



INSTITUTO POLITÉCNICO NACIONAL

**Centro Interdisciplinario de Investigación para el
Desarrollo Integral Regional Unidad Oaxaca**

Tesis

**“Patrones de diversidad de aves en las regiones Valles
Centrales y Sierra Sur de Oaxaca, México”**

Que para obtener el grado de:

**Doctor en Ciencias en Conservación y
Aprovechamiento de Recursos Naturales**

Presenta

Omar Suárez García

Director de tesis

**Dr. Matthias Rös
Dr. John Newhall Williams**



INSTITUTO POLITÉCNICO NACIONAL

SECRETARIA DE INVESTIGACIÓN Y POSGRADO

SIP-13
REP 2017

ACTA DE REGISTRO DE TEMA DE TESIS Y DESIGNACIÓN DE DIRECTOR DE TESIS

Ciudad de México, a 08 de junio del 2021

El Colegio de Profesores de Posgrado de CIIDIR UNIDAD OAXACA en su Sesión
(Unidad Académica)

Ordinaria No. 11 celebrada el día 14 del mes diciembre de 2020, conoció la solicitud presentada por el alumno:

Apellido Paterno:	Suárez	Apellido Materno:	García	Nombre (s):	Omar
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Número de registro: B 1 6 0 2 3 7

del Programa Académico de Posgrado: Doctorado en Ciencias en Conservación y Aprovechamiento de Recursos Naturales

Referente al registro de su tema de tesis; acordando lo siguiente:

1.- Se designa al aspirante el tema de tesis titulado:

"Patrones de diversidad de aves en las regiones Valles Centrales y Sierra Sur de Oaxaca, México"

Objetivo general del trabajo de tesis:

Analizar la diversidad de aves en dos paisajes modificados por el hombre: un paisaje variegado en la Sierra Sur y un paisaje relictual en Valles Centrales, durante las temporadas reproductiva y migratoria

2.- Se designa como Directores de Tesis a los profesores:

Directora: Dr. Matthias Rös 2° Director: Dr. John Newhall Williams
No aplica:

3.- El Trabajo de investigación base para el desarrollo de la tesis será elaborado por el alumno en:

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que cuenta con los recursos e infraestructura necesarios.

4.- El interesado deberá asistir a los seminarios desarrollados en el área de adscripción del trabajo desde la fecha en que se suscribe la presente, hasta la aprobación de la versión completa de la tesis por parte de la Comisión Revisora correspondiente.

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Matthias Rös

Dr. Matthias Rös

Aspirante

Suárez García Omar

Suárez García Omar

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SIP-14
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ACTA DE REVISIÓN DE TESIS

En la Ciudad de Santa Cruz Xoxocotlán, Oax., siendo las 12 horas del día 30 del mes de Junio del 2021 se reunieron los miembros de la Comisión Revisora de la Tesis, designada por el Colegio del Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, unidad Oaxaca (CIIDIR UNIDAD OAXACA) para examinar la tesis titulada:

"Patrones de diversidad de aves en las regiones Valles Centrales y Sierra Sur de Oaxaca, México "

del alumno:

Apellido Paterno:	Suárez	Apellido Materno:	García	Nombre (s):	Omar
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Número de registro: B 1 6 0 2 3 7

Aspirante del Programa Académico de Posgrado: Doctorado en Ciencias en Conservación y

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Una vez que se realizó un análisis de similitud de texto, utilizando el software antiplagio, se encontró que el trabajo de tesis tiene **2%** de similitud. **Se adjunta reporte de software utilizado.**

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El estudiante público un artículo y dos capítulos de calidad para publicar.

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En la Ciudad de Oaxaca el día 30 del mes de junio del año 2021, el que suscribe Omar Suárez García, alumno del Programa de Doctorado en Ciencias en Conservación y Aprovechamiento de Recursos Naturales con número de registro B160237, adscrito a CIIDIR-Oaxaca, manifiesta que es autor intelectual del presente trabajo de Tesis bajo la dirección de Dr. Matthias Rös y cede los derechos del trabajo intitulado “Patrones de diversidad de aves en las regiones Valles Centrales y Sierra Sur de Oaxaca, México” al Instituto Politécnico Nacional para su difusión, con fines académicos y de investigación.

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Overview

Since their origins, human beings have transformed their surrounding environment. These transformations have varied in both spatial and temporal dimensions, being especially intensive as mankind invented the agriculture and established in settlements. However, despite the long history of human interactions with the physical space, the impact of these transformations in the human surroundings and particularly over the biodiversity have been studied only recently from a scientific perspective, and under the lens of landscape and community ecology.

Community ecology is the branch of ecology that studies the distribution and abundance of assemblages (Morin 2011). Within this field, diversity patterns have been a main research interest (Maurer and MacGill 2011). Since the XIX century, naturalists like Alexander von Humboldt, Charles Darwin and Alfred Russel Wallace noted and described the differences in species number of the different places they visited and studied around the globe, starting to unveil some global diversity patterns. During the XX century, with ecology established and developed as a formal discipline, the study of the patterns and processes regarding the differences in distribution and abundance of species around the world started (Pianka 1966).

During the second half of the XX century, several analytical tools were developed to account for and measure species diversity (Hubalek 2000). The English mathematician Alan Turing made great advances in information theory during the first half of the XX century, while decoding top German messages during the World War II, and therefore funding the basis of information theory (Chao and Jost 2012). Later, ecologists borrowed these informatic theoretical advances to express the diversity of ecological communities: for instance, they started to use the Shannon-Wiener entropy to quantify it. Since then, some popular and widely used diversity measures were

species richness, entropies and Hill numbers or true diversity. Although they are mathematically distinct, all are calculated by using two basic community data: 1) Number of species and 2) Abundances (Gotelli 2008).

The effect of spatial patterns on ecological processes began to be explored in the 1980's (Turner 2001). Particularly, the relationships between spatial heterogeneity and ecological communities were first explored by using the island biogeography theory (MacArthur and Wilson 2001) as a landscape model (reviewed in Haila 2002, Arroyo-Rodriguez et al. 2019). Under this view, the landscape was composed by either habitat or non-habitat components, and a once extensive pristine habitat could suffer a reduction in area (mainly due to human activities but also by natural forces) and subsequent fragmentation, or the formation of fragments or patches of different size, shape, and isolation (Fahrig 2019). Soon, the process of fragmentation could give place to the matrix, or the most extensive land cover in the landscape (usually agricultural or human-made land cover), and corridors or fragments that improve the connectivity between patches (Lindenmayer and Fisher 2006). By nature, the model of landscape fragmentation is binary; in other words, it considers that the landscape is constituted by both suitable (habitat patches and corridors) and non-suitable (matrix) land covers (Forman and Godron 1986).

As landscape ecology research advanced, the landscape binary model proved to be insufficient to explain some patterns and processes (Haila 2002; Manning et al. 2004). In the 1990's alternative models like the variegated landscape approach appeared in the scene (McIntyre and Barret 1992). Under this view, there could be different landscape scenarios depending on the amount of original vegetation cover in the landscape (McIntyre and Hobbs 1999). Additionally, the most of species do not perceive landscapes in a binary way, but they can differentially use the land covers present in each place (Manning et al. 2004). According to this view, landscape scenario

is species or group depending, so while it could be perceived as fragmented for a few species or groups it could not be the case for most of the others (Brudvig et al. 2017).

The role of scale in landscape studies has been acknowledged but rarely addressed in landscape ecology. We can define scale as the spatial or temporal dimension of an object or process (Turner et al. 2001). There are two main concepts in defining the scale: 1) Grain, or the smallest spatial resolution in a set of data and, 2) Extension, or the size of the study area. We can say that a process or phenomenon is scale dependent when they change as scale does. Scale has a great importance in ecology because all biological systems are hierarchical and have emergent properties (Bertalanffy 2011).

Theoretical framework

a) Diversity

Ecology is the study of the distribution and abundance of living beings, as well as their mutual interactions and relationships to abiotic factors (Begon et al. 2006). There are different levels of organization in ecology: from the individuals (autoecology), to populations (population ecology) and communities (community ecology). The focus of this doctoral thesis will be put in communities, which can be defined as groups of two or more species that coexist in the same place at the same time (Morin 2011). Ecological communities have three main attributes: 1) Richness, or the number of species; 2) Equitability, or the degree of balance in the abundance of each species and, 3) Composition, or the identity of the species that compounds the community.

It is common to express species richness and equitability (or dominance, its counterpart) as a single attribute: species diversity (hereafter diversity). Essentially, diversity is higher in communities with high richness values and high evenness, while diversity is lower in depauperated communities in which one or few species are dominant in abundances over the others (Stiling 2012). It is remarkable that species diversity is a component of biodiversity, which is defined as the variety of forms of life that inhabits the planet (Gaston and Spicer 2004). Besides species diversity, biodiversity also includes genetic diversity (the variety of alleles or alternative forms of a gen present in a population), and ecological diversity (the set of interactions among living beings and their environment; Begon et al. 2006).

Since the middle of the XX century, the study of diversity patterns became a central topic in ecology (Maurer and MacGill 2011). At a global scale, the best documented diversity pattern is the latitudinal gradient: the highest species diversity is located within the tropics and decreases as latitude increases (Pianka 1966; Gaston 2000). Diversity is also positively correlated to area (MacArthur and Wilson 2001), primary productivity (Mittlebach et al. 2001) and environmental heterogeneity (Connell, 1978; Stiling 2012).

Typically, diversity has been quantified and expressed by indices, which are single values that measure both richness and equitability (Morin 2011). The more basic and simplest diversity index (although the hardest to quantify) is the species richness (Gotelli and Colwell 2011). Indices (at least the most used) are not diversities per se, but entropies, or measures derived from the informatics theory that express the degree of uncertainty in the identity of a new element picked at random from a set of elements (Jost 2007). For instance, the Shannon-Wiener index (the commonest of entropies) expresses the average number of operations carried out to get an outcome, while the Gini-Simpson index is the probability that two elements randomly picked from a set of elements have the same identity (Jost 2006).

Hill (1973) found the way to convert entropies to number of effective species, or the number of equally abundant elements needed to obtain a given entropy value. The mathematical formulae that he found was:

$${}^qD = (\sum_{i=1}^S p_i^q)^{1/1-q}$$

Where qD is the diversity *per se*, p_i is the relative abundance of the i -est species and q is the diversity order, or the degree of sensitiveness of the formulae to the relative abundances of the species. When $q=0$, relative abundances are not considered; hence diversity of order 0 is the number of species or species richness. When $q=1$, species are weighted by their observed proportional abundances, and their value in the formulae is not defined, but the function limit does and is the exponential of the Shannon-Wiener index. When $q=2$, the relative abundances of the dominant species have a major role, and its reciprocal is the Simpson dominance concentration index. Values of q higher than 2 give even more weight to the dominant species, and as q tends to infinite the diversity value reaches its limit, which is the reciprocal of the Berger-Parker index.

b) Landscape ecology

Despite the landscape concept was first conceived and developed at the beginning of the XX century by two independent schools (the European and the North American), it was until the 1980s that the effects of spatial pattern on ecological processes were formally explored (Turner 1989). In that way, a bunch of landscape definitions arose; however, all of them highlighted the spatial heterogeneity as the main landscape characteristic (Wu 2013). For example, Turner (1989) simply defined landscape as a heterogeneous spatial unit, while Halffter and Rös (2013) defined it as a geographical space with unique physical and climatic features, with a particular biogeographic history and delimited in space and time. Landscape ecology can then be defined as the discipline

that focuses on the effect of spatial patterns over the processes that define the distribution and abundance of living beings (Fahrig 2005).

Landscape has two main properties: 1) Composition, or the type and number of elements or land covers that compose the landscape and, 2) Configuration, the shape and spatial arrangement of the different landscape elements (Wiens 2002). The first theoretical model to study the landscapes was derived from the island biogeography (MacArthur and Wilson 2001). Under this idea, habitat fragments were considered as analogous to islands, which were surrounded by inhospitable land (the landscape matrix) analogous to the sea. Besides, this model also considered the existence of corridors, which species might use to move between patches (Gardner et al. 1993). In that way, the patch-corridor-matrix model were conceived.

The binary landscape model has been very useful to advance the discipline and even to develop important approaches such as the metapopulation dynamics (Hanski 1998) and the fragmentation framework (Forman and Godron 1986). However, as more research was developed, the binary model of landscape proved to be insufficient because in most cases the landscape matrix is not inhospitable to species, but they can use it in some degree (Brudvig et al. 2017).

As an alternative to the patch-corridor-matrix, the continuous landscape model was developed (McIntyre and Barret 1992). This landscape model is based on the amount of original vegetation present in a landscape. According to this approach, there are four possible landscape scenarios (McIntyre and Hobbs 1999). One of the main differences of this landscape model with respect to the fragmentation approach is that continuous model is not binary: there are not only habitat-non habitat covers, but there is a gradient of land covers which species can use in some degree (Fisher et al. 2009). Obviously, even in this continuous model there are species (mostly

specialists) which perceive the landscape as binary, but most of the local species can occupy in some degree the different elements of the landscape.

Currently, the variegated landscape model is not the mainstream; it even does not appear in the recent landscape literature reviews (Arroyo-Rodriguez et al. 2019), which are plenty of fragmentation examples. I consider that this model deserves a better place in the landscape ecology and this thesis will try to vindicate, spread, and apply the concepts related to this approach.

Justification

Oaxaca is the most biodiverse state of Mexico, mainly because it is located within the boundaries of the Mexican Transition Zone (Halffter 2019), besides its geological history and winding topography which gives place to environmental heterogeneity and therefore a complex biogeographic history (García-Mendoza et al. 2004). Additionally, the different land use histories and management strategies carried out by the locals (mainly peasant communities and indigenous people) of Oaxaca have promoted the persistence of a great number of biological species (Robson et al. 2017).

It has been documented that there are about 1,150 bird species in Mexico, 736 out of which have been registered in Oaxaca (Navarro-Sigüenza et al. 2014). Also, Oaxaca has 11 Important bird areas and 6 Endemic Bird Areas (Birdlife International 2020), as well as 6 federal protected areas (CONABIO 2020). Despite this importance, the ecological information about birds in Oaxaca is scarce and somehow outdated, so this work is expected to contribute and improve that knowledge and serve as a new starting point to make ecological research at the landscape scale at the state.

Objetives

- a) Know alpha and beta bird diversity patterns in the different studied landscapes and modification scenarios, at different spatial scales.
- b) Assess the effect of landscape characteristics over bird diversity.
- c) Analyze individual species and group responses to landscape modification.
- d) Find out if there are bird guilds associated to specific modification scenarios.
- e) Assess the effect of scale in both Alpha and beta diversity patterns.

Chapter 1

Life in two contrasting worlds: bird diversity patterns in relictual landscapes of the Central Valleys of Oaxaca, Mexico

Omar Suárez García¹, Matthias Rös², Citlali Paola Martínez López¹ and John N. Williams³

¹ , CIIDIR Oaxaca, Instituto Politecnico Nacional, Mexico

² CONACYT, CIIDIR Oaxaca, Instituto Politecnico Nacional, Mexico

³ Dept. of Environmental Science & Policy, University of California, Davis, USA

Corresponding Author:

Matthias Rös²

Email address: iguarana@gmail.com

Abstract

Under a continuum landscape approach, relictual landscapes represent the most modified scenario, where the original vegetation remains only in a small extension, and the original bird community might be strongly and negatively affected. However, relictual landscapes can vary in a number of physical characteristics, which already influence ecological processes. In this research, bird diversity at two contrasting relictual landscapes (urban and agricultural) of the Oaxaca Central Valleys, in Southern Mexico, was investigated. A hierarchical sampling design was used in order to evaluate alpha and beta diversity patterns at different scales. Three sampling windows of 1km² each, divided into 16 plots, were set in each of the two landscapes. In the center of each plot a 5-minute point count was performed during three different days at two different seasons (breeding and non-breeding) in order to register bird species and relative abundances. NDVI, tree cover and

abundance and diversity of tree species was recorded. Bird alpha and beta diversity was analyzed under the true diversity approach. The agricultural landscape was consistently more alpha-diverse than the urban landscape across all considered scales, diversity orders, and seasons. Compositional similarity was high inside the landscapes but low between-landscape. Neotropical, widespread and restricted-range bird species were excluded from the urban landscape, while non-native species were positively associated with it. In the breeding season, bird diversity was related with tree cover at both landscapes, and in non-breeding season bird diversity was positively associated with both tree coverage and tree abundance only in the agricultural landscape. The results of this work highlight the importance of the agricultural landscape for local bird diversity, playing a major role during non-breeding season, when several north American migratory species, reported as declining populations, use this landscape.

Keywords

Mexican Transition Zone, agricultural landscape, urban landscape, beta diversity, biotic homogenization, true diversity, community ecology, sampling windows, point counts, vegetation cover, spatial scale

Introduction

Landscapes are spatially heterogeneous areas that influence ecological patterns and processes (Fahrig et al., 2011). Changes in landscapes can be due to either natural forces or human activities, but in recent times the latter have acquired singular importance due to their impacts on biodiversity (Fischer and Lindenmayer, 2007; Chazdon et al. 2009). Much research has focused on the effects of human landscape modification through the lens of how fragmented a landscape is (Haila, 2002; Brudvig et al. 2017), but this approach does not adequately capture the composition and configuration complexities of many landscapes, especially in the tropics (Pulsford et al. 2017; Paize

et al. 2019, Halffter & Rös 2013). Instead, other landscape concepts have been developed, such as the continuum landscape model (McIntyre and Barret 1992; McIntyre and Hobbs, 1999).

The model includes so-called relictual landscapes, where only a small fraction (<10%) of original vegetation cover is left. Based on this definition, most, if not all urban landscapes are relictual landscapes, despite some of them maintain significant areas of native vegetation in green spaces and lining streets. Agricultural landscapes are also typically highly modified, but can be both relictual and fragmented landscapes with 10 to as much as 60% of original vegetation cover intact (McIntyre and Hobbs, 1999). Arguably, fragmentation and habitat loss may be seen as the most important drivers of biodiversity patterns in human-modified landscapes (Fahrig 1997, Brottons et al. 2005), but in relictual landscapes, where there are no fragments or patches, it is the loss of any remnant habitat that risks populations of native species (Fahrig 1997). Consequently, studies in relictual landscapes have reported negative effects on plant and animal species via a reduction in recruitment and the presence of certain vegetal elements (Damian et al. 2008; González-Varo et al. 2012).

Although the effect of both spatial and temporal scale in landscape ecology has been widely acknowledged (Turner 1990; Arroyo-Rodriguez et al. 2017; Newman et al. 2019), multi-scale studies have been rarely made. On the one hand, hierarchical sampling designs are especially suitable for studying landscapes at different spatial scales (Halffter and Rös 2013), given their complex-system nature (King 1997). On the other hand, addressing seasonal variation in landscape studies is important because factors at the population (e. g. organismal life span, Fahrig 1992) and community (e. g. bird seasonal dynamics, Maron et al. 2005) levels can influence community dynamics.

Diversity and distribution patterns are main topics in ecology (Townsend, Begon and Harper 2004). In landscape ecology, the influence of spatial features in the definition of species

diversity is widely acknowledged, but mainly under the fragmentation perspective, even in landscapes with no clear patch-matrix structure (Manning and Lindenmayer 2004). The positive impact of vegetation features on bird diversity has been well documented both in urban (Aronson et al. 2014; Amaya-Espinel and Holstreter 2019) and agricultural lands (Cunningham et al. 2008; Wilson et al. 2019), highlighting the role of vegetation cover (Fernandez-Juricic and Jokimaki 2001; Hughes et al. 2002; Evans et al. 2009; Carbo and Zuria 2011) and native plant presence (Burghardt, Tallamy and Shriver, 2009; Fontana et al. 2011; Goddard, Dougill & Benton, 2010) in increasing the bird diversity at the landscape level. Also, bird distribution at the species and guild (groups of species that exploit certain resources in similar ways, Morin 2011) levels has been documented to depend on certain vegetation characteristics because it promotes high food abundance (Burghardt et al. 2008) and nesting substrates (Tomoff 1974). While the amount of vegetation cover and tree abundances has proven to be important for birds in urban areas (Amaya-Espinel and Holstreter 2019), in agricultural lands, bird species depend upon open areas and grassy and shrubby vegetation to thrive there (Rosin et al. 2016; Valdez-Juarez et al. 2018). In addition, seasonal dynamics of habitat use by birds has been documented, so that in the non-breeding season birds become habitat generalists, mainly because they move actively searching for cues related to food availability (Hutto 1985; Dybala et al. 2015), but the habitat use at different seasons by all-year residents in the tropics remain poorly studied.

Beta diversity is the spatial or temporal variation in species composition between sampling units (Anderson et al. 2011). At the landscape level, spatial heterogeneity is directly related to increased beta diversity, and such heterogeneity can be promoted by human activities (Rös et al. 2012). However, in highly transformed landscapes (such as the relictual landscapes), activities like urban development and agriculture cause spatial uniformization, which in turn promotes biotic homogenization (Blair 1996; López-Vázquez et al. 2017). This phenomenon is likely to cause a

decrease in beta diversity, via species additions or subtractions (Socolar et al. 2016). To the best of our knowledge, beta diversity patterns has not been explored under the relictual landscape approach.

