecting the appropriate scale(s) of management in conservation strategies could have important implications for conservation of bird communities in Cuetzalan region.

Introduction

There is increasing recognition that community structure, species richness and abundances may depend on multiple spatial and temporal scales. Because ecological patterns, processes, and species responses are scale-dependent, issues of scale are central to ecology (Meentemeyer and Box 1987; Wiens 1989; Levin 1992, 1993; Dale *et al.* 1994; Bissonette 1997). Besides, biological communities are organised at multiple functional spatial scales and interactions between these scales determine both local and regional patterns of species richness (Loreau 2000; Mouquet *et al.* 2003; Kneitel and Chase 2004; Borcard *et al.* 2004). Understanding the species-environment interactions and how this affects the richness and abundance of biological communities will require integrating information from scaling effects in ecology.

Despite the recognition that diversity patterns are scale-dependent in species-environment relationships, many ecologists have neglected the influence of scale on these patterns and processes. Studies addressing relationships between community patterns and single causes at single hierarchical levels can be misleading (Wiens 1989; Borcard *et al.* 1992; Cushman and McGarigal 2002). Traditional community studies usually compare the marginal effects of factors at single scale. However, understanding relationships between community structure and environmental factors is greatly benefited by partitioning species-environment relationships to quantify the magnitude of the independent and confounded effects of each component (Cushman and McGarigal 2002). Recently, approaches to explain species diversity patterns using environmental variables at multiple scales have been attempted, where the independent and confounded effects are partitioned (Borcard *et al.* 1992; Liu and Brakenhielm 1995; Cushman and McGarigal 2002; Borcard *et al.* 2004; Cushman and McGarigal 2004). Despite these efforts, there is a lack of multi-scale and hierarchical approaches to understand the patterns in ecological communities' organisation, and the processes and causal mechanisms that act as driving forces.

In this paper we investigate the influence of spatially explicit bio-physical variables on a bird community at different taxonomic levels, incorporating different class groups (i.e.; migrants, endemics and species with special protection status), using a multiple scale approach applying three scales: plot, patch and landscape. We presented our approach using the data from a bird community study in Cuetzalan region, Mexico. We studied shade coffee plantations, a habitat with large ecological benefits, widely documented by many researchers (Greenberg *et al.* 1995; Moguel and Toledo 1998; Gobbi 2000; Liang *et al.* 2001; Soto-Pinto *et al.* 2000). We analysed both species abundance and presence-absence data because the different analysis may produce different results regarding the relative influence of species-environmental relationships among various spatial scales, as recoding from abundance to presence-absence data removes information regarding the ecological relationships between species abundance patterns and environmental gradients (Cushman and McGarigal 2004). Moreover, it has been suggested that descriptors of landscape structure and composition are stronger predictors of bird species assemblages and community composition (O'Neill *et al.* 1997; Miller *et al.* 2004). We therefore hypothesised that landscape-scale explanatory variables would be stronger predictors of bird species assemblages than patch-scale or plot-scale variables.

The variation in community structure, furthermore, is often sensitive to the number of variables (i.e.; taxa) used to describe each observation (i.e.; community) (Bouwman and Bailey1997). Most studies deal with species-level data to predict diversity patterns; however family-level data have the advantage that could facilitate interpretation of sources and sinks of biodiversity along spatial scales. Moreover, the distribution of whole families is often less complex, facilitating interpretation of the mechanisms leading to the observed patterns (Jacobsen 2004). It is therefore relevant to identify the taxonomic level at which the variation in community structure is best explained across different spatial scales. Thus, our second hypothesis is that the variation in community structure will be best described at family-level than genera- or species-level independent of the spatial scale of the analysis.

Methods

The species data set consisted of 170 bird species recorded in nine landscape frames of 10 x 10 km in 120 visits during the migratory and breeding seasons from November 2002 to November 2003 in the North Eastern Mountain range of Puebla, within the Cuetzalan region, Mexico. We used standard point count techniques for bird detection (Bibby *et al.* 1992). A number of ±10 point counts per site were performed. A modified double-observer approach was used for visual and sound avian detection (Parker 1991). Bird observations were recorded using over 360° with a fixed-radius of 25 m, and counting period (single count) of ten minutes (Dawson *et al.* 1997; Vielliard 2000). A distance of 100 m between point counts was used to avoid dependency between points' data.

The bio-physical data set consisted of three sub-sets of variables at three different scales: plot (0.025 hectares, n=36), patch (>1 to <3 km, n=12) and landscape (radius of 1, 3, 5, and 5-10 km, n=28). The plot sub-set included floristic, stand structure and vegetation cover variables (Table 1). The patch sub-set included patch configuration, human disturbance, water resource availability, Normalised Difference Vegetation Index (NDVI) average (as a proxy for vegetation vigour), average slope, and altitude variables. Subsequently, we derived a landscape sub-set that consisted of landscape composition metrics measured for each landscape frame at three different radiuses. We extracted variables at plot-scale *in situ* from 0.025 ha plots located in shade coffee plantations in each of the nine sampled landscape frames using standard quadrants (Kent and Coker 1992). For patch and landscape variables, we computed a multi-spectral image classification using an ETM satellite image (year 2003; 30 meters of spatial resolution). We applied a maximum likelihood classifier method, including prior probabilities to generate a land cover map, which contained seven classes (i.e.; agricultural land, grazing land, coffee plantations, forest, secondary vegetation, urban areas and water bodies). For patch-scale variables (i.e.; patch defined as the polygon containing bird point counts) we derived patch-configuration properties. Human disturbance variables were calculated using distance operations. As for distance to human settlements we used an increasing radius from 500, 1000, 1500 and 2000 meters, computed from the central point of each patch. Additionally, we calculated distance to primary or secondary roads, and also distance to water resources using the shortest linear path in any direction. Vegetation vigour variables were derived from NDVI values computed from a two–band combination index (Lillesand and Kiefer 1979). In addition, for altitude and slope variables, average values of each patch were calculated. In all patch variables calculations we used ILWIS 3.2 (Integrated Land and Water Information System, 1997).

Table 1 Explanatory variables contained by plot, patch and landscape sets, both for abundance and presence-absence analyses.

Explanatory set	Explanatory variable class	Description
Plot	Floristic	Total number of tree species in a plot of 0.1 ha per site within coffee plantations
		Total number of herb species in a plot of 0.1 ha per site within coffee plantations
	Stand structure	Standard deviation of overall tree heights
		Average height of coffee shrubs (m) in a plot of 0.1 ha per site
		Calculated density of tree species per hectare within coffee plantations
		Average number of coffee individuals in a plot of 0.1 ha per site within coffee plantations
	Vegetation cover	Total amount of crown spread of canopy in a plot of 0.1 ha per site within coffee plantations
		Standard deviation of crown spread of canopy in a plot of 0.1 ha per site within coffee plantations
		Average crown spread of canopy in a plot of 0.1 ha per site within coffee plantations
Patch	Configuration	Area (ha) of coffee plantation patch in which plot was located
		Perimeter of coffee plantation patch in which plot was located
	Disturbance factors	Distance from patch to human settlements in an increasing radius of 500, 1000, 1500 and 2000 m (total of 4 variables per patch)
		Distance from patch to the nearest primary or secondary road (m) per site
	Water availability	Distance from patch to the nearest water body (m) per site
	Vegetation vigour	Average of the Normalised Difference Vegetation Index for patch
		Standard deviation of the Normalised Difference Vegetation Index for patch
	Physical (abiotic)	Average elevation for bird point counts contained in a patch
		Average percentage of slope for bird point counts contained in a patch
Landscape	Landscape composition	Proportion of cp, f, sv, u, ag, g, w land covers (ha) with an increasing radius from 1, 3, 5 and >5 kilometres (total of 28 variables). Abbreviations: cp, Coffee plantations; f, Forest; sv, Secondary vegetation; u, urban settlements; ag, Agricultural area; g, grazing land; w, water bodies.

We conducted a series of multiple linear regressions with forward selection of independent variables for each species with the zero-truncated abundance data ($\alpha = 0.05$). Zero counts were only used in the logistic regression. Abundance data were checked for normality, and untransformed abundance data used in the analysis. First, we partitioned the total variance (R^2) of the species data, for each of the 114 species, explained for by the explanatory variables of seven different sets representing the individual and confounded influence of variables at plot, patch and landscape scales (Figure 1). This latter was calculated for the total number of species models and also for only those with $P \leq 0.05$.

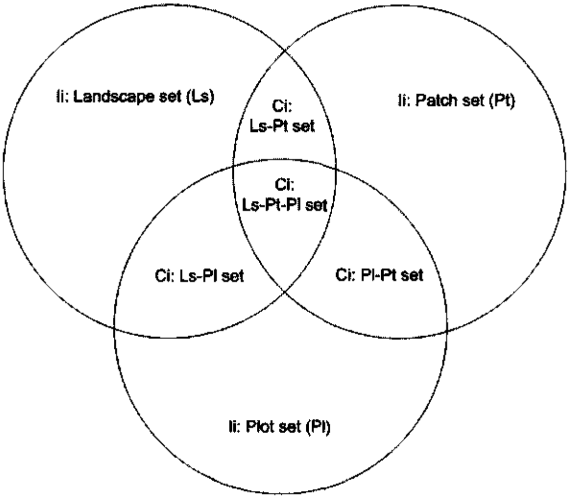

Figure 1. Explanatory sets representing the individual and confounded influence of variables at plot, patch and landscape scales. Abbreviations: Ii, Individual influence; Ci, confounded influence (adapted from Cushman and McGarigal 2004).

In addition, we calculated the total percentage of bird species with models with $P \leq 0.05$ for all individual explanatory sets and for those representing the influence of the largest explanatory sets. We also calculated the percentage of species for which each of the independent variables had an influence ($P \leq 0.05$), so that we could filter out the relative importance of specific independent variables within an explanatory set. However, the number of models with $P \leq 0.05$ increases when variables are added to the model due to spurious correlations. We therefore compared the observed number of species models against the expected number, calculated from a set of random variables (created by a random number generator) regressed against species, with 10,000 permutations. Finally, we grouped the species data to genera and families, and estimated the percentage of models at family and genera level with $P \leq 0.05$, for all explanatory sets. This approach enabled the comparison of the effect of taxonomic resolution on the analysis. A similar comparison of the multiple regression performance was executed to compare different species groups (resident-migrants, endemics and species with protection status). For presence-absence analyses we used a series of binary logistic regression with LR forward selection of independent variables, and consequently used the same modified variance partitioning approach, as used for the abundance analyses to quantify the variation (Nagelkerke R^2) in bird species presence explained by the single and confounded explanatory sets. Finally, we also checked for spurious correlations comparing the observed number of species models against the expected number following the same method as for abundance analyses.

Results

The explained variance (R^2) for the regression models for species abundance analysis varied between 0.43-0.60, whereas when only considering statistically significant models ($P \leq 0.05$) the range of explained variance decreased to 0.39-0.54 (Table 2). Results indicated that for statistically significant models, the total variance explained by the Landscape explanatory set individually (0.52) shows a marginal improvement compared to the Patch set (0.51), whereas compared to the Plot set (0.39) is much higher. The Landscape-Plot explanatory set increased the fraction of explained variance to 0.65. The largest Landscape-Patch-Plot set explained 54 % of the total variation, whereas Landscape-Patch set resulted in a total $R^2 = 0.50$. The marginal effect of the Landscape component in all explanatory sets was significantly higher than for the plot or patch subsets. The conditional effect of all components in each different explanatory sets had lower explanatory power than any individual component with the exception of the Patch-Plot set where the conditional effect was higher than the marginal effect of Patch or Plot. The explanatory sets for all models showed a general higher explained variance compared to only statistically significant models, with the exception of LS-Plot, LS and Patch sets.

The total percentage of species that presented regression models with $P \leq 0.05$ was between 54-65 % for all explanatory sets. The highest percentage of bird species that presented regression models with $P \leq 0.05$ was accounted for by the confounded influence of Landscape-Patch (65 %), whilst within this explanatory set, the highest percentage of species was obtained by the Landscape variables. However, in comparison to the expected values, the Landscape set presented less regression models with $P \leq 0.05$ (62%) than expected on the basis of spurious correlations alone (76%). The cause of this low explanatory power after accounting for spurious correlations could be the result of a large number of landscape variables in the analysis.

*Table 2 Results of the analyses of bird species abundance using multiple linear regressions, utilising forward selection for different explanatory sub-sets landscape, patch and plot. Mean R^2 for all species and R^2 for only the species that presented regression models with $P \leq 0.05$ are listed. Additionally, the percentage of species that presented regression models with $P \leq 0.05$ is given ($N = 114$), together with the expected percentage from spurious correlations. Also the percentage of species that presented regression models with $P \leq 0.05$ for each of the explanatory sets is given. * $P \leq 0.005$; ^{1} Expected. Abbreviations: Landscape (LS), Patch (PT) and Plot (PL).*

	Total variance			Variance explained (%)*						
	All species	Model	% species*^{1}	Individual			Confounded			
Set	R^2	R^2		LS	PT	PL	LS/PT	LS/PL	PT/PL	LS/PT/PL
LS-PT-PL	0.60	0.54	64 (92)	25	11	4	5	5	3	1
LS-PT	0.59	0.50	65 (87)	30	15	-	5	-	-	-
LS-PL	0.50	0.65	62 (85)	47	-	12	-	7	-	-
PT-PL	0.55	0.14	63 (66)	-	0.9	0	-	-	14	-
LS	0.46	0.52	62 (76)	52	-	-	-	-	-	-
PT	0.48	0.51	55 (46)	-	51	-	-	-	-	-
PL	0.43	0.39	54 (37)	-	-	39	-	-	-	-

A more appropriate way to study the impact of individual variables is to calculate the average number of regression models ($P \leq 0.05$) per variable for the different sets (Figure 2). Especially, in the larger spatial scale Landscape, explanatory variables produced more significant results than Patch or Plot variables. The percentage of regression models ($P \leq 0.05$) were significantly higher when increasing the spatial extent of the variables in the Landscape set (Spearman-$r = 0.587$, $P < 0.001$, $N = 28$). The most significant variables in Landscape-Patch set were landscape composition (46 % of the species with significant models; Table 3) and human disturbances (8 %). Landscape configuration, vegetation cover and human disturbance variable groups accounted for the majority of the significant regression models in the other explanatory sets.

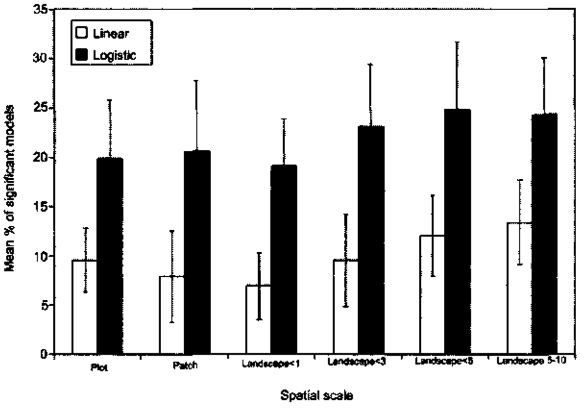

Figure 2. The average percentage (±s.d.) of models with $P \leq 0.05$, per variables for the spatial scales at which the variables were measured: Plot, Patch and Landscape sets (<1 km, <3 km, <5 km, and 5-10 km) for both the multiple linear regression and binary the logistical regression.

Table 3 Results of the analyses of bird species presence-absence using binary logistic regressions, utilising forward selection for different explanatory sub-sets landscape, patch and plot. Mean Nagelkerke R^2 for all species, and mean Nagelkerke R^2 for only the species that presented models with $P \leq 0.05$ are listed. Additionally the percentage of species that presented models with $P \leq 0.05$ is given ($N = 114$), together with the expected percentage from spurious correlations, as well as the percentage of species that presented models with $P \leq 0.05$ for each of the explanatory sets. $P \leq 0.005$; (1) Expected. Abbreviations: Landscape (LS), Patch (PT) and Plot (PL).*

		Total variance explained		Variance explained (%)*						
		All models	Models *	Marginal			Conditional			
Set	% species* 1	R^2	R^2	LS	PT	PL	LS/PT	LS/PL	PT/PL	LS/PT/PL
LS-PT-PL	71 (92)	0.68	0.69	26	16	6	8	8	4	0.9
LS-PT	70 (87)	0.67	0.68	35	19	-	14	-	-	-
LS-PL	67 (85)	0.61	0.62	40	-	11	-	11	-	-
PT-PL	66 (66)	0.49	0.48	-	21	11	-	-	16	-
LS	63 (76)	0.58	0.58	58	-	-	-	-	-	-
PT	63 (46)	0.42	0.42	-	42	-	-	-	-	-
PL	61 (37)	0.30	0.34	-	-	34	-	-	-	-

For presence-absence analysis the explained variance (Nagelkerke R^2) varied between 0.0.30-0.68, whereas when only considering statistically significant models ($P \leq 0.05$) the range of explained variance increased to 0.34-0.69. For only statistically significant models, the total variance explained by the Landscape (LS) explanatory set (0.58) was much higher than for Patch or Plot sets. The largest Landscape-Patch-Plot set had a Nagelkerke R^2 of 0.69, showing a marginal improvement compared to the Landscape-Patch set (Nagelkerke R^2 = 0.68). The Landscape-Plot and Patch-plot explanatory sets decreased the fraction of explained variance to 0.62 and 0.48 respectively. Similar to the species abundance analysis, the marginal effect of the Landscape sub-component in all explanatory sets was significantly higher than for the Patch and Plot subsets. The conditional effect of all components in each different explanatory sets had a lower explanatory power than any individual component with the exception of the Patch-Plot set where the conditional effect was higher than the marginal effect of Patch and Plot. For all the models, the explained variance for the largest LS-Patch-Plot showed a marginal improvement compared to LS-Patch and LS-Plot, whereas compared to Patch-Plot is much higher. The LS explanatory set explained a higher variance than Patch or Plot.

In the presence-absence analysis, the percentage of statistically significant models ($P \leq 0.05$) varied between 61-71 % for the different explanatory sets. In all explanatory sets, Landscape explanatory set accounted for the highest percentage of statistically significant models ($P \leq 0.05$) (Table 4). However, also here the patterns are concealed by the different number of variables used in the models. The Landscape set presented a lower percentage of models with $P \leq 0.05$ than expected, whereas the Patch and Plot sets produced a higher number of models with $P \leq 0.05$ than expected from spurious correlations. The most significant variables were also landscape configuration presenting the highest percentages of models with $P \leq 0.05$ of all explanatory sets, followed by human disturbance, stand structure and vegetation cover variable groups (Table 5).

Table 4 Percentage of species ($N = 114$) using abundance analysis ($P \leq 0.05$) for each of the different variables per explanatory set. Abbreviations: Landscape (LS), Patch (PT) and Plot (PL), Configuration (C), Abiotic (A), Human Disturbance (HD), Water availability (WA), Vegetation vigour (VV), Floristic (F), Stand Structure (SS) and Vegetation Cover (VC).

	Partial contribution of independent variable group (%)								
Set	LS variables	PT variables					PL variables		
	LSC	PTC	A	HD	WA	VV	F	SS	VC
LS-PT-PL	48	2	5	11	0	5	4	8	15
LS-PT	46	0.9	7	8	0	5	-	-	-
LS-PL	46	-	-	-	-	-	3	6	12
PT-PL	-	4	9	10	5	13	8	10	26
#variables per class	28	2	2	4	1	2	2	4	3

Table 5 Percentage of species ($N = 114$) using presence-absence analysis ($P \leq 0.05$) for each of the different variables per explanatory set. Abbreviations: Landscape (LS), Patch (PT) and Plot (PL), Configuration (C), Abiotic (A), Human Disturbance (HD), Water availability (WA), Vegetation vigour (VV), Floristic (F), Stand Structure (SS) and Vegetation Cover (VC).

	Partial contribution of explanatory variables group (%)								
Set	LS variables	PT variables					PL variables		
	LSC	PTC	A	HD	WA	VV	F	SS	VC
LS-PT-PL	49	3	4	16	0	8	4	13	5
LS-PT	61	4	6	18	2	7	-	-	-
LS-PL	64	-	-	-	-	-	4	18	24
PT-PL	-	4	10	22	0.9	9	4	25	30
# variables per class	28	2	2	4	1	2	2	4	3

Furthermore, the highest percentage of regression models with $P \leq 0.05$, was obtained by a family-level analysis for both analysis types, which increased the percentage of models from 54-65 % to 77-80 % (abundance analysis) or from 61-73 % to 73-80 % (presence-absence analysis; Table 6). However, a shift in the predictive power can be seen when comparing the two types of analyses. The presence-absence analysis typically performed better than the abundance analysis at species level, whereas the abundance analysis performed better at family level. Patch and landscape variable sets had, when grouping species to genera or families, the highest percentage of bird species that presented regression models with $P \leq 0.05$.

Table 6 Percentage of species for abundance and presence-absence analyses ($P \leq 0.05$) for each of the different explanatory set over different taxonomic levels: family, genera, and species.

	Levels of taxonomic resolution					
	Abundance analysis			Presence-absence analysis		
Set	Family	Genera	Species	Family	Genera	Species
LS-PT-PL	70	68	64	80	73	73
LS-PT	80	67	65	80	72	70
LS-PL	80	68	62	77	72	67
PT-PL	80	76	63	80	72	66
LS	80	67	62	77	72	63
PT	77	59	55	73	68	63
PL	80	61	54	73	68	61

Migrants and endemics

Neo-tropical migrants analyses (Table 7), showed more models with $P \leq 0.05$ than resident bird species analyses, with 44-72 % for the abundance analysis and 52-76 % for the presence-absence analysis, whereas permanent residents showed between 40-46 % and 45-53 %, respectively. For endemic species the percentage of models with $P \leq 0.05$ for only meso-American endemics for abundance and presence-absence analysis was 71-81 % and 71-90 % respectively, whereas for quasi-endemics and Mexican endemics this was far less, although this is based on only 8 bird species. The analysis of species with a protection status (special protected, or threatened) produced a higher percentage of species with models with $P \leq 0.05$ for presence-absence data than for species without protection (Table 7). The threatened species accounted for a higher percentage of models with $P \leq 0.05$ in the abundance analysis than the non-protected species.

Table 7 Percentage of species with regression models ($P \leq 0.05$) for abundance and presence-absence analyses for each of the different explanatory sets for different species groups. Abbreviations: MWR, Migratory winter resident; TM, Transitional migratory; SR, Summer resident; PR, Permanent resident; EMA, Endemic to Mesoamerica; QM, Quasi-endemic to Mexico; EMX, Endemic to Mexico; NE, Not endemic; SP, Special protection; T, Threatened; NP, No Protection Status. TNSC, Total number of species per category.

	Bird species per category of functional group (%)																	
	Abundance analysis									Presence-absence analysis								
	Migratory status			Endemic status			Protection			Migratory status			Endemic status			Protection		
Set	MWR	TM	PR/SR	EMA	QM/EMX	NE	SP	T	NP	MWR	TM	PR/SR	EMA	QM/EMX	NE	SP	T	NP
LS-PT-PL	72	71	44	76	53	58	50	75	54	76	57	53	90	75	65	81	88	70
LS-PT	72	71	45	81	50	57	63	75	63	72	57	51	86	63	64	81	75	68
LS-PL	64	43	46	76	63	56	63	75	61	68	57	47	71	50	63	75	75	63
PT-PL	68	71	43	71	50	58	56	75	62	64	43	49	90	63	57	69	75	64
LS	60	57	45	76	50	56	56	75	60	68	57	45	71	75	57	63	75	62
PT	56	43	40	76	38	44	56	63	54	64	29	47	90	25	64	63	63	63
PL	44	71	40	71	38	49	56	63	53	52	57	46	76	63	54	69	75	58
TNSC	25	7	82	21	8	89	16	8	90	25	7	82	21	8	89	16	8	90

Discussion

Our results supported our first hypothesis. Landscape variables explained most of the variation in bird species in both abundance and presence-absence analyses in all explanatory sets. Most previous studies suggested that landscape attributes (e.g.; composition and heterogeneity) are important factors in explaining species richness (Söderström and Pärt 2000; Wagner *et al.* 2000; Weibull *et al.* 2000). Titeux *et al.* (2004) had found that landscape variables explained most variation in bird species composition (27.5 %); others observed that landscape level factors explained a slightly larger amount of variation (12 %) than patch (8 %) or plot (11 %) factors (Grand and Cushman 2003). One possible reason explaining this landscape effect is that these large-scale spatial factors encompass processes and patterns (e.g.; dispersal, habitat heterogeneity) that strongly affect local species dynamics. In contrast, other studies (Miller *et al.* 2004; Cushman and McGarigal 2004) found that landscape variables had relatively lower explanatory power for bird community structure and composition. However, when there are strong differences among landscape elements that affect habitat quality (heterogeneity), landscape variables are likely to have greater explanatory power (Wiens *et al.* 1987).

For the analysed bird community, the fraction of explained variance in species assemblage did not differ considerably in abundance and presence-absence coded analysis. However, the total percentage of species that presented models with $P \leq 0.05$ was higher in the presence-absence analysis than in the abundance analysis, implying that presence-absence analysis gives a better explanation of single species responses. In contrast, Cushman and McGarigal (2004) found that abundance data provided a better general measure of species-environment relationships at community level than presence-absence data.

Additionally, based on our results, vegetation cover and stand structure variables, as well as the proportion of shade coffee plantations within the landscape, presented significant influence on bird species. Furthermore, human disturbances showed a significant influence on bird species. However, there is a risk of extrapolating results based on community analyses to individual species. Habitat affinities for certain species may be specific to a particular region, or a set of landscapes (Miller *et al.* 2004). Further work is needed to determine if the different patterns observed, associated with explanatory variables at different spatial scales, are broad ecological patterns. Individual species responses are associated to one or several scales, and it is therefore necessary to repeat the analysis for individual target species.

Consistent with our second hypothesis, the results demonstrated that the variation in community structure was described best at family-level than at genera- or species-level. Grouping species from species level to genera and then to family increased the percentage of species that presented models with $P \leq 0.05$. Grouping reduced the noise in responses of individual species, increasing the fit with the regression models. This is especially true for the multiple regression models and to a lesser extent to the logistic regression models. This has important consequences, as measuring richness at higher taxonomic levels, such as families, could help us to understand large-scale patterns in diversity. Previous studies suggested that using higher taxa to estimate the distribution of biological diversity retains some information on the complementarities of biotas (Williams and Gaston 1994; Williams *et al.* 1994; Gaston *et al.* 1995). However, because there are fewer higher taxa than species, a minimum representative set of areas also tends to be smaller. Nevertheless, this is not a serious limitation because it is the more realistic case for conservation questions regarding large-scale biodiversity (Williams 1997). Additionally, higher taxa can also be used to study hotspots of endemism (Williams *et al.* 1994).

The results of this study provide some insight into the spatial scale-dependency of diversity patterns in species-environment relationships, partitioning the effects of scale and their confounded influence on species patterns. Our study emphasizes the spatial scale-dependency of local and regional bird community structure in Cuetzalan region, Puebla, Mexico. We believe that our results give a better understanding of the relative importance of environmental factors over multiple spatially scales in explaining bird species assemblages. Furthermore, diversity patterns are dynamic at a given scale, influenced by factors at broader scales (Wiens 1989). Species diversity of a local community, for example, is influenced by speciation and extinction, and by range dynamics at regional or biogeographic scales (Ricklefs 1987). Besides, individual species as well as community level analyses can be derived from this approach, which has strong implications on understanding how habitat patterns at multiple scales influence bird community structure. However, is important to emphasise that conclusions about the relative importance of explanatory variables to explain patterns are restricted by the size of the individual units of observation. What is more, a difficulty in statistical models is the assumption of causality inherent to hypotheses, because direct causal relationships may be caused by common links to other factors (Wiens 1989).

Furthermore, these results could have important implications for conservation and management, specifically for bird communities of Cuetzalan region, Mexico. Conservation strategies strongly depend on aiming at the appropriate scale(s) of management, which is functionally significant for the involved species (Grand and Cushman 2003). Moreover, shade coffee plantations represent one of the main land uses in the region, and therefore by managing shade coffee plantations it is possible to provide habitat for neo-tropical migrants and forest-dependent birds, likewise endemic species or protected birds, as shown in our analysis.

Acknowledgements

We acknowledge the important contribution of S. Lopez de Aquino during the fieldwork phase; we also thank all members of Tosepan Titataniske Cooperative that allowed us to perform our field observations in their properties and for logistic support. We thank Idea Wild Organisation for providing essential fieldwork material. This research was supported by the CONACYT grant 149557 to E. Leyequién.

References

American Ornithologists' Union. 1998. Check-list of North American Birds, 7th ed: American Ornithologists' Union, Washington, D.C.

Bibby C.J., Burgess N.D. and Hill D.A. 1992. Bird census techniques. Academic Press, California

Bissonette, J.A., Harrison, D.J., Hargis, C.D. and Chapin, T.G. 1997. The influence of spatial scale and scale sensitive properties in habitat selection by American Martins. In: Bissonette, J.A. (ed.) Wildlife and landscape ecology: effects of patterns and scale. Springer-Verlag, New York, pp 310-330.

Borcard, D, Legendere, P, and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology 73(3):1045-1055

Borcard, D. and Legendere, P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecol Modell 153:51-68

Borcard, D., Legendere, P., Avois-Jacquet, C. and Tuomisto, H. 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology 85(7):1826-1832

Bowman, M.F. and Bailey, R.C. 1997. Does taxonomic resolution affect the multivariate description of the structure of freshwater benthic macro-invertebrate communities? Can J Fish Aquat Sci 54: 1802–1807

Cushman, S.A. and McGarigal, K. 2002. Hierarchical, multiscale decomposition of species-environment relationships. Landscape Ecology 17:637-646

Cushman, S.A. and McGarigal, K. 2004. Patterns in the species-environment relationship depend on both scales and choice of response variables. Oikos 105:117-124

Dale, V.H., Pearson, S.M., Offerman, H.L. and O'Neill, R.V. 1994. Relating patterns of land use change to faunal biodiversity in the central Amazon. Conserv Biol 8:1027-1036

Dawson, D.K., Smith, D.R. and Robbins, C.S. 1997. Point count length and detection of forest Neotropical migrant birds. In: Ralph, C.J., Sauer, J.R. and Droege, S. (eds) Monitoring Bird populations by point counts. General technical Report PSW-GTR-149. Albany, California, pp 35-43.

Gaston, K. J., Williams, P.H., Eggleton, P., Humphries, C.J. 1995. Large scale patterns of biodiversity: spatial variation in family richness. Proc R Soc Lond B 260:149-154

Gobbi, J.A. 2000. Is biodiversity-friendly coffee financially viable? An analysis of five different coffee production systems in western El Salvador. Ecol Econ 33:267-281

Grand, J. and Cushman, S.A. 2003. A multi-scale analysis of species-environment relationships: breeding birds in a pitch pine-scrub oak (*Pinus rigida-Quercus ilicifolia*) community. Biol. Conserv. 112:301-317

Greenberg, R., Salgado-Ortiz, J., Warkentin, I., Bichier, P. 1995. Managed forest patches and the conservation of migratory birds in Chiapas, Mexico. In: Wilson, M., Sader, S. and Santana, E. (eds.) The conservation of migratory birds in Mexico. Technical Publications, University of Maine, School of Natural Resources, pp 178-190.

ILWIS (Integrated Land and Water Information System) 1997. Application and reference guides. ILWIS Department,ITC, Enschede, The Netherlands, p. 352

Jacobsen, D. 2004. Contrasting patterns in local and zonal family richness of stream invertebrates along an Andean altitudinal gradient. Freshwater Biol. 49:1293–1305

Kent, M. and Coker, P. 1992. Vegetation description and analysis. A practical approach. John Wiley & Sons, New York.

Kneitel, J.M. and Chase, J.M. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecol. Letters 7:69-80

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967

Levin, S.A. 1993. Concepts of scale at the local level. In: Ehleringer, J.R. and Field, C.B. (eds.) Scaling physiological processes: leaf to globe. Academic Press, New York, New York, USA.

Liang, L., Stocking, M., Brookfield, H. and Jansky, L. 2001. Biodiversity conservation through agrodiversity. Global Environmental Change. 11:97-101

Lillesand, T.M. and Kiefer, R.W. 1979. Remote Sensing and Image Interpretation. John Wiley & Sons, New York.

Liu, Q.H. and Brakenhielm, S. 1995. A statistical approach to decompose ecological variation. Water, Air, and Soil Poll.1-4:61-87

Loreau, M. 2000. Are communities saturated? On the relationship between α, β and γ diversity. Ecol. Letters 3:73-76

Meentemeyer, V. and Box, E.O. 1987. Scale effects in landscape studies. In: M. G. Turner (ed.) Landscape heterogeneity and disturbance. Springer- Verlag, New York, USA, pp 15-34

Miller, J.R., Dixon, M.D. and Turner, M.G. 2004. Response of avian communities in larger-river floodplains to environmental variation at multiple scales. Ecological applications 14(5):1394-1410

Moguel, P. and Toledo, V.M. 1998. Biodiversity conservation in traditional coffee systems of Mexico. Conserv. Biol.13(1):11-21

Mouquet, N., Munguia, P., Kneitel, J.M. and Miller, T.E. 2003. Community assembly time and the relationship between local and regional species richness. Oikos 103:618-626

O'Neill, R.V., Hunsaker, C.T., Jones, K.B., Ritters, K., Wickham, J.D., Schwartz, P.M., Goodman, I.A., Jackson, B.L. and Baillargeon, W.S. 1997. Monitoring environmental quality at the landscape scale. Bioscience 47:513-519

Parker, T.A. 1991. On the use of tape recorders in avifaunal surveys. The AUK 108(2):443-444

Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. Science 235:167-171

Söderström, B. and Pärt, T. 2000. Influence of Landscape Scale on Farmland Birds Breeding in Semi-Natural Pastures. Conserv. Biol. 14(2):522-533

Soto-Pinto, L., Perfecto, I., Castillo-Hernandez, J. and Caballero-Nieto, J. 2000. Shade effect on coffee production at the northern Tzeltal Zone of the state of Chiapas, Mexico. Agric., Ecosyst. and Environ. 80:61-69

Titeux, N., Dufrene, M., Jacob, J.P., Paquay, M. and Defourny, P. 2004. Multivariate analysis of a fine-scale breeding bird atlas using a geographical information system and partial canonical correspondence analysis: environmental and spatial effects. J. Biogeogr. 31:1841-1856

Van Langevelde, F. 2000. Scale habitat connectivity and colonization in fragmented nuthatch populations. Ecography 23:614-622

Vielliard, J.M. 2000. Bird community as an indicator of biodiversity: results from quantitative surveys. Brazil. A. Acad. Bras. Ci. 72(3):323-330

Wagner, H.H., Wildi, O., Ewald, K.C. 2000. Additive partitioning of plant species diversity in an agricultural mosaic landscape. Landscape Ecol. 15(3):219-227

Weibull, A.C., Bengtsson, J. and Nohlgren, E. 2000. Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. Ecography 23:743–750

Wiens, J.A., Rotenberry, J.T. and Van Horne, B. 1987. Habitat occupancy patterns of North American shrub steppe birds: the effects of spatial scale. Oikos 48:132-147

Wiens, J.A. 1989. Spatial scaling in ecology. Func. Ecol. 3:385-397

Williams. P.H. and Gaston, K.J. 1994. Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? Biol. Conserv. 67:211-217

Williams, P.H., Humphries, C.J., Gaston, K.J. 1994. Centres of seed-plant diversity: the family way. Proc. R. Soc. Lond. B 256:67-70

Williams, P.H., Gaston, K.J. and Humphries, C.J. 1997. Mapping biodiversity value worldwide: combining higher-taxon richness from different groups. Proc. R. Soc. Lond. 264:141-148

Chapter 6

Capturing the fugitive: applying remote sensing to terrestrial animal distribution and diversity. A review.

Euridice Leyequien, Jochem Verrelst, Martijn Slot, Gabriela Schaepman-Strub, Ignas M. A. Heitkönig, Andrew Skidmore

Abstract

Amongst many ongoing initiatives to preserve biodiversity, the Millennium Ecosystem Assessment again shows the importance to slow down the loss of biological diversity. However, there is still a gap in the overview of global patterns of species distributions. This paper reviews how remote sensing has been used to assess terrestrial faunal diversity, with emphasis on proxies and methodologies, while exploring prospective challenges for the conservation and sustainable use of biodiversity. We grouped and discussed papers dealing with the faunal taxa mammals, birds, reptiles, amphibians, and invertebrates into five classes of surrogates of animal diversity: 1. habitat suitability, 2. photosynthetic productivity, 3. multi-temporal patterns, 4. structural properties of habitat, and 5. forage quality. It is concluded that the most promising approach for the assessment, monitoring, prediction, and conservation of faunal diversity appears to be the synergy of remote sensing products and auxiliary data with ecological biodiversity models, and a subsequent validation of the results using traditional observation techniques.

Introduction

The importance of biodiversity conservation is widely recognised as there is a general concern about its current status and about the responses by society to present and future environmental changes (Gaston, 2000; Mace, 2005, Millennium Ecosystem Assessment, 2005). Biodiversity definitions include different levels of organisation of biological variation and richness, from genes and species to ecosystems. Noss (1990) expressed the variation at each of these hierarchical levels in terms of three spheres: composition (e.g. the genes of different cattle races), structure (e.g. the ratio of large versus small bodied animals), and function (e.g. forage consumption). However, this multi-faceted nature of the term biodiversity makes it a difficult concept to capture in one definition or description, so it cannot be measured in a single parameter (Noss, 1990; Wolfang, 2003; Scholes and Biggs, 2005). The challenge to measure these levels and spheres of organisation of biological variation has led to the search of relevant biological indicators from which biodiversity could be measured. These indicators include species, habitats, and eco-regional characteristics, which can be sampled in the field, categorized, and interpreted.

Despite the efforts of scientists and policy makers to reduce the rate of species loss, there is still a gap in the overview of continental and global patterns of species distributions (Brooks *et al.*, 2001; Ceballos *et al.*, 2005). Remotely sensed data contribute to the assessment and monitoring of biodiversity from local to global scales (Murthy *et al.*, 2003), and over time, with spatially continuous coverage. Since the 1980s, satellite multispectral imagery became a common tool, particularly in exploring the composition of biodiversity, i.e., species richness (e.g. Saxon, 1983; Nagendra, 2001). Several articles reviewed the potential and contribution of remote sensing data products to assess terrestrial vascular plant species diversity (e.g., Stohlgren *et al.*, 1997; Gould 2000; Griffiths *et al.*, 2000; Nagendra 2001). This review article has the purpose to summarise the historical development and prospective approaches in which remote sensing was used to assess and monitor terrestrial faunal diversity. While an important methodology of plant diversity consists in direct mapping of species and associations (Nagendra 2001), the fugitive and secretive nature of animals requires approaches based on proxies and surrogates. Based on the currently applied methodologies, the following broad categories were identified, reflecting chronological approaches in this field: 1. habitat suitability mapping, relying on species-habitat associations, 2. spatial heterogeneity assessment based on primary productivity, 3. temporal heterogeneity assessment, 4. mapping of structural properties of habitat, and 5. mapping of plant chemical attractants, relying of the influence of land cover attractants on fauna, such as forage quality. These latter categories enclose the range from the most frequently used methodologies applied to terrestrial animal taxa to the latest approaches found in literature. In addition, direct and indirect measurements of species diversity and distribution are illustrated. Within each approach, the literature was furthermore grouped following the taxonomical system: mammals, avifauna, reptiles, amphibians, and invertebrates. These taxonomic groups represent the most frequently studied taxa, and reflect different challenges to the application of remote sensing to assessing animal species presence. The discussion evaluates theory development and the potential use of remote sensing techniques for terrestrial animal ecology studies related to species diversity, and the prospective direction of remote sensing approaches applied to this field.

Assessing species richness through habitat suitability mapping

The most straightforward approach to estimate animal distribution or species richness from remotely sensed data is to identify and detect animal habitat suitability. A habitat is the local environment in which an organism normally lives and grows. In order to map habitat, knowledge of habitat preferences and the requirements of the species of interest is combined with airborne or satellite data, biophysical, geophysical data, and meteorological data.

For ecological biodiversity assessments, field surveys are usually executed to collect data on species distribution, habitat use or characteristics of nesting, breeding or burrowing sites. Additionally, habitat use patterns can be derived from analysis of movements of radio or satellite collared individuals (e.g. Kanai *et al.*, 1994; Bechtel *et al.*, 2004). Using remote sensing, these local measurements can be extrapolated to cover a large region of interest, and estimate habitat suitability. After collecting field survey data, spectral *in situ* measurements at the locations of the ecological assessments or the spectral properties of the pixel corresponding to this location are used as training data to classify the imagery for a larger area. Resulting maps with spatially discrete habitat types can then be analysed using a wide array of statistical techniques to validate classified habitat with species population data. The main problem with this approach is the assumption that empirical conditions at the field survey point may be extrapolated over a large area. Such an assumption needs to be carefully tested otherwise the resulting maps will be biased by the sample points. In other words, habitats may not be described and stratified in ecologically meaningful terms, which could limit the predictive value of the relationships between reflectance data and species distribution within and beyond the study area. The following sections demonstrate how widely remote sensing approaches are applied to estimating habitat suitability in terrestrial environments throughout many animal taxa.

Mammals

One of the earliest publication involving satellite imagery to detect mammalian species dates from 1980, when Loffler and Margules estimated the distribution of hairy nose wombat (*Lasiorhinus latifrons*) in southern Australia by identifying burrows and mounts from Landsat imagery. Also in Australia, Saxon (1983) used Landsat imagery to locate a habitat suitable for the re-introduction of rufous hare-wallabies *Lagorchestes hirsutus*. Later in the 1980s this approach of relating remotely sensed land cover types to habitat suitability, was used amongst others for assessment of the habitat of the giant panda, *Ailuropoda melanoleuca* (De Wulff *et al.*, 1988), elk, *Cervus elaphus* (Eby and Bright, 1985) and white-tailed deer, *Odocoileus virginianus borealis*, (Ormsby and Lunetta, 1987). The method of habitat mapping by means of signature classification was applied throughout the 1990s (e.g. Huber and Casler, 1990; Del Valle *et al.*, 1997; Fuller *et al.*, 1998; Cardillo *et al.*, 1999; Richards, 1999) and is still used today (e.g. Oindo *et al.*, 2003; Sharma *et al.*, 2004).

Other authors tried to derive general patterns of species richness in relation to habitat (White *et al.*, 1997; Mason *et al.*, 2003). Fuller *et al.* (1998) combined field surveys of plants and animals with satellite remote sensing of broad vegetation types to map biodiversity in the Sango Bay area in Uganda. They identified 14 land-cover classes from reflectance characteristics and validated the results with field surveys, recording 86% correspondence between field and map data. The field surveys included flowering plant species, dragonflies, butterflies, fish, amphibians, reptiles, birds and mammals. These species data were used to generate biodiversity ratings, based on species 'richness' and 'rarity', which could be related to the vegetation cover. Similarly, Cardillo *et al.* (1999) predicted species richness and occurrences of terrestrial mammals from Principal Component Analysis (PCA) ordinated land cover variables from the Land Cover Map of Great Britain. Because of the high proportion of species with geographic distributions changing independently of land cover, the predictive strength of the land cover data for species richness assessment was however limited.

Heitkönig *et al.* (2003) directly correlated the distribution of large mammalian herbivores in the Okavango delta in Botswana with Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM+) reflectance data. Animal distribution was sampled along field transects, while registering the locations with a Global Positioning System (GPS), and the recorded animal presence was related to the spectral signature of the location. A multivariate approach allowed for the distinction of occurrence of several mammalian species, including elephant (*Loxodonta africana*), zebra (*Equus burchelli*), and impala (*Aepyceros melampus*). However, species with low densities in the field, including giraffe (*Giraffa camelopardis*) and wildebeest (*Connochaetes taurines*), were not successfully distinguished. Bechtel *et al.* (2004) used a comparable method for woodland caribou (*Rangifer tarandus caribou*). Because habitat maps were incomplete for their study area, they correlated spectral information obtained from Landsat 5 TM satellite data with Global Positioning System (GPS) locations of satellite collared, and Very High Frequency Radio locations of collared animals. First, a statistical approach was used to automate the classification of each satellite imagery pixel to generate landscape classes based on characteristic spectral signatures. These classes were then regrouped corresponding to their relation with the GPS-registered animal presence. The resulting map indicated the woodland caribou use and avoidance of areas, based on corresponding identified spectral classes of the satellite imagery.

Coops and Catling (1997) used airborne multispectral videographic data to accurately predict the complexity of fauna habitat across forested landscapes. This video system provides a tool for stratifying the forest into fauna habitats to predict the composition, spatial distribution and abundance of faunal groups that are known to prefer the eucalypt forests (Coops *et al.*, 1998; Catling *et al.*, 2000). Coops and Catling (2002) then related habitat quality based on complexity scores, to predict future relative abundance of the long-nosed potoro (*Potorous tridactylus*) and the large wallabies (red-necked wallaby, *Macropus rofogriseus*, and swamp wallaby, *Wallabia bicolour*) across landscapes.

Mammals are relatively well studied and their habitat preference is quite well documented, which is of vital importance for successfully correlating mammal occurrence to remotely sensed habitat data. Many species however, (e.g. generalist species) use more than a single distinct vegetation type, and non-herbivore species tend to have little direct association with a habitat or vegetation type that can be remotely sensed (e.g. Cardillo *et al.*, 1999; Cowley *et al.*, 2000). In other cases, there is a limitation to the use of remotely sensed data due to the animals' elusive nature. The predictive value of mammal-habitat relationships will also be limited for species for which the habitat preference changes with geographical position (e.g., Cardillo *et al.*, 1999). Another issue that complicates the link between species presence and habitat characteristics is the socio-biology of the species. The predicted distribution of guanaco (*Lama guanicoe*), for example, proved to have little correlation with the real distribution and densities (Del Valle *et al.*, 1997). The socio-biology of the species, classified as 'resource defence polygyny' (Franklin, 1983) where a dominant male will defend his territory against other males, in combination with interspecific competition with sheep and anthropogenic influences, was identified as the possible reason for the inaccuracy of the predictions.

Avifauna

Since the 1980s, remote sensing has been widely used in assessing and monitoring bird distribution and habitats (e.g. Baines *et al.*, 1986; Perras *et al.*, 1988, Minton *et al.*, 2003; Venier *et al.*, 2004). Habitat maps are aggregated from land cover maps that are generally produced from Landsat or radar imagery. The habitat maps are then combined with data from bird composition and abundance surveys, yielding distribution and density maps (e.g. Palmeirim, 1988; Schwaller *et al.*, 1989; Avery and Haines-Young, 1990; Kanai *et al.*, 1994; Morrison, 1997; Debinski *et al.*, 1999; Osborne *et al.*, 2001; Taft *et al.*, 2003; Fuller *et al.*, 2005; Prins *et al.*, 2005).

Apart from Miller and Conroy (1990), who classified data from the Satellite Probatoire d'Observation de la Terre (SPOT) to predict Kirtland's warbler (*Dendroica kirtlandii*) occurrence in the Bahamas based on vegetation types, most studies applied Landsat TM data for the prediction of single bird species habitat suitability. Knowledge and ground studies on habitat preferences for nesting and feeding were combined with Landsat data for sedentary (e.g. Osborne *et al.*, 2001; Johnson *et al.*, 1998; Hurlbert and Haskell, 2003) as well as migratory birds (e.g. Green *et al.*, 1987; Avery and Haines-Young, 1990; Sader *et al.*, 1991). Environmental criteria (i.e. vegetation cover, landscape characteristics) derived from Landsat data were used to assess the location of nesting sites of buzzards, *Buteo buteo*, (Austin *et al.*, 1996) and great sandhill cranes, *Grus canadensis*, in Minnesota (Herr and Queen, 1993). Further, the probability of occurrence of 14 out of 23 species of land birds in Maine (Hepinstall and Sader, 1997), as well as winter distributions of sage grouse (*Centrocercus urophasianus*) in Utah (Homer *et al.*, 1993) were successfully predicted using Landsat imagery. Kanai *et al.* (1994) analysed data of satellite collared red crowned cranes (*Grus japonensis*), hooded cranes (*Grus monacha*) and white-naped cranes (*Grus vipio*) to determine habitat use and species distribution. Subsequently, a combination of Landsat with Marine Observation Satellite- Multi-spectral Electronic Self-scanning Radiometer (MOS1 MESSR) data was used to derive the characteristics of seven sites that were identified as crane habitat. The method proved very helpful, because the large crane habitats cannot easily be monitored through ground studies.

Some recent studies focus on avifaunal diversity, leading from single species assessments to diversity predictions for whole taxa. Nøhr and Jørgensen (1997) related avian diversity in northern Senegal to landscape diversity, while Debinski *et al.*, (1999) categorized habitats in the Greater Yellowstone ecosystem based on Landsat data and then determined the relationship between habitat categorizations and plant, bird, and butterfly species distribution patterns. They found that sites of highest species richness coincided for plants, birds, and butterflies. This coincidence of 'hotspots' of different taxa shows those indicator taxa could be used to assess an areas' biodiversity status. Also in the Greater Yellowstone ecosystem Saveraid *et al.* (2001) assessed potential bird habitats for 11 types of montane meadows. Landsat imagery was further analyzed to identify habitats for migratory birds in Costa Rica (Sader *et al.,* 1991), and to predict bird species richness in boreal agricultural-forest mosaics in south-western Finland (Luoto *et al.*, 2004). Fuller *et al.* (1998) related the diversity of various taxa, including flowering plant species, dragonflies, butterflies, fish, amphibians, reptiles, birds and mammals in Uganda to vegetation cover derived from Landsat. Areas of bird endemism in East Africa were related to remotely sensed climatic variables by Johnson *et al.* (1998), to obtain general patterns of bird species richness. It was concluded that contemporary environmental conditions, ultimately determined by climate, appear to account for a substantial fraction of the observed variation in the distribution of endemic bird areas.

The above bird studies demonstrate that habitat classifications based on remote sensing data can be successful for sedentary and migratory birds, as well as bird communities. However, the spatial and spectral scale of the data appears to be a crucial factor in the prediction of bird occurrence patterns. Laurent *et al.* (2005) investigated the potential of using unclassified spectral data for predicting the distribution of three bird species by varying 1) the window size used to average spectral values in signature creation, and 2) the threshold distance for recording bird observations. Accuracy statistics for each species were affected by the detection distance of point count surveys used to stratify plots into presence and absence classes. Thus, the accuracy of wildlife occurrence maps classified from spectral data will differ given the species of interest, the spatial precision of occurrence records used as ground references and the number of pixels included in spectral signatures. Akin to mammal studies, a low number of bird records per habitat type decrease the power of the statistical tests to distinguish differences between habitat use and availability in bird studies (Garshelis 2000).

Reptiles and amphibians

Only two studies on mapping reptilian or amphibian habitats using remote sensing data were identified, but both were innovative and successful. Raxworthy *et al.* (2003) assessed and predicted the distribution of known and unknown chameleon species in Madagascar, using a combination of satellite data (Moderate Resolution Imaging Spectroradiometer (MODIS) and historical and recent chameleon observations on the island. A generic algorithm for rule-set prediction (GARP) was used to delineate ecological niches, based on environmental geographical information system (GIS) data, and to predict geographical distributions of species. This study leads to the discovery of seven new species of chameleon.

Scribner *et al.* (2001) used in situ and remotely sensed data of the aquatic and terrestrial environment, to examine the correlation of habitat characteristics with population demographic and genetic characteristics of the common toad (*Bufo bufo*). This study was the only one (encountered) that focussed on the sub-species level. Allelic (i.e. genetic) richness, population size, and toad presence were mostly associated with terrestrial habitat variables, like pond density, availability of woodlands, hedgerows, and anthropogenic development.

While remotely sensed data for animal diversity assessment using habitat characteristics is increasingly used, its application to reptile and amphibian diversity remains poorly explored. Despite the success of the above presented studies, there is still a gap between ecological theory and the application of remotely sensed data. One of the problems is that there is no clear understanding over which spatial scales the species-habitat relationships apply for species of interest, specifically those of limited vagility. The complex life histories of amphibians and their secretive behaviour add to the challenge of successfully using remotely sensed data.

Invertebrates

Remotely sensed imagery is increasingly used to detect insect habitats or the effects of insects on their environment (Riley, 1989; Hay, 1997). Habitat patch characteristics essential for many insects, such as micro-variations in wetlands, grasslands and forests are too small to be identified using conventional imagery (Fisher, 1997; Cracknell, 1998). A recent study tackled the problem of sampling scale inherent to insect habitat mapping by comparing two satellite sensors with different spatial resolution (SPOT and Landsat) and, as a result, optimized insect species richness mapping at a landscape level (Chust *et al.*, 2004).

One of the most common cases of insect habitat mapping deals with swarming insects that have the potential to destroy their habitat. Defoliating insects, once present in a food-endowed environment, quickly expand to a devastating outbreak consuming their primary resource. This allows a precise distribution mapping through classification of vegetation defoliation or discoloration using remote sensing. For instance, Joria *et al.* (1991) successfully classified gypsy moth (*Choristoneura fumiferana*) defoliation into three damage classes by delineating affected areas with Landsat data. Franklin and Baske (1994) differentiated four defoliation levels of spruce budworm (*Choristoneura fumiferana*) in a balsam fir forest analyzing SPOT HRV data. The spectral response of the Jack Pine (*Pinus banksiana*) canopy, attacked by the Jack Pine budworm (*Choristoneura pinus pinus*), was first described by Hall *et al.* (1995). Landsat TM images before and after defoliation were acquired to map the top-kill severity. Another aggressive defoliator actor widely documented is the mountain pine beetle (*Dentroctonus ponderosa*) which is primarily hosted by the lodgepole pine (*Pinus contorta*). Combinations of SPOT multispectral and panchromatic bands and PCA-transformations were evaluated by Sirois and Ahern (1988) to determine their ability to detect mountain pine beetle mortality ('red attack'). A conceptual model based on spectral brightness-greenness was developed and tested (Price and Jakubauskas, 1998) to relate beetle infestation to spectral properties. Similar examples are reported for pear thrips (*Taeniothrips inconsequens*) (Vogelmann and Rock, 1989); the black-headed budworm (*Acleris variana*) (Franklin *et al.*, 1994; Luther *et al.*, 1997); the aspen tortrix (*Choristoneura conflictana*) (Hall *et al.*, 2003); and the Douglas-fir beetle (*Dendroctonus pseudotsugae*) (Lawrence and Labus, 2003).

In more diverse ecosystems, notable efforts to create habitat maps from remotely sensed data were made for butterfly and beetle species. Butterfly species are often host-specific and their diversity may correlate with underlying plant diversity. Thus, Debinski *et al.* (1999) reported that several rare butterfly species significantly correlated with remotely sensed habitat types in the Greater Yellowstone Ecosystem. The modelling of Luoto *et al.* (2002) supported the findings that specialist butterfly species distribution is closely related to remotely sensed habitat types. British ground (*Coleoptera, Carabidae*) (Eyre *et al.*, 2003a) and water beetle (*Coleoptera spec.*) species pool distribution (Eyre *et al.*, 2003b) strongly correlated with satellite-derived land cover data. Chust *et al.* (2004) successfully assessed woodland invertebrate taxa distribution based on satellite imagery.

Compared to other taxonomic groups, the ability of remote sensing data to contribute to the mapping and prediction of occurrence of invertebrate diversity appears to be poorly investigated. The current trend of studies on terrestrial invertebrates shows an emphasis on insects, whereas for other taxa there is no literature known to the authors. The majority of articles concentrated on insects that are considered pests, and their effects on crops or forests. However, very few studies deal with conservation efforts. Besides, the approach is limited to habitat-insect relationships using only beta diversity (i.e. local diversity, within-community component) whereas gamma diversity (i.e. total regional diversity) is not taken into account.

Summary

Habitat suitability is widely used as a remotely sensed proxy for species distribution and richness. It mainly covers the *composition sphere* of biodiversity. Though successful in many of the discussed examples, the micro-heterogeneity of an area required for many species does not always allow a discrete classification approach. Many species (e.g. generalist species) use more than a single distinct vegetation type and some non-herbivore species may show low strength of association with a habitat or vegetation type because many species, regardless of the degree of habitat-specificity, do not occupy the full extent of their preferred habitat type that can be remotely sensed (e.g. Cardillo *et al.*, 1999; Cowley *et al.*, 2000). Current habitat classification is based on discrete maps and the resulting representation of class boundaries may not capture the meaningful ecological functional variability for each species.