Mexican tropical semi-dry region lies within the boundaries of the so-called Mexican Transition Zone, which is a broad region of Mexico and central America characterized by the overlapping distribution of both Nearctic and neotropical biotas, plus a set of endemic species (Halffter 2020). Although the Mexican Transition Zone is a biogeographical concept, it can be useful at an ecological scale because it has been documented that certain biogeographical groups are more prone to be affected by environmental variables (Moreno-Rueda and Pizarro 2008). For example, Gonzalez-Oreja (2011) discussed higher local extinction risks due to urbanization based on birds biogeographical affinity, finding that Nearctic and Non-Native species were favoured by increased urbanization in a Mexican city.

Recently, a significant decrease in bird numbers across North America during the last 50 years has been documented (Rosenberg et al. 2019). For instance, regarding breeding biome, grassland and arid-land birds have declined 53.3% and 17.0%, respectively. A large fraction of these birds is migratory and spend their non-breeding season in tropical regions, where information about bird community patterns at the landscape level is scarce, especially in Southern Mexico, which is known to be a continental biodiversity hotspot (Robson 2007). The information generated in this study will help to better understand the use of the tropical relictual landscapes by migratory species, helping to design conservation strategies of Nearctic-Neotropical migrants that include their non-breeding grounds.

The main objective of this study was to compare the alpha and beta bird diversity of two relictual landscapes (urban and agricultural) at four different scales and two contrasting seasons (breeding and non-breeding) in the Central Valleys region of Oaxaca, Mexico. Individual bird

distribution patterns based on guild and nesting substrate (only in case of resident species) were explored, and also the relationships between zoogeographical groups and the studied landscapes. Tree cover, tree diversity, and abundance were analyzed to know if they are predictive variables of bird diversity in agricultural and urban landscapes, as literature typically suggests. A lower bird alpha diversity in the urban landscape compared with the agricultural landscape was expected due to spatial homogenization and loss of ecological niches in the city (Blair 2001). Between-landscapes beta diversity was expected to be high due to the contrasting characteristics of both studied landscapes; however low within-landscape beta diversity was expected to be low due to the homogeneous within-landscape features. Also, a direct and positive relationship between tree diversity, tree coverage, and tree abundances, and bird diversity was predicted (MacArthur and MacArthur 1965, Rotenberry 1985). Finally, the absence of ground and shrub nesters in the urban landscape was expected due to the lacking of nesting substrates for those species (Lim & Sodhi, 2004) during the breeding season, a high occurrence of tree dependent migratory species in the urban landscape in non-breeding season (Amaya-Espinel and Hosteler 2019) and a decrease in neotropical and restricted range species in the urban landscape compared to the agricultural landscape (González-Oreja 2011).

Methods

Study area

The study was conducted in the physiographic province Central Valleys of Oaxaca , within the city of Oaxaca de Juarez (17° 33'55" N, 96° 43' 25" W) and the municipality of Zimatlán de Álvarez (16° 52' N, 96° 47' W, Fig. 1). The Central Valleys of Oaxaca have an average altitude of 1500 m, a mainly plain terrain dominated by agricultural lands, urban settlements of different sizes (Ortiz-Pérez, Hernández-Santana, and Figueroa-Mah-Eng, 2004). Following Köppen climatic

classification, the region is considered as warm-semiarid (BSh), with an average annual temperature of 20 °C and annual mean precipitation of 676 mm, with most of the rains occurring during summer. This region has been occupied and modified by humans since pre-Columbian times, for example, Monte Alban, an ancient Zapotec city, was one of the main urban centers in Mesoamerica. This city reached its maximum splendor between 400 and 600 A. D., when it sheltered a population of approximately 35 000 persons (Marcus et al. 2001).

The two studied landscapes were separated by 18 km. The average altitude of the sites was 1500 masl. The Urban landscape (UL) was characterized by the presence of commercial and residential buildings with different proportions of green spaces and scattered trees on its streets and gardens. In contrast, agricultural landscape (AL) was dominated by low-intensity cultivation plots (both rainfed and irrigated) worked rustically by peasants with oxen plow, mainly traditional “milpa” (with maize, squash and beans), with scattered trees. Following a continuous landscape approach, they fall into the “relictual” category established by McIntyre & Hobbs (1999), because they contain less than 10% of original vegetation cover. Nowadays, no larger areas of original vegetation typical for the plain part of Central Valleys exist, which hypothetically had been tropical dry forest, probably dominated by *Prosopis* trees/shrubs.

Sampling

Sampling design. The sampling design was hierarchical following Halffter and Rös (2013). In each landscape, and across a north-south axis, three sampling windows (equivalent spaces, placed to maximize representativeness through the landscape) of 100 ha at 1x1 km (6 in total) were established, where windows were located at a minimum distance of 1 km apart. Each window was subdivided into 16 plots of 6.25 ha, 250x250 m (Fig. 2). Four adjacent plots formed a frame (4 frames of 25 ha in each window), which results in a four-scale sampling design (from smallest to largest: plot, frame, window, and landscape; see Fig. 3 caption). To control the effects of adjacent

mountain slopes on the avifauna of plain terrains in our study area, each window was located exactly at the same distance from the adjacent piedmont, fully over the plain part of each landscape. Birds. In the center of each plot, one observer (OSG) conducted fixed radius point counts (Gregory, Gibbons & Donald, 2004; Ralph, Sauer & Droege, 1995). At each point, bird species and the number of individuals seen or heard within a 50-m radius were recorded for 5 minutes. Bird individuals flying overhead or not evidently using the landscape elements for foraging, perching or nesting, were not recorded. There were 250 m between each point count to ensure the independence of plot data; this distance is adequate because the non-overlapping 125 m radius between adjacent points is beyond the limit of movement of most small land bird species (Hutto, Pletschet & Hendricks, 1986).

Bird counts were made during May and June 2017 (breeding season), and November and December of the same year (non-breeding season), from dawn to 4 hours afterward, and each window was visited three times (one per day). The order of daily visits to each point count was changed to avoid sampling bias. All bird species detected at the study sites were recorded, but only passerines, doves, woodpeckers, hummingbirds, and anis were included in the diversity analysis. Raptors, waterbirds, and mostly aerial species (e. g. swallows and swifts) were excluded. It is important to note that individuals of the genus *Empidonax* and *Spizella*, found at the non-breeding season at the agricultural landscape, could not be determined at the species level (due to the facts that they did not sing and moved in flocks), and were considered only at the genus level in the diversity analysis, being aware that these two groups may contain at least two species, so our bird diversity calculations are biased downwards in such landscape and season.

Tree census. During 2016 and 2017, tree species richness and abundance were recorded by CPML in the same windows of urban and agricultural landscapes, and all trees were georeferenced. In the AL, each tree was recorded and determined to species level. In the UL only trees in the streets

could be determined to species level. Trees of house gardens could not be determined (due to the impossibility to get permission to enter each house) but were counted via GoogleEarth satellite images. Based on the sampling of selected house-gardens and GoogleStreetView images, we assumed that diversity measured by street trees is representative of windows and cells. To quantify tree cover at each window, we digitalized all trees using aerial imagery with a resolution of 15 cm per pixel (Bing Maps 2018) and qGIS software (QGIS Development Team 2019). Additionally, we analyzed vegetation heterogeneity using the Normalized Difference Vegetation Index (NDVI) in both, breeding and migratory, seasons.

Data analysis

We analyzed bird and tree count data using the true diversity approach (Jost, 2006), which is calculated from the formulae $qD = (\sum p_i^q)^{1/(1-q)}$, where p_i is the proportional abundance of each species, q is the degree of sensitiveness to the relative abundances, and qD is the true diversity of order q (Jost 2006). We followed a multiplicative partitioning of diversity, which yields independent alpha and beta components (Jost, 2007).

With the purpose of assessing sampling efficiency, Chao 1 richness estimator was calculated at each considered scale with Estimates 8.1 (Colwell 2016) from the raw abundances. The ratio (expressed as a percentage) between observed and estimated species was used as a measure of sample completeness.

To make fair comparisons of alpha diversity among the different sampling units at the landscape and window scales, intrapolation and extrapolation curves (Chao et al. 2014) of diversity of order 0, 1 and 2 were computed with iNEXT package, and then standardized at a given value of coverage to avoid bias due to sample completeness (Chao and Jost 2012); this diversity is expressed as number of effective species. Differences in alpha diversity between seasons at each landscape were assessed by comparing values at cell and frame scale using Wilcoxon tests.

Pairwise compositional similarity (CS) were calculated for sampling units at each of the 4 considered scales by using PAST software (Hammer et al. 2001). Specifically, Jaccard and Morisita-Horn indices were used; these two CS indices are directly related to beta diversities $0D$ and $2D$, respectively (Jost, Chao and Chazdon 2011). Also, to graphically represent the similarities of sample units regarding their bird community composition, Non-Metric Multidimensional Scaling were performed using raw abundances of the species with PAST. NMDS is an ordination method well suited to data that are non-normal (McCune, Grace & Urban, 2002), and it works with different similarity measures, such as the here used Jaccard and Morisita. NMDS stress, which is a measure of departure from monotonicity in the relationships between the distance in the original p -dimensional space and distance in the reduced k -dimensional ordination space was reported (McCune, Grace & Urban, 2002). Typically, when stress is below 0.20, NMDS is considered valid.

Wilcoxon tests were used for pairwise comparisons of both frames and cells to evaluate seasonal differences in compositional similarity. To assess the particular contribution of all-year residents and migratory species to CS, Jaccard and Morisita-Horn indexes were calculated in two ways: 1) comparing all bird species registered in each of the two seasons and; 2) comparing only year-round residents registered in each of the two seasons.

To explore if there were differences between landscapes due to the biogeographic origin of their bird species we made a Chi-squared test regarding species and abundances. We grouped birds in seven zoogeographic categories: 1) nearctic; 2) neotropical; 3) endemic to Mexico; 4) quasi-endemic to Mexico (species whose distribution ranges include Mexico and $<35,000$ Km² outside the Mexican territory); 5) semi-endemic to Mexico (species that are endemic to Mexico during any season of the year); 6) widespread and; 7) non-native (Palomera-García et al. 1994; González García and Gómez de Silva 2003).

Rank-abundance plots were used to compare the structure of the different bird communities at the landscape level (McGill et al., 2007). Also, the inequality factor was calculated by the formulae $H' = -\sum_{i=1}^S p_i \ln p_i$ to assess the degree of dominance relative to the maximum and minimum amount possible given the observed richness (Jost 2010). In such equation, S denotes species richness, p_i represents the proportional abundance of the i species, and q is the diversity order as abovementioned.

Correspondence analysis using raw bird frequencies observed in each landscape and season was applied. This analysis also allowed to explore the affinities of species both to UL and AL based on their guilds and nesting substrates (only in the case of all year-resident species). Only species whose expected abundances were more than five in any of the studied landscapes or seasons were included in the analysis (Gotelli and Ellison 2004).

To assess the extent to which within-landscape bird diversity was driven by tree diversity, abundance and cover, as well as NDVI values, linear regressions were made for bird 1D and 2D, since both measures are continuous variables (Sokal & Rohlf, 1995). In this case, the normality of the residuals was assessed using a Kolmogorov-Smirnov test. In the case of 0D (species richness) and abundances, which are discrete variables, generalized linear models (GLM's) were constructed considering a Poisson error distribution and using a logarithmic link (Buckley 2015). GLM's are appropriate to analyze relationships between richness and abundance data and environmental variables. These analyses were made using data at cell scale.

Results

Observed species and sample completeness

We summarized 1440 minutes of bird observation (5 minutes x 16 plots x 6 windows x 3 days; 720 minutes in each landscape) in each season. In the breeding season, we counted 2104 individuals of 28 species belonging to 4 orders and 14 families in the urban landscape and 2209 individuals of 39

species belonging to 5 orders and 17 families in the agricultural landscape. In the non-breeding season, we counted 1672 individuals of 44 species belonging to 4 orders and 17 families in the UL and 1621 individuals of 61 species belonging to 5 orders and 20 families in the AL (Table 1). The Chao1 richness estimator showed that sampling was efficient, between 88.7% to 100% of species were observed at the landscape scale.

Alpha diversity

When comparing true alpha diversity of the two landscapes in the two different seasons, there was a consistent higher bird diversity in the AL at all orders of q excepting 0D of the UL at the non-breeding season, which was more diverse than AL in the breeding season. UL at the breeding season had the lowest bird diversity at all considered orders (Table 3).

The three windows located in the AL were more diverse than any of the three windows in the UL at all considered orders, excepting 0D of urban windows in the non-breeding season, which showed a similar diversity as the windows of AL in both seasons (Table 3). Within the AL, the three windows showed similar qD at each of the seasons. Within the UL, UW1 was more diverse than UW2 and UW3 at order 0, but at orders 1 and 2 UW2 was more diverse than any of the other windows in the breeding season. In the non-breeding season, UW1 was the most diverse window in the UL at order 0, but at order 1 all windows had a similar diversity, and at order 2 UW2 was the most diverse window.

In general, we observed at both frame and cell scale a higher alpha diversity in the AL compared to the UL (except for UW1_F1, Fig. 3). Also, when comparing alpha diversity in each landscape between seasons at frame scale, a significantly higher alpha diversity in the non-breeding season was found in the AL at all orders and in the UL at 0D (Table S2), while at the cell scale statistical differences in alpha diversity only were found when 0D of both seasons was compared in the AL ($W=741$, $p<0.05$, Table S2).

Compositional similarity

Compositional similarity among landscapes and seasons decreased as q increased. In general, beta diversity was higher when contrasting landscapes were compared (e.g. UL vs AL in non-breeding season), while the highest compositional similarity was observed when UL at breeding and the non-breeding season was compared (Table S3).

The lowest compositional similarity (expressed as Jaccard and Morisita-Horn indices) was observed when windows of different landscapes were compared. For example, Jaccard values ranged from 0.37 to 0.53 for comparisons of UW vs. AW in the non-breeding season, meanwhile, Jaccard values ranged from 0.41 to 0.59 for comparisons between UW in the breeding vs. the non-breeding season (Table 4). Similarly, Morisita values ranged from 0.24 to 0.42 for comparisons of UW vs. AW in the non-breeding season, while values ranged from 0.35 to 0.62 for comparisons of AW in the breeding vs. non-breeding season (Table 4). Overall, the compositional similarity of windows of the same landscape at the same season was very high (e. g. Morisita-Horn index of UW in the non-breeding season ranged from 0.74 to 0.96).

NMDS analysis at the landscape scale showed that the two landscapes are different both in composition (Jaccard) and dominant species (Morisita) in both breeding and non-breeding seasons (Fig S2). At the window scale, NMDS put UW at the left side of the x axis and AW at the right side of such axis for both Jaccard and Morisita-Horn indices in breeding season (Fig. 4a). At the frame scale, patterns are consistent with the windows level analysis, with all urban frames well differentiated from the rural ones in breeding season (Fig. 4b), whereas at the cell scale all cells from the UL remained separated from the cells of the AL when Jaccard index was applied, meanwhile when Morisita-Horn index were used some cells of the UL appeared close to the ones from the AL and vice versa, indicating some similarity between dominant species of these cells in breeding

season. NMDS for the non-breeding season showed the same patterns as the breeding season (Fig. S3).

Finally, when we compared pairwise compositional similarity (expressed as Jaccard and Morisita-Horn indices) at frame and cell scales within landscapes, in all cases, we found significantly lower values in the non-breeding than in the breeding season, both when we considered all species and only all-year residents. Wilcoxon tests summaries can be seen in Table S4.

Community structure

At the landscape level, analysis of rank abundance by species showed that urban bird communities were more dominated by a small number of species than their agricultural counterparts, which showed greater evenness at both seasons (Fig. S4). Inequality factors IF_{0,1} and IF_{0,2} confirmed this pattern; the highest values were observed at the UL in both the breeding and non-breeding seasons (Table 1). The dominant species in the UL in the breeding season were *Passer domesticus*, *Haemorhous mexicanus*, *Zenaida asiatica*, and *Columba livia*, all of which are known for being regular city dwellers, whereas in non-breeding season all these species were also dominants plus *Setophaga coronata*, a neotropical migrant warbler. By contrast, dominant species in AL at breeding season were *Peucaea botterii*, *Sturnella magna*, *H. mexicanus*, and *Melospiza albicollis*, whereas in non-breeding season dominants were the latter two species plus *Tyrannus vociferans* and *Setophaga coronata*.

Species distribution

The correspondence analysis at landscape scale at both seasons was significant ($\chi^2=7331.1$, $df=150$, $p<0.001$); there were associations between particular bird species and landscapes at each season. In this ordination, first two axes (eigenvalues= 0.484 and 0.389 respectively) represented 49.3% and 39.6% of the total variance. Axis 1 was determined by the differences between AL in

the breeding season and UL at both seasons (AL at the negative end UL at the positive end, Fig. 7). Axis 2 was determined by species differences at the non-breeding season, mostly at AL, and to a lesser extent from the contributions of both UL and AL in the breeding season (a full summary is presented in Table S5). Species that contributed the most to the first axis were all-year residents which were situated at the positive end of the axis. By contrast, all-year resident species typical of open and shrubby areas of Southern Mexico were negatively associated with the first axis. Species that contributed the most to the second axis were migratory sparrows and other Nearctic-neotropical migrants which were situated at its positive end. At the guild level, omnivores, nectarivores, and granivores were located at the positive extreme of the first axis, meanwhile granivorous and insectivorous species were associated with the negative extreme of that axis. By contrast, granivores and insectivorous species were located to the positive extreme of the second axis. Regarding nesting substrates, species that nested in cavities, buildings, and trees were at the positive part of the first axis; while species that nest in the ground, shrubs, and trees were associated with the negative extreme of such axis. Graphical representation of the correspondence analysis can be viewed in Fig. 7.

Chi-squared test for zoogeographic categories and studied landscapes based on abundances was significant ($\chi^2=996.24$, $df=6$, $p<0.001$), Fig. 6a), whereas the analysis based on the number of species was not ($\chi^2=0.98$, $df=6$, $p>0.5$, Fig. 6b). Zoogeographic categories whose abundances were higher than expected in AL were neotropical, endemic, widespread, and semi-endemic, whereas quasi-endemic and non-native were higher than expected in UL. In the case of the category Nearctic, there was no significant association with any of the studied landscapes (Fig. 6).

Bird diversity and tree diversity

According to the Kolmogorov-Smirnov test, residuals of 1D and 2D were normal for all linear models. Linear regressions between 1D and 2D (bird diversity of order 1 and 2) and tree coverage

(but not for tree abundances) were significant for both seasons and landscapes, while 1D and 2D were significantly related to both tree coverage and tree abundances only for the AL during the non-breeding season (Table S6). There were no significant relationships between tree diversity and bird diversity at any scale nor season.

In the UL, GLM's showed only significant relations between 0D and bird abundances and tree coverage during the breeding season, whereas during the non-breeding season, there was only a significant relationship between bird abundances and tree abundances. In contrast, in the AL there were significant relations between bird richness and tree coverage during the breeding season, whereas during the non-breeding season, both bird richness and bird abundances were significantly related to tree coverage and tree abundances (Table S7).

Discussion

Relictual landscapes are defined generally by an original vegetation cover of less than 10% (McIntyre and Hobbs 1999); nevertheless, besides this key factor, they can have contrasting structures. In this study, the obvious difference was the dominance of fields vs. houses/streets in the agricultural and urban landscape, respectively, and the difference in tree cover (6.9 vs, 13.4%, AL, UL, respectively, Fig. 2). In general, higher bird species diversity was found in the agricultural landscape at all seasons and diversity orders. These results are in concordance with several works in temperate latitudes (Clergueau et al. 1998; Ciach 2012), and partially in the tropics (Chamberlain et al. 2016); however, both highly urbanized and intensively cultivated landscapes have shown low diversity values (Smith 2003; Faggi 2006, Ludwig et al. 2009, Muñoz and Miller 2020). Similar bird abundances were accounted in both landscapes at each season, contrary to the findings of Blair (1996) and Chace and Walsh (2004), who reported more individuals in the city. The higher

abundance in urban areas might be due to the constant input of food resources, but the highest numbers are usually of few, exotic species (Ortega-Álvarez and MacGregor-Fors 2011).

Scale is a main topic in landscape ecology because the processes that act at one scale do not necessarily act at subsequent scales, thus affecting patterns observed (Turner et al. 2001). The hierarchical, multiscale sampling design used in this work (Halffter and Rös 2013) allowed to gather enough data to detect trends in relationships between bird diversity and vegetational variables at two spatial scales (cell and frame); the patterns we found were similar (i. e. higher diversity in the agricultural landscape than in the urban landscape, significant relationships between richness and vegetation cover) across landscapes. Conversely, the sampling design used in this work allowed to get good sample coverages at the two higher scales (window and landscape) in a relatively small sampling period. Our method (sampling windows) can be considered as a Rapid Biodiversity Assessment (Alonso and Naskrecki 2011), which could be implemented for gathering data at low time and money costs.