Correspondence between field data and remotely sensed imagery aimed at species communities was found to be high in some studies (Fuller *et al.*, 1998; Bechtel *et al.*, 2004), but limited in others (e.g. Cardillo *et al.*, 1999; Heitkönig *et al.*, 2003). One factor limiting the accuracy in this approach appears to be the application of proxies at inappropriate spatial, spectral, and temporal resolutions. Remote sensing studies involving species diversity need to consider different levels of taxonomic resolution. Several studies used a higher or lower taxonomic resolution approach as proxy for estimating species richness for other taxa (Baldi, 2003; Olsgard *et al.*, 2003; Doerries and Van Dover, 2003; Sauberer *et al.*, 2004; Ward and Larivière, 2004). Cross-taxon congruence in biodiversity across different groups of organisms was also investigated as potential surrogates for each other (Negi and Gadgil, 2002; Heino *et al.*, 2005). However, correlations and congruencies in species richness among different taxonomic groups are difficult to generalise as they differ to environmental gradients. Accuracy of assessing species diversity in particular may further increase by adding environmental variables to the analysis. Moreover, despite the potential of remotely sensed data for habitat suitability analysis, ground survey data (e.g., species composition, abundance, and density maps) are essential to provide the basis for finding ecologically meaningful interpretations and for predicting species distribution and diversity.

Assessing species richness through spatial heterogeneity based on primary productivity

Spatial heterogeneity is one of the driving factors in the explanation of species richness (Stoms and Estes, 1993). It has long been accepted that environmental heterogeneity may support richer species assemblages compared to simple ecosystems (Simpson, 1949; MacArthur and Wilson, 1967; Lack, 1969; Huston, 1994) because of the creation of niche differentiation (Tilman *et al.*, 1997; Loreau, 1998). This is of particular relevance for dealing with the structural sphere of biodiversity. Here, we are concerned not only with the species composition, but also with the relationships of species towards one another. Factors contributing to the environmental heterogeneity include the temporal and spatial variation in the biological, physical, and chemical features of the environment that create different conditions that species can preferentially exploit (Morin, 2000). In comparison with the previously discussed discrete classification approach, the biological, physical, and chemical features are represented in a continuous way. Depending on the spatial, spectral, temporal, and angular resolution of the remotely sensed data, different levels of differentiation are reached, while post-processing techniques (e.g. density slicing, thresholds) allow the assignment of a discrete class to every pixel, if necessary. Plant productivity and biomass of ecosystems vary in space and time, and the spatial heterogeneity in productivity is hypothesized to influence species distribution and local abundance of individuals (Brown, 1988; Currie, 1991; Brown and Lomolino, 1998; Gaston and Blackburn, 2000; Oindo and Skidmore, 2002; Seto, 2004).

The most commonly used parameter for quantifying productivity and above-ground biomass of ecosystems is the Normalized Difference Vegetation Index (NDVI) (Tucker, 1979). It is based on the strong absorption of the incident radiation by chlorophyll in the red, and the contrasting high reflectance by plant cells in the Near infrared (NIR) spectral region. Because it is based on the normalized ratio of the reflectance in these two spectral bands (i.e., NDVI = (NIR-red)/(NIR+red)), it is an indicator of the greenness of vegetation canopies and able to separate vegetation from other materials. NDVI values proved to be a suitable indicator for vegetation parameters including biomass and above-ground primary productivity (e.g., Sellers, 1985, 1987; Tucker and Sellers, 1986; Box *et al.*, 1989), and it is therefore often correlated to faunal species occurrence and diversity.

Mammals

Since the late 1990s, an increasing number of studies is analysing NDVI to predict wildlife habitat suitability. Verlinden and Masogo (1997) found a significant positive relationship between NDVI and grass greenness in the Kalahari of Botswana. The relationship between NDVI and animal distribution using animal census data turned out to be more complex. Results using presence/absence data indicated a significant selection for higher NDVI signatures only for ostrich (*Struthio camelus*) and wildebeest (*Connochaetes taurinus*), the latter only when present in high numbers. The gemsbok (*Oryx gazelle*), the less abundant eland (*Taurotragus oryx*), and the locally concentrated springbok (*Antidorcas masupialis*) did not show significant relationships with greenness and NDVI. Musiega and Kazadi (2004) found, that the great seasonal migration of herds of wildebeest (*Connochaetes taurinus*) in the Serengeti-Mara ecosystem is primarily driven by green vegetation availability, as detected using NDVI. In another African case, Zinner *et al.* (2001) described habitat quality in central Eritrea through NDVI derived from Landsat MSS satellite data for three baboon species ((*Papio hamadryas hamadryas*, *Papio hamadryas anubis* and *Chlorocebus aethiops*). Hamadryas (*Papio h. hamadryas*) and olive baboons (*Papio h. anubis*) tended to select better quality habitats, characterized by a higher NDVI than the average in four out of five ecogeographical zones in Eritrea. Moreover, Hamadryas baboons showed a greater ecological plasticity than olive baboons, which are confined to riverbeds with extended gallery forest. Although successful in some studies (e.g. Zinner *et al.*, 2001), difficulties in correlating NDVI with the mammal distribution of less abundant species (Verlinden and Masogo, 1997) remain unsolved. Results suggest that relationships between less abundant species and greenness might become insignificant because of a large number of unoccupied suitable habitats. Moreover, the biomass-based approach is successful only with herbivorous species that are sensitive to differences in vegetation characteristics across an area.

Avifauna

Jørgensen and Nøhr (1996) and Nøhr and Jørgensen (1997) used a combination of satellite image analysis and ornithological surveys to assess avian biodiversity in the Sahel. A Landsat image was used to derive landscape diversity and NDVI, the latter being an indicator for the annual biomass production. Both variables were significant factors in a multiple regression model explaining species diversity. Hurlbert and Haskel (2003) analysed avian species richness in relation to primary productivity and habitat heterogeneity in America. They found that NDVI was a good predictor of seasonal species richness at fine spatial scales, whereas habitat heterogeneity best predicted richness at coarser spatial resolutions. Hawkins *et al.* (2003, 2004) showed that productivity indicators (NDVI and actual evapotranspiration) correlated well with bird diversity data in North America. A positive correlation between NDVI and bird and butterfly species richness was found by Seto (2004), though this relation did not have a definite functional shape. The relationship between NDVI and species richness of butterflies was strongest at high spatial resolutions, whilst that of birds was better at a lower resolution. In a comparable study, Bailey *et al.* (2004) distinguished between both habitat primary productivity and habitat heterogeneity by using estimated maximum NDVI and the spatial variation therein. This, in turn, was correlated with species richness of birds and butterflies. They found positive linear relationships between maximum NDVI and the number of functional guilds of birds and species richness of neotropical migrant birds, but a negative association between NDVI and the number of functional guilds of birds and species richness of resident birds. Alternatively, Lee *et al.* (2004) found a hump-shaped relationship between NDVI and bird species richness in Taiwan, but this became insignificant when effects of roads and elevation were accounted for.

Generally, NDVI proves to be a suitable proxy reflecting primary production or heterogeneity. Nevertheless, the correlations with bird species diversity were positive, hump-shaped, or even negative. The differences in results suggest that a functional link between NDVI and diversity remains elusive, underpinning the importance of ground truth data and validation. Results from several studies (e.g., Bailey *et al.*, 2004; Cushman and McGarigal, 2004) suggest that taxa related scale issues are to be considered when setting up a monitoring scheme using remote sensing.

Reptiles and Amphibians

In a study on two genetically differentiated forms of the Golden-striped salamander (*Chioglossa lusitanica*) in Portugal, Arntzen and Alexandrino (2004) applied GIS-based rules in addition to NDVI data, and found that the southern form of the salamander tended to encounter harsher environmental conditions, with lower precipitation, air humidity, summer temperatures and NDVI, but with a higher number of frost months than the northern form. This is the only study on amphibians using NDVI to assess or monitor species richness.

Invertebrates

Very few studies use remote sensing data to assess or predict invertebrate species richness beside cases cited above as pests or acting as disease vectors. Nevertheless, Seto *et al.* (2004) and Bailey *et al.* (2004) found strong correlations between NDVI values and butterfly species' richness in the Great Basin of western North America.

Insect outbreaks may result in such a dramatic reduction in standing biomass, that it enables vegetation indices to precisely indicate the affected location. Amongst the earliest reports on remote insect detection, Nelson (1983) analysed Landsat data for detecting significant forest canopy alteration caused by gipsy moth (*Lymantria dispar*) defoliation. The author found that the transformed vegetative index difference (VID = NIR- red) most accurately delineated forest change, and thus was able to map gypsy moth outbreak. More recently, MODIS NDVI data was successfully analysed to map a locust (*Locust migratoria manilensis*) plague in China (Ma *et al.*, 2005). The NDVI difference image between the data before and after the peak damage of the locust plague accurately mapped the geographical extent and severity of the affected areas.

Many invertebrate studies used NDVI in combination with the reflectance in the middle infrared, land surface temperature, and rainfall to predict abundance, distribution and seasonality of diseases transmitted by an invertebrate vector. Robinson *et al.* (1997) used satellite data to make predictions of the probable distribution of tsetse fly (*Glossina spp.*) species in southern Africa. For some subspecies (e.g. *Glossina morsitans centralis*) the distribution was best correlated with NDVI and the average maximum temperature (75% correct predictions). Relative abundances of the midge *Culicoides imicola*, the vector of bluetongue virus and African horse sickness virus, at various sites in Morocco and Spain, were compared with climatic variables, altitude and NDVI of the same sites (Baylis *et al.*, 1998). No significant correlations were found, although wind speed and NDVImin explained over 50% of the variance in abundance. Using broadband NOAA AVHRR data, Hay *et al.* (1998) successfully correlated NDVI-series with malaria presence in Kenya, and malaria admissions could be predicted across Kenya in an average year with regression analysis. NOAA AVHRR data of a site in Brazil (Bavia *et al.*, 2001) and sub-Saharan Africa (Kristensen *et al.*, 2001; Malone *et al.*, 2001) was similarly used to produce NDVI maps, and analyzed for relationships with the prevalence of schistosomiasis, hosted by snails. Results indicated that NDVI, together with climate data, predicted snail distributions accurately enough for schistosomiasis risk assessment.

As in the case of habitat characteristics used to predict species distribution, the use of NDVI has a strong emphasis on insects considered a pest and those that act as vector diseases, thus there is a lack of conservation-oriented studies for species which are not considered as pests. The use of NDVI has proven to be successful, however it depends directly on the species life history and ecology whether NDVI can act as a surrogate itself or in combination to other remotely sensed data.

Summary

The approach of assessing species distribution and richness through spatial heterogeneity based on primary production, can be considered as a functional, non-discrete correlation. Here, animal occurrence and diversity are related to terrestrial features by means of an ecological link. The link emphasised in this review is a trophic one (i.e. food-related), e.g. the case of herbivore animals being correlated with local vegetation biomass or primary productivity (Oindo, 2002; Seto *et al.*, 2004), and heterogeneity therein. The heterogeneity hypothesis affirms a positive relationship between ecosystems diversity and biological diversity (Simpson, 1949; MacArthur and Wilson, 1967; Lack, 1969; Hutson, 1994). The spatial and temporal heterogeneity in primary productivity is an explanatory variable to assess species occurrence and richness.

Although successful in some studies (Zinner *et al.*, 2001; Ito *et al.*, 2005), difficulties to correlate NDVI and animal distribution of less abundant mammal species (Verlinden and Masogo, 1997) remains unsolved. Moreover, the biomass-based approach is successful only with species sensitive to differences across an area. More elaborate studies, including additional explanatory environmental variables together with primary productivity heterogeneity (e.g. landscape diversity, evapotranspiration, land surface temperature, rainfall, altitude), explained considerable variation in species richness, but - here too - the explanatory power of each variable differed among spatial scales (Robinson *et al.*, 1997; Baylis *et al.* 1998; Hurlbert and Haske, 2003; Hawkins *et al.*, 2003, 2004; Bailey *et al.* 2004).

One of the factors influencing the accuracy of predictions of species richness using primary productivity indicators (NDVI) is scale or resolution, where the variation of species diversity - within and between taxa - is better explained using a specific scale, e.g. finer spatial resolution, whereby other variables explains more of the variation at another scale, e.g. coarser spatial resolution (Bailey *et al.*, 2004; Cushman and McGarigal, 2004; Hawkins *et al.*, 2003; Lee *et al.*, 2004; Hurlbert and Haskel, 2003). Another aspect leading to ambiguous accuracy is that the results are based on NDVI and other environmental variables, such as (e.g. average maximum temperature, rainfall, altitude) where the independent marginal effect of each variable is unknown. However, this conditional effect can be as high as 50 to 75 % of the explained variation (Baylis *et al.*, 1998; Robinson *et al.*, 1997).

The major drawback of using vegetation NDVI, however, is the asymptotical approach to a saturation level above a certain biomass density and leaf area index (Tucker, 1977; Sellers, 1985; Todd *et al.*, 1998; Gao *et al.*, 2000;), and has therefore limited value in assessing biomass during, for example, the peak of seasons (Thenkabail *et al.*, 2000). This problem could be overcome by using more recent remote sensing products and techniques, such as the enhanced vegetation index (EVI) from the MODIS product suite (Huete *et al.*, 2002). The EVI was developed to optimize the vegetation signal with improved sensitivity in high biomass regions and improved vegetation monitoring through a de-coupling of the canopy background signal and a reduction in atmosphere influences. Further, several studies explored the possibilities of narrow band vegetation indices for biomass estimation at high canopy density: Todd *et al.* (1998) and Clevers and Jongschaap (2001) reported a widening and deepening of the red absorption pit with an increase in biomass. Mutanga and Skidmore (2004a) successfully estimated biomass based on band depth analysis for densely vegetated areas where NDVI values reached an asymptote. In a similar approach it was demonstrated that imaging spectrometer data enhance the estimation of forest stand variables (leaf area index and crown volume) compared to broadband multispectral data. (Schlerf *et al.*, 2005).

As indicated above, novel indices developed as proxies for biomass and primary productivity, which are based on spectrometer data, encompass the capability of moving beyond conventional NDVI analysis, particularly suitable for identifying habitats in heterogeneous, densely vegetated areas.

Assessing species richness through temporal heterogeneity.

Ecoclimatic dynamics are highly complex, ranging from the impact of changing weather, seasonal variation in climate, including interannual cycles, to climate changes such as the global Pleistocene glacial periods. Seasonal variations in climate govern differences in plant species growth and establishment patterns, leading to changes in species composition and distributions (Hobbs, 1990). Consequently, annual variations in vegetation can induce changes in the spatial distribution of plant phenology and growth (Tucker and Selles, 1986). Therefore, analysis of multi-annual land cover data potentially provides a key to understanding the influence of climate variability on shaping ecosystems - which form the overarching hierarchical layer in biodiversity assessment. Continuous data to study ecoclimatic dynamics are available from 1980, with the establishment of the AVHRR meteorological satellite series. The coefficient of variation of AVHRR-derived NDVI data for a number of years indicates the relative variability of the vegetation cover for a given region. Consequently, regions with a high coefficient of variation should reflect large variations in vegetation composition and growth, following unstable and unpredictable climatic conditions over a number of years. On the other hand, low coefficients of variation should indicate regions with small variations in vegetation composition and growth. The use of temporal heterogeneity as a proxy is limited to a small number of studies, therefore all taxa are treated within the same chapter.

Species richness and abundance of large mammals in Kenya were correlated with yearly variation in vegetation, as assessed by the interannual variation of the maximum AVHRR-derived NDVI (Oindo 2002). In line with the findings above, maximum numbers of species were found in regions with current ecoclimatic stability. These studies support the hypothesis that high species diversity occurs in stable, predictable environments (Sanders and Hessler, 1969; Fjeldsa and Lovett, 1997). Fjeldsa *et al.* (1997) correlated interannual variability of NDVI with biodiversity 'hotspots' of tropical Africa, linking local endemism with local ecoclimatic stability. Similarly, Fjeldsa *et al.* (1999) correlated interannual differences in NDVI with endemism of 789 Andean bird species, thereby linking biodiversity with short-term and long-term ecoclimatic stability. Their results suggest that high ecoclimatic stability allows species to 'accumulate' in an area, whereas large interannual variation limits the community to species able to withstand large fluctuations in habitat quality resulting from interannual climatic variation.

Rodriguez *et al.* (2005) used regression analyses to examine the relationship between reptile and amphibian species richness and a set of environmental variables related to five hypotheses for geographical patterns of species richness based on productivity, ambient energy, water-energy balance, habitat heterogeneity, and climatic variability. For reptiles, annual potential evapotranspiration (an index of atmospheric energy) explained 71% of the variance. For amphibians, annual actual evapotranspiration (an index of the joint availability of energy and water in the environment), and the global vegetation index derived from satellite data, both described about 60% of the variance. Their results were consistent with reptile and amphibian environmental requirements, where the former depend strongly on solar energy, and the latter on both warmth and moisture for reproduction. On a somewhat different vein, Carey *et al.* (2001) attempted to identify the causes of amphibian declines around the globe. Four relatively undisturbed areas in northeastern Australia, Costa Rica-Panama, central Colorado, and Puerto Rico were chosen for examination of environmental correlates coincident with mass mortalities at these localities. They compiled a database including descriptions of 120 localities, both at which declines have been documented and at which no declines were known at the time. For each locality, the number of species, dates and degree of declines, habitat characteristics, and other factors were provided. The authors then used data predicted by models or collected by satellites, airplanes, or direct sampling on the ground to evaluate variations over time in temperature, precipitation, wind direction, UV-B radiation, and concentrations of contaminants. They considered the variation in certain environmental variables unlikely to have directly caused amphibian deaths, but suggested that correlations between these environmental changes and the occurrence of amphibian die-offs need further investigation into synergistic interactions among environmental variables and possible indirect causal relationships.

Summary

This approach assesses species richness based on temporal heterogeneity, The multi-temporality of habitat heterogeneity, indicated through the heterogeneity in NDVI, was suggested to be an appropriate proxy to predict species richness patterns (Sanders and Hessler, 1969; Fjeldsa and Lovett, 1997). The literature review showed that temporal studies were mostly performed across large regional areas. Further, conflicting results highlight the need to select relevant taxa (refer to taxonomic resolution) and to tune the methodology (Oindo and Skidmore, 2002). Even though NOAA-AVHRR data currently offer the longest time series, they are limited in their spatial and spectral resolution. The variability in vegetation cover as assessed using AVHRR data is the result of multiple influences: intrinsic characteristics of climate such as interannual variability in rainfall and temperature, long-term climate trends, vegetation succession, anthropogenic land-cover changes, and variability in the state of atmosphere (Fjeldsa *et al.*, 1997). However, the prospective for the temporal analysis is promising as alternative long-term satellite data series evolve. In the future, the combination of multitemporal satellite data with historical meteorological, ecological and paleological data has the potential of describing interactions among seasonal, annual and long-term climate variability to understand species diversity. Multi-temporal data offer possibilities to overcome the limitations of 'static' habitat studies needed for conservation purposes. Given the fact that many species are extremely mobile over time, e.g. migratory species, single-date studies do not cover the complete range of their habitats. In such cases only multitemporal data can provide a more complete assessment of the species' occurrence and distribution.

Assessing species richness through heterogeneity based on landscape structural properties

Brokaw and Lent (1999) stated that, in general, the more vertically diverse a forest is, the more diverse is its biota. Remote sensing has the potential to estimate structural properties and assess their heterogeneity. Most studies relating remote sensing derived structural properties to animal diversity relied on height measuring technologies such as airborne lasers (i.e., airborne LiDAR) and Synthetic Aperture Radar (SAR). They are tools to map vegetation height and its variability, field boundary height, shape of individual agricultural fields, fractional vegetation cover, and aboveground biomass (e.g., Ritchie *et al.*, 1995; Blair *et al.*, 1999; Lefsky *et al.*, 2002; Lim *et al.*, 2003; Mason et al, 2003, Santos *et al.*, 2003; Lefsky *et al.*, 2005).

Recently, Nelson *et al.* (2005) analyzed LiDAR measurements and video to identify and locate forested sites that might potentially support populations of a mammal, the Delmarva fox squirrel (*Sciurus niger cinereus*). Results indicated that the largest part of the area (78%) met certain minimum length, height, and canopy closure criteria to support squirrel populations. This is the only study addressing a faunal taxa other than the avifauna.

Beier and Drennan (1997) demonstrated that Northern Goshawks (*Accipiter gentilis*) selected foraging sites based on structure rather than on prey abundance, while (Jansson and Andrén, 2003) found that forest structure is related to species richness. Imhoff *et al.*, (1997) used SAR and aerial photography to map vegetation heterogeneity and relate this to field studies of bird abundances in Australia's Northern Territory. The abundances of individual species changed significantly across floristic and structural gradients, implying that bird habitat can be predicted from SAR data. Hinsley *et al.* (2002) and Hill *et al.* (2003) used an airborne laser scanning (ALS) system to map forest structure and related canopy heights to chick mass (i.e., nestling weight), a surrogate for breeding success, which, in turn, is a function of 'territory quality'. They found that, for one species, chick mass increased with increasing forest canopy height, and for a second species, chick mass decreased. Hence, Hill *et al.* (2003) concluded that airborne laser scanning data can be used to predict habitat quality and to map species distributions as a function of habitat structure. Davenport *et al.* (2000) devised a technique to measure the height of crops in farmland fields using LiDAR scanning, as crop height is an important predictor of bird species population and, in turn, can be used as a proxy for bird suitability. Using a population model of skylark (*Alauda arvensis*) they concluded that the achieved structural accuracy - less than 10 cm - would be sufficient to discriminate suitable from unsuitable habitat from LiDAR data. Incorporating high resolution multi-spectral images, these techniques can be used over large geographical areas and could therefore have wide application in ecological monitoring of change in habitat structures and the associated effects on wildlife (Mason *et al.*, 2003).

Summary

The fourth approach, assessing species richness through heterogeneity based on landscape structural properties, involves the assessment of species diversity using structural properties of habitat heterogeneity. This is a more complicated approach that not only relies on primary productivity and its heterogeneity, but also on structural properties of ecosystems. Vegetation height, height variability, percent canopy cover, and aboveground biomass are structural properties defining habitat heterogeneity (e.g. Ritchie *et al.*, 1995; Blair *et al.*, 1999; Lefsky *et al.*, 2002, 2005; Lim *et al.*, 2003; Santos *et al.*, 2003). Such structural habitat properties were successfully correlated to species distributions (Imhoff *et al.*, 1997; Brokaw and Lent, 1999; Hinsley *et al.*, 2002; Jansson and Andrén, 2003; Hill *et al.*, 2003). In addition to the applied laser and radar systems, optical multiangular sensor products (e.g., from the Multiangular Imaging SpectroRadiometer (MISR)) describing structural properties, such as the leaf area index and leaf angle distribution have the potential to contribute to the assessment and monitoring of terrestrial faunal species richness. In addition to more traditional approaches, the use of structural characteristics of habitats, their change and influence on faunal species distribution has a high potential for further studies covering large geographical areas (Nelson *et al.*, 2005).

Assessing species richness through heterogeneity based on plant chemical constituents

Animal species have a preference for the spatial and structural composition of habitat, but another attractant is the forage quality that an animal perceives in that habitat. Studies in the African savannah demonstrated that the occurrence and spatial distribution of many wildlife species is influenced by the variation in grass quality (Grant *et al.*, 2002; Heitkönig and Owen-Smith, 1998; McNaughton, 1988). Techniques that can estimate canopy quality on a large scale appear relevant in understanding wildlife diversity. Broadband satellites such as Landsat TM or SPOT lack the potential to capture detailed spectral features needed to detect or estimate the concentration of chemical constituents. Alternatively, imaging spectrometers can measure canopy reflectance in narrow and contiguous spectral bands in a wide wavelength range (e.g. 400 – 2500 nm). A wide range of plant compounds and their concentration can be identified from the many subtle absorption features of the spectrometer data (Curran, 1989; Elvidge 1990). The relationships with spectral properties and foliar chemicals, nitrogen amongst others, have been studied from dried and fresh leaves (e.g. Grossman *et al.*, 1996; Dury and Turner, 2001; Ebbers *et al.*, 2002), to entire canopies (e.g. Jago *et al.*, 1999; Curran *et al.*, 2001). However, there are many complicating factors to consider when estimating biochemicals of entire canopies. These include the masking effect of leaf water absorption (Fourty and Baret, 1998), the complexity of the canopy architecture, variation in leaf internal structure and directional, atmospheric and background effects. Several methods were developed to maximize sensitivity to the vegetation characteristics while minimizing confounding factors, including band ratios, difference indices, and derivative analysis (e.g., Huang *et al.* 2004; Schmidt and Skidmore, 2004; Becker *et al.*, 2005).

Regarding forage quality assessment as proxies for animal studying, McIlwee *et al.* (2001) investigated the utility of in situ reflectance spectroscopy as a means of rapidly assaying chemical constituents of leaves of four Eucalyptus species to predict herbivory by greater gliders (*Petauroides volans*) and common ringtail possums (*Pseudocheirus peregrinus*).

Resulting concentrations of nitrogen, neutral detergent fibre, condensed tannins and total phenolics, and thus leaf palatability, were predicted accurately and were consistent with documented food preferences of greater gliders. Dury *et al.* (2001) estimated concentrations of nutrients in Eucalypt tree foliage using airborne imaging spectrometer data. They determined secondary compounds of the group diformylphloroglucinols known to be deterrents for herbivores. Consequently, they derived palatability of Eucalypt leaves for foliovorous marsupials to map potential koala and possum habitats.

Mutanga *et al.* (2004c) investigated the ability of field spectroscopy to discriminate different levels of sodium concentration in grass, as sodium is a scarce element needed and sought by mammals (e.g. Brady *et al.*, 2002; Grant *et al.*, 2002). Using field spectrometer measurements of pasture grass, they were able to detect several sodium concentrations. They concluded that with the knowledge of grass species distribution, imaging spectrometer data would help to understand the distribution of mammals in nutrient limited savannas. This approach was successfully applied to large geographical areas linking forage quality to species richness and distribution particularly in areas with limited nutrients (Ferwerda, 2005).

Summary

This last approach is based on the use of plant chemical constituents to define habitat heterogeneity and ultimately assess and predict species richness. Attractants and deterrents related to the structural and trophic composition of habitat are important criteria to be considered in habitat-species associations. These attractants can be forage quality (Grant *et al.*, 2002; Heitkönig and Owen-Smith, 1998; McNaughton, 1988). Consequently the estimation of forage quality is essential to understand species richness patterns. Imaging spectroscopy with its ability to record reflected radiance in narrow spectral bands, allows the detection and quantification of canopy biochemical components. The overview of these initial studies demonstrated the utility of imaging spectrometer data to map foliar nutrient concentration in savannas and woody ecosystems. The above mentioned studies provide a first step towards understanding the movement and distribution of wildlife, particularly in areas where herbivorous wildlife is known to be limited by nutrients. The correlations between animal presence-abundance/habitat and forage quality were consistent with results derived from imaging spectroscopy; McIlwee *et al.*, 2001; Mutanga *et al.*, 2004c d), whilst other studies successfully upscaled those correlations to large geographical areas (Dury *et al.*, 2001, Mutanga *et al.*, 2004b), particularly in areas with limited nutrients (Ferwerda, 2005).

Some authors recommended that future studies should focus on monitoring seasonal changes in foliar nutrient concentration as well as extending the method to predict other macro nutrients (P, K, Na, Mg, Ca) and secondary compounds in both grass and tree canopies. Nevertheless a major constraint remains that foliar chemicals contribute only a little to the canopy optical properties. Radiative transfer models incorporating the involved optical mechanisms at varying complexity have some success at biochemical parameter retrieval (e.g. Jacquemoud *et al.*, 2000; Kötz *et al.* 2004), however typically many inputs of canopy parameters are required. At the current stage extensive in situ investigations on spectral features of attractants and deterrents of forage and their influence on faunal species distributions is a prerequisite to successfully upscale these findings to large areas for monitoring and conserving faunal species.

Conclusion

It is important for conservation purposes to generate consistent and reliable information about species distribution and diversity in order to develop plans for species protection and sustainable use (Riede, 2000). Remote sensing is generally regarded to be able to contribute to this aim, mainly by its ability to provide continuous spatial information. It is rapidly developing, capable of coping with environmental heterogeneity - and thus biodiversity - in its broadest range, by measuring increasingly detailed variation on a spatial, temporal, and structural scale, and recently by measuring variation in biochemical composition. This development is clearly highlighted in the presented review.

A major issue complicating the assessment of species occurrence and richness across all techniques is the mobility of faunal species, especially migrants which can move long distances occupying a wide range of natural and anthropogenic habitats. Techniques used in plant oriented diversity studies are generally based on characteristic spectral reflectance features of plant species or plant communities. For this purpose, objects need to be sessile to be accurately assessed. The techniques of remote sensing that have aided the studies on plant species distribution and diversity cannot be applied to animal studies in a similar fashion. Although commercial satellites with 61 cm pixel size are now capable of locating elephants in Kenya's Amboseli National Park and surrounding ecosystem (see e.g. http://media.digitalglobe.com/file.php/binaries/51/AmboseliF.pdf), most animal species remain undetectable. The often cryptic existence of fauna poses an additional general problem, akin to that of undergrowth species in vegetation.

Table 1 presents a summary of the various approaches discussed in this paper, including aspects of methodology, data requirements, techniques involved, and the biodiversity aspects covered. Most of the earlier studies on the application of remote sensing to biodiversity research were published in ecological, rather than remote sensing journals. This review is mainly based on peer-reviewed literature. Two main biases can be identified in the selected studies: a strong emphasis on NDVI-based approaches and on spaceborne sensor data. The development and application of new remote sensing techniques and products appears to undergo a lag time before they enter the realm of ecological research. We acknowledge that new methodologies (e.g., narrow-band vegetation indices), and less operational systems (e.g., airborne imaging and in situ spectroradiometers, lidar) have a high potential to provide a new generation of vegetation products representing proxies to estimate animal distribution.

Table 1. *Summary of the main remote sensing approaches to biodiversity research, and the biodiversity spheres and levels (cf. Noss, 1990) to which they were applied, according to the literature analysed in this review.*

Aim	Approach	Field data	RS data	Biodiv.	Biodiv. level
Discrete mapping					
Spatial. Habitat suitability mapping (single species and species richness) based on reflectance of landscape characteristics	Image classification of expected habitat correlated with in-situ species data	• Knowledge of, or ground studies on habitat preferences • Ground truth data of reflectance characteristics • Ancillary data (e.g.; ecological and/or meteorological data)	• Multispectral imagery (e.g.; Landsat, SPOT) • Videographic tracking	Composition	Species, community
Continuous mapping					
Spatial. Species distribution or diversity prediction and mapping based on variation in primary productivity	NDVI, or other vegetation indices correlated with in-situ species data	• Species distribution data • Ancillary data (e.g.; ecological and/or meteorological data)	• Multispectral imagery (e.g.; Landsat, SPOT, MODIS)	Composition Function	(Sub)species, community Production
Temporal. Species diversity prediction and mapping based on eco-climatic stability in productivity	Interannual NDVI variability correlated with in-situ species data	• Species distribution data • Ancillary data (e.g.; long-term meteorological data)	• Meteorological imagery: NOAA-AVHRR	Composition Function	Species, community Production
Structural. Habitat suitability mapping (single species and species richness) based on structural habitat characteristics	Structural characteristics estimation using radar or laser altimetry correlated with species data	• Validation data structural characteristics • Species distribution data • Data of proxy (e.g. ;bird	• Radar • LiDAR	Composition Function	Species Production
Biochemical. Species distribution or diversity prediction and mapping based on biochemical compounds of canopy (in the future)	Estimation of biochemical compounds of canopy correlated with in situ species data	• Validation data biochemical compounds • Signature library • Species distribution data	• Imaging spectroscopy	Composition Function	Species Production, quality

A more recent – and most promising - development in terms of methodology was observed in the assimilation of remote sensing data in ecological species distribution models. Although the reviewed papers mostly emphasise the composition and functional part of animal biodiversity and distribution, rather than population structures, for instance, it is expected that the approaches described here, particularly those with an emphasis on functional ecological relationships, will aid in the ultimate goal of biodiversity conservation.

Finally, this review has focussed on the use of remote sensing for estimating terrestrial animal distribution and diversity. Geostatistical methods are more and more being used incorporating remote sensing and field measurements. The use of ancillary data such as climate, terrain, soils, human infrastructure and footprint, access to water and so on, have been extensively used in geographic information systems. Many of these GIS modelling exercises also incorporate remotely sensed imagery. Corsi et al (2000) provide an overview of these models and ancillary data sources.

Acknowlegments

The authors wish to acknowledge Michael Schaepman and Jan Clevers for including the review article in this special issue, and two anonymous reviewers for their comments.

References

Asner, G.P., Vitousek P.M., 2005. Remote analysis of biological invasion and biogeochemical change. PNAS, 102 (12), 4383-4386.

Arntzen, J.W., Alexandrino, J., 2004. Ecological modelling of genetically differentiated forms of the Iberian endemic golden-striped salamander, Chioglossa lusitanica. Herpetol. J. 14, 137.

Austin, G.E., Thomas, C.J., Houston, D.C., Thompson, D.B.A., 1996. Predicting the spatial distribution of buzzard Buteo buteo nesting areas using a geographical information system and remote sensing. J. Appl. Ecol. 33, 1541-1550.

Avery, M.I., Haines-Young, R.H., 1990. Population estimates for the dunlin *Calidris alpina* derived from remotely sensed satellite imagery of the Flow Country of northern Scotland. Nature 344, 860-862.

Bailey, S.A., Horner-Devine, M.C., Luck, G., Moore, L.A., Carney, K.M., Anderson, S., Betrus, C., Fleishman, E., 2004. Primary productivity and species richness: relationships among functional guilds, residency groups and vagility classes at multiple spatial scales. Ecography 27 (2), 207-217.

Baines, L. M., Collins, W. G., Robins, P., 1986. The application of remote sensing to urban bird ecology. Remote sensing for resources development and environmental management. Proc. 7th ISPRS Commission VII symposium, Enschede, Vol. 2 (1): 795-799.

Baylis, M., Rawlings, P., 1998. Modelling the distribution and abundance of *Culicoides imicola* in Morocco and Iberia using climatic data and satellite imagery. Arch.Virol.14, 137-153.

Báldi, A., 2003. Using higher taxa as surrogates of species richness: a study based on 3700 Coleoptera, Diptera, and Acari species in Central-Hungarian reserves. Basic Appl. Ecol. 4, 589-593.

Barnsley, M.J., Hobson, P., Lewis, P., O'Dwyer, S., Disney, M.I., Cutter, M., Lobb, D., 2000. On the potential of CHRIS/PROBA for estimating vegetation canopy properties from space. Rem. Sens. Rev.19 (1-4), 171-189.

Bavia, M.E., Malone, J.B., Hale, L., Dantas, A., Marroni, L., Reis, R., 2001. Use of thermal and vegetation index data from earth observing satellites to evaluate the risk of schistosomiasis in Bahia, Brazil. Acta Trop. 79 (1), 79-85.

Bechtel, R., Sánchez-Azofeifa, A., Rivard, B., Hamilton, G., Martin, J., Dzus, E., 2004. Associations between Woodland Caribou telemetry data and Landsat TM spectral reflectance. Int. J. Rem. Sen. 25 (21), 4813-4821.

Beier, P., Drennan, J.E., 1997. Forest structure and prey abundance in foraging areas of Northern Goshawks. Ecol. Applic. 7 (2), 564-571.

Blair J.B., Rabine, D.L., Hofton, M.A., 1999. The Laser Vegetation Imaging Sensor: A medium-altitude, digitisation-only, airborne laser altimeter for mapping vegetation and topography. ISPRS J. Photogram. Rem. Sen. 54 (2-3), 115.

Box, E.O., Holben, B. N., Kalb, V., 1989. Accuracy of the AVHRR Vegetation Index as a predictor of biomass, primary productivity and net CO2 flux. Vegetatio 80, 71–89.

Brady, R.C., Trock, S.C., Jones, C.J., Ross, P.F., 2002. Stunted growth and mortality associated with sodium deficiency. Avian Dis. 46, 740-744.

Brokaw N.V., Lent, R.A., 1999. Vertical structure. in Hunter, M. (Editor). Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, pp. 373–399.

Brooks, T., Balmford, A., Burgess, N., Fjeldså, J., Hansen, L.A., Moore, J., Rahbek, C., Williams, P., 2001. Toward a blueprint for conservation in Africa. BioScience 51(8), 613-624.

Brown, J.H., 1988. Species diversity. in Myers, A. A. and P. S., Giller, (Editors). Analytical Biogeography: An Integrated Approaches to the Study of Plant and Animal Distribution Chapman & Hall, New York, pp. 57-89.

Brown, J.H., Lomolino, M.V., 1998. Biogeography, 2nd ed. Sinauer Associates, Sunderland, Massachusetts, 691 p.

Cardillo, M., Macdonald, D.W., Rushton, S.P., 1999. Predicting mammal species richness and distributions: testing the effectiveness of satellite-derived land cover data. Landscape Ecol. 14 (5), 423-435.

Carey, C., Heyer, W.R., Wilkinson, J., Alford, R.A., Arntzen, J.W., Halliday, T., Hungerford, L., Lips, K.R., Middleton, E.M., Orchard, S.A., Rand, A.S., 2001. Amphibian declines and environmental change: Use of remote-sensing data to identify environmental correlates. Conserv. Biol. 15 (4), 903-913.

Catling P.C., Burt, R.J., Forrester, R.I., 2000. Models of the distribution and abundance of ground-dwelling mammals in the eucalypt forests of north-eastern New South Wales in relation to habitat variables. Wildlife Res. 27 (6), 639-654.

Ceballos, G., Ehrlich, P.R., Soberon, J., Salazar, I., Fay, J.P., 2005. Global mammal conservation: What must we manage? Science 309, 603-607.

Chust, G., Pretus, J.L.l., Ducrot, D., Ventura, D., 2004. Scale dependency of insect assemblages in response to landscape pattern. Landscape Ecol. 19 (1), 41-57.

Clevers, J.G.P.W., Jongschaap, R., 2001. Imaging spectrometry for agricultural applications. in Van der Meer, F. D., and S. M., De Jong, (Editors). Imaging spectrometry: Basic principles and prospective applications. Kluwer Academic Publishing. Dordrecht, pp. 175-179.

Coops, N.C., Catling, P.C., 1997. Predicting the complexity of habitat in forests from airborne videography for wildlife management. Int. J. Rem. Sen. 18 (12), 2677-2682.

Coops, N., Culvenor, D., Preston, R., Catling, P., 1998. Procedures for predicting habitat and structural attributes in eucalypt forests using high spatial resolution remotely sensed imagery. Aust. Forestry 61 (4), 244-252.

Coops, N.C., Catling, P.C., 2002. Prediction of the spatial distribution and relative abundance of ground-dwelling mammals using remote sensing imagery and simulation models. Landscape Ecol. 17 (2), 173-188.

Corsi, F., de Leeuw, J., Skidmore, A.K., 2000. Modelling species distribution with GIS. In: Boitani, L., Fuller, T.K. (Eds.), Research Techniques in Animal Ecology Controversies and Consequences. Columbia University Press, New York. pp. 389-434.

Cowley, M.J.R., Wilson, R.J., Leon-Cortes, J.L., Gutierrez, D., Bulman, C.R., Thomas, C.D., 2000. Habitat-based statistical models for predicting the spatial distribution of butterflies and day-flying moths in a fragmented landscape. J. Appl. Ecol. 37 (1), 60-72.

Cracknell, A.P., 1998. Synergy in remote sensing - what's in a pixel? Int. J. Rem. Sen.19 (11), 2025-2047.

Curran, P.J., 1989. Remote sensing of foliar chemistry - Rem. Sen. Environ.. Rem. Sen. Environ. 30, 271-278.

Currie, D.J., 1991. Energy and large-scale patterns of animal-and plant-species richness. Am. Nat. 137(11), 27-49.

Cushman, S.A., McGarigal, K., 2004. Patterns in the species-environment relationship depend on both scales and choice of response variables. Oikos 105,117-124.

Davenport, I.J., Bradbury, R.B., Anderson, G.Q.A., Hayman, G.R.F., Krebs, J.R., Mason, D.C., Wilson, J.D., Veck, N.J., 2000. Improving bird population models using airborne remote sensing. Int. J. Rem. Sen. 13-14, 2705-2717.

Debinski, D.M., Kindscher, K., Jakubauskas, M.E., 1999. A remote sensing and GIS-based model of habitats and biodiversity in the Greater Yellowstone Ecosystem. Int. J. Rem. Sen. 20 (17), 3281-3291.

Del Valle, H.F., De Lamo, D.A., Gagliardini, D.A., 1997. Environmental affinity of the guanaco (Lama guanicoe M³ller, Camelidae) in two selected areas of Central Patagonia supported by ERS-1 SAR data. Earth Obs. Quart. 55, 14-19.

De Wulf, RR, Goossens, R.E., McKinnon, J.R. and Cai, W.S., 1988. Remote sensing for wildlife management: Giant panda habitat mapping from LANDSAT MSS images. Geocarto Int. 1, 41–50.

Diner D.J., Braswell, B. H., Davies, R., Gobron, N., Hu, J., Jin, Y. Kahn, R., Knyazikhin, Y., Loeb, N., Muller, J.P., Nolin, A., Pinty, B., Schaaf, C. B., Seiz, G., Stroeve, J., 2005. The value of multiangle measurements for retrieving structurally and radiatively consistent properties of clouds, aerosols, and surfaces. Rem. Sen. Environ. 97, 495-518.

Doerries, M.B., Van Dover, C.L., 2003. Higher-taxon richness as a surrogate for species richness in chemosynthetic communities. Deep-Sea Res. I 50, 749–755.

Dury, S.J., Turner, B., Foley, W.J., 2001. The use of high spectral resolution remote sensing to determine leaf palatability of eucalypt trees for folivorous marsupials. Int. J. Appl. Earth Observ.Geoinf. 3 (4), 328-336.

Eby, J.R., Bright, L.R., 1985. A digital GIS based on Landsat and other data for elk habitat effectiveness analyis. in Proceedings of the 19th International Symposium on Remote Sensing of the Environment, Environmental Research Institute of Michigan, Ann Arbor, MI., pp. 855-864.

Eyre, M.D., Foster, G.N., Luff, M.L., Staley, J.R., 2003. An investigation into the relationship between water beetle (Coleoptera) distribution and land cover in Scotland and northeast England. J. Biogeogr. 30 (12), 1835-1849.

Eyre, M.D., Luff, M.L., Staley, J.R., Telfer, M.G. 2003. The relationship between British ground beetles (Coleoptera, Carabidae) and land cover. J. Biogeogr. 30 (5), 719-730.

Ferwerda, J.G., 2005. Charting the quality of Forage: measuring and mapping the variation of chemical components in foliage with hyperspectral remote sensing. PhD thesis, ITC, The Netherlands.

Fisher, P., 1997.The pixel: A snare and a delusion. Int. J. Rem. Sen. 18 (3), 679-685.

Fjeldså, J., Lovett, J.C., 1997. Biodiversity and environmental stability. Biodivers.Conserv. 6, 315-323.

Fjeldså, J., Ehrlich, D., Lambin, E., Prins, E., 1997. Are biodiversity 'hotspots' correlated with current ecoclimatic stability? A pilot study using the NEA-AVHRR remote sensing data. Biodivers. Conserv. 6 (3), 401-422.

Fjeldså, J., Lambin, E., Mertens, B., 1999. Correlation between endemism and local ecoclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. Ecography 22 (1), 63-78.

Fourty, T., Baret, F. 1998. On spectral estimates of fresh leaf biochemistry, Int. J. Rem. Sen. 19 (7), 1283-1297.

Franklin, W.L., 1983. Contrasting socioecologies of South America's wild camelids: The vicuna and guanaco. Advances in the Study of Mammalian Behaviour. in Eisenberg, J.F., and D.G., Kleiman, (Editors). The American Society of Mammalogists. Shippensburg, PA. pp. 573-629.

Franklin, S.E., Raske, A.G., 1994. Satellite remote sensing of spruce budworm forest defoliation in western newfoundland. Can. J. Rem. Sen.20 (1), 37-48.

Franklin, S.E., Hansen, M.J., Stenhouse, G.B., 2002. Quantifying landscape structure with vegetation inventory maps and remote sensing. Forest. Chron. 78 (6), 866-875.

Fuller, R.M., Groom, G.B., Mugisha, S., Katende, A., Ipulet, P., Pomeroy, D., Bailey, R., Ogutu-Ohwayo, R., 1998. The integration of field survey and remote sensing for biodiversity assessment: A case study in the tropical forests and wetlands of Sango Bay, Uganda. Biol. Conserv. 86 (3), 379-391.

Fuller, R.M., Devereux, B.J., Gillings, S., Amable, G.S., Hill, R.A., 2005. Indices of bird-habitat preference from field surveys of birds and remote sensing of land cover: A study of south-eastern England with wider implications for conservation and biodiversity assessment. Global Ecol. Biogeogr. 14 (3), 223-239.

Gao, X., Huete, A.R., Ni, W., Miura, T., 2000. Optical-biophysical relationships of vegetation spectra without background contamination. Rem. Sen. Environ. 74 (3), 609-620.

Gaston, K.J., Blackburn, T.M., 2000. Patterns and process in macroecology. Blackwell Science, Oxford.

Gould, W., 2000. Remote sensing of vegetation, plant species richness, and regional biodiversity hotspots. Ecol. Appl. 10 (6), 1861-1870.

Grant, C.C., Davidson, T., Funston, P.J., Pienaar, D.J., 2002. Challenges faced in the conservation of rare antelope: A case study on the northern basalt plains of the Kruger National Park. Koedoe 45 (2), 1-22.

Green, K.M., Lynch, J.F., Sircar, J., Greenberg, L.S.Z., 1987. Landsat remote sensing to assess habitat for migratory birds in the Yucatan Peninsula, Mexico. Vida Silvestre Neo- Trop. 1, 27–37.

Griffiths, G.H., Lee, J., Eversham, B.C., 2000. Landscape pattern and species richness; regional scale analysis from remote sensing. Int. J. Rem. Sen. 21 (13-14), 2685-2704.

Hall, R.J., Hall, R.J., Crown, P.H., Titus, S.J., Volney, W.J.A., 1995. Evaluation of LANDSAT thematic mapper data for mapping top kill caused by Jack Pine budworm defoliation. Can. J. Rem. Sen. 21 (4), 388-399.

Hall, R.J., Hogg, E.H., Brandt, J.P., Case, B.S., Fernandes, R.A., Butson, C., Leblanc, S.G., 2003. Relating aspen defoliation to changes in leaf area derived from field and satellite remote sensing data. Can. J. Rem. Sen. 29 (3), 299-313.

Hawkins, B.A., Porter, E.E., 2002. Does Herbivore Diversity Depend on Plant Diversity? The Case of California Butterflies. Am. Nat. 161 (1), 40-49.

Hawkins, BA., 2004. Summer vegetation, deglaciation and the anomalous bird diversity gradient in eastern North America. Global Ecol. Biogeogr. 13 (4), 321-25.

Hawkins, B.A., Porter, E.E., Diniz-Filho, J.A.F., 2003. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. Ecology 84, 1608-1623.

Hay, S.I., 1997.Remote sensing and disease control: Past, present and future. T. Roy. Soc. Trop. Med. H. 91 (2), 105-106.

Hay, S.I., Rogers, D.J., Snow, R.W., 1998. Predicting malaria seasons in Kenya using multitemporal meteorological satellite sensor data. T. Roy. Soc. Trop. Med. H. 92 (1), 12-20.

Heino, J., Soininen, J., Lappalainen, J., Virtanen, R., 2005. The relationship between species richness and taxonomic distinctness in freshwater organisms. Limnol. Oceanogr. 50 (3), 978-986.

Heitkönig, I.M.A., Owen-Smith, N., 1998. Seasonal selection of soil types and grass swards by roan antelope in a South African savanna. African J. Ecol. 36 (1), 57-70.

Heitkönig, I.M.A., Ringrose, S., Epema, G.F., Bonyongo, C., Veenendaal, E., Stein, A., Breeuwer, A., Hasselt, M. van, Klop, E., Goethem, J., Slot, M., 2003. Watching Wildlife from Space. In: Bernard, T., Mosepele, K., Ramberg, L. (Eds.), Int. Wetlands Conference, Botswana.

Hepinstall, J.A., Sader, S.A., 1997. Using Bayesian statistics, thematic mapper satellite imagery, and breeding bird survey data to model bird species probability of occurrence in Maine. Photogramm. Eng. Rem. Sen. 63 (10), 1231-1237.

Herr, A.M., Queen, L.P., 1993. Crane habitat evaluation using GIS and remote sensing. Photogramm. Eng. Rem. Sen. 59, 1531-1538.

Hill, R.A., Hinsley, S.A., Bellamy, P.E., Balzter, H., 2003. Ecological applications of airborne laser scanner data: Woodland bird habitat modeling. in Hyypä, J., Næsset, E., Olsson, H., Granqvist Pahlén, T. and H., Reese, (Editors) Proceedings of the Scandlaser Scientific Workshop on Airborne Laser Scanning of Forests, Umeå, Swedish University of Agricultural Sciences, pp. 78–87.

Hinsley, S.A., Hill, R.A., Gaveau, D.L.A., Bellamy, P.E., 2002. Quantifying woodland structure and habitat quality for birds using airborne laser scanning. Funct. Ecol. 16 (6), 851-857.

Hobbs, R.J., 1990, Remote sensing of spatial and temporal dynamics of vegetation. in Hobbs, R. J., and H. A., Mooney, (Editors). Ecological Studies 79, Rem. Sen. of Biosphere Funct., New York: Springer-Verlag, pp. 203-219.

Homer, C.G., Edwards, T.C. Ramsey, R.D., Price, K.P., 1993. Use of remote sensing menthods in modelling sage grouse winter habitat. J. Wildlife Manage. 57, 78-84.

Huang, Z., Turner, B.J., Dury, S.J., Wallis, I.R., Foley, W.J., 2004. Estimating foliage nitrogen concentration from HYMAP data using continuum removal analysis. Rem. Sen. Environ. 93 (1-2), 18-29.

Huber, T.P., Casler, K.E., 1990. Initial analysis of Landsat TM data for elk habitat mapping. Int. J. Rem. Sen. 11 (5), 907-912.

Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X. and Ferreira, L. G., 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Rem. Sen. Environ. 83 (1-2), 195-213.

Hurlbert, H., Haskell, J.P., 2003. The Effect of Energy and Seasonality on Avian Species Richness and Community Composition. Am. Nat. 161, 83-97.

Huston, 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge, 701 p.

Imhoff, M.L., Sisk, T.D., Milne, A., Morgan, G., Orr, T., 1997. Remotely sensed indicators of habitat heterogeneity: Use of synthetic aperture radar in mapping vegetation structure and bird habitat. Rem. Sen. Environ. 60 (3), 217-227.

Ito, T.Y., Tsunekawa, A., Miura, N., Lhagvasuren, B., Enkhbileg, D., Takatsuki, S., Jiang, Z., 2005. Preliminary evidence of a barrier effect of a railroad on the migration of Mongolian gazelles. Conserv. Biol. 19 (3), 945-948.

Jansson, G., Andrén, H., 2003. Habitat composition and bird diversity in managed boreal forests. Scand. J. Forest Res. 18 (3), 225-236.

Johnson, C.G., Clausnitzer, R.R., Mehringer, P.J., Oliver, C.D., 1994. Biotic and abiotic processes of eastside ecosystems: the effects of management on plant and community ecology, and on stand and landscape vegetation dynamics. U.S. Forest Service General Technical Report PNW-GTR-322, Pacific Northwest Research Station, Portland, Oregon.

Johnson, D.D.P., Hay, S.I., Rogers, D.J., 1998. Contemporary environmental correlates of endemic bird areas derived from meteorological satellite sensors. P. Roy. Soc. Lon. B. Bio. 265 (1400), 951-959.

Jørgensen, A.F., Nøhr, H., 1996. The use of satellite images for mapping of landscape and biological diversity in the Sahel. Int. J. Rem. Sen. 17 (1), 91-109.

Joria, P.E., Ahearn, S.C., Connor, M., 1991. A comparison of the SPOT and Landsat Thematic Mapper satellite systems for detecting gypsy moth defoliation in Michigan. Photogramm. Eng. Rem. Sen. 57 (12), 1605-1612.

Kanai, Y., Kondoh, A. Higuchi, H., 1994. Analysis of crane habitat using satellite images. In: Higuchi, H., Minton, J. (Eds.) The Future of Cranes and Wetlands, Tokyo. Japan, pp. 72-81.

Kokaly, R.F., Despain, D.G., Clark, R.N., Livo, K.E., 2003. Mapping vegetation in Yellowstone National Park using spectral feature analysis of AVIRIS data. Rem. Sen. Environ. 84 (3), 437-456.

Kötz, B., Schaepman, M., Morsdorf, F., Bowyer, P., Itten, K., and Allgower, B., 2004. Radiative Transfer Modeling within a Heterogeneous Canopy for Estimation of Forest Fire Fuel Properties. Rem. Sen. Environ. 92(3): 332-344.

Kristensen, T.K., Malone, J.B., McCarroll, J.C., 2001. Use of satellite remote sensing and geographic information systems to model the distribution and abundance of snail intermediate hosts in Africa: A preliminary model for Biomphalaria pfeifferi in Ethiopia. Acta Trop. 79 (1), 73-78.

Kumar, L., Schmidt, K.S., Dury, S., Skidmore, A.K., 2001. Imaging spectrometry and vegetation science. in Van der Meer, F., and S.M., De Jong, (Editors). Imaging spectrometry. Kluwer Academic Publishers, Dordrecht, pp. 111-115.

Lack, D., 1969. The numbers of bird species on islands. Bird Study 16, 193-209.

Laurent, E.J., Shi, H., Gatziolis, D., LeBouton, J.P., Walter, M.B., Liu, J., 2005. Using the spatial and spectral precision of satellite imagery to predict wildlife occurrence patterns. Rem. Sen. Environ. 97, 249-262.

Lauver, C.L., 1997. Mapping species diversity patterns in the Kansas shortgrass region by integrating remote sensing and vegetation analysis. J. Veg. Sci. 8 (3), 387-394.

Lawrence, R., Labus, M., 2003. Early detection of Douglas-fir beetle infestation with subcanopy resolution hyperspectral imagery. West. J. Appl. For. 18 (3), 202-206.

Lee, P.F., Ding, T.S., Hsu, F.H., Geng, S., 2004. Breeding bird species richness in Taiwan: Distribution on gradients of elevation, primary productivity and urbanization. J. Biogeogr. 31 (2), 307-314.

Lefsky, M.A., Cohen, W.B., Parker, G.G., Harding, D.J., 2002. Lidar Remote Sensing for Ecosystem Studies. BioScience 52 (1), 19-30.

Lefsky, M.A., Hudak, A.T., Cohen, W.B., Acker, S.A.., 2005. Geographic variability in lidar predictions of forest stand structure in the Pacific Northwest. Rem. Sen. Environ. 95 (4), 532-548.

Lim, K., Treitz, P., Wulder, M., St-Ongé, B., Flood, M., 2003. LiDAR remote sensing of forest structure. Prog. Phys. Geog. 27 (1), 88-106.

Liu, J., Linderman, M., Ouyang, Z., An, L., Yang, J., Zhang, H., 2001, Ecological degradation in protected areas: The case of Wolong Nature Reserve for giant pandas. Science 292, 98-101.

Loffler, E., Margules, C., 1980. Wombats detected from space. Rem. Sen. Environ. 9 (1), 47-56.

Loreau, M., 1998. Separating sampling and others effects in biodiversity experiments. Oikos 82 (3), 600-602.

Luoto, M., Kuussaari, M., Toivonen, T., 2002. Modelling butterfly distribution based on remote sensing data. J. Biogeogr. 29 (8), 1027-1037.

Luoto, M., Virkkala, R., Heikkinen, R.K., Rainio, K., 2004. Predicting bird species richness using remote sensing in boreal agricultural-forest mosaics. Ecol. Appl. 14 (6), 1946-1962.

Luther, J.E., Hudak, J., Meades, J.P., Franklin, S.E., 1997. Forecasting the susceptibility and vulnerability of balsam fir stands to insect defoliation with Landsat thematic mapper data. Rem. Sen. Environ. 59 (1), 77-91.

Ma, J., Han, X., Hasibagan, A., Wang, C., Zhang, Y., Tang, J., Xie, Z., Deveson, T., 2005. Monitoring East Asian migratory locust plagues using remote sensing data and field investigations. Int. J. Rem. Sen. 26 (3), 629-634.

MacArthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. Princeton University Press, Princeton, 203 p.