From an ecological perspective, it has been documented that urbanization favors omnivorous, ground granivorous, cavity-nesting species, and in less extent frugivorous and nectarivorous (McKinney and Lockwood 1999; MacGregor-Fors and García-Arroyo 2017), as opposed to habitat-specialist, bark and foliage gleaners, and ground nesters (Marzluff 2001; Chace and Walsh 2004). In agricultural lands, intensification promotes generalist species while unfavors specialists (Doxa et al. 2010). Other studies have highlighted the importance of available nesting sites for the occurrence of some bird species in the breeding season (Tomoff 1974); in the agricultural landscape, most all-year resident birds depend on grassy, shrubby vegetation, cacti and agaves, plant forms that are absent from the city. Besides, ground and shrub nesters could be more vulnerable to urban predators such as dogs, cats, and rodents, or sensible to traffic (Shanahan et al., 2011). In addition, most species of agricultural landscape (especially migratory species) feed on

seeds and insects and need an amount of open land for foraging (reviewed in Howell and Webb 1995), which is only available in the Central Valleys countryside. From a biogeographical approach, cities favor both nearctic and non-native species (Gonzalez-Oreja 2011). In the urban landscape, the dominant species in both seasons were year-round generalists (*C. livia*, *P. domesticus* and *H. mexicanus*), which take advantage of the urban infrastructure for perching and nesting, and food resources may be abundant (e.g. leftovers, Haemig et al. 2015). The fact that the urban landscape in this study appears to have filtered out neotropical and restricted range species may show its limited capacity to conserve species that may be able to survive in other types of relictual landscapes but not in cities, such as the resident Boucard's Wren, and the migrant species Bullock's Oriole, Varied bunting, and Virginia's Warbler. The Central Valleys of Oaxaca are within the Mexican Transition Zone (Halffter 2020), which is characterized by its particular avifauna composed of species of both Nearctic and Neotropical realms, as well as restricted range species with recent origin.

The low compositional similarity between the two studied landscapes may be the result of two combined processes in the urban landscape: 1) subtracting homogenization and; 2) additive homogenization (Socolar et al. 2016). The city of Oaxaca has been extended over the adjacent agricultural landscape, so the urban landscape is more recent. During this urbanization process, first, its bird community would have been defined by the loss of some species from the agricultural landscape (subtracting homogenization), and later by the establishment of new, non-native species (additive homogenization). The main role of agricultural lands in preventing regional biotic homogenization have been recognized (Doxa et al. 2012). In this work, the importance of the agricultural landscape in increasing local beta diversity (a reverse process of biotic homogenization) has been documented: several bird species can still persist despite the increase in urban surface. In a recent work, the biotic homogenization in a tropical semi-dry zone of

Mexico across an elevational gradient was documented (Vázquez-López et al. 2017); where bird communities in urban settlements were subsets of the communities in conserved seasonal forests. Cities act as ecological filters of both species and functional traits (Crocini et al. 2008, McKinney 2006); the same pattern could be observed here. In urban environments, the absence of appropriate nesting conditions and substrates limits its suitability for many passerine species (e.g. Chace and Walsh 2006; Lim and Sodhi 2004). Urban ecological filtering may also have long-term negative effects for regional conservation efforts if urban surface increased (Gonzalez-Oreja 2011) and might be opposed to studies highlighting the benefits of urban environments for bird diversity (Tzortzakaki et al. 2018; Callaghan et al. 2019).

In the agricultural landscape, a turnover in dominant species between seasons was observed, from reproductive granivorous and insectivorous in the breeding season to migratory insectivorous and granivores in the non-breeding season. which may be caused by the inner tropical migration of some dominant species (e.g. *Peucaea botterii*, Forcey 2002), as a strategy to avoid competition with migrant species (Poulin and Lefebvre 1996). By contrast, the constant environmental conditions in cities promote seasonal stability of bird communities (Leveau and Leveau 2016; Leveau 2018); therefore, the species composition in cities have minimal variations throughout the year. In addition, compositional similarity was found to be lower at the non-breeding season; this pattern suggests that in this season birds moved freely across the landscape, maybe tracking food resources (Hutto 1985), while in the breeding season they were bounded to territories and are less mobile, which coincides with other works assessing bird distribution between seasons (Dybala et al. 2015; Almazán-Nuñez et al. 2018). We hypothesized that birds perceive the landscapes as homogeneous by using it in the same degree across scales. In addition, the urban landscape bird composition changed little when both the breeding and non-breeding seasons were compared. Competition could be more important in the relationships between resident and migratory species

than the sole availability and distribution of food resources (Toms 2013). In contrast to the low compositional similarity among the landscapes, there was a high compositional similarity within each landscape in both of the sampling seasons. It is acknowledged that low beta diversity is mainly related to spatial homogeneity (Socolar et al. 2016), but also ecological processes like high dispersion rates and landscape connectivity (Martin and Winsley 2015) can play a role in defining within site low beta diversity.

At the landscape level, one critical factor for bird diversity both in the countryside as well as in the cities is the amount of vegetation cover (Ortega-Álvarez and Macgregor-Fors 2011). For instance, studies have found that the amount of vegetation directly correlates with the biological diversity in urban (Chace and Walsh 2006, Fischer et al. 2011) and suburban environments (MacGregor-Fors 2008; Lessi et al. 2016). The same pattern has arisen in tropical agricultural landscapes: vegetation margins in cultivated areas are important for biological diversity (Zuria and Gates 2006), while the key role of life fences, tree remnants, and isolated trees in modified landscapes has been highlighted in tropical lowland fields (Estrada et al. 2000; Martin et al. 2009; Fisher et al. 2010; Cadavid-Flores et al. 2020). It seems, therefore, that the vegetation in general and especially arboreal elements of the landscape would be essential for the persistence of bird diversity in the agricultural lands. However, although positive relationships between bird diversity and abundance and structural vegetation features were found in this work, no significant relationships between bird diversity and tree diversity were detected. The most tree-diverse landscape was the urban one, but as found in other works in urban environments (Wania et al. 2006; Lessi 2016; Martínez-López et al. 2017), it was mainly dominated by non-native species such as Weeping Fig (*Ficus benjamina*), Flamboyant (*Delonix regia*) and Jacaranda (*Jacaranda mimosifolia*). The native Monkeypod (*Pithecelobium dulce*) was the dominant tree in the agricultural landscape. It seems that native tree species play an important role in the occurrence of

certain bird species in the tropics (Karr 1971; Douglas et al. 2013), and low numbers of such tree species in the urban landscape could explain the lower bird diversity in Oaxaca City.

Conservation implications

Historically, biodiversity conservation in Oaxaca has involved the management of natural landscapes by peasants and indigenous communities (Robson, 2007); the development of low impact activities such as small-scale timber extraction, coffee production and low intensity agriculture has produced spatially heterogeneous and biodiverse landscapes (Robson 2009). This has not been the case in the Central Valleys region of Oaxaca, where high intensity human impacts on natural landscapes date to pre-Columbian times (García-Mendoza et al. 2004). However, even in these relictual landscapes (urban and agricultural) an important diversity of bird species was observed, as it is possible to see when information about other birding spots at the area (i. e. Dainzú Archaeological site and Jardín Etnobotánico de Oaxaca) is consulted (eBird 2020). Especially remarkable was the fact that the agricultural landscape shelter bird species which cannot live in forests or cities, which is the case of the migratory birds from North American aridlands and grasslands. They spend their non-breeding season at the Oaxaca Central Valleys. Their numbers have declined in their breeding area in the last 50 years (Rosenberg et al. 2019). This shows the need to develop conservation strategies for the agricultural landscapes of the Oaxacan Valleys.

The agricultural landscape was shown to be essential for the maintenance of regional alpha and beta bird diversity in the tropical seasonally-dry zone of the Central Valley of Oaxaca, Mexico. This landscape had 30% more species than the urban landscape. Some bird species typical of agricultural landscapes can use to a certain degree the urban areas in the breeding season, but most of them cannot. In contrast, some migratory species cannot use the urban landscape. This study documented that from a biogeographical approach, the urban landscape selects against neotropical

and restricted-range birds while favoring non-natives. In contrast, at the ecological level, it selects against shrub and ground nesters, and migratory granivores and insectivores. There is an urgent need for developing conservation strategies for the agricultural landscape, which assures the persistence of the current bird community, as well as a strategy for the urban landscape to increase permeability for the surrounding native bird community.

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Figures

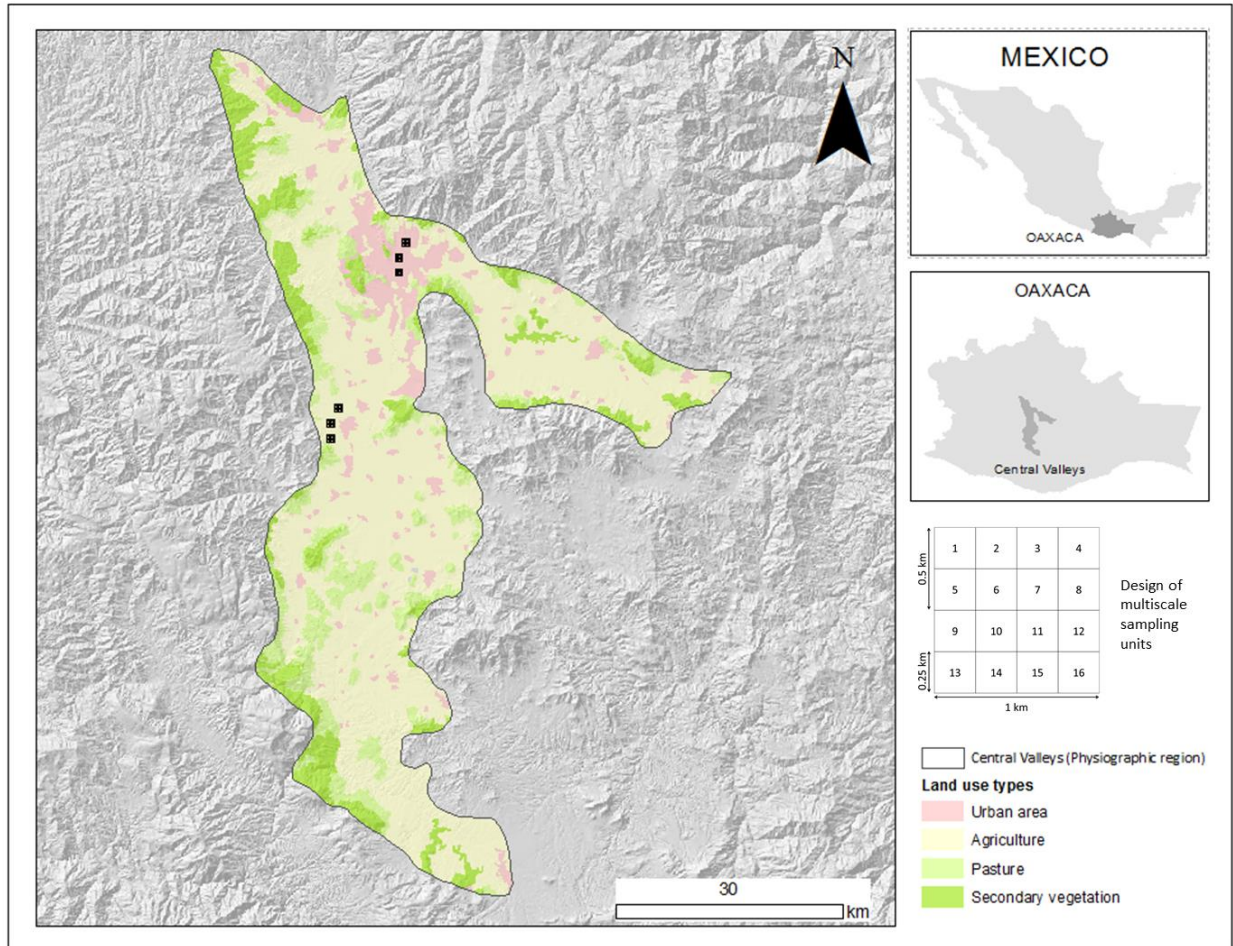
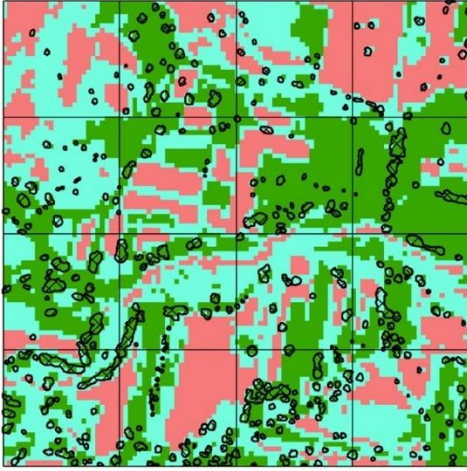


Fig. 1. Land use types and sampling units in the Central Valleys of Oaxaca. Three multiscale sampling units were situated in each urban and agricultural landscapes. A schematic view of a sampling window with standard cell numeration is shown above the legend. Scales are: cells (4 per frames, 16 per window, extension 6.25 ha, 0.25 km x 0.25 km), frames (4 per window; 25 ha; 0.5 km x 0.5 km), window (100 ha, 1 km x 1 km). Digital elevation model and land use map (based on vegetation series VI) were provided by INEGI (downloadable at <http://www.inegi.org.mx>).

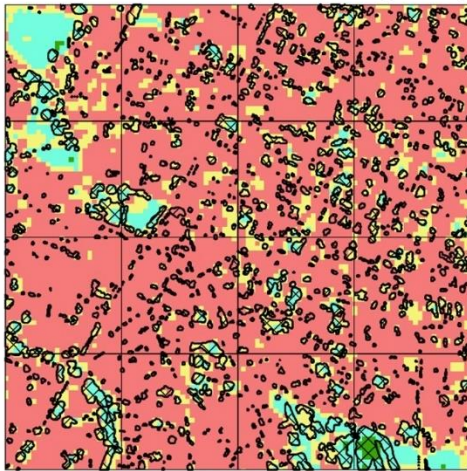


Fig. 2 Landscape scenarios of the Central Valleys of Oaxaca: relictual landscapes in the bottom of the Valley, formerly of shrub and dry forest, and adjacent to mountainous landscapes of oak forests . A) agricultural landscape near Zimatlan b) urban landscape in the center of Oaxaca.

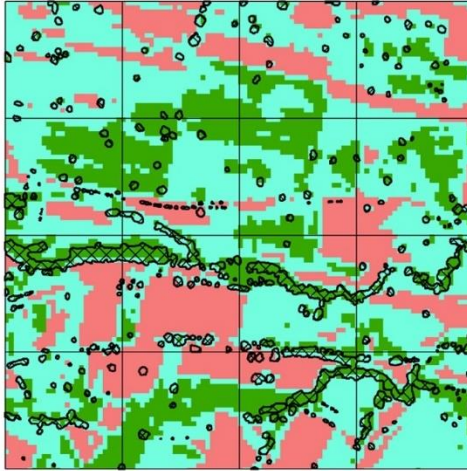
AW1 8.2 % (634)



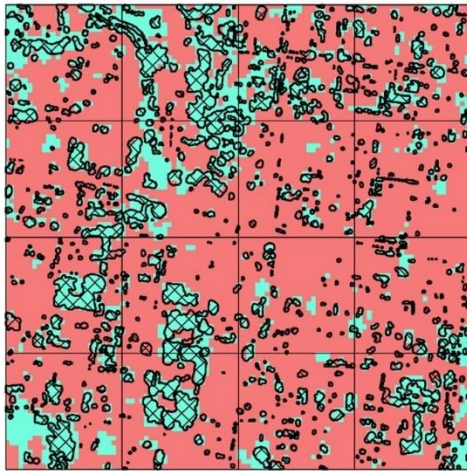
UW1 16.1 % (1754)



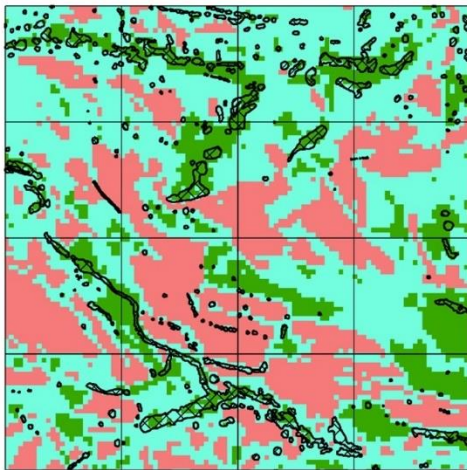
AW2 12.0 % (993)



UW2 20.2 % (1374)



AW3 9.5 % (1185)



UW3 11.2 % (1409)

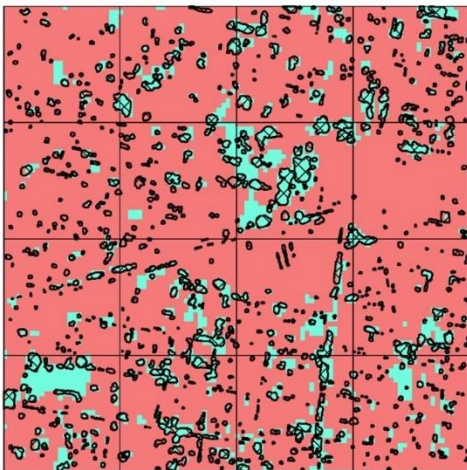


Fig. 3. NDVI, tree cover and tree abundance of each window at the two studied landscapes during the breeding season. Each window at each landscape was numbered from north to south.

Percentages shows vegetation cover of window area (100 ha), tree abundance in parenthesis.

NDVI categories: 1 (0-0.25), 2 (0.25-0.5), 3 (0.5-0.75), 4 (0.75-1)

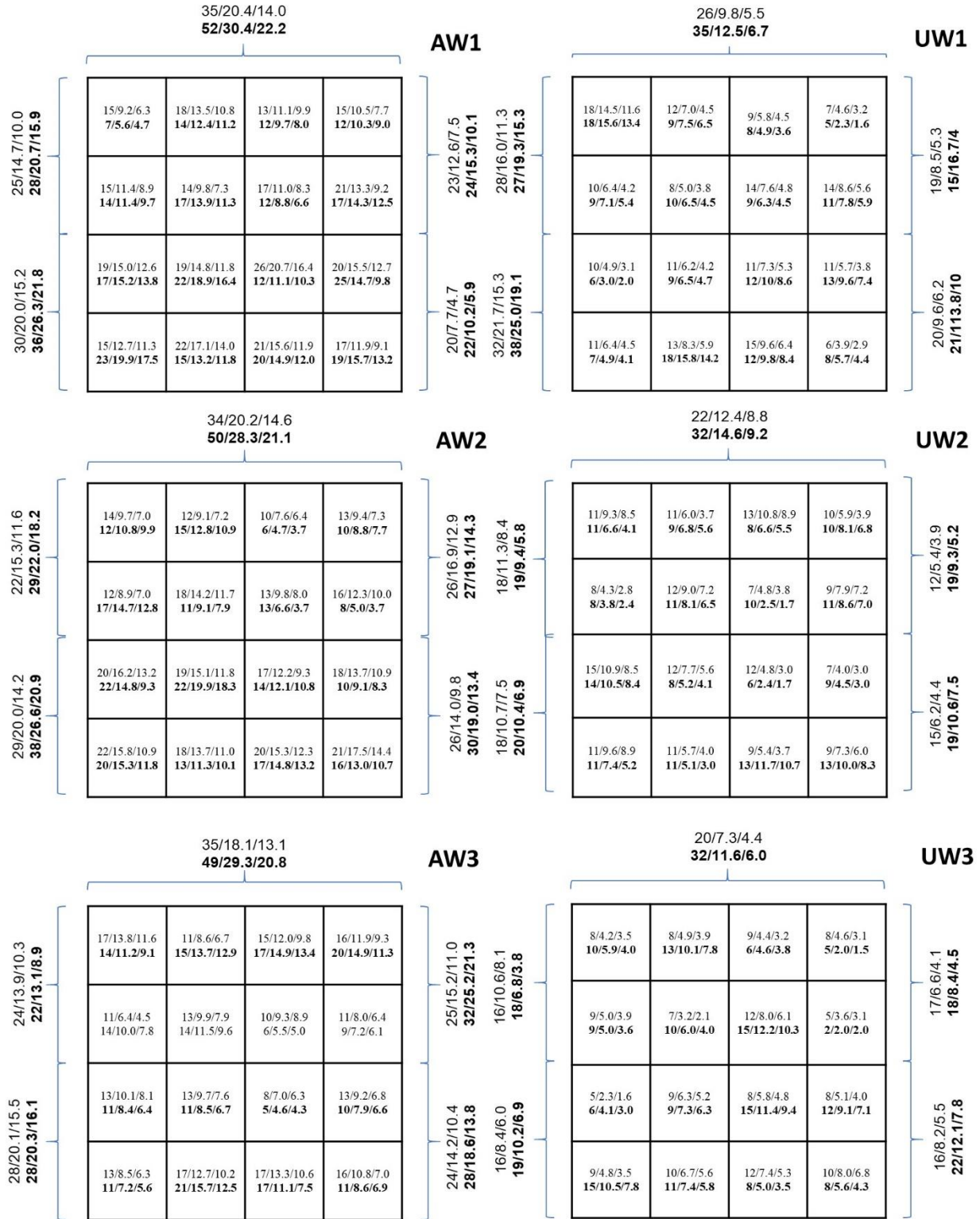
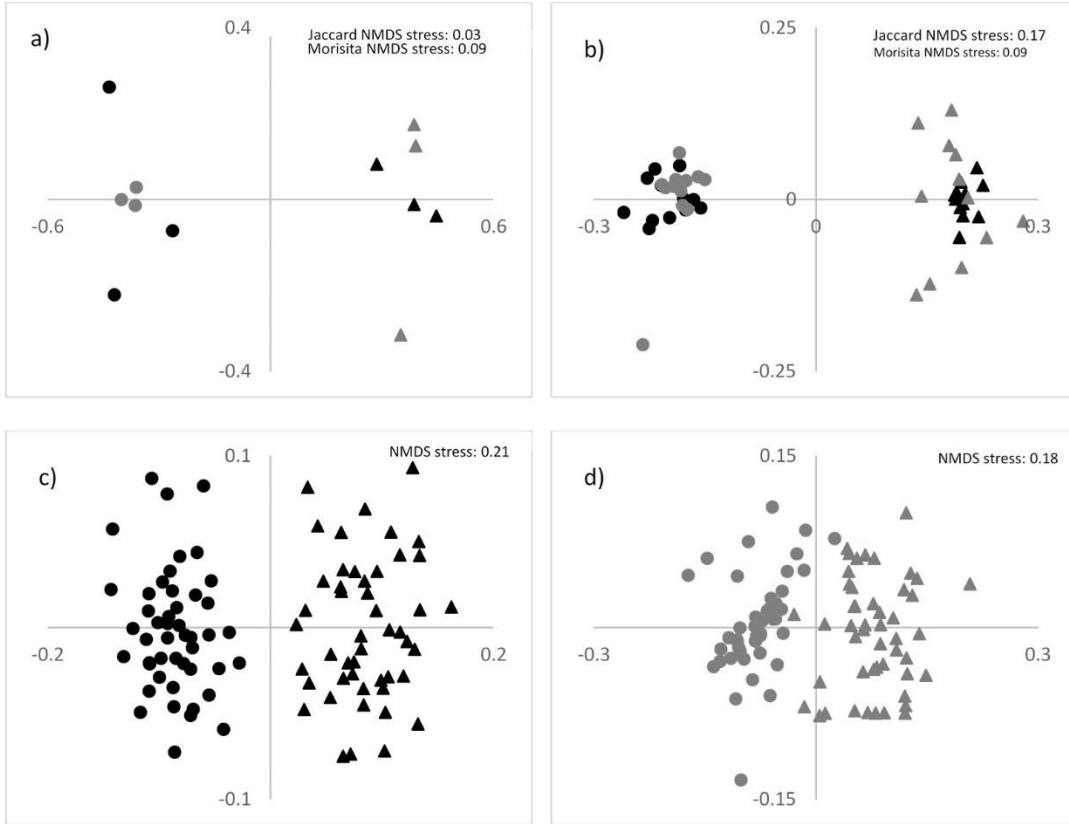