Mace, G.M., 2005. An index of intactness. Nature 434: 32-33.

Malone, J.B., Yilma, J.M., McCarroll, J.C., Erko, B., Mukaratirwa, S., Zhou, X., 2001. Satellite climatology and the environmental risk of Schistosoma mansoni in Ethiopia and east Africa. Acta Trop. 79 (1): 59-72.

Mapaure, I.N., 1994. The distribution of *Colophospermum mopane* (leguminosae - caesalpinioideae) in Africa. Kirkia 15, 1-5.

Mason, D.C., Anderson, G.Q.A., Bradbury, R.B., Cobby, D.M., Davenport, I.J., Vandepoll, M., Wilson, J.D., 2003. Measurement of habitat predictor variables for organism-habitat models using remote sensing and image segmentation. Int. J. Rem. Sen. 24 (12), 2515-2532.

McCoy, E.D., Bell, S.S., 1991. Habitat structure: the evolution and diversification of a complex topic. in Bell, S.S., McCoy, E.D., and H.R., Mushinsky, (Editors). Habitat structure: the physical arrangement of objects in space. Chapman and Hall, London, pp. 3-27.

McCullough, D.G., 2000. A review of factors affecting the population dynamics of jack pine budworm (*Choristoneura pinus pinus* Freeman). Popul. Ecol. 42 (3), 243-256.

McIlwee, A.M., Lawler, I.R., Cork, S.J., Foley, W.J., 2001. Coping with chemical complexity in mammal-plant interactions: Near-infrared spectroscopy as a predictor of Eucalyptus foliar nutrients and of the feeding rates of folivorous marsupials. Oecologia 128 (4), 539-548.

McNaughton, S.J., 1988. Mineral nutrition and spatial concentrations of African ungulates. Nature 334 (6180), 343-345.

Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC., 85 p.

Miller, K.V., Conroy, M.J., 1990. SPOT satellite imagery for mapping Kirtland's warbler wintering habitat in the Bahamas. Wildlife Soc. Bull. 18, 252-257.

Minton, J.S., Halls, J.H., Higuchi, H., 2003. Integration of satellite telemetry data and land cover imagery: a study of migratory cranes in northeast Asia. T. in GIS 7 (4), 505-528.

Morin, PJ., 2000. Biodiversity's ups and downs. Nature 406 (6795), 463-464.

Morisson, R.I.G., 1997. The use of remote sensing to evaluate shorebird habitats and populations on Prince Charles Island, Foxe Basin, Canada. Arctic 50, 55–75.

Murthy, M.S.R., Giriraj, A., Dutt, C.B.S., 2003. Geoinformatics for biodiversity assessment. Biol. Lett. 40 (2), 75-100.

Musiega, D.E. and Kazadi, S.-N., 2004. Simulating the East Afircan wildebeest migration patterns using GIS and remote sensing. African J. Ecol. 42, 355-362.

Mutanga, O., Skidmore, A.K., 2004a. Narrow band vegetation indices overcome the saturation problem in biomass estimation. Int. J. Rem. Sen. 25 (19), 3999-4014.

Mutanga, O., Skidmore, A.K., 2004b. Integrating imaging spectroscopy and neural networks to map grass quality in the Kruger National Park, South Africa. Rem. Sen. Environ. 90 (1), 104-115.

Mutanga, O., Skidmore, A.K., Prins, H.H.T., 2004c. Discriminating sodium concentration in a mixed grass species environment of the Kruger National Park using field spectrometry. Int. J. Rem. Sen. 25 (20), 4191-4201.

Mutanga, O., Skidmore, AK, Prins H.H.T., 2004d. Predicting in situ pasture quality in the Kruger National Park, South Africa, using continuum-removed absorption features. Rem. Sen. Environ. 89 (3):393-408.

Nagendra, H., 2001. Using remote sensing to assess biodiversity. Int. J. Rem. Sen. 22 (12), 2377-2400.

Nagendra, H., Gadgil, M., 1999. Biodiversity assessment at multiple scales: Linking remotely sensed data with field information. P. Natl. Acad. Soc. 96, 9154-9158.

Negia, H.R., Gadgil, M., 2002. Cross-taxon surrogacy of biodiversity in the Indian Garhwal Himalaya. Biol. Conserv. 105, 143–155.

Nelson, R.F., 1983. Detecting forest canopy change due to insect activity using landsat MSS. Photogramm. Eng. Rem. Sen. 49 (9), 1303-1314.

Nelson, R., Keller C., Ratnaswamy, M., 2005. Locating and estimating the extent of Delmarva fox squirrel habitat using an airborne LiDAR profiler. Rem. Sen. Environ. 96 (3-4), 292-301.

Nøhr, H., Jørgensen, A.F., 1997. Mapping of biological diversity in Sahel by means of satellite image analyses and ornithological surveys. Biodiv. Conserv. 6 (4), 545-566.

Noss, R.F., 1990. Indicators for monitoring biodiversity: A hierarchical approach. Conserv. Biol. 4 (4): 355-364.

Oindo, B.O., 2002. Patterns of herbivore species richness in Kenya and current ecoclimatic stability. Biodiv.Conserv. 11 (7), 1205-1221.

Oindo, B.O., Skidmore, A.K., 2002. Interannual variability of NDVI and species richness in Kenya. Int. J. Rem. Sen. 23 (2), 285-298.

Oindo, B.O., Skidmore, A.K., De Salvo, P., 2003. Mapping habitat and biological diversity in the Maasai Mara ecosystem. Int. J. Rem. Sen. 24 (5), 1053-1069.

Olme, C.D.L., Davies, R.G., Burguess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T-S., Rasmussen, P.C., Ridgley, R.S., Stattersfield, A.J., Bennet, P.M., Blackburn, T.M., Gaston, K.J., Owens, P.F., 2005. Global hotspots of species richness are not congruent with endemism or threat. Nature 436, 1016-1019.

Olsgrad, F., Brattegard, T., Holthe, T., 2003. Polychaetes as surrogates for marine biodiversity: lower taxonomic resolution and indicator groups. Biodiv. Conserv. 12, 1033-1049.

Oppelt, N., and Mauser, W., 2004. Hyperspectral monitoring of physiological parameters of wheat during a vegetation period using AVIS data. Int. J. Rem. Sen. 25 (1), 145-159.

Ormsby, J.P. and Lunetta, R.S., 1987. Whitetail deer food availability maps from Thematic Mapper data. Photogramm. Engin.Rem. Sen. 53, 1585-1589.

Osborne, P.E., Alonso, J.C., Bryant, R.G., 2001. Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. .J. Appl. Ecol. 38 (2), 458-471.

Palmeirim, J.M., 1988. Automatic mapping of avian species habitat using satellite imagery. Oikos 52 (1): 59-68.

Perras, S., Bonn, F., Gwyn, Q. H. J., Babin, M., Couture, R., 1988. Inventory of the habitat of the American woodcock (*Scolopax minor*) by remote sensing. Photo Interpretation: Images Aeriennes et Spatiales 88, 1-19.

Price, K.P., Jakubauskas, M.E., 1998. Spectral retrogression and insect damage in lodgepole pine successional forests. Int. J. Rem. Sen. 19 (8), 1627-1632.

Prins, E., Petersen, B.S., Aunins, A., Priednieks, J., 2005. Using Landsat TM and field data to produce maps of predicted bird densities in Latvian farmland. Int. J. Rem. Sen. 26 (9), 1881-1891.

Raxworthy, C.J., Martinez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A., Peterson, A.T., 2003. Predicting distributions of known and unknown reptile species in Madagascar. Nature 426, 837-841.

Richards, B.J., 1999. Relationships between white-tailed deer distribution and habitat characteristics in Hamilton County, Illinois. NCASI Technical Bull. 2 (781), 440-441.

Riede, K., 2000. Conservation and modern information technologies: the global register of migratory species (GROMS). J. Int. Wildlife Law Policy 3 (2), 152-164.

Riley, J.R., 1989. Remote sensing in entomology. Annual Review of Entomology 34, 247-271.

Ritchie, J.C., Humes, K.S., Weltz, M.A., 1995. Laser altimeter measurements at Walnut Gulch watershed, Arizona. J. Soil Water Conserv. 50, 440–442.

Robinson, T., Rogers, D., Williams, B., 1997. Mapping tsetse habitat suitability in the common fly belt of Southern Africa using multivariate analysis of climate and remotely sensed vegetation data. Med. Vet. Entomol. 11 (3), 235-245.

Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D.C., da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Long, J.S., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J., Yan, X., 2004. Effectiveness of the global protected area network in representing species diversity. Nature 428, 640-643.

Rodríguez, M.A., Belmontes, J.A., Hawkins, B.A., 2005. Energy, water and large-scale patterns of reptile and amphibian species richness in Europe. Acta Oecologica 28 (1), 65-70.

Sader, S.A., Powell, G.V.N., Rappole, J.H., 1991. Migratory bird habitat monitoring through remote sensing. Int. J. Rem. Sen. 12, 363-372.

Sanders, H.L., Hessler, R.R., 1969. Ecology of the deep-sea benthos. Science 163 (874), 1419-1424.

Santos, J.R., Freitas, C.C., Araujo, L.S., Dutra, L.V., Mura, J.C., Gama, F.F., Soler, L.S., Sant'Anna, S.J.S., 2003. Airborne P-band SAR applied to the aboveground biomass studies in the Brazilian tropical rainforest. Rem. Sen. Environ.87 (4), 482-493.

Sauberer, N., Zulka, K.P., Abensperg-Traun, M., Berg, H.M., Bieringer, G., Milasowszky, N., Moser, D., Plutzar, C., Pollheimer, M., Storch, C., 2004. Surrogate taxa for biodiversity in agricultural landscapes of eastern Austria. Biol. Conserv. 117 (2), 181-190.

Saveraid, E.H., Debinski, D.M., Kindscher, K., Jakubauskas, M.E., 2001. A comparison of satellite data and landscape variables in predicting bird species occurrences in the Greater Yellowstone Ecosystem, USA. Landscape Ecol. 16, 71–83.

Saxon, E.C., 1983. Mapping the habitats of rare animals in the Tanami wildlife sanctuary (Central Australia): An application of satellite imagery. Biol. Conserv.27 (3), 243-257.

Schlerf, M., Atzberger, C., Hill, J., 2005. Remote sensing of forest biophysical variables using HyMap imaging spectrometer data. Rem. Sen. Environ. 95 (2), 177-194.

Scholes, R.J. and R. Biggs, 2005. A biodiversity intactness index. Nature 434: 45-49.

Schwaller, M.R., Olson, Jr. C., Ma, Z., Zhu, Z., Dahmer, P., 1989. A remote sensing analysis of Adelie penguin rookeries. Rem. Sen. Environ. 28, 199-206.

Scribner, K.T., Arntzen, J.W., Cruddace, N., Oldham, R.S., Burke, T., 2001. Environmental correlates of toad abundance and population genetic diversity. Biol. Conserv. 98, 201-210.

Sellers, P.J., 1985. Canopy reflectance, photosynthesis and transpiration. Int. J. Rem. Sen. 6 (8), 1335-1372.

Sellers, P.J., 1987. Canopy reflectance, photosynthesis, and transpiration. II. The role of biophysics in the linearity of their interdependence. Rem. Sen. Environ. 21 (2), 143-183.

Seto, K.C., Fleishman, E., Fay, J.P., Betrus, C.J., 2004. Linking spatial patterns of bird and butterfly species richness with Landsat TM derived NDVI. Int. J. Rem. Sen. 25 (20), 4309-4324.

Sharma, B.D., Clevers, J., De Graaf, R., Chapagain, N.R., 2004. Mapping Equus kiang (Tibetan Wild Ass) Habitat in Surkhang, Upper Mustang, Nepal. Mt. Res. Dev. 24 (2), 149-156.

Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688.

Sirois, J., Ahern, F.J., 1988. An investigation of SPOT HRV data for detecting recent mountain pine beetle mortality. Can. J. Rem. Sen. 14 (2), 104-108.

Smallie, J.J., O'Conner, T.G., 2000. Elephant utilization of *Colophospermum mopane*: possible benefits of hedging. African J. Ecol. 38, 352-359.

Smith, M.L., Martin, M.E., Plourde, L., Ollinger, S.V., 2003. Analysis of hyperspectral data for estimation of temperate forest canopy nitrogen concentration: Comparison between an airborne (AVIRIS) and a spaceborne (Hyperion) sensor. IEEE Transactions on Geoscience and Remote Sensing 41 (6)(I), 1332-1337.

Stohlgren, T., Coughenour, M., Chong, G., Binkley, D., Kalkhan, M., Schell, L., Buckley, D., Berry, J., 1997. Landscape analysis of plant diversity. Landscape Ecol. 12: 155–170.

Stoms, D.M., Estes, J.E., 1993. A remote sensing research agenda for mapping and monitoring biodiversity. Int. J. Rem. Sen. 14 (10), 1839-1860.

Styles, C.V., Skinner, J.D., 1997. Seasonal variations in the quality of mopane leaves as a source of browse for mammalian herbivores. African J. Ecol. 35, 254-265.

Taft, O.W., Haig, S.M., Kiilsgaard, C., 2003. Use of radar remote sensing (radarsat) to map winter wetland habitat for shorebirds in an agricultural landscape. Environ. Manage. 32 (2), 268–281.

Thenkabail, P.S., Smith, R.B., De Pauw, E., 2000. Hyperspectral vegetation indices and their relationships with agricultural crop characteristics. Rem. Sen. Environ. 71 (2), 158-182.

Tilman, D., Lehman C.L., Thomson K.T., 1997. Plant diversity and ecosystem productivity: Theoretical considerations. Proc. Natl. Acad. Sci.USA 94 (5), 1857-1861.

Tobler, M.W., Cochard, R., Edwards, P.J., 2003. The impact of cattle ranching on large-scale vegetation patterns in a coastal savannah in Tanzania. J. Appl. Ecol. 40 (3), 430-444.

Todd, S.W., Hoffer, R.M., Milchunas, D.G., 1998. Biomass estimation on grazed and ungrazed rangelands using spectral indices. Int. J. Rem. Sen. 19 (3), 427-438.

Tucker, C.J., 1977. Asymptotic nature of grass canopy spectral reflectance. Appl. Optics 16 (5), 1151-1156.

Tucker, C.J., 1979. Red and photographic infrared linear combinations for monitoring vegetation. Rem. Sen. Environ. 8 (2), 127-150.

Tucker, C.J., Sellers. P.J., 1986. Satellite remote sensing of primary production. Int. J. Rem. Sen. 7 (11), 1395-1416.

Verlinden, A., Masogo, R., 1997. Satellite remote sensing of habitat suitability for ungulates and ostrich in the Kalahari of Botswana. J. Arid Environ. 35 (3), 563-574.

Venier, L.A., Pearce, J., McKee, J.E., McKenney, D.W., and Niemi, G.J., 2004. Climate and satellite-derived land cover for predicting breeding bird distribution in the Great Lakes Basin. J. Biogeogr. 31, 315-331.

Vogelmann, J.E., Rock, B.N., 1989. Use of thematic mapper data for the detection of forest damage caused by the pear thrips. Rem. Sen. Environ. 30 (3), 217-225.

Ward, D.F., Larivière, M-C., 2004. Terrestrial invertebrate surveys and rapid biodiversity assessment in New Zealand: lessons from Australia. New Zealand. J. Ecol. 28 (1), 151-159.

White, D., Minotti, P.G., Barczak, M.J., Sifneos, J.C., Freemark, K.E., Santelmann, M.V., Steinitz, M.J., Kiester, A.R., Preston, E.M., 1997. Assessing risks to biodiversity from future landscape change. Conserv. Biol. 11 (2), 349-360.

Wolfgang, B., 2003. Biodiversity and agri-environmental indicators—general scopes and skills with special reference to the habitat level. Agriculture, Ecosystems and Environment 98, 35–78.

Zinner, D., Pelaez, F., Torkler, F., 2001. Distribution and Habitat Associations of Baboons (*Papio hamadryas*) in Central Eritrea. Int. J. Primatology 22 (3), 397-413.

E.J. Bell and R.C. Hinoja, Markov analysis of land use change: continuous time and stationary processes. Socio-Econ. Plan. Sci. 11 (1977), 13–17.

Chapter 7

Synthesis: Spatial complexity in the diversity puzzle: implications for conservation planning

Eurídice Leyequién Abarca

Introduction

To understand the environmental and controls on species diversity, we need to explore the relative differences of species richness patterns over a variety of spatial scales. Current debates about patterns and processes regulating species diversity, do not explicitly consider the spatial scale (Huston 1999, Olff *et al.* 2002). Previously, two levels of spatial scales were distinguished, i.e.; local and regional (Ricklefs and Schluter 1993). Subsequently, a hierarchical framework explaining the processes influencing species diversity has emerged (Table 1) (Willis and Whittaker 2002). In fact, it has been claimed that the impact of processes at different spatial and/or temporal scales is central to understanding global variation in biodiversity (Gaston 2000). However, studies at the species assemblage level usually focus only on a single spatial scale (e.g.; McGarigal and McComb 1995, Trzcinski *et al.* 1999, Holland and Fahrig 2000). It is plausible that species richness and abundance patterns respond differently to their environment at various scales (e.g.; Roland and Taylor 1997, Clarke and Lidgard 2000, Crawley and Harral 2001, Lennon *et al.* 2001, Rahbek and Graves 2001, Leyequien *et al.* submitted). Often there is limited knowledge about the scales at which species respond to environmental factors, and this uncertainty may limit the effectiveness of study designs, and the applicability of results (Holland *et al.* 2004). Thus, untangling the relative contribution of environment-species relationships in shaping ecological attributes at different spatial scales, such as species richness and abundance may provide valuable insights for solving the diversity puzzle (Meentemeyer and Box 1987, Wiens 1989, Levin 1992, 1993, Borcard *et al.* 1992, Dale *et al.* 1994, Bissonette 1997, Cushman and McGarigal 2002).

Table 1. Processes influencing species diversity in a hierarchical framework across spatial scales (modified from: Willis and Whittaker 2002).

Spatial scale	Scale of species richness	Processes	Important environmental variables responsible
Local scale	Species richness within communities, within habitat patches	Resource partitioning, competition, predation, facilitation	Resource availability, interacting species, physical habitat, precipitation, disturbance (e.g.; fire)
Landscape scale	Species richness between communities; turnover of species within the landscape	Dispersal, migration, colonisation/extinction, (Metacommunity dynamics)	Topography, landscape complexity, peninsula effect
Regional scale	Species richness of large geographical areas within continents	Migration/extinction dynamics, regional constraints on persistence	Radiation budget and water availability, area, latitude
Continental scale	Differences in species lineages and richness across continents	Speciation, colonisation, extinctions, biogeographical history	Acidification events, mountain-building episodes, e.g.; tertiary uplift of the Andes
Global	Differences reflected in the biogeographical realms, e.g.; distribution of mammal families between continents	Biogeographical hitstory, productivity	Latitude, climate, glacial/interglacial cycles of the Quaternary, continental plate movements, sea level change

In this research, we studied how biological and physical factors influence species diversity across different spatial scales in a Neotropical bird community (Chapter 5). The results showed the responses of bird species richness and abundance to biophysical variables can be explained at a landscape scale. This is especially the case for different migratory species such as warblers (e.g.; *Wilsonia pusilla*, *Wilsonia citrina*, *Wilsonia canadensis*, *Dendroica townsendi*, *Dendroica virens* and *Parula americana*), and forest dependant species (e.g.; *Aulacorhyncus prasinus*, *Lepidocolaptes affinis*, *Trogon elegans*). Despite the fact that the landscape scale explained most of the variation in the species data, it is important to consider that the relationships between species richness/abundance and environmental variables vary at different spatial scales. In particular, there may be confounding effects between species richness and environmental variables,. A key result from this thesis is that appropriate spatial scales should be selected when studying how species respond to environmental variables. Properly identified scale is crucial for scientific studies or conservation planning, as scale is functionally significant for the target species (Grand and

Cushman 2003). The multi-scale approach presented in Chapter 5 could, besides the interest of the effect on community level, be useful for species-specific analysis, for example for studies on Neartic-Neotropical migrant species that currently show evidence of decline (e.g.; in this research: *Chaetura vauxi*, *Contopus cooperi*, *Empidonax traillii*, *Empidonax hammondii*, *Empidonax wrightii*, *Empidonax difficilis*, *Oporornis tolmiei*) (Seavey 2002); or for species falling under the Mexican category of special protection (e.g.; in this research: hawks, *Accipiter striatus* and *Buteo platypterus*; toucans, *Aulacorhyncus prasinus*; woodpeckers, *Campephilus guatemalensis*; or vireos, *Hylophilus ochraceiceps*) or endangered species (e.g.; in this research: solitaires, *Myadestes unicolor*; thrushes, *Catharus frantzii*; quail-doves, *Geotrygon albifacies*; or parrots, *Pionus senilis*).

Processes such as habitat loss and fragmentation are relevant in understanding the differences in species diversity and are crucial factors affecting species diversity at landscape scale that could threaten species survival (Fahrig 1998, 2003, Rosenzweig 1995). How these inherently spatial processes affect species diversity across different levels, i.e.; low, intermediate or high levels of habitat loss and fragmentation may have important consequences for conservation planning. As concluded by Fahrig (2003), most researchers view habitat fragmentation as a process involving both the loss of habitat and the breaking apart of habitat, and this has produced inconsistencies and difficulties in the interpretation of the effects of both spatial processes on biodiversity. If conservation efforts are to be successful, particularly when considering species assemblages, the individual effect of habitat loss and fragmentation on species richness needs to be elucidated. In our research we found that, when separating the individual effects of fragmentation and habitat loss, the bird species richness show a unimodal response to habitat fragmentation at landscape level with highest levels of species richness at intermediate fragmentation levels, whereas a negative linear response to habitat loss (Chapter 3). The relative importance of both spatial processes did not prove significantly different in explaining species richness, and the interaction effect of these two single processes was not significant. These results emphasise that both, habitat loss and fragmentation, are important factors influencing bird species diversity and that the individual effects of habitat loss do not outweigh the effects of fragmentation on bird species richness. We propose that conservation efforts should focus on both spatial processes together rather than on the factors separately, and we suggest that influencing fragmentation levels may mitigate the negative effects of habitat loss on species richness (i.e.; the spatial arrangement of habitat). At local scales, fragmentation of resources has frequently been shown to be associated with higher species richness (Tilman, 1982; Chaneton and Facelli, 1991; Huston, 1994; Knapp *et al.*, 1999), because such differentiation prevents exclusion by a single superior competitor (Olff and Ritchie 2002). These results have important conservation implications if the *design* of the landscape matrix is set out to optimise bird species richness in a particular area. However, special attention should be drawn to the deterioration of natural habitat as a result of habitat fragmentation as it may produce unsuitable conditions for species and therefore the chances for local coexistence of species can be counteracted (Olff and Ritchie 2002), or if fragmentation negatively affect the balance between the colonization and extinction rate of suitable habitat patches as it has been found in a regional scale (Hanski and Simberloff 1997).

The diversity in species assemblages can be regulated by factors such as interspecific competition, and great attention had been devoted to understand the role of competition in the structure and dynamics of ecological communities (Ricklefs 1975, Giller 1984, Wiens 1989, Keddy 2001). Despite the large amount of research on the mechanisms of interspecific competition, the impact of competition on community composition has remained unclear. Similarity in body mass is an easily determined animal characteristic that probably could serve as a proxy for competition strength in ecological communities. However, the impact of a large overlap in body mass in structuring ecological communities remains unproven, and there is an ongoing debate about the relationship between species coexistence and body size differences among ecologically similar species. The thresholds for body size differences above which competition is minimized, are still not understood. In this thesis we addressed how interspecific competition is influenced by differences in body mass among ecologically comparable species (Chapter 4). The results showed that there is a significant negative relationship between the body mass ratio and the strength of competition, suggesting that a large difference in body sizes among sympatric species promotes coexistence in communities. The species pairs range from relatively high body masses like granivorous birds like parrots or oropendola, i.e.; *Pionus senilis-Psarocolius montezuma*, to small body masses like hummingbirds, e.g.; *Amazilia candida-Campylopterus curvipennis* (nectarivorous). This allometric relationship, though not causal, proves that the body mass ratio influences the strength of competition, and possibly ultimately the community species composition.

Apart from understanding the factors controlling species diversity, and how spatial patterns and processes at various spatial scales influence species richness and community patterns, it is crucial for conservation planners to efficiently monitor and assess trends in ecological communities. Specifically, in avian studies the selection of different techniques (e.g.; point counts and mist netting) to sample bird species richness and abundances may have profound consequences for the reliability and completeness of the study, and subsequently for the knowledge on the patterns in avian communities. The evaluation performed in Chapter 2 demonstrated that even after a large sampling effort, point counts perform better in detecting species richness with a lower total effort and costs, than mist netting. However, we suggest that when possible both techniques should be used to benefit from their individual strengths (e.g.; detection of understory, canopy species or secretive species). The relatively higher costs of mist netting compared to point counts, if we would have aimed at recording 90 % of the species, would be 3297 USD, which is 2090 USD (calculated for the period 2033-2004) or almost twice total costs for point counts. Nonetheless, the higher costs of mist netting could be balanced by the higher efficiency in registering for example understory species that were missed by point counts (i.e.; *Mionectes oleagineus*, *Catharus aurantiirostris, Catharus mexicanus*, *Helmitheros vermivorus*, *Oporornis formosus*, *Seiurus motacilla*, *Basileuterus belli*, *Melospiza lincolnii*, *Cyanocompsa parellina*, *Passerina cyanea* and *Passerina ciris*), but this depends on the research objectives (Chapter 2). Furthermore, the generation of consistent and reliable information about species distribution and diversity is critical in biodiversity conservation (Riede 2000). One promising approach for the assessment, monitoring and prediction of animal diversity is the synergy of remote sensed information and auxiliary data with ecological models, and a subsequent validation using traditional field techniques (Chapter 6). An example of this is the relatively recent development of methods using remotely sensed data in ecological species distribution models (see Chapter 6 for a review). However, despite the potential of remote sensing applications in ecology, there is still a considerable time lag time between the developments of new remote sensing techniques and their use in ecological research.

Conservation implications: shade coffee plantations as a refuge for Neotropical birds

Biogeographical position of the study area: its importance for conservation

The extended region of the study area of this thesis, the northeastern mountain range of Puebla, is located in a strategic zone along the border of the Neotropical region and the Nearctic region (Rzedowski 1966). It is situated in the meridional extreme of the Sierra Madre Oriental and borders two major landscapes: the Mexican Transvolcanic Belt ('Eje neovolcánico') and the Coastal lowlands. The study area covers the vegetation belts of lower montane rain forest and lowland rain forest (both tropical evergreen forests). This geographic position of the northeastern mountain range of Puebla is a key biogeographical location characterized by high biodiversity. For example, there are 558 registered plant species in different tropical evergreen forests in Sian Ka'an (Quintana Roo), 737 in Tuxtepec (Oaxaca), 800 in Uxpanapa (Veracruz), 814 in Los Tuxtlas (Veracruz) and 984 in Montes Azules (Chiapas). For other taxa such as mammals the recorded species richness is 85 in Montes Azules (Chiapas) and 90 in Los Tuxtlas (Veracruz). In particular, avian diversity is high in the tropical evergreen forests in Mexico, for example, 150 species in Uxpanapa (Veracruz), 301 in Peten (Yucatan) and 341 in Los Tuxtlas (Veracruz).

The study area, as part of the northeastern mountain range of Puebla, is an important region for bird conservation and is also part of the migratory route for the Nearctic-Neotropical birds. Specifically, during the fieldwork for this thesis we documented a total of 181 bird species within the traditional shade coffee plantations, representing a total of 12 orders, 31 families and 123 genera (Annex 1). The 181 bird species represent 61 % of the total bird species (298) registered for the northeastern mountain range of Puebla and 17 % of all Mexican birds (1060 species).The predicted species richness (S_{max}) for the study area shows that the asymptote was nearly reached (Figure 1), indicating that the sampling effort in this study enabled us to detect the far majority of all bird species. From the 181 species, 124 (69 %) were resident birds and 57 (31 %) Neartic-Neotropical migrants, 9 (5 %) were forest-dependent species, 4 (2 %) endemics, 10 (5 %) were subject to special protection and 4 (2 %) were endangered (Norma Oficial Mexicana NOM-059-ECOL-2001).

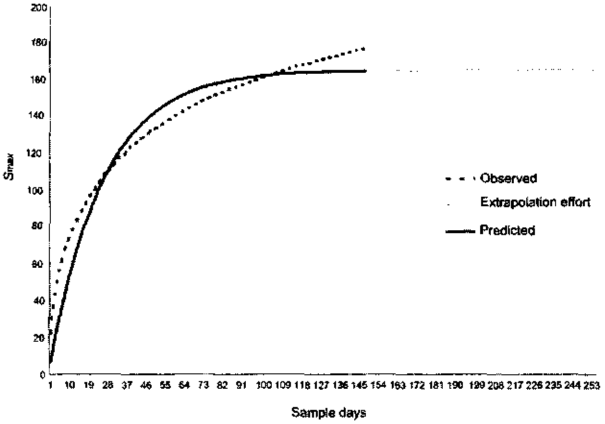

Figure 1. Accumulation curve (total observed species richness of 182) and predicted S_{max} *(164.77), the light line shows the extrapolation effort reaching an asymptote at* S_{max} *of 165.24.*

Despite the biogeographical and ecological importance of the northeastern mountain range of Puebla, deforestation has caused a serious loss of habitat for wildlife species in the last thirty years, mainly due to deforestation and conversion to agricultural lands and pasturelands (Lugo-Hubp *et al.* 2005). In Mexico, annual deforestation rates for tropical evergreen forests are estimated at 1.9 % for lower montane rain forest and 2 % for lowland rain forest. This is considerably higher than for temperate (upper montane) forests with 0.64 %/y, specifically for coniferous and broadleaved forests (Masera *et al.* 1997). Some of the major causes that threaten both the Neotropical birds and the migrants are habitat loss and fragmentation by wide-spread deforestation. In particular, important declines in Neotropical migrants have been found (Rappole 1995, Robbins *et al.* 1995), and it has been suggested that one of the major causes for these declines is caused by problems in their wintering areas (Estrada and Coates-Estrada 2005).

At present, an important agricultural land cover within the tropical evergreen forests is coffee, the majority of which belong to the traditional shade system. In Mexico, coffee-growing regions fall largely within areas identified as biodiversity hotspots. Evidence suggests that shade coffee agro-ecosystems have important ecological functions, such as biodiversity maintenance and protection (for a review see Perfecto and Armbrecht 2003), water, health and production, soil fertility, capture of carbon and rain, refuges for biological control agents and pollinators, and maintenance of climatic balance (Toledo and Moguel, 2006). Shade coffee plantations are also characterised by a high diversity and abundance of plants. A floristic survey carried out in the region at 31 sites with traditional shade coffee plantations (Toledo *et al.* 2004), reported between 35 and 150 plant species per hectare, with an estimated total of 250 species (Figure 2). These *coffee gardens* are man-made systems reflecting in their structure and composition the traditional management of plant species (e.g.; domesticated and introduced species). In the northeastern mountain range of Puebla, 96% of the recorded species in the traditional shade coffee plantations are useful, with a clear dominance of species serving for food (almost 50%), followed by species serving for medicines, materials for construction, fuelwood and others. A remarkable group are the edible fruits that also constitute food resources for birds: sapotes (14 varieties), avocados (8 varieties), berries (17 species), citrus species (14 varieties) and others. Similarly, there are abundant plant taxa that constitute nectar sources for birds: 11 varieties of platanillos (*Heliconia* spp.), 4 species of Zingiberaceae, 3 species of Marantaceae and others. Thus, as habitats for the avifauna, coffee gardens are not only forest refuges, but also provide abundant food resources for birds (e.g.; nectar, fruit and insects) (Wunderle and Latta 1998; Greenberg *et al.* 1997a, b). Some examples of the most common plant species are *Pimenta dioica*, *Inga lactibracteata* and *Hamelia patens* as source of insects and nectar, and *Bursera simaruba*, *Trema micrantha*, *Psidium guajava* and *Persea americana* as source of fruits. Thus, the maintenance of traditional shade coffee agroecosystems in this landscape mosaic can assist in the conservation of Neotropical avifauna, and help maintain multiple ecological services.

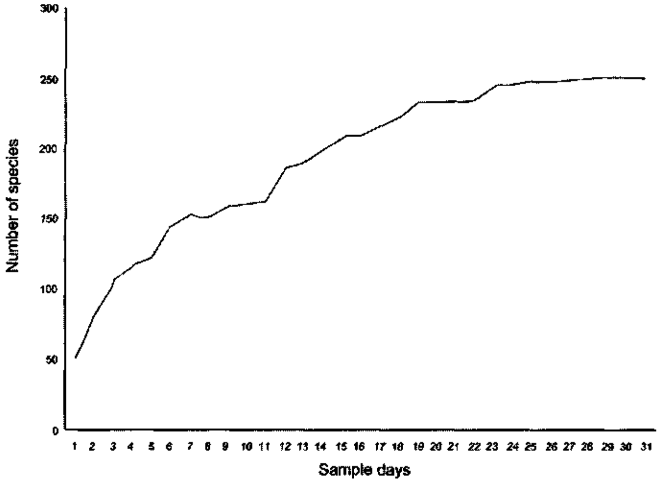

Figure 2. Accumulation curve of recorded plant species at 31 sites with shaded grown coffee in the northeastern mountain range of Puebla. Source: Toledo, et al. 2004.

Shade coffee plantations and the anthropogenic matrix

From the total research area (151,367.5 ha), 56,364 ha (31 %) comprise agricultural lands (i.e.; non-arboreal crops) and 11,925 ha (7 %) are shade coffee plantations. In addition there are 15527 ha (9 %) of tropical evergreen forest (i.e.; lowland rain forest and lower montane forest) and 67,552 ha (37 %) of a diversity of forest formations (i.e.; at different succession and/or management stages), whilst the remaining area is composed by urban areas and water bodies. As noted above shade coffee plantations represent a forested habitat for wildlife, including avifauna (i.e.; 124 resident birds, 57 migratory birds and 9 forest dependent species in our research area), which is particularly important in areas with high degree of fragmentation and habitat loss. According to Perfecto and Armbrecht (2003), shade coffee agroecosystems could provide a high-quality matrix for many bird forest species or bird species that originally required natural closed-canopy forests. In fact, we found that the total area covered by coffee plantations has a significant positive influence ($p = 0.05$) on species richness (Chapter 3). This confirms other studies which have shown that the expected species richness (of migrant birds) in shade coffee plantations is significant higher than in other agricultural systems (Figure 3) (Estrada and Coates-Estrada 2005). The area of traditional shade coffee plantations as well as their ecological qualities constitute a key element in the design of a landscape that aims at optimising biological conservation and providing human subsistence. We suggest that the conservation plans of this region could incorporate the paradigm of reconciliation ecology (Rosenzweig 2005) or bioregional conservation (Toledo 2005) and adopt some the results found here. The value of protected areas for the preservation and maintenance of biological diversity is doubtful if the conservation strategies do not actively incorporate areas managed for human use (Bengtsson *et al.* 2003).

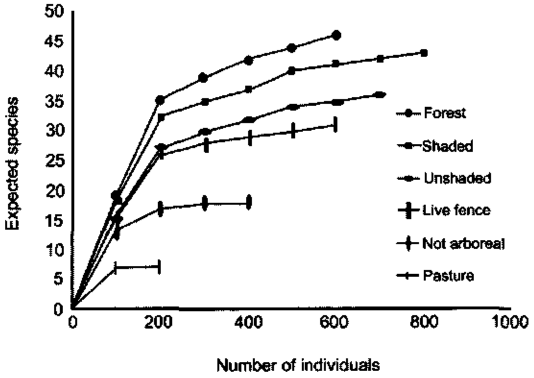

Figure 3. Rarefaction curves for different agroecosystems: shade plantations, unshade plantations, live fences, non-arboreal crops and pasture lands (source: Estrada and Coates-Estrada 2005).

Traditional shade coffee plantations in the international context: scenarios for biodiversity conservation and carbon sequestration

Biodiversity conservation and carbon sequestration are key ecological issues that are subject of a common international concern and numerous cooperation programmes. As has been mentioned in the introduction of this thesis the current trend in northern Latin America (Colombia, Panama, Costa Rica, El Salvador, Guatemala, Nicaragua, Honduras and Mexico) is to reduce shade cover plantations and convert them into unshaded coffee plantations or other open non-arboreal agricultural systems. If this trend continues it could have important implications for the loss of biodiversity including bird species, and also loss of important ecological services that the shade coffee plantations provide such as carbon sequestration. Here we present scenarios of the potential consequences on: a) species richness (specifically avifauna) and b) carbon sequestration, if the area of shade coffee plantations continues to be reduced.

a) *Species richness.* The Convention on Biological Diversity in Rio de Janeiro in 1992 is the result of international cooperation to anticipate, prevent and battle the causes of a significant reduction or loss of biological diversity. Traditional shade coffee plantations support a high biodiversity compared to open sun coffee plantations or other non-arboreal open agricultural systems, and therefore they represent a suitable habitat for a wide range of species. Specifically in Latin America, the bird diversity had been studied in shade coffee plantations and the results show a relatively high avian diversity of resident birds and also migrants (Table 2) (Aguilar-Ortiz 1982, Robbins *et al.* 1992, Vennini 1994, Wunderle and Latta 1996, Greenberg *et al.* 1997, Van der Voort and Greenberg 1999, Dietsch 2000, Johnson 2000).

Therefore, the loss of this man made habitat (i.e.; traditional shade coffee plantations) could have a deleterious effect on the bird species richness. If we take the example of the resident birds in our research area with an observed species richness of 124 and S_{max} of 113.59 (Figure 4), we found that based on our analyses (Chapter 3) using the extended species-area curve, we can expect an estimated decline of 0.006 in species richness for every hectare the coffee area is reduced. These results could have significant consequences for conservation strategies as the amount of traditional shade coffee plantations has a positive linear relationship with the species richness of resident birds (p <0.001).

Table 2. Bird species richness found in tropical forest, shade coffee plantations, rustic coffee and unshaded coffee S, Species richness; n.a., Not Available.

Habitat	Observed S	Estimated S	Country	Country
Tropical forest	75	n.a.	Mexico	Greenberg *et al.* (1997b)
	86	77	Mexico	Tejeda-Cruz and Sutherland (2004)
	131	n.a.	Panama	Petit *et al.* (1999)
	82	81.6	Mexico	Greenberg *et al.* (1997a)
	85	78	Mexico	Tejeda-Cruz and Sutherland (2004)
	138	n.a.	Mexico	Aguilar-Ortiz (1981)
	96	n.a.	Mexico	Navarro (1992)
	51	46	Mexico	Tejeda-Cruz and Sutherland (2004)
Shade coffee	56	55.5	Mexico	Greenberg *et al.* (1997)
	136	n.a.	Mexico	Aguilar-Ortiz (1981)
	65	64.7	Guatemala	Greenberg *et al.* (1997b)
	90	n.a.	Mexico	Calvo and Blake (1998)
	41	n.a.	Mexico	Johnson (2000)
	87	n.a.	Guatemala	Petit *et al.* (1999)
	79	69	Jamaica	Tejeda-Cruz and Sutherland (2004)
	65	n.a.	Mexico	Cruz-Angon and Greenberg (2005)
	99	n.a.	Mexico	Arangon and Paniagua (1989)
	182	164.77	Mexico	Leyequien (2006)
	99	n.a.	Mexico	Borrero (1989)
Rustic coffee	69	68.7	Mexico	Greenberg *et al.* (1997b)
	80	70	Mexico	Tejeda-Cruz and Sutherland (2004)
Unshaded	49	49.2	Mexico	Greenberg *et al.* (1997b)
	75	n.a.	Mexico	Calvo and Blake (1998)
	6	4	Guatemala	Tejeda-Cruz and Sutherland (2004)

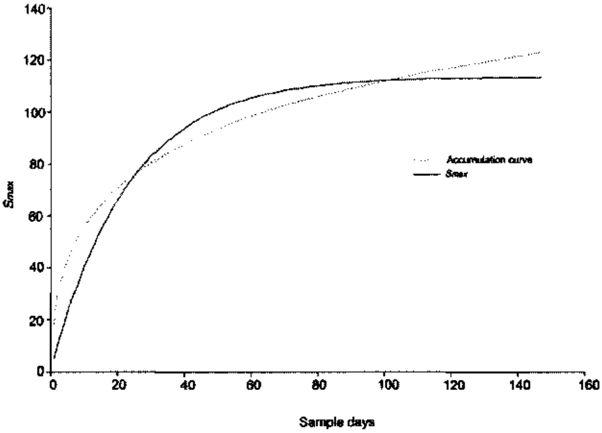

Figure 4. Accumulation curve for resident birds (observed species richness of 125) and predicted S_{max} (113.59).

b) *Carbon sequestration.* Under the Kyoto Protocol, several countries agreed to adopt specific targets for a reduction in greenhouse gas emissions within the first Kyoto commitment period (2008-2012), and carbon credits in the Certified Emission Reductions market have been offered to reduce the CO_2 emissions with an actual market value of USD$ 5/tCO_2eq (Teixeira-Coelho *et al.* 2005). One form of emissions offset is the capture of carbon in carbon sinks. Carbon sequestration involves the transfer of atmospheric CO_2 into secure long-lived pools thus preventing the immediate reemission to the atmosphere. Therefore, through judicious land use and management practices, soil carbon sequestration can increase the soil organic carbon and the soil inorganic carbon stocks (Lal 2004). Agroforestry systems have a high and attainable soil carbon sequestration potential with a rate of 100-200 kg C/ha per year compared to extractive farming practices (Lal 2004). Traditional shade coffee plantations fall in the category of agroforestry, and therefore have clear benefits for carbon sequestration (Kursten and Burschel 1993, Schroeder 1994, De Jong *et al.* 1997, Kursten 2000, Avila *et al.* 2001, Noordwijk *et al.* 2002, Pandey 2002, Suárez-Pascua 2002, Albrecht and Kandji 2003) , moreover traditional shade coffee agroecosystems add high amounts of biomass to the soil and prevent soil loss, conserve water (Beer *et al.* 1998) and enhance activity and species diversity of soil fauna (Nestel 1995).

Hence, carbon-trading markets offering C-credits may be a solution to mitigate the negative impacts of climate change and other ecological problems (e.g.; soil degradation and disturbance in hydrological cycles). The calculated carbon stock by the area under traditional shade coffee plantations in Mexico (70 % of the total coffee area) is 11,255,973 t C, based on an average carbon stock of 21.6 t C ha^{-1} of the total aerial C-stock including shade trees, coffee bushes and leaf litter (derived from Alpizar *et al.* 1985, Avila-Vargas 2000, Suárez-Pascua 2002, Potzol 2004). This represents approximately 56,279,864 USD in carbon credits (USD5/ t C). However, the deforestation in shade coffee plantations has been estimated at a rate of 0.4 % per year (Blackman *et al.* 2005)With this rate of deforestation in twenty years there will be a reduction of 89 % of carbon stock if it converts into pasture lands or extractive farming. In our research area the calculated carbon stock of the total area covered by shade coffee plantations is 257,789 t C based on the same average carbon stock of 21.6 t C ha^{-1}, representing 1,288,943 USD in carbon credits. Moreover, if the conversion rate would be 0.4 % the results in carbon loss will be devastating in just one year. However, the conversion rate for the research area is unknown and we approximate an almost negligible rate of conversion compared to the previously reported. The potential for the coffee producers as suppliers of carbon sequestration is calculated in approximately 105 USD/ha, which represents a considerable income compared to approximately an average of 59 USD/ha per coffee harvest.

Traditional shade coffee plantations in the regional context: Adaptative management by indigenous people

In Mexico, the coffee regions overlap largely with areas supporting a high biological richness (Moguel and Toledo 1999). It is estimated that 60-70 % of coffee plantations in Mexico are shade coffee plantations (Moguel and Toledo *in prep*). Traditional shade coffee plantations are cultivated mainly by small-scale community-based growers, the majority of them belong to some indigenous group (Moguel and Toledo 1999). The indigenous mode of utilisation of this tropical agroecosystems denotes a multiple use strategy (MUS), which can be called adaptative management (Toledo *et al.* 2003). This indigenous adaptative management has obvious socio-economic as well as ecological benefits. The ecological advantages of shade coffee agroecosystems are clear: a) high biodiversity maintenance, b) regulation of carbon cycle, c) soil protection, d) regulation of hydrological cycle and e) preservation of forest cover. The economic benefits derived from this tropical agroecosystems are sources of goods, services and energy for household subsistence and products for local, regional and international markets. For example, shaded coffee plantations hold a high proportion of useful plant diversity. Estimates of useful plants are in a range of 35 to 150 species per hectare (mainly tropical fruits, spices, ornamentals, bamboos and medicinal plants) (Moguel and Toledo *in prep.*) This plant species richness has a substantial potential for international markets oriented to organic agricultural products as well as for conventional products. Indigenous multiple use management creates a diverse landscape mosaic which could be approached in a three dimensional view in space, in its horizontal axis as multiple land covers at different stages of use (e.g.; the use of succession stages of vegetation for agriculture), in a vertical axis as the structural complexity of the MUS (e.g.; vegetation structural complexity) and the third axis as the biological diversity and composition resulted from the MUS. Maintaining such a functional and productive landscape with diverse land uses and ecosystems seems to be an optimal strategy to maintain biodiversity (Pimentel *et al.* 1992, Toledo *et al.* 2003).

Moreover, since the coffee crisis in the last decade as a result of overproduction in Vietnam and Brazil (ICO 2003), and the conversion of shade plantations into unshaded plantations in countries like Colombia or Costa Rica (Perfecto *et al.* 1996) new market alternatives as for example the "sustainable coffee" or the "shade coffee" certification programs emerge as a way to improve the economic situation of coffee producers in Latin America together with the maintenance of biodiversity (Perfecto *et al.* 2005). Several studies had approached the problem between yield and biodiversity maintenance in which the construction of a yield set from functions of shade cover proved to be successful for optimising both yield and biodiversity (Staver *et al.* 2001, Perfecto *et al.* 2005). Perfecto *et al.* (2005) concluded already that there are two critical factors for decision making in these certification programmes: a) the relationship between shade and yield is not linear (it has been found in many studies that this relation is best described by a humped-shape curve) (Soto-Pinto *et al.* 2000, Staver *et al.* 2001), and b) different taxa or species could differ in their sensitivity to changes in the structural and floristic composition of vegetation (i.e.; reduce of shade trees). Another feasible market option for coffee farmers is the transformation from conventional to organic coffee, which represents an increase of yield ranging from 15 % (Bray *et al.* 2001) to 67 % (Damiani 2002). Thus, the balance between yield and the maintenance of biodiversity needs to be accounted if successful shade coffee certifications programs are to be implemented and most likely this process should involve producers as well as government and non-government institutions.

In the research area of this thesis, the main managers of the shade coffee plantations are indigenous people from two groups, i.e.; nahuats and totonacos. One of the major indigenous organisations in the northeastern mountain range of Puebla is Tosepan Tatataniske, which has approximately 30,000 members corresponding to 60 % of the regional total population (Moguel and Toledo *in prep*). Currently they manage approximately 5,800 ha of shade coffee plantations, which play a crucial role in the maintenance of the forested cover in the landscape along with the associated ecological services. Furthermore, the ecological knowledge on the regional avifauna enables these indigenous groups to influence the structural and floristic design of the shade coffee plantations to a certain extent, where food resources for birds are explicitly maintained in the plantations (Leyequién *et al. in prep.*). Coffee farmers identified plant species within their coffee plantations that are food resources for a variety of birds, mainly maintained in the plantation as sources of cash crops or self-subsistence products, but also to attract birds for mere contentment. This ecological indigenous knowledge acquired over a long history of natural resources utilisation, should be considered in the conservation strategies if we successfully want to maintain and preserve the biological diversity within the complexity of the anthropogenic matrix.

References

Aguilar-Ortiz, F. 1982. Estudio ecológico de las aves del cafetal, in Estudios Ecológicos en el Agroecosistema Cafetalero, Jiménez-Ávila, E and Gómez-Pompa, A. (eds.) INIREB, Xalapa, Veracruz, México.

Albrecht, A. and Kandji, S.T. 2003. Carbon sequestration in tropical agroforestry systems. Review. Agriculture, Ecosystems and Environment 99: 15-27.

Alpizar, L., Fassbender, H.W. and Heuvelop, J. 1985. Sistemas agroforestales de café (*Coffea arabica*) con laurel (*Cordia alliodora*) y con Poró (*Erythrina poeppigiana*) en Turrialba, Costa Rica. I. Biomasa y reservas nutritivas. Turrialba 35(3): 233-242.

Ávila, G., Jiménez, F., Beer, J., Gómez, M. and Ibrahim, M. 2001. Almacenamiento, fijación de carbono y valoración de servicios ambientales en sistemas agroforestales en Costa Rica. Agroforesteria en las Américas 8(30): 32-35.

Ávila Vargas, G. 2000. Fijación y Almacenamiento de Carbono en Sistemas de Café Bajo Sombra, Café a Pleno Sol, Sistemas Silvopastoriles y Pasturas a Pleno Sol. Turrialba, Costa Rica: CATIE thesis.

Beer, J., Muschler, R., Kass, D. and Somarriba, E.1998. Shade management in coffee and cacao plantations. Agroforestry Systems 38: 139-164.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F. and Nyström, M. 2003. Reserves, resilience and dynamics landscapes. Ambio 32(6): 389-396.

Bissonette, J.A., Harrison, D.J., Hargis, C.D. and Chapin, T.G. 1997. The influence of spatial scale and scale sensitive properties in habitat selection by American Martins. In: Bissonette, J.A. (ed.) Wildlife and landscape ecology: effects of patterns and scale. Springer-Verlag, New York.

Blackman, A., Albers, H., Avalos-Sartorio, B. And Crooks, L. 2005. Deforestation and shade coffee in Oaxaca, Mexico. Key research findings. RFF DP 05-39. Washington, D.C.

Borcard, D., Legendere, P. and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology 73(3):1045-1055.

Borrero, H. 1986. La substitución de cafetales de sombrío por caturrales y su efecto negativo sobre la fauna de vertebrados, Caldasia, 15: 725-7326.

Bray, D.B., Plaza Sanchez, J.L. and Murphy, E.C. 2001. Social dimensions of organic coffee production in Mexico: lessons for eco-labeling initiatives. Soc. Nat. Resour. 15: 429– 446.

Clarke, A. and Lidgard, S.J. 2000. Spatial patterns of diversity in the sea: bryozoan species richness in the north Atlantic. J. Anim. Ecol.69: 799-814.

Crawley, M.J. and Harral, J.E. 2001. Scale dependency in plant biodiversity. Science 291: 864-868.

Cushman S.A. and McGarigal, K. 2002. Hierarchical, multiscale decomposition of species-environment relationships. Landscape Ecology 17:637-646.

Chaneton, E.J. and Facelli, J.M. 1991. Disturbance effects on plant community diversity: spatial scales and dominance hierarchies. Vegetatio 93: 143–156.

Dale, V.H., Pearson, S.M., Offerman, H.L. and O'Neill, R.V. 1994. Relating patterns of land use change to faunal biodiversity in the central Amazon. Conserv Biol 8:1027-1036.

Damiani, O. 2002. Organic Agriculture in Guatemala: A Study of Producer Organizations in the Cuchumatanes Highlands. Office of Evaluation and Studies, IFAD, Rome.

De Jong, B.H. *et al.* 1997. Forestry and agroforestry land-use systems for carbon mitigation: an analysis in Chiapas, Mexico. In: Adger, W.N., Whitby, M., and Pettenella, D.M. (eds.) Climate-Change Mitigation and European Land-Use Policies, CAB International,
New York.

Dietsch, T.V. 2000. Assessing the conservation value of shade-grown coffee: a biological perspective using neotropical birds. Endangered Species Update 1750-72 [Electronic version]. Retrieved January 2, 2006, from http://www.umich.edu/-esupdatel

Donald, P., 2004. Biodiversity Impacts of Some Agricultural Commodity Production Systems. Conservation Biology 18:17-37.

Estrada, A. and Coates-Estrada, R. 2005. Diversity of Neotropical migratory landbird species assemblages in forest fragments and man-made vegetation in Los Tuxtlas, Mexico. Biodiversity and Conservation 14: 1719-1734.

Fahrig L. 1998. When does fragmentation of breeding habitat affect population survival? Ecol. Model. 105:273–92

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Syst. 34: 487-515.

FAO 1996. Forest Resources Assessment 1990: Survey of Tropical Forest Cover and Study of Change Processes. Rome, Italy: FAO, FAO Forestry Paper 130: 152 pp.

FRA 2005. Global forest resources assessment update 2005. Specification of national reporting tables for FRA 2005. Rome, Italy: FAO, FAO Forestry Paper 81: 37 pp.

Gaston, K.J. and Blackburn, T.M. 2000. Patterns and process in macroecology. Blackwell.

Giller, P.S. 1984. Community structure and the niche. Chapman and Hall, London.

Grand, J. and Cushman, S.A. 2003. A multi-scale analysis of species-environment relationships: breeding birds in a pitch pine-scrub oak (*Pinus rigida-Quercus ilicifolia*) community. Biol. Conserv. 112:301-317.

Greenberg, R., Bichier P. and Sterling J. 1997. Bird populations in rustic and planted shade coffee plantations of Eastern Chiapas, México. Biotropica 29: 501–514.

Hanski, I. and Simberloff, D. 1997. The metapopulation approach, its history, conceptual domain and application to conservation. In: Hanski, I. and Gilpin, M.E. (eds.) Metapopulation Biology. Ecology, Genetics and Evolution. Academic Press, San Diego.

Holland, J.D. and Fahrig, L. 2000. Effect of woody borders on insect density and diversity in crop fields: A landscape-scale analysis. Agriculture, Ecosystems and Environment 78: 115–122.

Holland, J.D., Bert, D.G. and Fahrig, L. 2004. Determining the spatial scale of species' responses to habitat. BioScience 54(3): 227-233.

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

Huston, M.A. 1994. Biological diversity. The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge.

ICO 2003. Website of the International Coffee Organisation: http://www.ico.org

Johnson, M.D. 2000. Effects of shade-tree species and crop structure on the winter arthropod and bird communities in a Jamaican shade coffee plantation. Biotropica 32: 133–145.

Keddy, P.A. 2001. Competition. Kluwer Academic Publishers, Dordrecht.

Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C. and Towne, E.G. 1999. The keystone role of bison in North American tall grass prairie: bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. Bioscience 49, 39–50.

Kursten, E. 2000. Fuelwood production in agroforestry systems for sustainaible land use and CO_2-mitigation. Ecological Engineering 16: S69-S72. S?

Kursten, E. and Burschel, P. 1993. CO2-mitigation by agroforestry. Water, air and soil 70: 533-544.

Lal, R. 2004. Soil carbon sequestration impacts on global climate change and food security. Science 304: 1623-1627.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. and Gaston, K.J. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. J. Anim. Ecol. 70: 966–979.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967.

Levin, S.A. 1993. Concepts of scale at the local level. In: J. R. Ehleringer and Field, C. B. (eds.) Scaling physiological processes: leaf to globe. Academic Press, New York, New York, USA.

Leyequien *et al.* (*in prep*) Etno-ornithology in the northeastern mountain range of Puebla.

Leyequien, E., De Boer, W.F. and Skidmore, A.K. (*submitted*) Linking species-environment relationships and multiple spatial scales in community ecology.

Lugo-Hubp, J., Zamorano-Orozco, J.J., Capra, L., Invar., M. and Alcantara-Ayala, I. 2005. Revista Mexicana de Ciencias Geológicas 22(2): 212-228.

Masera, O.R., Ordones, M.J. and Dirzo, R.1997. Carbon emissions from Mexican forests: current situation and long-term scenarios. Climatic Change 35: 265-295.

Mcgarigal, K. and McComb, W.C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecol. Monogr. 65: 235-260.

Meentemeyer, V. and Box, E.O. 1987. Scale effects in landscape studies. In: Turner, M.G. (ed.) Landscape heterogeneity and disturbance. Springer-Verlag, New York, USA.

Moguel, P. and Toledo, V.M. 1999. Biodiversity conservation in traditional coffee systems in Mexico. Conservation Biology 13: 1–12.

Moguel, P. and Toledo, V.M. (*in prep*) Indigenous resistance, shaded coffee and globalization: the "Tosepan Titataniske" Cooperative of Mexico.

Nestel, D. 1995.Coffee in Mexico: international market, agricultural landscape and ecology. Ecol. Econ.15: 165-178.