Fig. 4. Bird diversity values at each scale at each window. True diversity values are expressed as number of effective species. Diversity values for breeding season in normal and non-breeding season in bold (${}^0D/{}^1D/{}^2D$). UW-Urban Windows; AW-Agricultural Windows

A)



B)

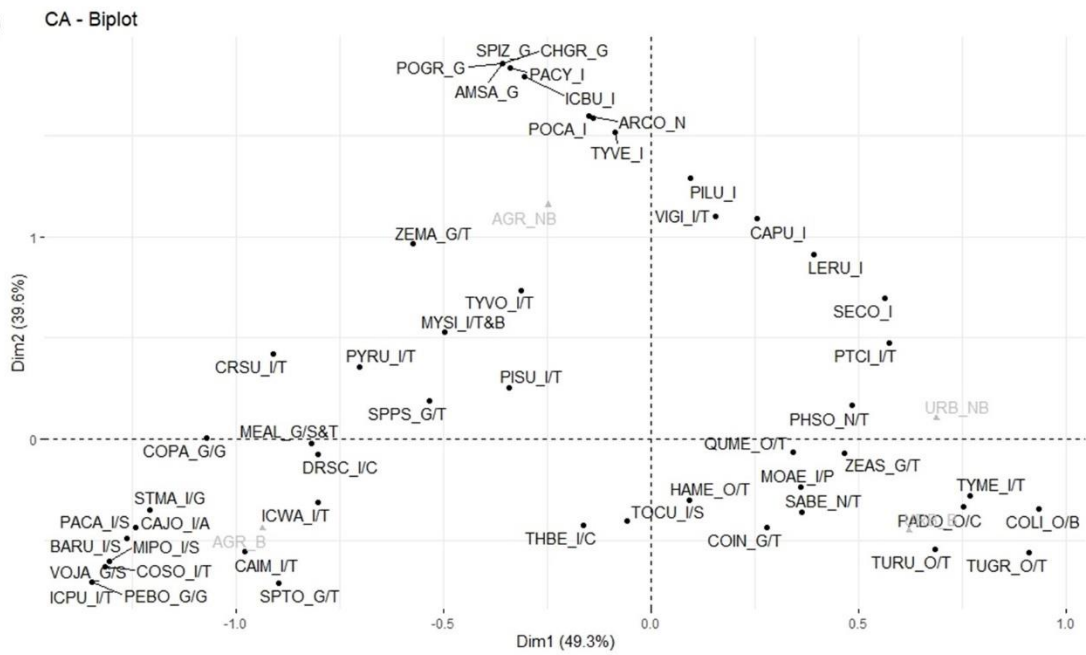


Fig. 5. A) NMDS biplots based on Jaccard and Morisita-Horn indices of sampling units at different scales in the breeding season: a) window; b) frame; c) Jaccard at plot level; d) Morisita at plot level. The solid markers depict samples ordinated with the Jaccard index, whereas open markers depict samples ordinated with the Morisita index. Circular markers are samples from the urban landscape; triangular markers are samples from the agricultural landscape. B) Correspondence analysis biplot of bird species. Each species is depicted with the first two letters of the genus and the first two letters of the specific epithet, followed by an abbreviation of their nesting substrate and an acronym of the feeding guild after the diagonal bar. The keys are depicted in Table 1.

Tables

Table 1. Summary of sampling measures of bird communities at each landscape in two different seasons. Sample completeness was assessed as 1) Sampling efficiency, the ratio (expressed as a percentage) between the observed and estimated number of species according to Chao 1 richness estimator, and; 2) Sample coverage, the probability that a newly sampled individual belongs to any species already represented at the sample. S_{obs} -Observed number of species, Cov-Sample coverage, E-Sampling efficiency, UL: Urban Landscape, AL: Agricultural Landscape, B: Breeding Season; NB: Non-breeding Season, $IF_{0,q}$: Inequality Factor

	Individuals	S_{obs}	Chao 1	E (%)	Singletons	Doubletons	$IF_{0,2}$
UL_B	2104	28	28	100	1	3	4.38
UL_NB	1672	44	49.6	88.7	8	4	4.74
AL_B	2209	39	39.3	99.2	2	2	2.41
AL_NB	1621	61	62	98.4	4	5	2.30

Table 2. Bird species checklist with ecological information. Species were used in the correspondence analysis biplot and were abbreviated by the first two letters of the genus and the first two of the specific epithet.

Scientific Name	Common Name	Species code	Feeding guild	Landscape	Nest substrate	Abundances (UL-B/AL-B/UL-NB/AL-NB)	Zoogeographical affinity
Columbidae							
<i>Columba livia</i>	Rock Pigeon	COL I	O	U	B	141/0/107/0	NN

Scientific Name	Common Name	Species code	Feeding guild	Landsc ape	Nest substrate	Abundances (UL-B/AL-B/UL-NB/AL-NB)	Zoogeographical affinity
<i>Columbina inca</i>	Inca Dove	COIN	G	U/A	T	123/52/53/15	WD
<i>Columbina passerina</i>	Common Ground-Dove	COPA	G	A	G	0/13/0/5	NT
<i>Zenaida asiatica</i>	White-winged Dove	ZEAS	G	U/A	T	162/44/110/57	WD
<i>Zenaida macroura</i>	Mourning Dove	ZEMA	G	U/A	T	1/34/6/71	WD
Cuculidae							
<i>Crotophaga sulcirostris</i>	Groove-billed Ani	CRSU	I	A	T	0/19/0/15	NT
Picidae							
<i>Dryobates scalaris</i>	Ladder-backed Woodpecker	DRSC	I	U/A	C	5/32/2/12	NA
Trochilidae							
<i>Archilochus colubris</i>	Ruby-throated Hummingbird	ARCO	N	U/A	-	0/0/4/22	NA
<i>Phaeoptila sordida</i>	Dusky Hummingbird	PHSO	N	U/A	T	15/04/19/10	MX
<i>Saucerottia beryllina</i>	Berylline Hummingbird	SABE	N	U/A	T	55/36/54/2	SE
<i>Saucerottia cyanocephala</i>	Azure-crowned Hummingbird	SACY	N	A	T	0/1/0/0	NT
Tyrannidae							
<i>Camptostoma imberbe</i>	Northern Beardless-Tyrannulet	CAIM	I	U/A	T	2/28/3/1	NT
<i>Contopus pertinax</i>	Greater Pewee	COP E	I	A	-	0/0/0/10	NT
<i>Contopus sordidulus</i>	Western Wood-Pewee	COSO	I	A	T	0/31/0/1	NA
<i>Empidonax sp.</i>		EMPID	I	U/A	-	0/0/0/10	

Scientific Name	Common Name	Species code	Feeding guild	Landsc ape	Nest substrate	Abundances (UL-B/AL-B/UL-NB/AL-NB)	Zoogeographical affinity
<i>Myiarchus cinerascens</i>	Ash-throated Flycatcher	MYC I	I	A	-	0/0/0/13	NA
<i>Myiozetetes similis</i>	Social Flycatcher	MYS I	I	U/A	T/B	3/17/5/20	NT
<i>Pitangus sulphuratus</i>	Great Kiskadee	PISU	I	U/A	T	26/46/11/44	NT
<i>Pyrocephalus rubinus</i>	Vermilion Flycatcher	PYR U	I	U/A	T	9/59/4/49	WD
<i>Tyrannus crassirostris</i>	Thick-billed Kingbird	TYC R	I	A	-	0/0/0/6	SE
<i>Tyrannus melancholicus</i>	Tropical Kingbird	TYM E	I	U/A	T	63/8/57/3	NT
<i>Tyrannus verticalis</i>	Western Kingbird	TYV E	I	U/A	-	0/0/12/48	NA
<i>Tyrannus vociferans</i>	Cassin's Kingbird	TYV O	I	U/A	T	8/66/49/120	SE
Laniidae							
<i>Lanius ludovicianus</i>	Loggerhead Shrike	LAL U	I	A	S/T	0/5/0/5	NA
Vireonidae							
<i>Vireo gilvus</i>	Warbling Vireo	VIGI	I	U	T	2/0/5/11	NA
Troglodytidae							
<i>Campylorhynchus jocosus</i>	Boucard's Wren	CAJ O	I	A	A	0/17/0/2	MX
<i>Cistothorus palustris</i>	Marsh Wren	CIPA I		A	-	0/0/0/3	NA
<i>Thryomanes bewickii</i>	Bewick's Wren	THB E	I	U/A	C	40/45/11/8	NA
<i>Troglodytes aedon</i>	House Wren	TRA E	I	A	-	0/0/0/2	MX
Turdidae							
<i>Turdus grayi</i>	Clay-colored Thrush	TUG R	O	U	T	35/0/8/0	NT

Scientific Name	Common Name	Species code	Feeding guild	Landsc ape	Nest substrate	Abundances (UL-B/AL-B/UL-NB/AL-NB)	Zoogeographical affinity
<i>Turdus rufopalliatu</i> s	Rufous-backed Thrush	TUR U	O	U/A	T	130/18/34/1	QE
Mimidae							
<i>Melanotis caerule</i> scens	Blue Mockingbird	MEC A	I	U/A	S/T	2/1/0/4	MX
<i>Mimus polyglott</i> os	Northern Mockingbird	MIP O	I	A	S	0/94/0/4	NA
<i>Toxostoma curviro</i> stre	Curve-billed Thrasher	TOC U	I	U/A	S	9/7/1/2	NA
Ptiligonatidae							
<i>Ptiliogonys cinere</i> us	Grey-silky Flycatcher	PTCI	I	U/A	T	21/2/76/37	QE
Polioptilidae							
<i>Polioptila caerule</i> a	Blue-gray Gnatcatcher	POC A	I	U/A	-	0/0/15/78	NA
Alaudidae							
<i>Eremophila alpe</i> stris	Horned Lark	ERA L	G	A	-	0/0/0/11	WD
Parulidae							
<i>Basileuterus rufif</i> rons	Red-capped Warbler	BAR U	I	A	S	0/43/0/4	QE
<i>Cardellina pusilla</i>	Wilson's Warbler	CAP U	I	U/A	-	0/0/25/30	NA
<i>Leiothlypis celata</i>	Olive Warbler	LEC E	I	U/A	-	0/0/2/1	NA
<i>Leiothlypis ruficap</i> illa	Nashville Warbler	LER U	I	U/A	-	0/0/88/70	NA
<i>Leiothlypis virginia</i> e	Virginia's Warbler	LEVI	I	U/A	-	0/0/1/5	SE
<i>Mniotilta varia</i>	Black and white Warbler	MN VA	I	U	-	0/0/1/0	NA
<i>Setophaga coronata</i>	Yellow-rumped Warbler	SEC O	I	U/A	-	0/0/189/87	NA

Scientific Name	Common Name	Species code	Feeding guild	Landsc ape	Nest substrate	Abundances (UL-B/AL-B/UL-NB/AL-NB)	Zoogeographical affinity
<i>Setophaga dominica</i>	Yellow-throated Warbler	SEDO	I	U	-	0/0/1/0	NA
<i>Setophaga nigrescens</i>	Black-throated Grey Warbler	SENI	I	U/A	-	0/0/4/6	SE
<i>Setophaga townsendi</i>	Townsend's Warbler	SETO	I	U/A	-	0/0/2/7	NA
Passerelidae							
<i>Ammodrammus savannarum</i>	Grasshopper Sparrow	AMSA	G	A	-	0/0/0/31	NA
<i>Chondestes grammacus</i>	Lark Sparrow	CHGR	G	A	-	0/0/0/47	NA
<i>Melospiza lincolni</i>	Lincoln's Sparrow	MELI	G	A	-	0/0/0/14	NA
<i>Melospiza albicollis</i>	White-throated Towhee	MEAL	G	U/A	S/T	40/249/8/106	MX
<i>Peucaea botterii</i>	Botteri's Sparrow	PEBO	G	A	G	0/266/0/0	WD
<i>Poocetes gramineus</i>	Vesper Sparrow	POGR	G	A	-	0/0/0/25	NA
<i>Spizella spp.</i>		SPIZ	G	A	-	0/0/0/39	-
<i>Spizella passerina+</i>	Chipping Sparrow		G	A	-	-	NA
<i>Spizella pallida+</i>	Clay-colored Sparrow		G	A	-	-	SE
Cardinalidae							
<i>Piranga ludoviciana</i>	Western Tanager	PILU	I	U/A	-	0/0/35/69	NA
<i>Piranga rubra</i>	Summer Tanager	PIRU	I	U/A	-	0/0/6/5	NA
<i>Passerina caerulea</i>	Blue Grosbeak	PACA	I	A	S	0/110/0/13	WD
<i>Passerina cyanea</i>	Indigo Bunting	PACY	I	U/A	-	0/0/1/79	NA
<i>Passerina versicolor</i>	Varied Bunting	PAVE	I	A	-	0/0/0/4	SE

Scientific Name	Common Name	Species code	Feeding guild	Landsc ape	Nest substrate	Abundances (UL-B/AL-B/UL-NB/AL-NB)	Zoogeographical affinity
<i>Pheucticus ludovicianus</i>	Rose-breasted Grosbeak	PHL U	I	U	-	0/0/2/0	NA
Thraupidae							
<i>Sporophila torqueola</i>	White-collared Seedeater	SPT O	G	U/A	T	19/76/0/0	NT
<i>Volatinia jacarina</i>	Blue-black Grassquit	VOC A	G	A	S	0/102/0/0	NT
Icteridae							
<i>Agelaius phoeniceus</i>	Red-winged Blackbird	AGP H	I	A	S	0/2/0/0	WD
<i>Icterus bullockii</i>	Bullock's Oriole	ICB U	I	U/A	-	0/0/1/25	SE
<i>Icterus pustulatus</i>	Streaked-backed Oriole	ICPU	I	A	T	0/28/0/0	NT
<i>Icterus spurius</i>	Orchard Oriole	ICSP	I	U/A	-	0/0/1/2	NA
<i>Icterus wagleri</i>	Black-vented Oriole	ICW A	I	U/A	T	4/19/1/4	NT
<i>Molothrus aeneus</i>	Bronzed Cowbird	MO AE	I	U/A	P	38/50/104/0	WD
<i>Quiscalus mexicanus</i>	Great-tailed Grackle	QU ME	O	U/A	T	57/19/26/23	WD
<i>Sturnella magna</i>	Eastern Meadowlark	STM A	I	A	G	0/141/0/23	WD
Fringillidae							
<i>Haemorhous mexicanus</i>	House Finch	HA ME	O	U/A	T	415/263/106/109	NA
<i>Spinus psaltria</i>	Lesser Goldfinch	SPPS	G	U/A	T	29/85/11/62	NA
Passeridae							
<i>Passer domesticus</i>	House Sparrow	PAD O	O	U/A	C	650/77/438/29	NN

Feeding guild: O-Omnivorous; G-Granivorous; I-Insectivore; N-Nectarivore

Landscape: U-Urban; A-Agricultural

Season: B-Breeding; NB-Non-Breeding

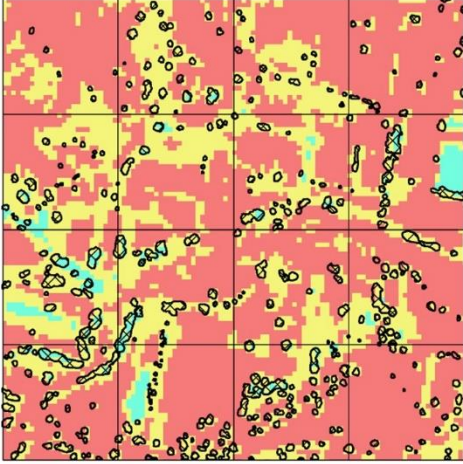
Nest substrate: B-Building; T-Tree; G-Ground; C-Cavity; S-Shrub; A-Agave

Table 3. Matrix of compositional similarity indices between windows. Jaccard index values are depicted in italics (above the x-diagonal). Morisita-Horn index values are shown under the x-diagonal. In both cases, the lowest possible value of the index can be 0 (when two communities are completely different), while the highest possible value can be 1 (when two compared communities are completely the same). UW: Urban Window; AW: Agricultural Window; B: Breeding Season, NB: Non-Breeding Season

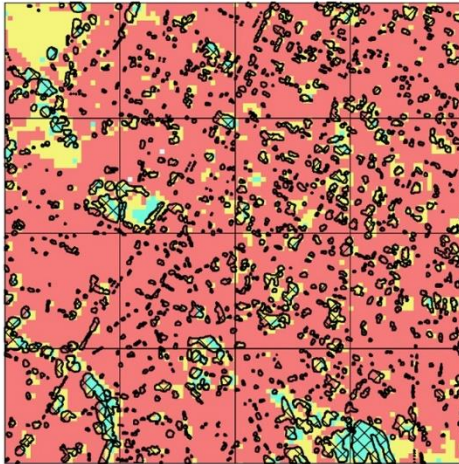
	UW1_B	UW2_B	UW3_B	UW1_NB	UW2_NB	UW3_NB	AW1_B	AW2_B	AW3_B	AW1_NB	AW2_NB	AW3_NB
UW1_B	x	<i>0.71</i>	<i>0.77</i>	<i>0.53</i>	<i>0.49</i>	<i>0.57</i>	<i>0.61</i>	<i>0.54</i>	<i>0.53</i>			
UW2_B	0.89	x	<i>0.68</i>	<i>0.50</i>	<i>0.59</i>	<i>0.54</i>	<i>0.50</i>	<i>0.44</i>	<i>0.39</i>			
UW3_B	0.98	0.85	x	<i>0.45</i>	<i>0.41</i>	<i>0.53</i>	<i>0.49</i>	<i>0.46</i>	<i>0.41</i>			
UW1_NB	0.85	0.73	0.81	x	<i>0.60</i>	<i>0.60</i>				<i>0.53</i>	<i>0.47</i>	<i>0.47</i>
UW2_NB	0.62	0.69	0.57	0.76	x	<i>0.68</i>				<i>0.50</i>	<i>0.39</i>	<i>0.40</i>
UW3_NB	0.93	0.84	0.92	0.96	0.74	x				<i>0.50</i>	<i>0.39</i>	<i>0.37</i>
AW1_B	0.37	0.39	0.35				x	<i>0.86</i>	<i>0.79</i>	<i>0.40</i>	<i>0.37</i>	<i>0.40</i>
AW2_B	0.37	0.37	0.32				0.79	x	<i>0.92</i>	<i>0.39</i>	<i>0.40</i>	<i>0.38</i>
AW3_B	0.39	0.39	0.36				0.85	0.76	x	<i>0.38</i>	<i>0.39</i>	<i>0.38</i>
AW1_NB				0.32	0.33	0.25	0.37	0.35	0.37	x	<i>0.70</i>	<i>0.68</i>
AW2_NB				0.40	0.42	0.35	0.40	0.38	0.42	0.80	x	<i>0.77</i>
AW3_NB				0.26	0.24	0.28	0.60	0.43	0.62	0.80	0.78	x

Supplementary Material

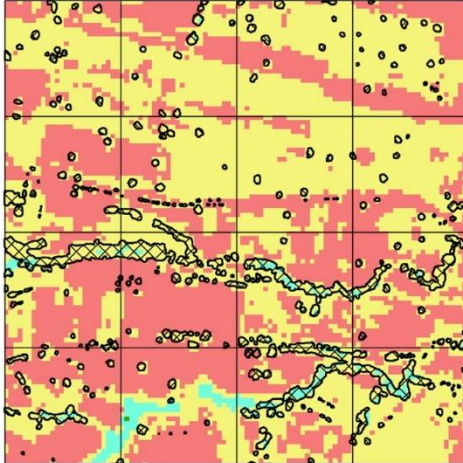
AW1 8.2 % (634)



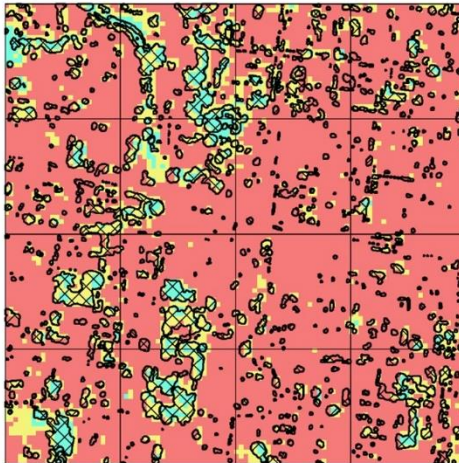
UW1 16.1 % (1754)



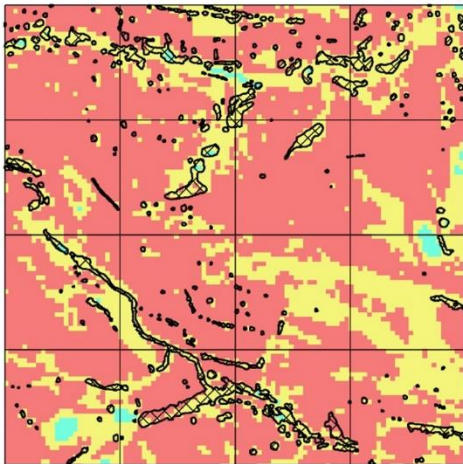
AW2 12.0 % (993)



UW2 20.2 % (1374)



AW3 9.5 % (1185)



UW3 11.2 % (1409)

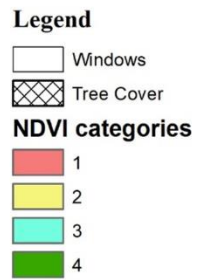
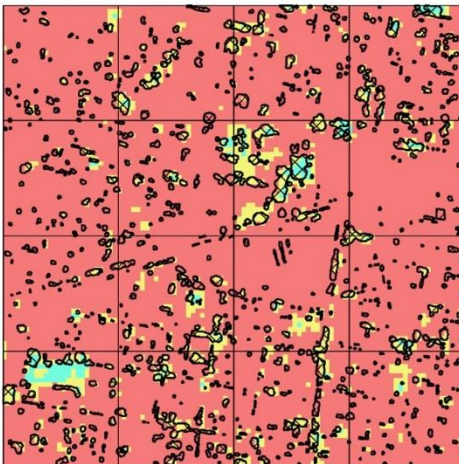


Fig. S1. NDVI and Vegetation cover of the studied windows at each landscape in non-breeding season. Each window at each landscape was numbered from north to south. Percentages shows vegetation cover of window area (100 ha), tree abundance in parenthesis. NDVI categories: 1 (0-0.25), 2 (0.25-0.5), 3 (0.5-0.75), 4 (0.75-1)

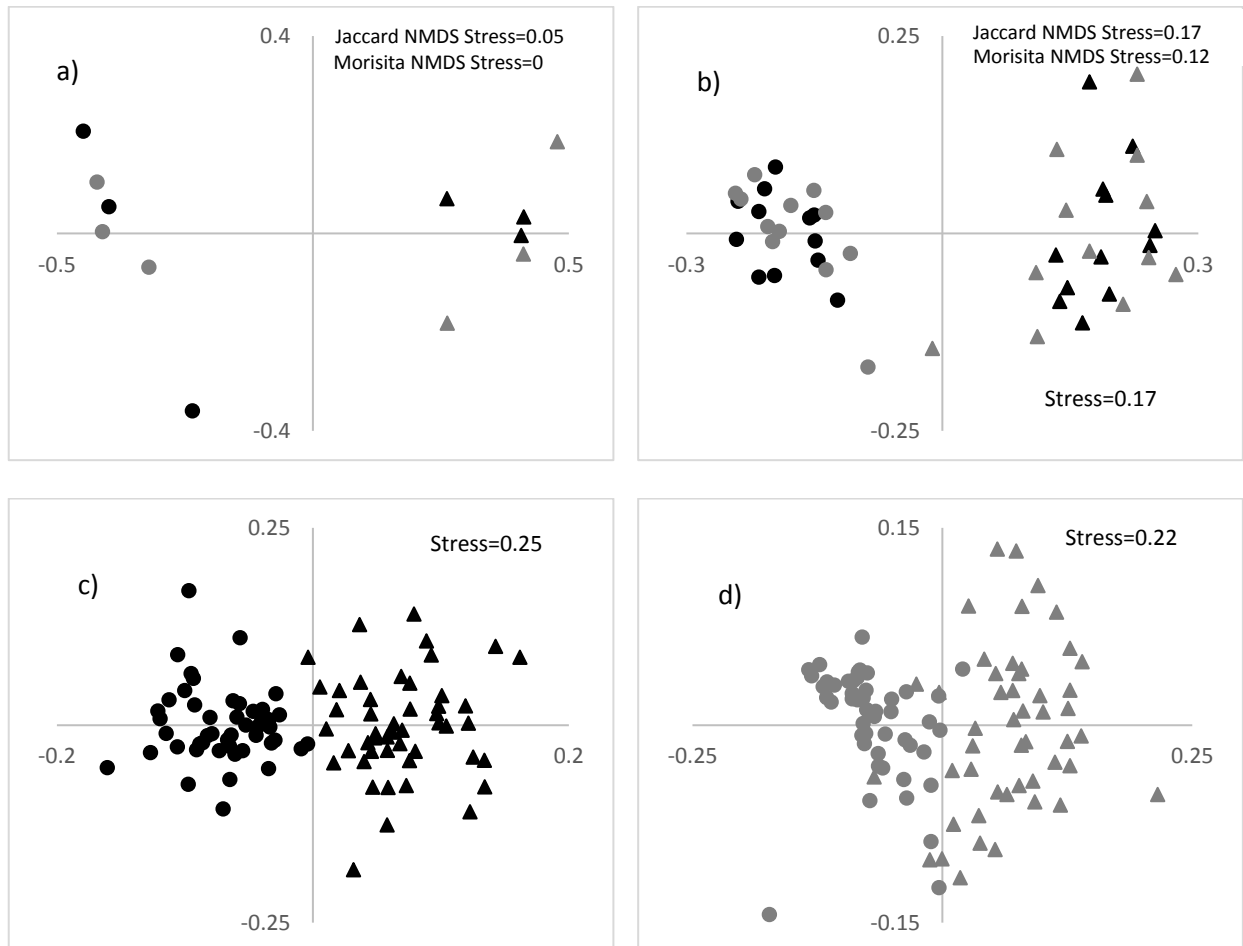


Fig. S2. NMDS biplot based on Jaccard and Morisita-Horn indices of sampling units at different scales in non-breeding season: a) Windows; b) Frames; c) Cells with Jaccard index; d) Cells with Morisita-Horn index. Black markers depict samples ordinated with the Jaccard index, whereas grey markers depict samples ordinated with the Morisita-Horn index. Circular markers are samples from the urban landscape; triangular markers are samples from the agricultural landscape.

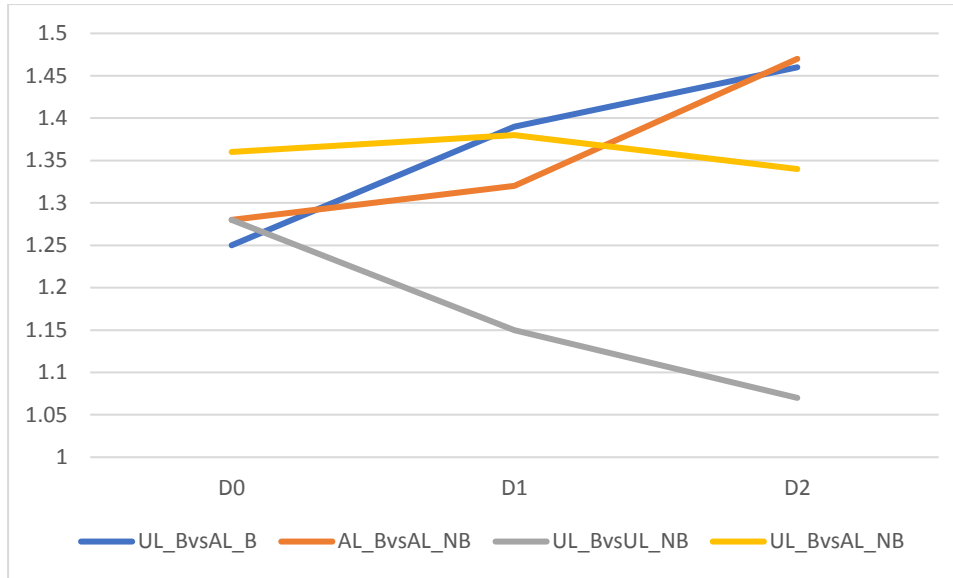


Fig. S3. Values of true beta diversity between landscapes and seasons at three different diversity orders are depicted in sequence (${}^0D/{}^1D/{}^2D$). Units of beta diversity are effective number of communities; the lowest possible value is 1 (when two compared communities are the same) whereas the highest possible value is 2 (when two compared communities are completely dissimilar). UL: Urban landscape, AL: Agricultural landscape, B: Breeding season, NB: Non-breeding season

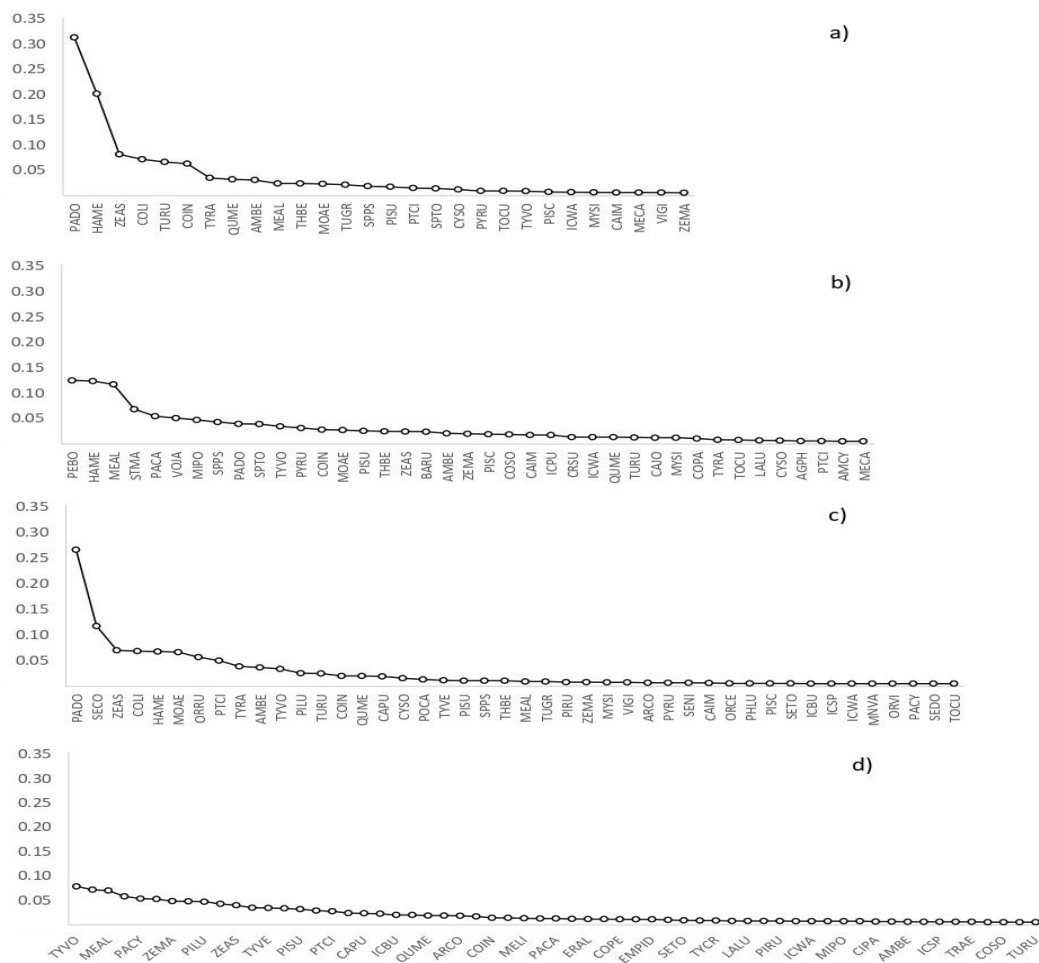


Fig. S4. Rank-abundance plot at the landscape level at two sampling seasons. a) Urban Landscape- Breeding; b) Agricultural Landscape-Breeding; c) Urban Landscape Non-breeding; d) Agricultural Landscape Non-breeding. Species keys are displayed in the x-axis (see Table 2; the y-axis represents proportional abundances.

Tables

Table S1. Summary of bird community numbers at each window in two different seasons. Sample completeness was assessed as 1) Sample efficiency, or the ratio (expressed as percentage) between the observed and estimated number of species according to Chao 1 richness estimator, and; 2) Sample coverage, or the probability that a new found individual belongs to any species already represented at the sample. Also, coverage based comparisons of alpha diversity with confidence intervals of the three studied windows at each landscape at both seasons are depicted. Ind-Number of individuals, S_{Obs} -Observed number of species, Cov-Sample coverage, E-Sampling efficiency, UW: Urban window, AL: Agricultural Window. UW: Urban window, AW: Agricultural window. UCL: upper confidence limit; LCL: lower confidence limit

	Window	Ind	S_{Obs}	Cov	Chao 1	E (%)	Singletons	Doubletons	0D	UCL	LCL	1D	UCL	LCL	2D	UCL	LCL
Breeding	UW1	730	26	0.997	26.3	98.7	2	2	23.1	24.6	21.5	10.1	9.2	11	5.9	5.3	6.6
	UW2	643	22	0.998	22	100	1	2	19.8	20.7	18.9	12.4	11.6	13.2	9.4	8.4	10.3
	UW3	731	20	0.999	20	100	1	4	17.1	18.3	15.9	7.1	6.4	7.9	4.5	4.1	5
	AW1	869	35	0.998	35.3	99.3	2	3	32	33.1	30.9	19.8	18.4	21.1	13.6	12.3	15
	AW2	723	34	0.997	34.2	99.5	2	5	31.1	32.8	29.5	20.1	19	21.3	14.9	13.6	16.3
	AW3	617	35	0.994	36.5	95.9	4	3	33.1	35.7	30.6	17.7	16.2	19.3	12.8	11.6	13.9
Non-breeding	UW1	463	35	0.978	50	70	10	2	43.2	52.6	33.9	13.8	12	15.5	7.3	6.1	8.4
	UW2	739	32	0.991	53	60.4	7	0	28.5	31.1	25.9	14.2	13.1	15.3	10.2	9.5	10.9
	UW3	470	32	0.989	33.4	95.7	5	6	31.4	34.7	28	12.5	11.2	13.7	6.7	5.6	7.7
	AW1	627	51	0.989	55.2	92.4	7	4	49.7	53.4	46	31.6	29.7	33.4	24.4	22.1	26.7
	AW2	501	49	0.986	51.6	94.9	7	7	49	52.6	45.4	28.8	26.2	31.5	22.2	19.9	24.6
	AW3	493	49	0.986	52.5	93.4	7	5	49	52.5	45.5	30.7	28.3	33.2	22.1	19.3	24.9

Table S2. Results of the Wilcoxon test to compare 0D at different seasons at cell and frame scale.

Black numbers indicate comparisons with significant differences. UL: Urban landscape, AL:

Agricultural landscape, B: Breeding season, NB: Non-breeding season, N: Number of paired data,

W: Wilcoxon value; p: probability value

	N	W	p
UL_Cell scale			
0D_B vs 0D_NB	48	427.5	>0.5
1D_B vs 1D_NB	48	692	>0.1
2D_B vs 2D_NB	48	743	>0.1
AL_Cell scale			
0D_B vs 0D_NB	48	741	<0.05
1D_B vs 1D_NB	48	688	>0.1
2D_B vs 2D_NB	48	609	>0.5
UL_Frame scale			
0D_B vs 0D_NB	12	68.5	<0.05
1D_B vs 1D_NB	12	62	>0.05
2D_B vs 2D_NB	12	50	>0.1
AL_Frame scale			
0D_B vs 0D_NB	12	61.5	<0.05
1D_B vs 1D_NB	12	76	<0.01
2D_B vs 2D_NB	12	76	<0.01

Table S3. Results of Wilcoxon tests for comparisons of compositional similarities within landscapes at different seasons. UL: Urban landscape, AL: Agricultural landscape, B: Breeding season, NB: Non-breeding season, N: Number of paired data, W: Wilcoxon value; p: probability value

Frame scale				Cell scale			
Jaccard	N	W	p	Jaccard	N	W	p
All species				All species			
UL B vs UL_NB	66	1972	<0.001	UL B vs UL_NB	1128	4.87E+05	<0.001
AL_B vs AL_NB	66	2138	<0.001	AL_B vs AL_NB	1128	5.64E+05	<0.001
Only all-year residents				Only all-year residents			
UL B vs UL_NB	66	1881	<0.001	UL B vs UL_NB	1128	4.80E+05	<0.001
AL_B vs AL_NB	66	2183	<0.001	AL_B vs AL_NB	1128	5.23E+05	<0.001
Morisita				Morisita			
All species				All species			
UL B vs UL_NB	66	2050	<0.001	UL B vs UL_NB	1128	4.71E+05	<0.001
AL_B vs AL_NB	66	1993	<0.001	AL_B vs AL_NB	1128	5.75E+05	<0.001
Only all-year residents				Only all-year residents			
UL B vs UL_NB	66	1963	<0.001	UL B vs UL_NB	1128	4.38E+05	<0.001
AL_B vs AL_NB	66	1816	<0.001	AL_B vs AL_NB	1128	5.08E+05	<0.001

Table S4. Summary of the correspondence analysis ($\chi^2=7331.1$, $df=150$, $p<0.001$) between species and landscapes at each season. Species code is depicted in Table 1.

	Dim. 1	Dim. 2					
Variance	0.484	0.389					
% of variance	49.311	39.606					
Cumulative % of var.	49.311	88.917					
Rows							
	Iner*1000	Dim. 1	Contribution	cos2	Dim. 2	Contribution	cos2
SABE_N/T	6.14	0.36	0.53	0.42	-0.36	0.65	0.41
AMSA_G	16.34	-0.36	0.11	0.03	1.86	3.68	0.88
ARCO_N	9.19	-0.15	0.02	0.01	1.60	2.28	0.97
BARU_I/S	11.81	-1.26	2.07	0.85	-0.49	0.39	0.13
CAIM_I/T	6.16	-0.98	0.90	0.71	-0.56	0.36	0.23
CAJO_I/A	4.51	-1.24	0.81	0.87	-0.44	0.13	0.11
CAPU_I	10.33	0.25	0.10	0.05	1.09	2.24	0.84
CHGR_G	24.77	-0.36	0.17	0.03	1.86	5.58	0.88
COLL_O/B	32.87	0.93	5.97	0.88	-0.34	1.00	0.12
COIN_G/T	12.67	0.28	0.46	0.18	-0.44	1.41	0.43
COPA_G/G	2.78	-1.07	0.57	1.00	0.01	0.00	0.00
COSO_I/T	9.39	-1.32	1.53	0.79	-0.63	0.43	0.18
CRSU_I/T	4.65	-0.91	0.78	0.81	0.42	0.21	0.18
PHSO_N/T	1.88	0.48	0.31	0.80	0.17	0.05	0.10
HAME_O/T	23.78	0.09	0.21	0.04	-0.30	2.76	0.45
ICBU_I	12.43	-0.31	0.07	0.03	1.79	2.87	0.90
ICPU_I/T	8.98	-1.35	1.41	0.76	-0.71	0.48	0.21
ICWA_I/T	2.78	-0.80	0.50	0.87	-0.31	0.09	0.13
MEAL_G/S&T	36.37	-0.82	7.47	0.99	-0.02	0.00	0.00
MIPO_I/S	27.97	-1.31	4.63	0.80	-0.60	1.23	0.17
MOAE_I/P	17.88	0.36	0.69	0.19	-0.24	0.37	0.08
MYSI_I/T&B	3.20	-0.50	0.31	0.47	0.53	0.43	0.53
LERU_I	29.01	0.39	0.67	0.11	0.92	4.56	0.61
PADO_O/C	108.42	0.75	18.68	0.83	-0.34	4.61	0.17
PACA_I/S	29.15	-1.24	5.25	0.87	-0.44	0.81	0.11
PACY_I	40.86	-0.34	0.26	0.03	1.84	9.28	0.88
PEBO_G/G	85.29	-1.35	13.35	0.76	-0.71	4.58	0.21
DRSC_I/C	4.44	-0.80	0.91	0.99	-0.07	0.01	0.01
PILU_I	23.46	0.10	0.03	0.01	1.29	5.94	0.98
PISU_I/T	3.75	-0.34	0.42	0.54	0.25	0.28	0.29
POCA_I	32.25	-0.14	0.05	0.01	1.58	8.03	0.97

POGR_G	13.18	-0.36	0.09	0.03	1.86	2.97	0.88
PTCI_I/T	15.70	0.57	1.23	0.38	0.48	1.06	0.26
PYRU_I/T	10.39	-0.70	1.65	0.77	0.36	0.54	0.20
QUME_O/T	3.01	0.34	0.40	0.65	-0.06	0.02	0.02
SECO_I	59.51	0.56	2.42	0.20	0.70	4.64	0.30
SPPS_G/T	8.64	-0.54	1.48	0.83	0.19	0.24	0.11
SPIZ_G	20.55	-0.36	0.14	0.03	1.86	4.63	0.88
SPTO_G/T	16.72	-0.90	2.13	0.62	-0.71	1.65	0.39
STMA_I/G	35.27	-1.21	6.62	0.91	-0.35	0.68	0.08
THBE_I/C	3.35	-0.16	0.08	0.11	-0.43	0.65	0.75
TOCU_I/S	0.83	-0.06	0.00	0.01	-0.40	0.11	0.49
TUGR_0/T	8.70	0.91	0.98	0.55	-0.56	0.47	0.21
TURU_O/T	24.06	0.68	2.36	0.48	-0.55	1.87	0.30
TYME_I/T	12.15	0.77	2.14	0.85	-0.28	0.35	0.11
TYVE_I	18.80	-0.09	0.01	0.00	1.52	4.76	0.99
TYVO_I/T	20.88	-0.31	0.66	0.15	0.73	4.51	0.84
VIGI_I/T	2.98	0.15	0.01	0.02	1.10	0.75	0.98
VOJA_G/S	32.70	-1.35	5.12	0.76	-0.71	1.76	0.21
ZEAS_G/T	11.27	0.47	2.23	0.96	-0.07	0.06	0.02
ZEMA_G/T	19.64	-0.58	1.02	0.25	0.96	3.59	0.71

Columns

	Iner*1000	Dim. 1	Contribution	cos2	Dim. 2	Contribution	cos2
URB_B	203.85	0.62	22.40	0.53	-0.45	14.86	0.28
AGR_B	318.69	-0.94	53.47	0.81	-0.44	14.74	0.18
URB_NB	167.30	0.69	21.54	0.62	0.10	0.61	0.01
AGR_NB	291.97	-0.25	2.60	0.04	1.16	69.80	0.93

Table S5. Regression parameters at cell scale between abundances of trees, tree cover, and bird diversity

(¹D and ²D) at each landscape at the two different seasons. Bold values are statistically significant.