NOM-059-ECOL. 2001. Environmental protection—native species from the flora and fauna of Mexico—risk categories and guidelines for their consideration in the list of species in danger of extinction, threatened or protected. List of species in danger of extinction. Official Paper of the Mexican Federation, March 6, 2002, Mexico (in Spanish).

Olff, H. and Ritchie, M.E. 2000. Fragmented nature: Consequences for biodiversity. 3rd International Workshop on Sustainable Land Use Planning, Wageningen, the Netherlands.

Olff, H., Ritchie, M. E. and Prins, H. T. 2002. Global environmental controls of diversity in large herbivores. Nature 415: 901–904.

Pandey, D.N. 2002. Carbon sequestration in agroforestry systems. Climate Change Policy 2: 367-377.

Perfecto, I., Rice, R., Greenberg, R. and Van der Voort, M. 1996. Shade coffee: a disappearing refuge for biodiversity. BioScience 46(8): 598-603.

Perfecto, I. and Armbrecht, I. 2003. The coffee agroecosystem in the Neotropics: combining ecological and economic goals. In: Vandermeer, J. (ed.) Tropical agroecosystems. CRC Press, Washington, D.C.

Perfecto, I., Vandermeer, J., Mas, A. And Soto-Pinto, L. 2005. Ecological Economics 54: 435-446.

Pimentel, D., Stachow, U., Takacs, D.A. and Brubaker, H.W. 1992. Conserving biological diversity in agricultural/forestry systems. Bioscience 42: 354-362.

Potzol, C. 2004. Carbon storage in coffee agroecosystems of southern Costa Rica: potential applications for the Clean development Mechanism. MSc thesis. York University, Toronto, Ontario, Canada.

Rahbek, C. and Graves, G.R. 2001. Multiscale assessment of patterns of avian species richness. Proc. Natl. Acad. U.S.A. 98(8): 4534-4539.

Rappole J.H. 1995. The Ecology of Migrant Birds. Smithsonian Institution Press, Washington, DC.

Ricklefs 1975. Patterns of growth in birds, part 3, Growth and development of the Cactus Wren. Condor 77: 34-45.

Ricklefs, R.E. and Schluter, D. 1993. Species diversity: regional and historical influences. In: Ricklefs, R.E., Schluter, D. (Eds.), Species Diversity in Ecological Communities. University of Chicago Press, Chicago.

Riede, K. 2000. Conservation and modern information technologies: the global register of migratory species (GROMS). J. of Int. Wildlife Law and Policy 3(2): 152-164.

Robbins, C.S. Dowell, B. A., Dawson, D. K., Colon, J. A., Estrada, R., Sutton, A., Sutton, R. and Weyer, D. 1992. Comparison of Neotropical migrant landbird populations wintering in tropical forests, isolated forest fragments, and agricultural habitats. In: Ecology and Conservation of Neotropical Migrant Landbirds, Hagan, J.M. and Johnson, D.W., Eds., Smithsonian Institution Press, Washington, D.C.

Robbins, C.S., Dawson, D.K. and Dowell, B.A. 1995. Changing land use problems and opportunities. In: Wilson, M. and Sader, S. (eds.), Conservation of Neotropical Migratory Birds in Mexico. Maine Agricultural and Forest Experiment Station Miscellaneous Publication 727, pp.1–14.

Roland, J. and Taylor, P.D. 1997. Insect parasitoid species respond to forest structure at different spatial scales. Nature 386: 710–713.

Rosenzweig, M.L. 1995. *Species diversity in space and time.* Cambridge University Press, Cambridge, united Kingdom.

Rosenzweig, M.L. 2005. Avoiding mass extinction: Basic and applied challenges. 24th Annual Midwest Ecology and evolution Conference. Dept. of ecology and Evolutionary Biology, University of Arizona, Tucson.

Rzedowski, J. 1966 Vegetación del estado de San Luis Potosí. Acta Científica Potosina 5: 5–291.

Rzedowski, J. 1978. Vegetación de México. Ed Limusa. Mexico, D. F.

Schroeder, P. 1994. Carbon storage benefits of agroforestry systems. Agroforestry Systems 27: 89-97.

Soto-Pinto, L., Perfecto, I., Castillo-Hernandez, J., Caballero-Nieto, J. 2000. Shade effect on coffee production at the northern Tzeltal Zone of the state of Chiapas, Mexico. Agric., Ecosyst. and Environ. 80:61-69.

Staver, C., Guharay, F., Monterroso, D. and Muschler, R.G. 2001. Designing pest suppressive multistrata perennial crop systems: shade grown coffee in Central America. Agrofor. Syst. 53: 151– 170.

Suárez Pascua, D. 2002. Cuantificación y Valoración Económica del Servicio Ambiental Almacenamiento de Carbono en Sistemas Agroforestales de Café en la Comarca Yassica Sur, Metagalpa, Nicaragua. Turrialba, Costa Rica: CATIE thesis

Teixeira-Coelho, S., Moreira, J.R., Martins, A.S., Gonzalez-Velazques, S.M.S. and Castelo-Branco, M.B. 2005. Gallery forest recovery and carbon credits. RIO 5 - World Climate and Energy Event, Rio de Janeiro, Brazil.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press, Princeton.

Toledo, V.M. 2005. Repensar la conservación: ¿áreas naturales protegidas o estrategia bioregional? Gaceta ecológica 77: 67-82.

Toledo, V.M., Ortiz-Espejel, B., Cortés, L., Moguel, P. and Ordoñez *et al.* 2003. The multiple use of tropical forests by indigenous peoples in Mexico: case of adaptative management. Conservation Ecology 7(3): 9. [online] URL: http://www.consecol.org/vol7/iss3/art9

Toledo, V. M. et al 2004. El Potencial Económico de la Flora útil de los cafetales de la Sierra Norte de Puebla. Informe Final del proyecto AE019 al Consejo nacional para la Conservación y Uso de la Biodiversidad (CONABIO).

Toledo, V.M. and P. Moguel. 2006. Multiple benefits of shade-grown coffee in bioregional conservation strategy Conservation Biology (accepted).

Trzcinski, M.K., Fahrig, L. and Merriam, H.G. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecological Applications 9: 586–593.

Van der Voort, M. and Greenberg, R. 1999. Why Migratory Birds are Crazy for Coffee. Smithsonian Migratory Bird Center. U.S.A.

Van Noordwijk, M., Rahayu, S., Hairiah, K., Wulan, Y.C., Farida, A. And Verbist, B.2002. Carbon stock assessment for a forest-to-coffee conversión landscape in Sumber-Jaya (Lampung, Indonesia): from allometric equations to land use change analysis. Science in China (Series C) 45: 75-86.

Vennini, J.P. 1994. Neartic avian migrants in coffee plantations and forest fragments of southwestern Guatemala, Bird Conserv. Int. 4: 209-232.

Wiens, J.A. 1989. Spatial scaling in ecology. Func. Ecol. 3: 385-397.

Willis, K.J. and Whittaker, R.J. 2002. Species Diversity – Scale matters. Science 295: 1245-1248.

Wunderle, J. and Latta, S. 1996. Avian abundance in sun and shade coffee plantations and remnant pine forest in the Cordillera Central, Dominican Republic. Ornitologia Neotropical 7: 19–34.

Annex

Family	Species	EN	S	PC	FG	FD
Cracidae	*Ortalis vetula*	NA	R	NA	F	NA
Ardeidae	*Bubulcus ibis*	NA	R	NA	C/I	NA
Cathartidae	*Coragyps atratus*	NA	R	NA	C	NA
	Cathartes aura	NA	R	NA	C	NA
Accipitridae	*Pandion haliaetus*	NA	M	NA	C	NA
	Accipiter striatus	NA	M	SSP	C	NA
	Buteo magnirostris	NA	R	NA	C	NA
	Buteo platypterus	NA	M	SSP	C	NA
Columbidae	*Patagioenas flavirostris*	NA	R	NA	G/F	NA
	Zenaida asiatica	NA	R	NA	G/F	NA
	Columbina inca	NA	R	NA	G	NA
	Columbina talpacoti	NA	R	NA	G	NA
	Leptotila verreauxi	NA	R	NA	G/F	NA
	Geotrygon albifacies	NA	R	E	G	FR
Psittacidae	*Pionus senilis*	NA	R	E	F	NA
	Amazona autumnalis	NA	R	NA	G/F	NA
Cuculidae	*Coccyzus erythropthalmus*	NA	M	NA	F/I	NA
	Piaya cayana	NA	R	NA	I	NA
	Crotophaga sulcirostris	NA	R	NA	I	NA
Strigidae	*Megascops guatemalae*	NA	R	NA	C	NA
	Glaucidium brasilianum	NA	R	NA	C	NA
	Ciccaba virgata	NA	R	NA	C	NA
Apodidae	*Streptoprocne zonaris*	NA	R	NA	I	NA
	Chaetura vauxi	NA	R	NA	I	NA
Trochilidae	*Campylopterus curvipennis*	NA	R	NA	N/I	NA
	Campylopterus hemileucurus	NA	R	NA	N	NA
	Anthracothorax prevostii	NA	R	NA	N/I	NA
	Hylochoris leucotis	NA	R	NA	N	NA
	Amazilia candida	NA	R	NA	N/I	NA
	Amazilia cyanocephala	NA	R	NA	N	NA

Family	Species	EN	S	PC	FG	FD
	Amazilia tzacatl	NA	R	NA	N/I	NA
	Amazilia yucatanensis	MX	R	NA	N	NA
	Lampornis amethystinus	NA	R	NA	N	NA
	Lampornis clemenciae	NA	R	NA	N	NA
	Eugenes fulgens	NA	R	NA	N	NA
	Archilochus colubris	NA	M	NA	N/I	NA
	Atthis heloisa	MX	R	NA	N	NA
	Selasphorus platycercus	NA	R	NA	N	NA
Trogonidae	*Trogon elegans*	NA	R	NA	O	FR
Momotidae	*Momotus momota*	NA	R	NA	O	NA
Ramphastidae	*Aulacorhyncus prasinus*	NA	R	SSP	O	NA
Picidae	*Melanerpes formicivorus*	NA	R	NA	O	FR
	Melanerpes aurifrons	NA	R	NA	I	NA
	Sphyrapicus varius	NA	M	NA	O	NA
	Veniliornis fumigatus	NA	R	NA	I	NA
	Piculus rubiginosus	NA	R	NA	I	NA
	Dryocopus lineatus	NA	R	NA	I	NA
	Campephilus guatemalensis	NA	R	SSP	I	NA
Dendrocolaptidae	*Sittasomus griseicapillus*	NA	R	NA	F/I	FR
	Xiphorhynchus flavigaster	NA	R	NA	I	NA
	Lepidocolaptes affinis	NA	R	NA	I	FR
Tyrannidae	*Camptostoma imberbe*	NA	R	NA	I/F	NA
	Mionectes oleagineus	NA	R	NA	F	NA
	Rhynchocyclus brevirostris	NA	R	NA	I	FR
	Platyrinchus cancrominus	NA	R	SSP	I	NA
	Mitrephanes phaeocercus	NA	R	NA	I	NA
	Contopus cooperi	NA	M	NA	I	NA
	Contopus pertinax	NA	R	NA	I	NA
	Contopus sordidulus	NA	M	NA	I	NA
	Contopus virens	NA	M	NA	I	NA
	Empidonax flaviventris	NA	M	NA	I	NA
	Empidonax alnorum	NA	M	NA	I/F	NA

Family	Species	EN	S	PC	FG	FD
	Empidonax traillii	NA	M	NA	I	NA
	Empidonax hammondii	NA	M	NA	I	NA
	Empidonax wrightii	NA	M	NA	I	NA
	Empidonax affinis	NA	R	NA	I	NA
	Empidonax difficilis	NA	R	NA	I	NA
	Empidonax occidentalis	NA	R	NA	I	NA
	Sayornis nigricans	NA	R	NA	I	NA
	Myiarchus tuberculifer	NA	R	NA	I/F	NA
	Myiarchus crinitus	NA	M	NA	O	NA
	Myiarchus tyrannulus	NA	R	NA	O	NA
	Pitangus sulphuratus	NA	R	NA	I/F	NA
	Megarynchus pitangua	NA	R	NA	O	NA
	Myiozetetes similis	NA	R	NA	I/F	NA
	Myiodynastes luteiventris	NA	R	NA	I	NA
	Tyrannus melancholicus	NA	R	NA	O	NA
	Tyrannus couchii	NA	R	NA	O	NA
	Tityra semifasciata	NA	R	NA	F	NA
Vireonidae	*Vireo griseus*	NA	M	NA	O	NA
	Vireo bellii	NA	M	NA	I	NA
	Vireo solitarius	NA	M	NA	O	NA
	Vireo huttoni	NA	R	NA	O	NA
	Vireo gilvus	NA	M	NA	O	NA
	Vireo leucophrys	NA	R	NA	F/I	NA
	Vireo olivaceus	NA	M	NA	I/F	NA
	Vireo philadelphicus	NA	M	NA	O	NA
	Hylophilus ochraceiceps	NA	R	SSP	I	NA
	Vireolanius melitophrys	NA	R	NA	I	NA
	Cyclarhis gujanensis	NA	R	NA	I	NA
Corvidae	*Cyanocorax yncas*	NA	R	NA	O	NA
	Cyanocorax morio	NA	R	NA	O	NA
Hirundinidae	*Stelgidopteryx serripenis*	NA	R	NA	I	NA
	Hirundo rustica	NA	R	NA	I	NA

Family	Species	EN	S	PC	FG	FD
Troglodytidae	*Campylorhynchus zonatus*	NA	R	NA	I	NA
	Catherpes mexicanus	NA	R	NA	I	NA
	Thryothorus maculipectus	NA	R	NA	I	NA
	Troglodytes aedon	NA	M	NA	I	NA
	Henicorhina leucosticta	NA	R	NA	I	NA
	Henicorhina leucophrys	NA	R	NA	I	FR
Regulidae	*Regulus calendula*	NA	M	NA	O	NA
Sylviidae	*Polioptila caerulea*	NA	M	NA	I	NA
Turdidae	*Sialia sialis*	NA	R	NA	O	NA
	Myadestes occidentalis	NA	R	SSP	F	NA
	Myadestes unicolor	NA	R	E	F	NA
	Catharus aurantiirostris	NA	R	NA	O	NA
	Catharus frantzii	NA	R	E	O	NA
	Catharus mexicanus	NA	R	SSP	O	NA
	Catharus ustulatus	NA	M	NA	F	NA
	Hylocichla mustelina	NA	M	NA	O	NA
	Turdus grayi	NA	R	NA	I/F	NA
	Turdus assimilis	NA	R	NA	I/F	NA
Mimidae	*Dumetella carolinensis*	NA	M	NA	O	NA
	Toxostoma longirostre	NA	R	NA	F	NA
	Melanotis caerulescens	MX	R	NA	F	NA
Bombycillidae	*Bombycilla cedrorum*	NA	M	NA	F/I	NA
Parulidae	*Vermivora pinus*	NA	M	NA	I	NA
	Vermivora celata	NA	M	NA	I	NA
	Vermivora ruficapilla	NA	M	NA	O	NA
	Parula americana	NA	M	NA	O	NA
	Parula pitiayumi	NA	R	NA	I	NA
	Dendroica magnolia	NA	M	NA	I	NA
	Dendroica coronata	NA	M	NA	I	NA
	Dendroica virens	NA	M	NA	I	NA
	Dendroica townsendi	NA	M	NA	I	NA
	Dendroica occidentalis	NA	M	NA	I	NA

Family	Species	EN	S	PC	FG	FD
	Mniotilta varia	NA	M	NA	I	NA
	Setophaga ruticilla	NA	M	NA	I	NA
	Helmitheros vermivous	NA	M	NA	I	NA
	Seiurus aurocapilla	NA	M	NA	I	NA
	Seiurus motacilla	NA	M	NA	I	NA
	Oporornis formosus	NA	M	NA	I	NA
	Geothlypis trichas	NA	M	NA	I	NA
	Geothlypis poliocephala	NA	R	NA	O	NA
	Wilsonia citrina	NA	M	NA	I	NA
	Wilsonia pusilla	NA	M	NA	I	NA
	Wilsonia canadensis	NA	M	NA	I	NA
	Myioborus miniatus	NA	R	NA	I	NA
	Euthlypis lachrymosa	NA	R	NA	I	NA
	Basileuterus culicivorus	NA	R	NA	I	NA
	Basileuterus rufifrons	NA	R	NA	I	NA
	Basileuterus belli	NA	R	NA	I	NA
	Icteria virens	NA	M	NA	O	NA
Thraupidae	*Chlorospingus ophthalmicus*	NA	R	NA	O	NA
	Piranga rubra	NA	M	NA	O	NA
	Piranga ludoviciana	NA	M	NA	O	NA
	Piranga leucoptera	NA	R	NA	O	NA
	Thraupis abbas	NA	R	NA	F	NA
	Cyanerpes cyaneus	NA	R	NA	O	NA
Emberizidae	*Volatinia jacarina*	NA	R	NA	G/I	NA
	Sporophila americana	NA	R	NA	G	NA
	Sporophila torqueola	NA	R	NA	G	NA
	Sporophila minuta	NA	R	NA	G	NA
	Tiaris olivaceus	NA	R	NA	O	NA
	Atlapetes albinucha	NA	R	NA	I	NA
	Buarremon brunneinucha	NA	R	NA	I	FR
	Arremonops rufivirgatus	NA	R	NA	G	NA
	Aimophila rufescens	NA	R	NA	G	NA

Family	Species	EN	S	PC	FG	FD
	Spizella passerina	NA	R	NA	G/I	NA
	Melospiza lincolnii	NA	M	NA	G/I	NA
Cardinalidae	*Saltator atriceps*	NA	R	NA	O	NA
	Pheucticus ludovicianus	NA	M	NA	O	NA
	Cyanocompsa parellina	NA	R	NA	O	NA
	Passerina caerulea	NA	R	ND	G	NA
	Passerina cyanea	NA	M	NA	G	NA
	Passerina ciris	NA	M	NA	G	NA
Icteridae	*Dives dives*	NA	R	NA	O	NA
	Quiscalus mexicanus	NA	R	NA	O	NA
	Molothrus aeneus	NA	R	NA	G/I	NA
	Icterus spurius	NA	M	NA	O	NA
	Icterus cucullatus	NA	M	NA	F/I	NA
	Icterus gularis	NA	R	NA	I/N	NA
	Icterus graduacauda	MX	R	NA	I/N	NA
	Icterus galbula	NA	M	NA	O	NA
	Amblycercus holosericeus	NA	R	NA	I	NA
	Psarocolius montezuma	NA	R	SSP	F	NA
Fringillidae	*Euphonia hirundinacea*	NA	R	NA	G/F	NA
	Euphonia elegantissima	NA	R	NA	F	NA
	Carduelis pinus	NA	R	NA	G	NA
	Carduelis psaltria	NA	R	NA	G	NA
	Coccothraustes abeillei	NA	R	NA	G	NA

Annex 1. Total list of observed, heard and/or captured birds in taxonomic order in the study area (according to AOU 1998). Abbreviations: EN, Endemic; PC, Protection Category; FG, Foraging Guild; FD, Forest Dependent; MX, endemic to Mexico; R, resident; M, migratory; E, endangered; SSP, subject to special protection; F, frugivorous; I, insectivorous; G, granivorous, N, nectarivorous; O, omnivorous; C, carnivorous; FR, forest dependent (species that breed exclusively in the forest); NA, not applicable.

Summary

Resumen

Samenvatting

Summary

As the current accelerated and increasing loss of biological diversity have become apparent land managers and ecologists have sought to identify significant habitats to the preservation of biodiversity. A critical component of biodiversity protection is the understanding of the ecological forces shaping the species diversity patterns. The aim of this study is to gain insight in the local and regional factors ultimately controlling species persistence and coexistence. The conceptual background of this study is that of a diversified multiple-use landscape matrix, that is used and managed and where "natural areas" can be embedded.

Neotropical bird species are currently under threat as their breeding grounds suffer from degradation and loss because of intensification of land use. The fieldwork of this thesis was conducted in the northeastern mountain range of Puebla, Mexico. This region represents an important area for the conservation of resident and migrant birds, as it is located in a strategic position at the Neartic and Neotropical biogeographic boundary. It also forms part of the migratory route for Nearctic-Neotropical birds. Moreover, despite the loss of primary forests in the region, one of the main land uses in the study area is traditional shade coffee plantations which remain as an important forested habitat for birds.

An important issue in conservation biology is the monitoring of community trends to provide reliable information of species diversity and their status, for fast and efficient identification of conservation priorities. In chapter 2, we analyse the use of a double-observer point count approach and mist netting for assessing bird species richness during migration. We assess the relative biases, costs and efficiency of both techniques to aim optimisation in the design of large-scale monitoring. We found that the double-observer point count technique was the most effective in the total species richness completeness and presented lower total effort in comparison to mist netting. The performance of point counts is higher than mist netting in the detection of new bird species in the research area, even after a large sampling effort. However, mist netting significantly detected a higher proportion of understory species in comparison to point counts, though we found opposite results for migrant species. Finally, the cost-efficiency analysis showed that the modified

double-observer point counts required less total effort thus decreasing total monetary costs compared to mist netting.

One of the main problems in conservation in Latin America is the accelerated deforestation and conversion to monocultures and grazing lands that has direct effects on Neotropical avian communities (i.e. resident and migrants) leading to a major loss of habitat, and landscape fragmentation. In chapter 3, we analyse how fragmentation and habitat loss in the landscape influences the bird species richness patterns. We examine the relative individual and combined influence of these two factors on species richness in an avian metacommunity. Moreover, we compare the difference in explanatory power of individual and combined influence of both factors. The response of species richness to habitat fragmentation shows a unimodal response at landscape level, and a negative response to habitat loss. The combined influence of fragmentation and habitat loss did not offer a better approximation of species richness response. This suggests that there is no interaction between the effects of fragmentation and habitat loss. Assessment of the effects of habitat fragmentation and loss under the current situation of growing human perturbation in natural habitat is fundamental in conservation and landscape management.

An important ecological force structuring ecological communities is interspecific competition. Body mass is an easily determined characteristic of animals that probably influences competition strength. In chapter 4, our objective is to examine the effect of body size (mass) on competitive interactions between competing pairs of bird species. Our results indicate that there is a significant negative relationship between bird body mass ratio and the competition strength i.e.; the larger the body mass ratio, the lower the competition strength thereby suggesting that high variation in body sizes amongst sympatric species may promote coexistence in communities. Moreover species that have a greater overlap in resource use tend to exhibit stronger competition than species that overlap less in their resource use.

In chapter 5, the influence of spatially explicit bio-physical variables at multiple scales on a bird community is analysed. We argue that biological communities are organised at multiple functional spatial scales and interactions between these scales determine both local and regional patterns of species richness. We use a multiple scale approach with plot, patch and landscape level variables using abundance and presence-absence data. Our results demonstrate that landscape variables explain most of the variation in bird species in both abundance and presence-absence analyses in all explanatory sets. Interestingly, results demonstrate that variation in community structure was described best at family-level than at genera- or species-level. Our results show that shade coffee plantations is one of the main land covers that positively influence the species richness, thus providing habitat for neo-tropical migrants and forest-dependent birds (e.g.; in this study some endemic and protected species). Thus, selecting the appropriate scale(s) of management in conservation strategies is essential in conservation of bird communities.

The use of remotely sensed data has great potential to aid in explaining species diversity and community assemblage patterns at multiple scales. Besides, it can help to optimise sampling strategies or to allow testing of hypotheses regarding the spatial correspondence of species diversity patterns among different taxonomic groups. In chapter 6, we review how remote sensing has been used to assess terrestrial faunal diversity, with emphasis on proxies and methodologies, while exploring prospective challenges for the conservation and sustainable use of biodiversity. We grouped and discussed papers dealing with the faunal taxa mammals, birds, reptiles, amphibians, and invertebrates into five classes of surrogates of animal diversity: 1. habitat suitability, 2. photosynthetic productivity, 3. multi-temporal patterns, 4. structural properties of habitat, and 5. forage quality. It is concluded that the most promising approach for the assessment, monitoring, prediction, and conservation of faunal diversity appears to be the synergy of remote sensing products and auxiliary data with ecological biodiversity models, and a subsequent validation of the results using traditional observation techniques.

In chapter 7, I present the conservation implications of shade coffee plantations as a refuge for Neotropical birds. The scenarios of loss and conversion of shade coffee plantations for biodiversity conservation and carbon sequestration emphasise on the ecological services that this agro-ecosystem provides. The reduction of shade coffee plantations in the studied region will have a deleterious effect on the species richness of e.g., resident birds with an estimated decline of 0.006 in species richness for every hectare the coffee area is reduced. These results could have significant consequences for conservation strategies as the amount of traditional shade coffee plantations has a positive linear relationship with the species richness of resident birds (p <0.001). Moreover, in our research area the calculated carbon stock of the total area covered by shade coffee plantations is 257,789 t C, which represents 1,288,943 USD in carbon credits. Thus, with a reported current conversion rate of 0.4 % the results in carbon loss will be devastating in just one year. Although the conversion rate for the research area is unknown we approximate an almost negligible rate of conversion compared to the previously reported. The potential for the coffee producers as suppliers of carbon sequestration is calculated in approximately 105 USD/ha, which represents a considerable income compared to approximately an average of 59 USD/ha per coffee harvest. In addition, the value of shade coffee plantations as a component of the *anthropogenic* matrix is stressed in this study. Traditional shade coffee plantations are cultivated mainly by small-scale community-based growers, the majority of them belong to some indigenous group.

The indigenous form of utilisation of this tropical agroecosystems denotes a multiple use strategy, which can be called adaptative management. This indigenous adaptative management has obvious socio-economic as well as ecological benefits. The ecological advantages of shade coffee agroecosystems are clear: a) high biodiversity maintenance, b) regulation of carbon cycle, c) soil protection, d) regulation of hydrological cycle and e) preservation of forest cover. The economic benefits derived from this tropical agroecosystems are sources of goods, services and energy for household subsistence and products for local, regional and international markets. To increase the effectiveness of conservation management, the value of suitable land for multiple uses, as a component of the *anthropogenic* matrix should be considered. For example, in the case of tropical bird species, such linkages could be maintained by using the man-modified landscapes, e.g.; traditional shade coffee plantations as these areas also harbour an ecological value as habitat

Resumen

Debido a la acelerada y creciente perdida de la diversidad biológica (subsecuentemente referida como biodiversidad) los manejadores de recursos naturales y ecólogos han buscado identificar los habitats relevantes para la preservación de la biodiversidad. Un componente crítico para la protección de la biodiversidad es el entendimiento de las fuerzas que configuran los patrones de la diversidad de especies. La meta de este estudio es el de comprender los factores locales y regionales que finalmente controlan la persistencia y coexistencia de las especies. El concepto sobre el cual se fundamenta este estudio es hacia el uso y manejo de una matriz diversificada del paisaje con múltiples usos en donde las "áreas naturales" se encuentran insertas.

Las aves Neotropicales se encuentran actualmente amenazadas ya que sus áreas de reproducción sufren degradación y perdida. El trabajo de campo realizado en esta tesis fue conducido en la Sierra Norte de Puebla, México. Esta región representa un área importante para la conservación de aves residentes y migratorias, ya que se encuentra localizada en una zona estratégica biogeográfica en el limite entre la región Neoártica y la Neotropical. Además, forma parte del corredor migratorio para las aves Neoárticas-Neotropicales. A pesar de la alta tasa de deforestación en la región, uno de los usos de suelo principales en el area de estudio es plantaciones tradicionales de café bajo sombra los cuales permanecen como importantes áreas forestadas que representan hábitat adecuado para la avifauna.

Una cuestión importante en la conservación es el monitoreo de las tendencias en las comunidades de especies para obtener información confiable de la biodiversidad y su estatus. En el capitulo 2, analizamos el uso del enfoque de puntos de conteo con doble-observador y el uso de redes de niebla para evaluar la riqueza de especies durante la época de migración. Evaluamos las biases y los costos relativos, y la eficiencia de ambas técnicas para conseguir la optimización en el diseño de monitoreos a gran escala. Nuestros resultados muestran que la técnica de puntos de conteo con doble-observador tiene un mejor desempeño en la detección del número total de especies y requiere un esfuerzo de

muestreo menor comparado a las redes de niebla. El desempeño de los puntos de conteo es mejor que las redes de niebla en la detección de nuevas especies, aun después de un esfuerzo de muestreo relativamente largo. Sin embargo, las redes de niebla detectaron significativamente una proporción mayor de especies del sotobosque en comparación a los puntos de conteo, no obstante encontramos resultados contrarios en relación a las especies migratorias. Finalmente, el análisis de costo-beneficio mostró que los puntos de conteo con doble-observador requieren de un esfuerzo de muestreo total por lo tanto los costos monetarios son menores en comparación a las redes de niebla.