Urban Landscape

	Slope	Intercept	r ²	p
¹D Birds B vs Tree Cov	0.00	3.95	0.17	0.002
²D Birds B vs Tree Cov	0.00	3.09	0.10	0.014
¹ D Birds B vs AB Tree	0.01	5.73	0.00	0.277
² D Birds B vs AB Tree	0.00	4.46	0.01	0.508
¹ D Birds NB vs Tree Cover	0.00	5.48	0.02	0.174
² D Birds NB vs Tree Cover	0.00	4.23	0.01	0.208
¹ D Birds NB vs AB Tree	0.01	6.51	0.01	0.545

² D Birds NB vs AB Tree	0.01	4.83	0.00	0.378
Agricultural Landscape	Slope	Intercept	r ²	p
¹ D Birds B vs Tree Cov	0.00	9.30	0.32	0.00
² D Birds B vs Tree Cov	0.00	7.22	0.32	0.00
¹ D Aves B vs AB Arboles	0.02	11.08	0.82	0.08
² D Aves B vs AB Arboles	0.01	8.73	0.04	0.08
¹ D Birds NB vs Tree Cov	0.00	7.22	0.53	0.00
² D Birds NB vs Tree Cov	0.00	5.99	0.46	0.00
¹ D Aves NB vs AB Arboles	0.03	9.58	0.18	0.00
² D Aves NB vs AB Arboles	0.03	8.14	0.12	0.01

Table S6. GLM parameters at cell scale between abundances of trees, tree coverage, and bird richness (⁰D) at each landscape at the two different seasons. Bold values are statistically significant. B: Breeding season, NB: Non-breeding season.

<i>Response</i>	<i>model variables</i>	<i>Parameter Estimates</i>	<i>SE</i>	<i>p-value</i>
<i>Urban Landscape</i>				
⁰ D Birds B	Intercept	2.01	0.124	<0.001
	Tree Coverage	0.00	0.00	<0.01
⁰ D Birds B	Intercept	2.22	0.10	<0.001
	Tree Abundance	0.00	0.00	0.331
⁰ D Birds NB	Intercept	2.15	0.12	<0.001
	Tree Coverage	0.00	0.00	0.185
⁰ D Birds NB	Intercept	2.30	0.10	<0.001
	Tree Abundance	0.00	0.00	0.953
AB Birds B	Intercept	3.76	0.05	<0.001
	Tree Coverage	0.00	0.00	0.726
AB Birds B	Intercept	3.81	0.05	<0.001
	Tree Abundance	0.00	0.00	0.445
AB Birds NB	Intercept	3.45	0.07	<0.001
	Tree Coverage	0.00	0.00	0.08
AB Birds NB	Intercept	3.68	0.05	<0.001
	Tree Abundance	0.00	0.00	<0.01
<i>Agricultural Landscape</i>				
⁰ D Birds B	Intercept	2.58	0.07	<0.001
	Tree Coverage	0.00	0.00	<0.001

⁰ D Birds B	Intercept	2.71	0.06	<0.001
	Tree Abundance	0.00	0.00	0.176
⁰D Birds NB	Intercept	2.30	0.07	<0.001
	Tree Coverage	0.00	0.00	<0.001
⁰ D Birds NB	Intercept	2.50	0.06	<0.001
	Tree Abundance	0.00	0.00	<0.001
AB Birds B	Intercept	3.76	0.04	<0.001
	Tree Coverage	0.00	0.00	<0.05
AB Birds B	Intercept	3.87	0.03	<0.001
	Tree Abundance	0.00	0.00	0.131
AB Birds NB	Intercept	3.22	0.05	<0.001
	Tree Coverage	0.00	0.00	<0.001
AB Birds NB	Intercept	3.40	0.04	<0.01
	Tree Abundance	0.00	0.00	<0.001

Chapter 2

Bird diversity patterns during breeding and migratory seasons in a variegated mountain landscape in Southern Oaxaca, Mexico

Omar Suarez Garcia¹, Matthias Rös^{2*}, Erwin Lopez Osorio¹

Abstract

Aim: To analyze bird diversity patterns at three representative land-use scenarios in a variegated mountain landscape during breeding and migratory seasons.

Location: Sierra Madre del Sur, a mountain landscape at an elevation between 2200 to 2900 masl consisting of a mosaic of a dominant pine-oak forest, agricultural lands, cattle pastures, orchards.

Methods: Three representative landscape scenarios were selected- fragmented, variegated, and conserved. In each scenario, one square of 100 ha subdivided into 16 plots was placed. Point counts were conducted at the center of each plot to register bird species and abundances at two contrasting breeding and migratory seasons. Vegetation was characterized at the center of each plot. NDVI was calculated from satellite imagery to determine the amount of remnant forest cover and the degree of landscape heterogeneity.

Results: No statistical differences were found between landscape modification scenarios for alpha diversities of order 0 and 1 at any season. Beta diversity was significantly high comparing the intact and the other two scenarios. A positive correlation between bird diversity and the

percentage of forest cover was found only during the migratory season. Neotropical and restricted range species were positively associated with the intact landscape scenario at both seasons.

Main conclusions: A moderate reduction in original vegetation cover might not affect alpha diversity in a variegated landscape; nevertheless, it is more evident in beta diversity, as a set of species found in the intact scenario were absent or present in lower abundance in the modified scenarios. Forest amount was important to both altitudinal and latitudinal migrants, while it was of no importance to bird diversity during the breeding season. Neotropical species seem to depend mainly upon forest cover, maybe due to ecological inertia.

Keywords

Beta diversity, Mexican Transition Zone, Endemic Bird Area, community ecology, true diversity, hierarchical sampling, Normalized Difference Vegetation Index

Introduction

Anthropic landscape modification is a major force shaping ecological patterns and processes (Fisher and Lindenmayer 2007). It has been so for millenia, when our ancestors exerted both negative (Faurby and Svenning 2015) and positive effects (Peters 2019) over biodiversity.

Although the empirical knowledge obtained by autoctonous and indigenous people through time and experience has indirectly promoted the persistence of high biodiversity levels, only recently it has been acknowledged that conservation initiatives must be (and have been) carried out in human-modified landscapes, where high biodiversity levels still persist (Fisher and Lindenmayer 2006). Especially important is to understand the effect of human interventions over the living beings at the landscape level.

Mountain forest landscapes in the tropics often have a land-use pattern characterized by less intensive practices in space and time compared to plane or lowland landscapes. Small scale crops based on slash and burn activities, with longer pauses for fallows and forest regrows are embedded in forest mosaics of different age and harvesting intensity (Pérez-García and del Castillo 2017, Van Vleet et al. 2016)

In this work we used the variegated landscape model (McIntyre and Barrett 1992), which considers that as there is a mixture of land covers with often indistinguishable boundaries, several landscape scenarios based on the amount of original vegetation cover can be considered (McIntyre and Barret 1992; McIntyre and Hobbs 1999). Several works have shown that this landscape models are especially useful in mountain landscapes (e.g., Numa et al. 2005, Rös et al. 2012).

Especially is the role of variegated landscapes (i. e., those retaining between 60 and 90% of original vegetation cover, Manning et al. 2004) for biodiversity maintenance. It has been observed that variegated landscapes can sustain as much diversity as intact landscapes (Rös et al. 2012; Costa et al. 2017), which is important in terms of conservation because it shows that proper landscape management can buffer the impacts of human activities on local biodiversity (Perfecto and Vandemeer 2010). On one hand, variegated landscapes are often the result of human intervention: when people do low-intensity activities like traditional agriculture, shade-coffee growing or forest management, they create biodiversity-friendly landscapes where most of species can still coexist and have healthy populations (DeClerck et al. 2010). On the other hand, mountain landscapes in the tropics often have a high level of natural disturbances due to landslides, fires, heavy storms (Feinsinger 1994, Rös et al. 2012)

Birds are an well known and used model group to study the effects of landscape modification on biodiversity, because they are a well-known biological group, with standardized survey methods, and because they exhibit an array of responses to environmental changes (Rueda-Hernández et al. 2015). While landscape ecology studies using bird communities as biological subjects are numerous, they have been carried out in both in the Nearctic and the Neotropics, being scarce at transitional biogeographic areas like the Mexican Transition Zone (MTZ, Halffter 2020), which is a broad region encompassing Mexico and Norther Central America where biotas from Nearctic and Neotropical origins overlap.

Biogeographically, the MTZ is largely the result of the Great American Interchange (Weir et al. 2009), a process that began 3.5 MY ago, when the lands from Southern Central America arose to connect North America to South America. The result was a big faunal intermixing between both subcontinents, which in turn gave place to a vast transitional region encompassing the mountains of Mexico and Central America, where evolutive processes continued to our days (Blancas-Calva et al. 2010). Now, Mesoamerican mountains are centers of richness and endemism (Ramírez-Albores et al. 2020) where only few studies have been accomplished despite the great importance they have to understand the effects of human modification at the biogeographical and ecological scales.

There are several hypotheses that have been developed to explain the empirical diversity patterns at the landscape scale. For instance, the habitat amount hypothesis states that fragmentation per se is not the most negative variable influencing species diversity, and that the decrease in habitat amount is the key factor impoverishing biological communities (Fahrig et al. 2019). Based on evidence, it is widely acknowledged that at least 40% of original forest vegetation is needed to conserve biodiversity at the landscape scale (Arroyo-Rodriguez et al.

2020). Also, the beta dominance hypothesis states that in heterogeneous landscapes, beta diversity is more important than alpha diversity to define regional (gamma) diversity (Tcharntcke et al. 2012). At the biogeographic scale, it has been postulated that Neotropical species can be more sensitive to forest loss due to ecological inertia, given that species from that biogeographic realm are better adapted to forest conditions (Halffter and Morrone 2017).

The objectives of this work were: 1) To analyze the spatiotemporal bird diversity patterns at three different landscape modification scenarios in a mountainous region of Southern Mexico; 2) To evaluate bird distribution at each of the studied landscape scenarios, as well as the relationships between both local and landscape characteristics and bird diversity and; 3) To assess the relationships between biogeographical affinity of birds and the amount of forest cover. The hypotheses were: 1) Both the intact and the variegated scenarios will have similar alpha diversities; 2) Beta diversity will be higher when the intact and the fragmented scenarios are compared; 3) Bird species distribution will be strongly determined by vegetation characteristics (especially the tree and shrub cover) at the local and by the amount of forest vegetation and landscape heterogeneity at the landscape scale and; 4) Bird species of Neotropical affinity will be more affected by forest loss than Nearctic ones.

Methods

Study area. - The study was done at the municipality of San Mateo Río Hondo, Oaxaca, in Southern Mexico (Fig. 1a). This location lies within the boundaries of the Sierra Madre del Sur, which comprises the Southern mountains of Mexico, in the so-called Mexican Transition Zone (Fig1b-c), a biogeographic region including the highlands and mountains of Mexico and Central America where Nearctic and Neotropical biotas overlap (Halffter 2020). The altitude ranged from 2200 to 2900 m.a.s.l., and the main vegetation types are pine and pine-oak forests present in

different amounts and successional stages; also, agricultural fields, open lands for grazing, and gardens associated with rural human settlements, and roads are present. The average annual temperature is 18 °C, the annual precipitation reaches 1,500 mm, the climate is considered as temperate semihumid according to Köppen modified classification (García 2004) with a defined rainy season in summer and scattered rains in winter. The main human activities in the region are logging, rainfed agriculture, grazing, and touristic activities.

Sampling design. - To identify locations with different landscape modification scenarios, a first exploratory remote survey was made by using Google Earth (Google 2019) and aerial imagery (QGIS 2019). Further visits to the selected locations were carried out to make terrain reconnaissance. Three suitable locations were found, each representing a landscape modification scenario according to McIntyre and Hobbs (1999): Intact, Variegated, Fragmented (Fig. 1a,d).

A multiscale, hierarchical sampling design was used to sample birds and local vegetation features (Halfpeter and Rös 2013). One 100 ha window (1x1 km each) was established in each landscape modification scenario (three windows in total). These windows were subdivided into 16 smaller cells of 6.25 ha (250x250 m each). In this way, our sampling design allowed to analyze data at four different spatial scales: 1) plot (the smallest sampling unit); 2) frame (four adjacent plots), 3) window (which we use interchangeably with landscape scenario) and, 4) landscape (the three sampling windows).

Field surveys. - Point counts were performed at the center of each cell to register bird species and abundances (Bibby et al. 1992; Ralph et al. 1995). Each point count was separated by a minimum distance of 250 m to ensure statistical independence (Hutto 1986) excepting cell 1 of the intact scenario, where terrain conditions were so rugged that only a point 90 m apart from the cell center was reached. Plots were visited during the migratory season (February-March 2019) and

the reproductive season (May-June 2019). Birds more than 50 m away from the observer or flying over without interacting with any landscape element surrounding the point count were omitted.

One observer (OSG) visited the center of each cell for two different days to make 5-minute observations; surveys were made from sunrise to 4 hours afterward in good meteorological conditions (e.g., no rain, calm wind). The order of the daily visits to each point was changed. While all observed species were recorded at the sites, only passerines and allies were considered for analysis. Also, 11 vegetation variables were estimated at the center of each cell: 1) Tree genera richness; 2) Tree density; 3) Maximum tree diameter; 4) Maximum tree height; 5) Percentage of tree cover; 6) Shrub morph richness; 7) Percentage of shrub cover; 8) Maximum shrub height; 9) Herb morph richness; 10) Percentage of herb cover; 11) Maximum herb height (Rueda-Hernández *et al.*, 2015).

Data Analysis. – Chao 1 richness estimator was calculated for the whole landscape and each landscape scenario, and the ratio (expressed as percentage) between this estimator and the observed number of species was used as a measure of sample completeness. To express species diversity, the true diversity approach was used (Jost 2006): alpha (site diversity), beta (variation in species composition between sites), and gamma diversity (regional diversity) were quantified under a multiplicative partitioning principle (Whittaker 1974) at each considered scale.

Comparisons between alpha diversities between sites and seasons were made based on the sample coverage (Chao and Jost 2012) at landscape and window scales by using the iNext R package (Hsieh *et al.* 2016) at three different diversity orders ($q=0, 1$ and 2), which have a mathematical relationship to the three most used diversity indices (species richness, Shannon's entropy and Simpson's concentration respectively, Jost 2006). The inequality factor of order 2

($IF_{0,2}$) was calculated. The values of this measure range from a maximum equal to species richness (indicating the dominance of one species) and a minimum of 1, indicating equal abundance of all species (Jost 2010).

Beta diversity was calculated by comparing pairwise samples (at all scales) and complete sets of samples (only at landscape and window scales) and expressed as the number of effective communities (Jost 2010; Baselga 2010) at the same three orders as alpha diversity. Gamma diversity was therefore calculated as the product of alpha and beta diversity (Jost 2006), which are independent of each other (Jost 2010).

To assess statistical differences in beta diversity between landscape scenarios a multivariate dispersion analysis (Anderson et al. 2006) was done by using the Vegan R package (Oksanen 2008). Test of multivariate dispersion is a statistical technique that evaluates the differences in dispersion between and among samples belonging to a specific group and can be used to assess differences in species composition. This test allows to incorporate compositional similarity indices to look for differences in species composition between groups of samples; in this work Jaccard and Morisita indices were used because they are related to true beta diversities of order 0 and 2, respectively (Jost 2010), and because both indices truly measure compositional similarity (Jost et al. 2011). Also, to test for specific differences between pairs of groups a PERMANOVA was carried out with the Vegan package.

Simple correlations (Spearman coefficients) were used to explore the relationships between the percentage of forest cover and bird diversity (0D , 1D and 2D) at both cell and frame scales. Community structure was depicted by rank-abundance plots. Birds were classified into eight different foraging guilds (see Table 1) and six different zoogeographical categories: endemic, nearctic, neotropical, quasiendemic, semiendemic, and widespread. According to

González-García and Gómez de Silva (2004) and Palomera et al. (1998), who consider a species as endemic when its range lies within the boundaries of the Mexican territory, quasiendemic when its range includes Mexican territory and <50, 000 km² outside of it, and semiendemic when its distributional range encompasses only the Mexican territory only in some stage of its annual cycle.

A canonical correspondence analysis (CCA) was performed to explore the relationships between bird species distribution (and guilds) and local vegetation features. Simple correlation tests between these variables were run in order to look for interdependency; then a set of four vegetation variables were selected to make the CCA analysis: 1) Tree density (TD), 2) Diameter at breast height (DBH), 3) Shrub cover (SC), 4) Maximum herb height (MHH). CCA significance was assessed by calculating pseudo F statistics with Montecarlo permutations (N=999). Chi-squared tests were used to explore the affinities of zoogeographic categories (using both number of individuals and number of species belonging to each category) in each of the landscape scenarios.

Spatial analyses were done with QGIS 3.12 (QGIS Development Team): to quantify the amount of original arboreal vegetation present at each window, Sentinel 2 satellite imagery from March 2019 was downloaded from Copernicus Open Data Hub (European Union 2020) and used to calculate NDVI values; a threshold of 0.6 was used as a criterion to classify a pixel as arboreal, as values below the threshold were considered as non-forest (Rios et al. 2016). Also, the standard deviation of NDVI was calculated and used to make simple correlations. NDVI standard deviation has been used as a proxy of heterogeneity at landscape scale (Souza et al. 2019). In this work, non-parametric correlations between bird diversity and both percentage of forest cover and

standard deviation of NDVI at both frame and cell scales were made to explore the relationships between birds and vegetation.

Results

A total time of 960 minutes of bird observation (5 minutes x 48 plots x 2 days x 2 seasons) were carried out, accounting for 76 bird species belonging to 25 families and five orders (Table 1). Sixty species were all-year residents, 14 Nearctic-neotropical migrants, and two altitudinal migrants. Regarding foraging guilds, foliage-gleaner insectivorous (26 species), ground insectivorous (11) and omnivorous (10) species were the most common, whereas nectarivores, aerial insectivorous, bark insectivorous, granivorous, , and frugivorous, , eight were less common (between eight and four species). Foliage insectivorous and omnivorous were the guilds with the highest abundances during non-breeding season, while ground insectivores and frugivorous were the most numerous guilds in the migratory season (Fig. S1). At the zoogeographical level, 27 neotropical, 14 Nearctic, 11 widespread, 12 endemic, six quasiendemic and five semiendemic species were recorded. One of the species (White-throated Jay *Cyanolyca mirabilis*) is listed as Vulnerable by the IUCN Red List.

At the landscape scale, there were 67 observed species in the migratory season and 52 species in the breeding season. According to Chao 1 richness estimator, sample completeness was 87.7% and 93.3%, respectively; sample coverage was 99% in the migratory season and 99.5% in the breeding season (Table S1). At the window scale, observed numbers of species ranged from 34 to 48, sample completeness from 83.6% to 98.2%, and sample coverage from 96.8% to 99% (Table 2). Inequality of species abundances were only higher in the fragmented window in the migratory season (4.0), in the other cases it was relatively low (ranging from 1.8 to 2.4), with the lowest value in the variegated window in the breeding season. (Table 2).