Uno de los problemas principales en América Latina es la acelerada deforestación y conversión a monocultivos y potreros lo cual tiene efectos directos en las comunidades de aves Neotropicales (i.e.; aves residentes y migratorias), lo que conlleva a la fragmentación y pérdida substancial de hábitat. En el capitulo 3, analizamos como la fragmentación y perdida de hábitat influencia los patrones de riqueza de especies. Examinamos la influencia relativa individual y combinada de ambos factores en la riqueza de especies en una metacomunidad de aves. Además, comparamos la diferencia del poder explicativo del efecto individual y combinado. La respuesta en la riqueza de especies a la fragmentación del hábitat muestra una respuesta unimodal a nivel del paisaje, y una respuesta lineal negativa a la perdida de hábitat. El efecto combinado de ambos factores (i.e.; fragmentación y pérdida de hábitat) no ofrece una mejor aproximación de la respuesta en la riqueza de especies. Esto sugiere que no hay interacción entre los efectos de fragmentación y pérdida de hábitat. La evaluación de los efectos de fragmentación y pérdida de hábitat bajo la situación actual de perturbación humana en los habitats es fundamental en el manejo y conservación de especies a nivel del paisaje.

Una fuerza ecológica importante que estructura las comunidades de especies es la competencia interespecífica. La masa corporal es una característica animal fácilmente determinable que probablemente influencia la intensidad de la competencia. En el capitulo 4, nuestro objetivo es examinar el efecto de la masa corporal en las interacciones de competencia de pares de especies. Los resultados indican que existe una relación lineal negativa entre la tasa de masa corporal y la intensidad de competencia, i.e.; entre mas grande la tasa de masa corporal, menor la intensidad de competencia por lo que esto sugiere que la mayor variación en la el tamaño de especies entre especies simpatétricas puede promover la coexistencia en las comunidades de especies. Además, las especies que tienen un sobrelapamiento en el uso de recursos tienden a exhibir un grado de competencia mayor que las especies con menor sobrelapamiento en el uso de sus recursos.

En el capitulo 5, analizamos la influencia de variables espaciales bio-fisicas en una comunidad de aves, bajo un contexto multi-escalas. Nosotros argumentamos que las comunidades de especies están organizadas en múltiples escalas espaciales funcionales y las interacciones entre estas escalas determinan los patrones locales y regionales de la riqueza de especies. Usamos un enfoque de escalas múltiples con variables a nivel de parcela, parche y paisaje utilizando datos de abundancia y presencia-ausencia de especies. Los resultados demuestran que las variables al nivel del paisaje explican la mayor parte de la variación en los datos de abundancia y presencia-ausencia de especies de aves en todos los grupos de variables independientes. Interesantemente, la variación en la estructura de la comunidad es descrita mejor a nivel de familia taxonómica que a nivel de género o especie. También, las plantaciones de café es uno de las coberturas de suelo que muestran una relación lineal positiva con la riqueza de especies, por lo que proveen hábitat adecuado para aves migratorias y dependientes del bosque (e.g.; en este estudio algunas especies endémicas y especies protegidas). Por lo que el seleccionar la escala(s) espacial apropiada en las estrategias de manejo y conservación puede tener implicaciones importantes para la conservación de las comunidades de aves en la región de estudio.

El uso de datos obtenidos a través de sensores remotos tiene un gran potencial auxiliando en explicar la diversidad de especies y los patrones de la estructura en las comunidades de especies en múltiples escalas. Además, puede auxiliar en la optimización de las estrategias de muestreo o permitiendo la verificación de hipótesis concernientes a la correspondencia espacial de los patrones de la diversidad de especies entre diferentes grupos taxonómicos. En el capitulo 6, realizamos una revisión de cómo los sensores remotos han sido usados para evaluar la diversidad de fauna terrestre, haciendo énfasis en las variable substitutas utilizadas para explicar la distribución y diversidad de especies, al igual que las metodologías usadas. También damos una perspectiva de los desafíos del uso de datos obtenidos a través de sensores remotos para la conservación y uso sustentable de la biodiversidad. Agrupamos y discutimos artículos científicos acerca de diferentes grupos taxonómicos, i.e.; mamíferos, aves, reptiles, anfibios, e invertebrados en cinco grupos de variables sustitutas utilizadas para explicar la distribución y diversidad de especies: 1. adecuación de hábitat, 2. productividad primaria, 3. patrones multi-temporales, 4. propiedades estructurales del hábitat, y 5. calidad de forraje. Concluimos que el enfoque mas prometedor para la evaluación, monitoreo, predicción, y conservación de la diversidad de especies de fauna terrestre resulta ser la sinergia de productos derivados de sensores remotos y datos auxiliares con modelos ecológicos de la biodiversidad, y la subsiguiente validación de los resultados utilizando técnicas de observación tradicionales.

En el capitulo 7, presento las implicaciones de conservación de los cafetales tradicionales bajo sombra como refugios para las aves Neotropicales. Los escenarios de pérdida y conversión de los cafetales tradicionales bajo sombra mostrados en este estudio, enfatizan sobre los servicios ecológicos que estos agroecosistemas proveen. La reducción de los cafetales bajo sombra en la región de estudio tendría un efecto perjudicial en la riqueza de especies de, por ejemplo, aves residentes, con una reducción en la riqueza de especies de 0.006 por cada hectárea perdida de café bajo sombra. Estos resultados pueden tener consecuencias significativas para las estrategias de conservación ya que la cantidad de área de cafetales bajo sombra tiene una relación lineal positiva con la riqueza de especies de aves residentes ($p<0.001$). Además, en nuestra área de estudio el abastecimiento calculado de carbono producido por el área total cubierta por cafetales bajo sombra es de 257,789 t C lo que representa 1, 288,943 USD en créditos de carbono. Por lo que si consideramos la tasa de conversión reportada para los cafetales bajo sombra en México de 0.4% los resultados en la perdida de carbono serian devastadores en solamente un año. Sin embargo, la tasa de conversión en la región de estudio es desconocida y estimamos que comparada con la tasa reportada relativamente pequeña. El potencial monetario para los productores de café como abastecedores de secuestración de carbono esta calculado en aproximadamente en 105 USD/ha, lo cual representa un substancial comparado con promedio aproximado de 59 USD/ha por cosecha de café. Más aun, el valor de las plantaciones de café bajo sombra como un componente de la matriz *antropogénica* se enfatiza en este estudio.

Los cafetales tradicionales bajo sombra son cultivados mayoritariamente por pequeños productores ejidatarios, la mayoría de ellos pertenecientes a algún grupo indígena. El modo de utilización indígena en México en estos agroecosystemas tropicales denota una estrategia de uso múltiple (EUM), la cual ha sido llamada manejo adaptativo. La EUM tiene beneficios socio-económicos obvios como también ecológicos. Las ventajas ecológicas de estos agroecosystemas es claro: a) mantenimiento de niveles altos de biodiversidad, b) regulación de ciclos de carbono, c) protección del suelo, d) regulación de ciclos hidrológicos, y e) preservación de la cobertura forestada. Los beneficios económicos derivados de este agroecosystema son como fuente de bienes y servicios, y energía para la subsistencia de los productores, y como fuente de productos para mercados locales, regionales e internacionales. Para incrementar la efectividad del manejo y conservación de especies, el valor de usos de suelo adecuados de usos múltiples como un componente de la matriz *antropogénica* debe ser considerada. Por ejemplo, en el caso de las especies de aves Neotropicales, tales vínculos pueden ser mantenidos usando los paisajes modificados, e.g.; los cafetales tradicionales bajo sombra ya que estas áreas tienen un alto valor ecológico como hábitat adecuado.

Samenvatting

Sinds de huidige afname van biologische diversiteit duidelijk werd, hebben natuurbeheerders en ecologen getracht die habitats te identificeren, die belangrijk zijn voor het behoud van die biodiversiteit te behouden. Om biodiversiteit te behouden is een goed begrip van de ecologische processen die patronen in soortsdiversiteit veroorzaken onontbeerlijk. Het doel van deze studie is inzicht verwerven in de ultimate lokale en regionale factoren die het voorkomen en de coëxistentie van soorten bepalen. De conceptuele achtergrond van de studie is het interpreteren van een landschap als een gevarieerde multifunctionele landschapsmatrix, waarin natuurlijke gebieden een plaats wordt gegeven.

Vogels in de neotropische zone staan onder bedreiging: hun broedgebieden raken gedegradeerd, of raken ongeschikt. De data voor deze studie werd verzameld in het noordoostelijke berggebied van Puebla, Mexico. Deze regio is een belangrijk gebied in het beheer van zowel stand- als trekvogels, aangezien het op de grens ligt van de Neartische en de Neotropische biogeografische zones. Daarnaast ligt het op een belangrijke trekroute van Neartische en Neotropische migrerende vogels. Ondanks het verlies van primair bos in deze regio, biedt het gebied nog steeds een belangrijk boshabitat, in de vorm van koffieplantages, waar de traditionele verbouwing van bosrijk schaduwplantage nog wordt toegepast.

Voor een passend en efficient natuurbeheer is monitoring van soorten essentieel: alleen zo verkrijgen beleidsmakers betrouwbare informatie over soort-diversiteit en status van soorten. In hoofdstuk 2 van dit proefschrift evalueren we twee monitorings-methodes: punt-tellingen met twee waarnemers en inventarisaties met behulp van mistnetten. We vergelijken de twee methodes wat betreft gevonden resultaten, maar ook wat betreft kosten en. Met deze kennis kunnen grote-schaal monitoring geoptimaliseerd worden. Punt-tellingen bleek het meest effectief: deze gaf de beste schatting van de totale soortenrijkdom en kostte minder inspanning. Punt-tellingen werkten ook beter in het vaststellen van nieuwe soorten dan de mist-net methode. Met mistnetten werden relatief meer soorten gevonden die in struwelen leven, maar de punt-tellingen gaf meer migrerende soorten. Kost-efficiency analyses toonde aan dat monitoring met punt-tellingen minder inspanning en dus minder geld kosten.

Een van de belangrijkste problemen in natuurbeheer in Latijns Amerika is de toenemende ontbossing. Bossen worden omgevormd tot monocultuur-plantages of weide. Dit proces lijdt tot verlies of fragmentatie van habitats, en heeft zo een sterke invloed op zowel migrerende als niet-migrererende neotropische avifauna. In hoofdstuk 3 analyseren we de invloed van fragmentatie en habitatverlies op patronen van soortdiversiteit van deze avifauna. We bepalen de individuele en gecombineerde invloed van deze twee factoren op soortsrijkdom in de metagemeenschap van vogels. Soortenrijkdom reageert unimodaal op fragmentatie van habitats of landschapsniveau, en negatief op habitat-verlies. Het gecombineerde effect van deze twee factoren verklaarde het patroon van soortenrijkdom niet beter. Dit suggereerd dat er geen interactie is tussen de effecten van fragmentatie en verlies van habitat. Met oog op de groeiende verstorende invloed van de mens in natuurlijke habitats is en beoordeling van de effecten van fragmentatie en verlies van habitat is een van groot belang bij landschapsbeheer.

Interspecifieke concurrentie is een belangrijke onderdeel van het proces van vorming van ecologische gemeenschappen. Lichaamsgrootte is een eenvoudig te bepalen eigenschap en is in potentie een belangrijke bepalende factor in concurrentie tussen soorten.. In hoofdstuk vier bestuderen we het effect van lichaamsgrootte (massa) op deze interactie tussen vogelsoorten. Onze resultaten tonen dat er een significante negatieve relatie bestaat tussen lichaamsgewicht van soorten en de mate waarin deze soorten concurreren: hoe hoger de lichaamsgrootte-ratio hoe lager de competitie-kracht. Dit suggereert dat de grote variatie in lichaamsgrootte in sympatrische soorten de coexistentie in gemeenschappen mogelijk maakt. Bovendien tonen soorten met een grotere overlap in gebruik van resources een sterkere concurrentie dan soorten die hierin minder overlap tonen.

In hoofdstuk 5 analyseren we de invloed van ruimtelijk expliciete biologische en fysieke variabelen op vogel-gemeenschappen. We doen dit op verschillende ruimtelijke schalen, omdat we verwachten dat biologische gemeenschappen op meerdere functionele ruimtelijke schalen georganiseerd zijn en dat interacties tussen deze schalen de locale en regionale patronen in soortsrijkdom bepalen. We doen dit door de abundantie en aan-afwezigheids- van de vogelsoorten te analyseren aan de hand van variabelen op het niveau van plot, patch of landschap. Onze resultaten tonen dat zowel abundantie als aan-afwezigheid van soorten het beste verklaard worden door variabelen die spelen op landschaps-schaal. Interessant is dat onze resultaten uitwijzen dat variatie in de structuur van de gemeenschappen het best beschreven wordt op het taxonomische niveau van familie, beter dan op genus of soorts-niveau. Traditionele koffieplantages vormen een van de landschaps-types die soortenrijkdom positief beinvloeden, en vormt zo een habitat voor zowel neo-tropische migranten als bosbewondende vogels, waaronder een aantal endemische, beschermde soorten. Het selecteren van de juiste geografische schaal bij opstellen en implementeren van beschermingsplannen voor vogel-gemeenschappen is uiterst belangrijk.

Het gebruik van remote sensing voegt opent nieuwe mogelijkheden in het onderzoek aan patronen in soortenrijkdom en structuur van gemeenschappen op verschillende schalen. Daarnaast kan het een goed gereedschap zijn bij het optimaliseren van bemonstering van soortsdiversiteit, of testen van hypotheses over relaties tussen soortenrijkdom in verschillende taxonomische groepen. In hoofdstuk 6 bespreken we hoe remote sensing wordt gebruikt om faunistische diversiteit te bepalen, met een nadruk op methodologie. We bespreken mogelijke uitdagingen op het gebied van beheer en duurzaam gebruik van biodiversiteit. We delen de studies van zoogdieren, vogels reptielen amfibieen en invertebraten op in 5 klassen van surrogaten voor daadwerkelijke-diversiteit: 1) geschiktheid van habitat, 2) fotosynthetische productiviteit, 3) tijdsreeks-patronen. 4). structurele eingeschappen van het habitat en 5) voedselkwaliteit. We concluderen dat de meest kansrijke aanpak van bepalen, monitoren, voorspellen en beheren van diversiteit in fauna gelegen is in de synergie van remote sensing en ecologische biodiversiteits-modellen, gevolgd door een validatie van de resultaten met behulp van de meer traditionele veldmethodiek.

In hoofdstuk 7 bespreek ik de implicaties die traditionele koffieplantages met schaduwbouw, in hun functie als refugium voor neotropische vogels, hebben op natuurbeheer. De scenarios van versies of omzetting van deze koffieplantages voor het beheer van biodiversiteit en koolstof-fluxen benadrukken de ecologische rol van dit agro-ecosysteem. De afname van koffieplantages in het studiegebied heeft een negatief effect op soortenrijkdom van standvogels, met een geschatte afname in soortenrijkdom van 0.0006 voor elke hectare plantage die verdwijnt. Deze resultaten kunnen behoorlijke consequenties hebben voor beheer-strategieen aangezien het oppervlakte aan koffieplantages een positieve lineaire relatie heeft met soorten-rijkdom van standvogels ($P < 0.001$). Bovendien is voor ons studiegebied te berekenen dat in deze koffieplantages 257,789 t C aan koolstof is vastgelegd, , wat correspondeert met 1,288,943 USD in *carbon credits*. De huidige omzetting van plantages naar niet-beboside landschappen van 0.4% per jaar voor heel Mexico, zou voor het studiegebied leiden tot een aanzienlijk verlies van gefixeerd koolstof aanzienlijk. Hoewel de omzettingssnelheid in het studiegebied onbekend is, voorspellen we een bijna verwaarloosbare omzettingssnelheid. Koffieproducenten zouden een koolstoffixatie kunnen leveren van ongeveer 105 USD ha^{-1}, wat een hoger inkomen zou geven dan de gemiddelde winst bij verbouwens van koffie (59 USD ha^{-1}). Daarnaast hebben de plantages waarde als antropogeen element van de landschaps-matrix: traditionele schaduwplantages worden beheerd door kleine kleine boeren uit lokale kleine gemeenschappen, waarvan er velen behoren tot een inheemse bevolkingsgroep. De inheemse wijze van gebruik van dit tropische agroecosysteem volgt een *multiple use strategie*, ook wel *adaptive management* genoemd. Zulke *adaptive management* strategieen kennen zowel socio-economische als ecologische voordelen. De ecologische voordelen van traditionele koffieplantages zijn duidelijk: a) ze bieden ruimte aan een hoge biodiversiteit. b) ze leggen koolstof vast. c). ze beschermen tegen bodem erosie. d) ze gaan uitdroging tegen. e) ze maken behoud van bos mogelijk. Vanuit een economisch perspectief vormen de koffieplantages een bron van goederen, service en energie voor lokale bewoners en van producten voor lokale, regionale en internationale handel. Om effectiviteit van het beheer te vergroten, moet waarde van dit soort landschappen in met meerdere functies worden onderkent, en moet een gebied worden gezien als onderdeel van de antropogene matrix. In het geval van tropische vogels kunnen zulke verbindingen kunnen worden beheerd door gebruik van die onderdelen van de landschapsmatrix die gebruikt worden door de mens, zoals traditionele schaduw-bebouwede koffieplantages, aangezien deze ook functioneren als habitat.

Acknowledgments

Curriculum vitae

List of publications

Affiliations of co-authors

PE&RC PhD Education Statement Form

Acknowledgments

I am grateful to all people mentioned here for their intellectual, moral and material support.

I express my gratefulness to Fred de Boer for his guidance, supervision and faith in my work. I also feel thankful for all the support given by Antoine Cleef during the long process of my PhD. My gratitude to Victor Toledo for introduced me to the coffee lands and giving me support when needed. My thanks to Andrew Skidmore for his supervision.

Without Samuel Lopez de Aquino that I wouldn't have been able to carry out my fieldwork, and I appreciate all the knowledge and friendship he offered me. I especially thank all the people of the Cooperative Tosepan Titataniske for all the help, support and honest interest in my study that made my fieldwork possible and that ended in a creative and productive process beyond science. I express my gratitude to the people in Cuetzalan region for making me feel at home, especially Doña Guille. My appreciation to Patricia Moguel for initiating the topic of my thesis. I appreciate the help given by the excellent birdwatchers, Garry Bakker and Reinoud Vermoolen, during their visit to my research area.

I am grateful to Javier López Caloca and Mario Gomes Soberon for providimg the digital geographic material. Néstor Matamoros, Sofia Morales Argüello, Yolanda Aguirre Montiel and Sandra Jimenes Peregrina assisted in processing the digital material. Lucia Almeida, Víctor Avila-Akerberg, Verónica Aguilar, Tanya González, José Hernández, Maarten Blaauw and Ernesto Anaya contributed with the vegetation survey. Nelly García Diego and Beatriz Ludlow performed the taxonomic identification of plant material. Frank van Langevelde, Gerard Reinink and Boudewijn van Leeuwen helped process the geographic information. My gratitude goes as well to Idea Wild for the field material provided for my research. I appreciate the help and camaraderie given by all the staff and PhD students at the Resource Ecology Group. Thanks to the family Drent for all their support.

I am indebted to my parents, Fernando and Chuy, for providing me with love and the moral and material environment that allowed me to reach this stage. Thanks to my friends, Bibiana, Rodrigo, Michiel, Manuel, Sergio, Emiliano, Adolfo, Lilia, Maarten, Max. Thanks to all my past and present housemates: Jasja, Ans, Jasper, Elise, Vena, Paul, Karin, Griet, Arthur, Sander, Maartje. I am thankful to Annelies and Ton for being honest, natural and loving.

Tijl, I am so grateful for your love, sharp mind, humour, patience, understanding, critics, fun, and for being there even in my worse moments.

And finally, I have to mention Yohuak, my faithful dog that no matter what, he drags me out to the sun or rain, giving my lungs and mind a moment of fresh air.

Euridice

Wageningen, March 2006

Curriculum vitae

Euridice Leyequién Abarca was born on September 21st 1973 in Mexico City, Mexico. In 1997 she obtained her BSc. Degree in Biology from the Universidad Autonoma Metropolitana Unidad Xochimilco (UAM-X), Mexico City, Mexico. During her studies at UAM-X she conducted a land use planning study based on forestry goals in the municipality Ecatzingo de Hidalgo, Estado de Mexico, Mexico. After graduating, she worked as assistant professor in the same University in the Laboratory of Geographical Information Systems. At the end of the year 1998 she started her MSc. Degree in Environmental System Analysis and Monitoring from the International Institute for Aerospace Survey and Earth Sciences (ITC), Enschede, the Netherlands. Her MSc. thesis was conducted in the Hurungwe and Nyaminyami rural districts, Zimbabwe and it dealt with the spatial and temporal assessment of grazing and water resources for livestock in communal lands. She obtained her MSc. Degree in 2000.

After graduating, she returned to Mexico and started to work in the project 'Etno-ecological Atlas for Mexico and MidAmerica" in the Laboratory of Etnoecology, Institute of Ecology (now Research Centre in Ecosystems), Universidad Nacional Autonoma de Mexico (UNAM). In 2002 she started her PhD in the Resource Ecology Group from Wageningen University, the Netherlands. Her research project entailed the study of the ecological forces shaping the bird species diversity, and was performed in the north eastern mountain range of Puebla, Mexico in a coffee region. Her research allowed her to collaborate with an indigenous Cooperation Tosepan Titataniske which groups coffee farmers with organic and/or traditional coffee production. The results of this thesis contribute to the conservation and management plans of the aforementioned coffee region that aims to a diversified multiple-use in the landscape matrix, where "natural areas" can be embedded.

List of Publications

Published or accepted

Toledo, V.M.; Alarcón-Cháires, P.; Moguel, P.; Olivo, M.; Cabrera, A.; Leyequién, E. y Rodríguez-Aldabe, A. 2001. El Atlas Etnoecológico De México y Centroamérica: Fundamentos, Métodos y Resultados. 6 (8): 7-41.

Toledo, V.M.; Alarcón-Chaires, P; Moguel, P.; Olivo, M; Cabrera, A.; Leyequién, E. y Rodríguez-Aldabe, A. Biodiversidad y Pueblos Indígenas En México y Centro América. 2002. Biodiversitas. 7 (43): 2-8.

Chávez-Cortés, J.M., Chávez-Cortés, M.M., Binnquist-Cervantes, G.S., Roldán-Aragón, I., Leyequien, E., Romano-Delon, G. 2003. Strategic Planning Of The Iztaccíhuatl - Popocatépetl Area, In: Heil, G.W., Bobbink, R and Trigo Boix Nuri (Eds.) Ecology and Man in Mexico's Central Volcanoes Area. Geobotany 29, Kluwer, Dordrecht

Toledo, V.M., Moguel, P., Durán, L., Albores, Ma. L., Leyequien, E., Ayón, A., Rodríguez-Aldabe, A. and Alarcón-Chaires, P. (Accepted in Etnobiología 2004). Etnobiología para la Resistencia Indígena: La Sierra Norte de Puebla.

Leyequien, E., Verrelst, J., Slot, M, Heitkonig, I., Schaepman, G. and Skidmore, A.K. (Accepted in International Journal of Applied Earth Observation and Geoinformation, Special Issue). Capturing the Fugitive: Applying Remote Sensing to Terrestrial Animal Distribution and Diversity. A Review

Submitted

Leyequien, E., De Boer, W.F. and Skidmore, A.K. Linking Species-Environment Relationships and Multiple Spatial Scales in Community Ecology.

Leyequien, E., De Boer, W.F. and Toledo, V.M. Fragmentation and Habitat Loss: Species Richness Responses in an Avian Metacommunity.

Leyequien, E., De Boer, F. and Cleef, A.M. Influence of Body Size on Coexistence of Bird Species.

Leyequien, E., De Boer, F., Bakker, G., Vermoolen, R. and Lopez de Aquino, S. (Submitted to Biodiversity and Conservation). Monitoring Neotropical Birds: Efficiency of a Modified Double-Observer Point Count Approach versus Mist-Netting.

In preparation

Leyequien, E. and Lopez De Aquino, S. Avifauna Diversity In The Coffee Agro-Ecological Zone in the Cuetzalan Region, Puebla, Mexico.

Leyequien, E., Toledo, V.M. and Lopez de Aquino, S. Etno-Ornithology in the North Eastern Mountain Range of Cuetzalan Region, Puebla, Mexico.

Leyequien, E. and Lopez de Aquino, S. The North eastern mountain range of Puebla, Mexico: a priority conservation area for Neotropical birds.

Affiliation of co-authors

Fred de Boer

Resource Ecology Group, Department of Environmental Sciences, Wageningen University,
Bornsesteeg 69, 6708 PD Wageningen, the Netherlands

Antoine M. Cleef

Resource Ecology Group, Department of Environmental Sciences, Wageningen University,
Bornsesteeg 69, 6708 PD Wageningen, the Netherlands

Victor M. Toledo

Centro de Investigación en Ecosistemas, National University of Mexico, Apdo. 41-H Sta.
María Guido, Morelia, Michoacan 58090, México

Andrew K. Skidmore

ITC, PO Box 6, 7500 AA Enschede, the Netherlands

Jochem Verrelst

Wageningen University, Laboratory for Geo-information Science and Remote Sensing,
Droevendaalsesteeg 3, Building 100+101, 6708 PB Wageningen, the Netherlands

Martijn Slot

Resource Ecology Group, Department of Environmental Sciences, Wageningen University,
Bornsesteeg 69, 6708 PD Wageningen, the Netherlands

Gabriela Schaepman-Strub

Wageningen University, Nature Conservation and Plant Ecology Group, Bornsesteeg 69,
Building 119, 6708 PD Wageningen, the Netherlands

Ignas M. A. Heitkönig
Resource Ecology Group, Department of Environmental Sciences, Wageningen University,
Bornsesteeg 69, 6708 PD Wageningen, the Netherlands

Garry Bakker
Resource Ecology Group, Department of Environmental Sciences, Wageningen University,
Bornsesteeg 69, 6708 PD Wageningen, The Netherlands

Reinoud Vermoolen
Resource Ecology Group, Department of Environmental Sciences, Wageningen University,
Bornsesteeg 69, 6708 PD Wageningen, The Netherlands

Samuel López de Aquino
Museo de Zoología "Alfonso L. Herrera", Facultad de Ciencias UNAM, Apartado Postal
70-399, México D. F., México

PE&RC PhD Education Statement Form

With the educational activities listed below the PhD candidate
has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 22 credits (= 32 ECTS = 22 weeks of activities)

Review of Literature (4 credits)

- Spatial complexity in agro-ecological systems: bird diversity and coffee plantations. Metacommunity model (2001)

Writing of Project Proposal (5 credits)

- Birds, traditional coffee plantations and spatial complexity: the diversity puzzle (2001)

Post-Graduate Courses (11.5 credits)

- Computer management of ecological data (2001)
- Sub(tropical) land use (2001)
- Advanced Statistics (2005)
- Multivariate Analysis (2005)
- Landscape ecology: its methods and their applications (2005)
- Community Ecology (2005)

Deficiency, Refresh, Brush-up and General Courses (2.8 credits)

- Scientific writing
- Techniques for writing and presenting a scientific paper (2002)
- Basic statistics (2005)

PhD Discussion Groups (3 credits)

- Statistics, maths and modelling in production ecology and resource conservation (2002/2005)

PE&RC Annual Meetings, Seminars and Introduction Days (0.75 credits)

- PE&RC annual meeting: "Food Insecurity" (2001)
- PE&RC annual meeting: "Biological Disasters" (2004)
- PE&RC annual meeting: "The truth of Science" (2005)

International Symposia, Workshops and Conferences (3.4 credits)

- IX Simposio, la investigación y el desarrollo tecnológico, México
- XX Congreso de Etnobiologia, Univ. Aut. Chapingo

- Symposium "Trends in geo-information' (2004)
- Master class "state-of-the art remote sensing in agro-ecosystems (2004)
- Landscape ecology in the Mediterranean: Inside and outside approaches IALE (2005)

Laboratory Training and Working Visits (2 credits)

- GIS and remote sensing processing, ITC, The Netherlands