Alpha diversity. At the landscape scale, diversities of order 0 and 1 (hereafter 0D and 1D respectively) were statistically higher in the migratory than in the breeding season; in contrast, diversity of order 2 (hereafter 2D) was similar between seasons (Table S2). At the window scale, all three modification scenarios had statistically similar 0D values at each season (Fig. 2). All three scenarios had similar 1D values during the non-breeding season, whereas the fragmented and variegated scenarios had similar diversity values but were more diverse than the intact scenario during the breeding season (Fig. 2). At 2D , the fragmented scenario was less diverse than the other two scenarios, which had similar values in non-breeding season, while in breeding season the intact scenario was the least diverse, with both variegated and fragmented presenting similar values (Fig. 2). Estimated richness was higher in migratory than in breeding season at both frame and cell scales (Table S3). All alpha diversity values at frame and cell scales can be viewed in Fig. 3. Alpha diversity was positively correlated to percentage of forest cover only during non-breeding season (excepting 0D at frame scale) at both cell and frame scales (Table S4).

Beta diversity. - At the landscape scale, beta diversity between modification scenarios was higher in the migratory than in breeding season (Fig. S2a). At the window scale, beta diversity was highest between the intact and the fragmented scenarios, and lowest between the variegated and the fragmented scenarios. The trends were similar between seasons (Fig. S2b). In general, compositional similarity (Jaccard and Morisita) at both cell and frame scales was lower in non-breeding than in breeding season (Table S5).

Permutational analysis of variance showed that there were statistical differences between landscape scenarios at both seasons when both Jaccard and Morisita indices were considered (pseudo $F=3.62$ and 2.34 respectively, $p<0.05$, 999 permutations). PERMANOVA analysis

showed significant differences between the intact and the fragmented scenarios using Jaccard index during the migratory season, but no differences using Morisita-Horn similarity. During the breeding season, the intact scenario was significantly different from the other two scenarios both when Jaccard and Morisita indices were used (Table 3). During the migratory season, dominant species were *Myadestes occidentalis*, *Ptiliogonys cinereus* and *Peucedramus taeniatus*, while in breeding season the dominant ones were *Oreotlypis superciliosa* and *Myioborus miniatus* (Fig. S3A).

Birds and vegetation variables.- The canonical correspondence analysis at landscape scale was significant at both seasons ($p < 0.05$ at first 2 axes, 999 permutations); in the migratory season the first two axes (eigenvalues=0.28 and 0.13 respectively) represented 57.7% and 26.3% of the total variance, while in the breeding season the first two axes (eigenvalues=0.25 and 0.11 respectively) represented 60.5% and 27.4% of the total variance, respectively. In the migratory season, axis 1 was positively related to DBH and shrub cover, while axis 2 was positively related to SC and MHH. In the breeding season, axis 1 was related to both DBH and SC and axis 2 was related to tree density and SC. During the migratory season, species positively related to axis 1 were *Arremon brunneinucha*, *Atthis heloisa*, *Basileuterus belli*, *Chlorospingus flavopectus*, *Cyanolyca mirabilis* and *Henichorhina leucophrys*, while *Aphelocoma wollweberi*, *Atlapetes pileatus*, *Ptiliogonys cinereus* and *Troglodytes aedon* were negatively related to this axis. Species positively related to axis 2 were *Bombycilla cedrorum*, *Lamprolaima rhami*, *Leiothlypis celata*, and *Psaltriparus minimus*. During the breeding season, species positively associated with axis 1 were *Catharus frantzii*, *Cardellina rubra*, *Mitrephanes phaeocercus*, *Leuconotopicus villosus*, *Basileuterus belli*, *Trogon mexicanus* and *Arremon brunneinucha*, while species positively associated with axis 2 were *Vireo gilvus*, *Vireolanius melitophrys*, *Aulacorhynchus wagleri* and *Myiarchus tuberculifer* (

Fig. S3Ba-b). Excepting positive relationships between TD and MHH and omnivorous birds in the non-breeding season, no other significant relationships between foraging guilds and vegetation variables were found.

Regarding zoogeographical affinities to landscape scenarios, abundance-based chi-squared test between zoogeographic categories and landscapes scenarios was significant ($\chi^2=118.76$, $df=10$, $p<0.001$, Fig. 7a), whereas species richness was not ($\chi^2=22.53$, $df=25$, $p>0.5$, Fig. 7b). During the migratory season, quasiendemic species were positively associated with the fragmented scenario, Neotropical birds with the intact scenario and Nearctic species with all three landscape scenarios. During the breeding season, Widespread species were positively associated with both the fragmented and the variegated scenarios, while Endemic, Neotropical and Semiendemic species were positively associated with the intact scenario (Fig. 4).

Finally, no significant relationships between bird alpha diversity and diversity of NDVI categories were found. NDVI categorization showed that the variegated scenario was the most diverse in terms of land cover, whereas the intact scenario was the most homogeneous (Fig. S4).

Discussion

According to the findings of this work, landscape modification due to human activities [in](#) pine-oak forest of the Sierra Sur physiographic region promotes small changes in alpha diversity but also a decrease in beta diversity, especially when the intact scenario vs variegated and fragmented scenarios are compared. Other works have found that vegetation types with some degree of human intervention can harbor a high proportion of the total species contained in an entire landscape (Chazdon et al. 2009), however, some specialist species can be regionally lost if original forest remnants are deforested (Carrara et al. 2015).

As suggested by other studies, the presence of different land covers can promote a high beta diversity (Socolar et al. 2012). According to the landscape complementation hypothesis (Tscharntke et al. 2012), vegetation types other than original forest can offer other resources that species take. However, several forest interior species are not able to leave the forest to explore open areas because of increased predation risks and vulnerability (Santos-Moreno et al. 2019). It is well known that forest species also depend on shrubs (Ortega-Álvarez et al. 2018), because such vegetation strata can offer new nest substrates, food resources and protection. In agricultural lands, aerial insectivorous and granivorous species can take their chances, and these species can occasionally use resources at forest edges to complement their life requirements (Carrara et al. 2015).

Zoogeographical origin of bird species can inform about their extinction risk regarding human activities. For instance, there has been found that Nearctic and Widespread species can thrive better in urban environments than Neotropical and restricted range species, which are more prone to extinction in such places (González-Oreja 2011). The landscape that was investigated in this work lies within the Mexican Transition Zone, which is a biogeographical area characterized by the overlap of Nearctic and Neotropical biotas plus restricted range species (Halfpter 2019). We found that the intact scenario favored Neotropical species, while Nearctic and restricted-range species seem to use the modified landscape scenarios more than expected. This could be due to the generalist habits of some migrant species, which have a Nearctic affinity.

At the local scale, vegetation features are variables important to bird diversity and distribution (MacArthur and MacArthur 1962). In tropical forest, there has been observed that both vegetation richness and structural complexity can exert an effect on bird richness (Karr 1981). In this work we found no significant relations between bird diversity and vegetation

features, but when these environmental variables were related to individual species distribution several patterns emerged. Especially, shrubby vegetation has proven to be especially important for understory birds (Santos-Moreno et al. 2019).

Although the fragmentation model has been useful to explain some patterns and processes in landscape ecology, studies around the world have proven such approach to be unrealistic at certain locations and scenarios (Haila 2002; Manning et al. 2004; Barlow et al. 2007; Tschardt et al 2012; Rös et al. 2012; Brudvig 2017). Most of the tropical landscapes have been transformed by human activities (Chazdon et al. 2009). Many landscapes of this region do not have a definite anthropic matrix, and because the concept of inhospitable is species or species-group dependent, there are different responses to landscape modification (Fisher et al. 2009). That is the main reason why other land covers than pristine vegetation are important for bird diversity, and in the future conservation decisions should be made to include modified landscape elements, because they have the potential to provide resources and conditions for a big amount of species (Didham et al. 2012). In Oaxaca, landscapes have a long history of human modification, but community-based decisions have been made (Robson 2008), and the result is a mixture of low-intensity activities that have allowed a set of species to survive in these transformed landscapes since at least half a century ago (Rowley 1965; Binford 1989). Landscapes and humans evolve together, and this work show that this coexistence can have positive effects to local biodiversity.

In the mountains of Mexico, there has been found that forest patch size is the main driver of alpha bird diversity in tropical cloud forests (Martínez-Morales 2005; Rueda-Hernández et al. 2015; MacGregor-Fors et al. 2018). However, at least in some regions of Southern Mexico, forest fragmentation is not the common observed landscape pattern, because the history of management

and land use have allowed the persistence of large proportions of original vegetation throughout the region (Van Vleet et al. 2016). Instead, mountain landscapes might often match the variegated model, with a small scale land use gradient and without clear boundaries (Lindenmayer and Fisher 2006). Bird diversity patterns in variegated landscapes have been poorly documented; by contrast, there has been observed that dung beetle diversity peaks in variegated scenarios (Rös et al. 2012; Costa et al. 2017; Correa et al. 2019).

Biogeographically, the Sierra Madre del Sur (SMS) lies within the boundaries of the Mexican Transition Zone (MTZ), a vast region where both Nearctic and Neotropical biotas, as well as restricted range taxa overlap, and that encompasses the mountainous regions of Mexico and Central America (Halffter and Morrone 2017). Regarding birds, it has been acknowledged that the mountainous regions of Mexico belong to a biogeographic transition zone (Kobelkowsky-Vidrio et al. 2014; Ferro et al. 2017); arguably, the MTZ corresponds with what some researchers have defined as the Mesoamerican or Middle America region (Winker 2011; Muñoz-Ríos and Navarro-Sigüenza 2012), which is considered as a global biodiversity hotspot (Myers et al. 2000; Harvey et al. 2008). The Sierra Sur of Oaxaca has a complex history that involves the establishment of species from both Northern and Southern regions result of the Great American Interchange (DaCosta and Klicka 2008) and incipient speciation processes promoted by orogeny and climatic fluctuations that continue to our days (Rocha-Mendez et al. 2019). Also, the SMS is important in terms of habitat availability to Nearctic-Neotropical migrants, which spend the winter season in the different vegetation types present at the region (Binford 1989; Navarro-Sigüenza 1992).

The predominance of Neotropical species in our studied landscape, the presence of birds of Nearctic affinity and a high proportion of restricted range species seems to confirm the idea

that the avifauna in the Sierra Sur physiographic region is the result of a combination of elements from both North and South plus autochthonous species and subspecies which originated *in situ* (Hernández-Baños et al. 1995). Indeed, this pattern is congruent to the one observed at multitaxon level, which gave place to the concept of the MTZ (Contreras-Medina et al. 2007; Halffter and Morrone 2017)

In a study that evaluated the effects of urbanization on bird communities, González-Oreja (2011) found that birds of Neotropical affinity and restricted range species were more prone to be affected by human activities than Nearctic ones. In our studied landscape scenarios, Neotropical species were positively associated with the intact scenario at both studied seasons, while restricted range species were more abundant than expected in the same scenario only during the migratory season. It could be possible that due to ecological inertia (Halffter and Morrone 2017) or niche conservatism (Wiens and Graham 2005), Neotropical species are somewhat unable to use or colonize open environments like agricultural fields and pastures, which were present in greater proportions at the variegated and fragmented scenarios.

Bird conservation in the mountains of Mexico and Central America is considered a challenge because of the high rates of forest loss and land use change (Ramirez-Albores et al. 2020; Hernández-Dávila et al. 2021). However, contrary to the trends observed in other places of the region, deforestation in the mountains of Oaxaca has been less severe, and large parts remain with large forest areas, which are under management schemes with varying intensity (Van Vleet et al. 2016). Currently, it is acknowledged that a combination of community governance (Bray et al. 2012), population dynamics (i. e. migration, age structure; Robson et al. 2017) and cosmogony have allowed the accomplishment of management schemes that have promoted the persistence of high levels of biodiversity (Navarro-Sigüenza et al. 2014; Pazos-Almada and Bray 2018).

It is worthy to note that despite Oaxaca has around 6% of its entire terrestrial area under formal protection (included in eight official Natural Protected Areas), it is one of the three Mexican states with the highest species richness and the first in bird richness (Navarro-Sigüenza et al. 2014). Based only on data analysis and modelling, some authors have urged the creation of more Natural Protected Areas at Oaxaca (Rojas-Soto et al. 2012; Ramírez-Albores et al. 2019). If the establishment of new NPA's took place, they maybe could generate unnecessary conflicts and tensions between the government and the communities that inhabit these high biodiversity spots. What is necessary is to know and understand the different historical, social, and physical factors that have interacted to make possible the prevalence of high levels of biodiversity (Van Vleet et al. 2016).

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Figures

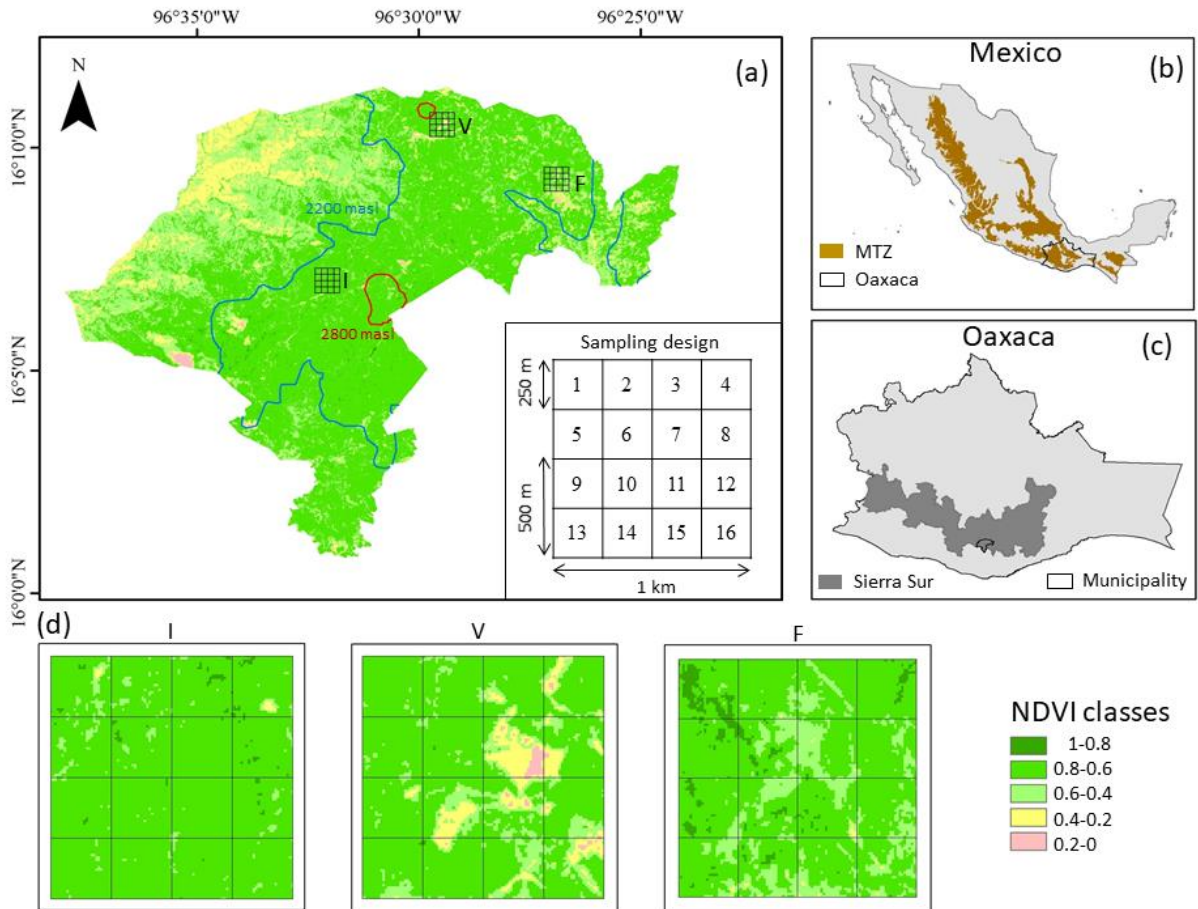


Fig. 1a-d. Study site in the Sierra Sur physiographic province (Ortiz-Perez et al. 2004), San Mateo Rio Hondo municipality, in the state of Oaxaca. Mexican Transition Zone according to Morrone (2017). The multiscale sampling design is shown consisting of the three landscape scenarios, each one a quadrat with 1km side length), divided into four frames (500 m) and 16 cells (250m).

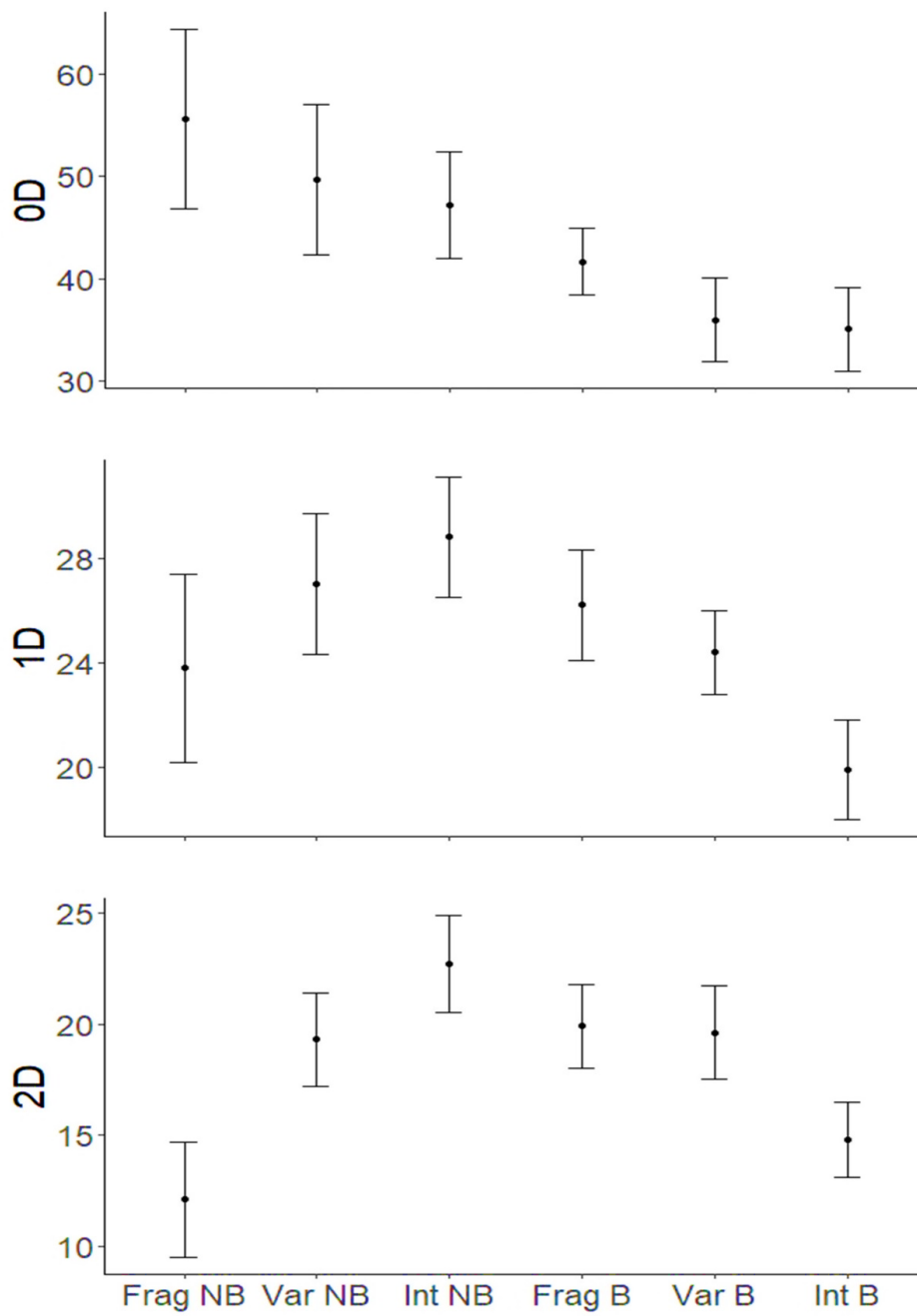


Fig. 2. Alpha diversity (from 0D to 2D) comparisons between landscape scenarios and seasons. Mean values and confidence intervals are depicted. Comparisons were made at sample coverage = 0.998. Diversity is expressed as number of effective species. Int-Intact; Var-Variegated; Frag-Fragmented. NBr-Non-Breeding Season, Br-Breeding season.

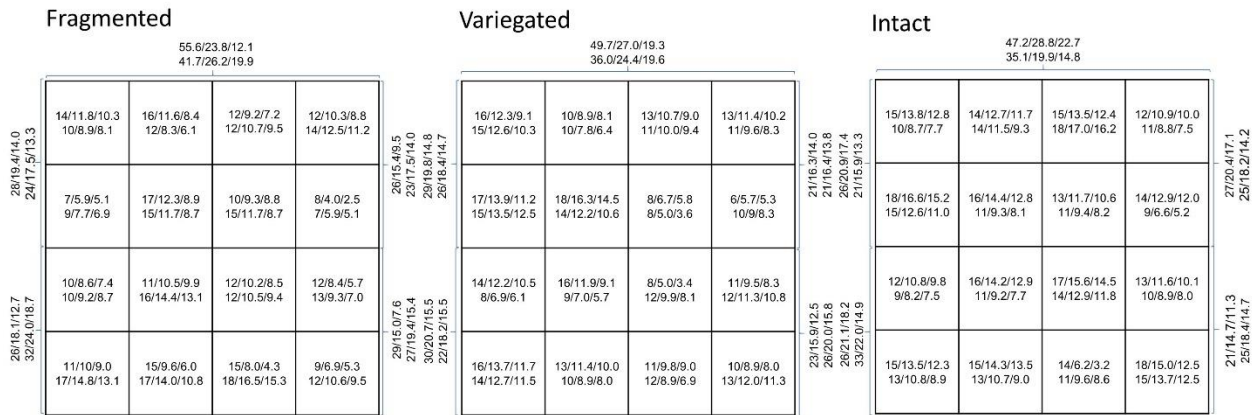


Fig. 3. Observed alpha diversity values at each scale. From each pair of lines, Non-breeding season values are at the upper line while breeding season values are depicted below. All values are number of effective species. Diversity values are depicted as ${}^0D/{}^1D/{}^2D$

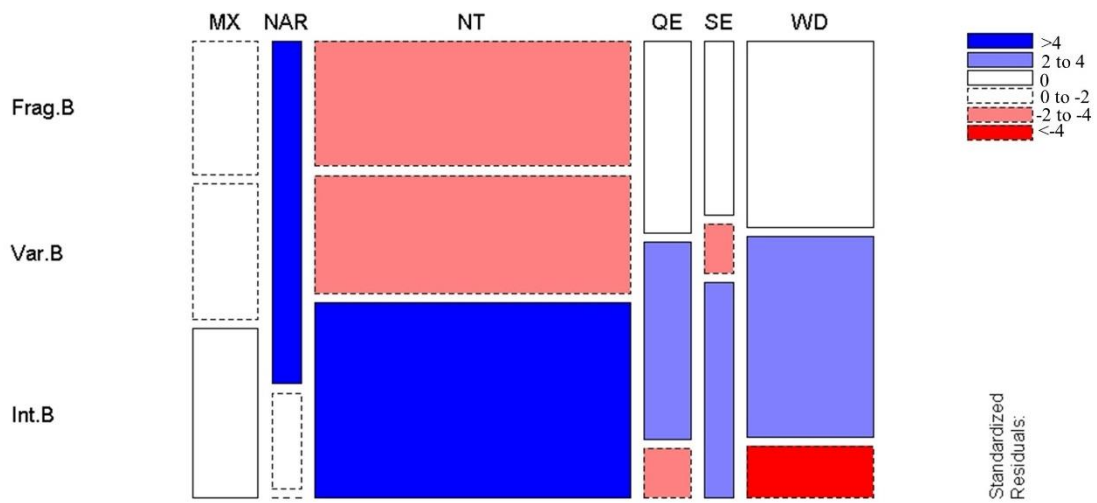
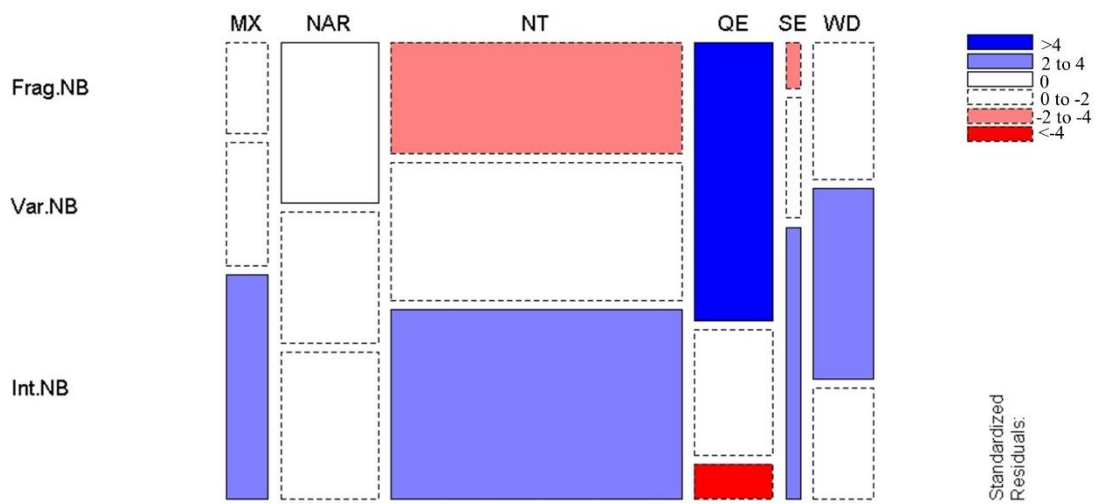


Fig. 4. Affinities between zoogeographical categories and landscape scenarios at two different seasons. Chi-square test was done using number of individuals per zoogeographic category. Upper: Non-breeding season; lower: Breeding season. MX: Endemic; NAR: Nearctic; NT:

Neotropical; QE: Quasiendemic; SE: Semiendemic; WD: Widespread. Frag-Fragmented; Var-Variegated; Int-Intact.

Tables

Table 1. Complete species checklist with codes. Guilds: G-Granivore; BI-Bark Insectivore; F-Frugivore; FI-Foliage Insectivore; N-Nectarivore; O-Omnivore; GI-Ground Insectivore; AI-Aerial Insectivore

Scientific Name	Common Name	Species code/Guild code	Seasonal Status
Columbidae			
<i>Leptotila verreauxi</i>	White-tipped Dove	LEVE/G	All-year Resident
<i>Patagioenas fasciata</i>	Band-tailed Pigeon	PAFA/G	All-year Resident
Picidae			
<i>Leuconotopicus villosus</i>	Hairy Woodpecker	LEVI/BI	All-Year Resident
<i>Melanerpes formicivorus</i>	Acorn Woodpecker	MEFO/BI	All-Year Resident
Ramphastidae			
<i>Aulacorhynchus prasinus</i>	Emerald Toucanet	AUWA/F	All-year Resident
Trogonidae			
<i>Trogon mexicanus</i>	Mountain Trogon	TRME/FI	All-Year Resident
Trochilidae			
<i>Atthis heloisa</i>	Bumblebee Hummingbird	ATHE/N	Altitudinal Migrant
<i>Colibri thalassinus</i>	Violet-eared Hummingbird	COTH/N	Altitudinal Migrant
<i>Eugenes fulgens</i>	Rivoli's Hummingbird	EUFU/N	All-year Resident
<i>Basilina leucotis</i>	White-eared Hummingbird	HYLE/N	All-year Resident
<i>Lampornis clemenciae</i>	Blue-throated Hummingbird	LACL/N	All-year Resident
<i>Lamprolaima rhami</i>	Garnet-throated Hummingbird	LARH/N	All-year Resident
<i>Selasphorus platycercus</i>	Broad-tailed Hummingbird	SEPL/N	Nearctic-Neotropical Migrant
Furnariidae			
<i>Lepidocolaptes affinis</i>	Spotted-crowned Woodcreeper	LEAF/BI	All-year Resident
<i>Lepidocolaptes leucogaster</i>	White-striped Woodcreeper	LELE/BI	All-year Resident
Tyrannidae			
<i>Contopus cooperi</i>	Olive-sided Flycatcher	COCO/AI	Nearctic-Neotropical Migrant
<i>Contopus pertinax</i>	Greater Pewee	COPE/AI	All-year Resident
<i>Empidonax affinis</i>	Pine Flycatcher	EMAF/AI	All-year Resident
<i>Empidonax albigularis</i>	White-throated Flycatcher	EMAL/AI	All-year Resident
<i>Empidonax occidentalis</i>	Cordilleran Flycatcher	EMOC/AI	All-year Resident
<i>Empidonax sp.</i>		EMPID/AI	
<i>Mitrephanes phaeocercus</i>	Tufted Flycatcher	MIPH/AI	All-year Resident
<i>Myiarchus tuberculifer</i>	Dusky-capped Flycatcher	MYTU/AI	All-year Resident
Corvidae			
<i>Aphelocoma woodhouseii</i>	Woodhouse's Scrub Jay	APWO/O	All-year Resident
<i>Cyanocitta stelleri</i>	Steller's Jay	CYST/O	All-year Resident

<i>Cyanolyca mirabilis</i>	White-throated Jay	CYMI/O	All-year Resident
Certhidae			
<i>Certhia americana</i>	Brown Creeper	CEAM/BI	All-year Resident
Vireonidae			
<i>Vireo brevipennis</i>	Slaty Vireo	VIBR/FI	All-year Resident
<i>Vireo gilvus</i>	Warbling Vireo	VIGI/FI	All-year Resident
<i>Vireo huttoni</i>	Hutton's Vireo	VIHU/FI	All-year Resident
<i>Vireolanius melitophrys</i>	Chesnut-sided Shrike-vireo	VIME/FI	All-year Resident
Troglodytidae			
<i>Henichorina leucophrys</i>	Grey-breasted Wood Wren	HELE/GI	All-year Resident
<i>Troglodytes aedon</i>	House Wren	TRAE/GI	All-year Resident
Turdidae			
<i>Catharus aurantiirostris</i>	Orange-billed Nightingale-thrush	CAAU/O	All-year Resident
<i>Catharus frantzii</i>	Ruddy-capped Nightingale-thrush	CAFR/GI	All-year Resident
<i>Catharus occidentalis</i>	Russet Nightingale-thrush	CAOC/GI	All-year Resident
<i>Myadestes occidentalis</i>	Brown-backed Solitaire	MYOC/F	All-year Resident
<i>Turdus infuscatus</i>	Black Thrush	TUIN/O	All-year Resident
<i>Turdus migratorius</i>	American Robin	TUMI/O	All-year Resident
Mimidae			
<i>Melanotis caerulescens</i>	Blue Mockingbird	MECA/GI	All-year Resident
Aegithalidae			
<i>Psaltriparus minimus</i>	Bushtit	PSMI/FI	All-year Resident
Bombycillidae			
<i>Bombycilla cedrorum</i>	Cedar Waxwing	BOCE/F	Nearctic-Neotropical Migrant
Ptilogonatidae			
<i>Ptiliogonis cinereus</i>	Grey-silky Flycatcher	PTCI/O	All-year Resident
Regulidae			
<i>Regulus calendula</i>	Buby-crowned Kinglet	RECA/FI	Nearctic-Neotropical Migrant
Paridae			
<i>Poecile sclateri</i>	Mexican Chickadee	POSC/FI	All-year Resident
Peucedramidae			
<i>Peucedramus taeniatus</i>	Olive Warbler	PETA/FI	All-year Resident
Parulidae			
<i>Basileuterus belli</i>	Golden-browed Warbler	BABE/FI	All-year Resident
<i>Cardellina pusilla</i>	Wilson's Warbler	CAPU/FI	Nearctic-Neotropical Migrant
<i>Cardellina rubra</i>	Red Warbler	CARU/FI	All-year Resident
<i>Geothlypis nelsoni</i>	Hooded Yellowthroat	GENE/FI	All-year Resident
<i>Mniotilta varia</i>	Black and White Warbler	MNVA/FI	Nearctic-Neotropical Migrant
<i>Myioborus miniatus</i>	Slate-throated Whitestart	MYMI/FI	All-year Resident
<i>Myioborus pictus</i>	Painted Whitestart	MYPI/FI	All-year Resident
<i>Oreothlypis celata</i>	Orange-crowned Warbler	ORCE/FI	Nearctic-Neotropical Migrant
<i>Oreothlypis superciliosa</i>	Crescent-chested Warbler	ORSU/FI	All-year Resident
<i>Setophaga coronata</i>	Yellow-rumped Warbler	SECO/FI	Nearctic-Neotropical Migrant

<i>Setophaga occidentalis</i>	Hermit Warbler	SEOC/FI	Nearctic-Neotropical Migrant
<i>Setophaga townsendi</i>	Townsend's Warbler	SETO/FI	Nearctic-Neotropical Migrant
Passerelidae			
<i>Arremon brunneinucha</i>	Chesnut-capped Brushfinch	ARBR/GI	All-year Resident
<i>Atlapetes pileatus</i>	Rufous-capped Brushfinch	ATPI/GI	All-year Resident
<i>Chlorospingus flavopectus</i>	Common Bush-tanager	CHFL/F	All-year Resident
<i>Junco phaeonotus</i>	Yellow-eyed Junco	JUPH/GI	All-year Resident
<i>Melospiza albicollis</i>	White-throated Towhee	MEAL/GI	All-year Resident
<i>Pipilo maculatus</i>	Spotted Towhee	PIMA/GI	All-year Resident
<i>Pipilo ocai</i>	Collared Towhee	PIOC/GI	All-year Resident
Cardinalidae			
<i>Pheucticus melanocephalus</i>	Black-headed Grosbeak	PHME/O	All-year Resident
<i>Piranga erythrocephala</i>	Red-headed Tanager	PIER/O	All-year Resident
<i>Piranga hepatica</i>	Hepatic Tanager	PIHE/O	All-year Resident
<i>Piranga ludoviciana</i>	Western Tanager	PILU/FI	Nearctic-Neotropical Migrant
Thraupidae			
<i>Diglossa baritula</i>	Cinammon-bellied Flowerpiercer	DIBA/N	All-year Resident
Icteridae			
<i>Icterus bullockii</i>	Bullock's Oriole	ICBU/FI	Nearctic-Neotropical Migrant
<i>Icterus graduacauda</i>	Audubon's Oriole	ICGR/FI	All-year Resident
<i>Icterus parisorum</i>	Scott's Oriole	ICPA/FI	Nearctic-Neotropical Migrant
<i>Icterus wagleri</i>	Black-vented Oriole	ICWA/FI	All-year Resident
Fringillidae			
<i>Haemorhous mexicanus</i>	House Finch	HAME/G	All-year Resident
<i>Spinus notatus</i>	Black-headed Siskin	SPNO/G	All-year Resident

Table 2. Summary of sampling measures of bird communities at each landscape scenario in two different seasons. Sample completeness was assessed as 1) Sampling efficiency, the ratio (expressed as a percentage) between the observed and estimated number of species according to Chao 1 richness estimator, and; 2) Sample coverage, the probability that a newly sampled individual belongs to any species already represented at the sample. S_{Obs} -Observed number of species, Cov-Sample coverage, E-Sampling efficiency, B: Breeding Season; NB: Non-breeding Season, $IF_{0,q}$: Inequality Factor

	Individuals	S_{Obs}	Chao 1	E (%)	Cov (%)	Singletons	Doubletons	$IF_{0,1}$	$IF_{0,2}$
Fragmented NB	370	48	57.4	83.6	96	12	5	2.13	4.04

Variegated NB	365	45	51.4	87.5	97	10	6	1.73	2.38
Intact NB	412	44	49.1	89.5	98	9	6	1.57	1.97
Fragmented B	409	42	42.8	98.2	99	4	7	1.60	2.11
Variegated B	364	35	38.3	91.3	99	5	2	1.45	1.80
Intact_B	374	34	37	91.9	98	6	4	1.72	2.32

Table 3. Matrix of permuted p-values (pairwise comparisons) from the Permutational Analysis of Variance. Permuted p-values of Jaccard comparisons are displayed above the main diagonal while those from Morisita comparisons can be read below the main diagonal. *Significant differences

	FRAG_NB	VAR_NB	INT_NB	FRAG_B	VAR_B	INT_B
FRAG_NB		0.55	0.03*	0.42	0.87	0.00*
VAR_NB	0.44		0.12	0.98	0.67	0.02*
INT_NB	0.06	0.33		0.09	0.04*	0.37
FRAG_B	0.72	0.63	0.11		0.6	0.01*
VAR_B	0.70	0.27	0.03*	0.83		0.00*
INT_B	0.01*	0.16	0.83	0.02*	0.01*	

Supplementary material

Figures

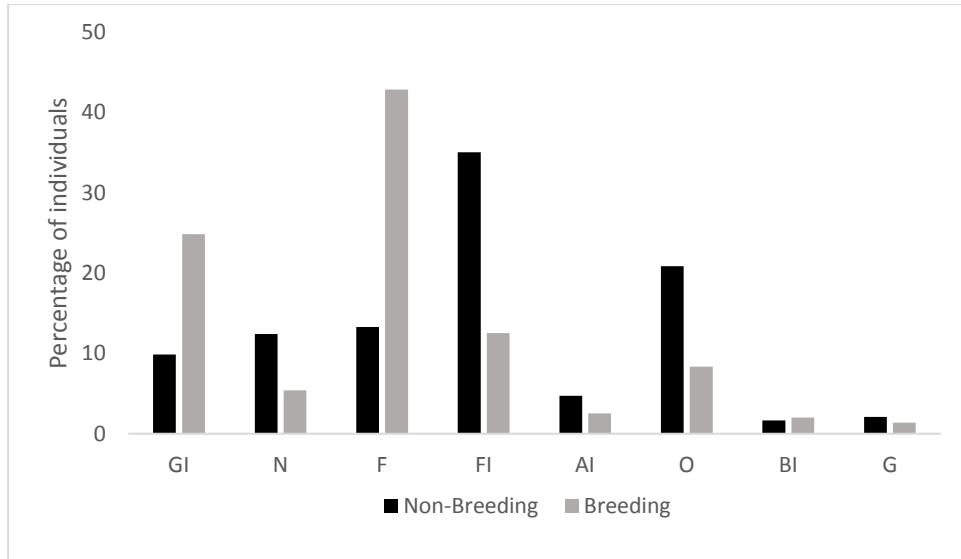


Fig. S1. Percentage of individuals belonging to each considered foraging guild at the two considered seasons. GI-Ground Insectivores; N-Nectarivores; F-Frugivores; FI-Foliage Insectivores; AI-Aerial Insectivores; O-Omnivores; BI-Bark Insectivores; G-Granivores

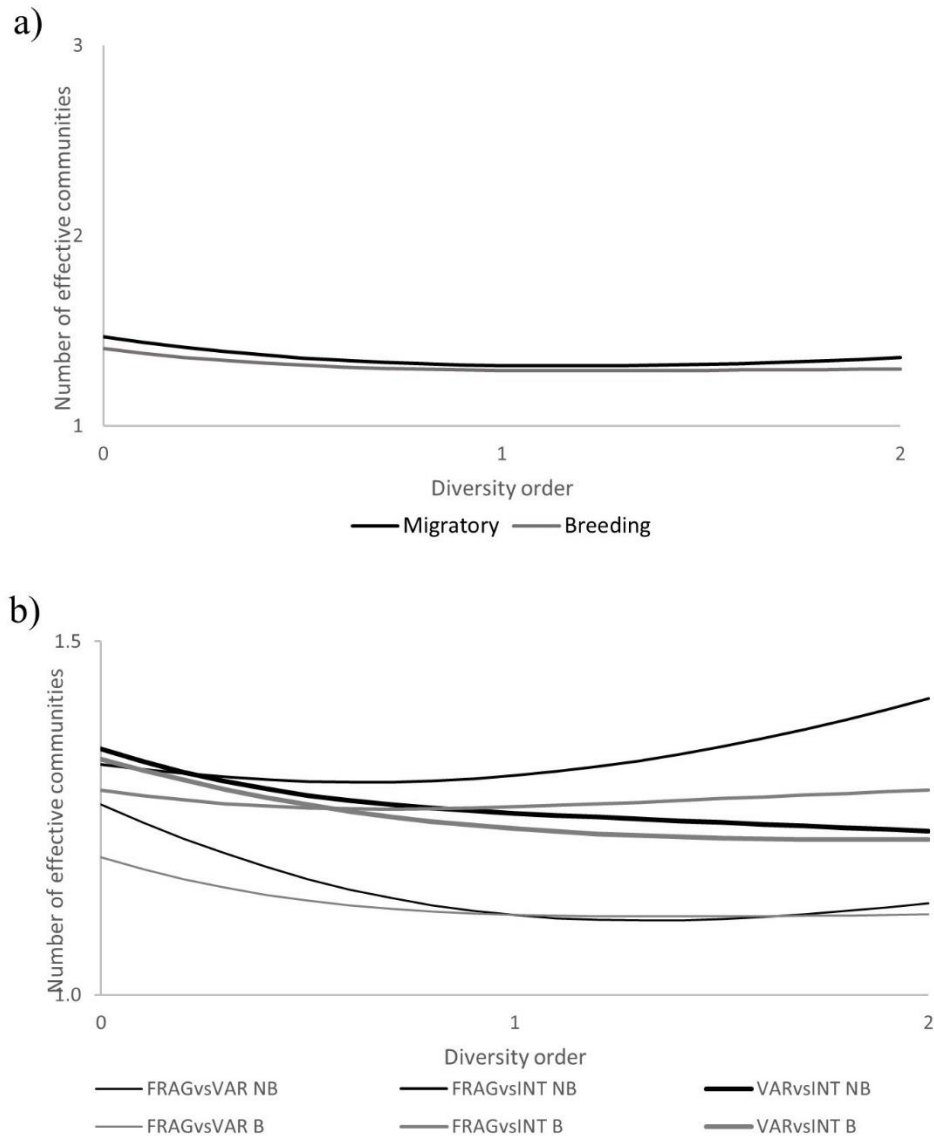


Fig. S2. Beta diversity profiles at different scales. a) comparing the landscape at both seasons; b) comparing the different landscapes scenarios at each season. FRAG-Fragmented, VAR-Variegated; INT-Intact, NB-Migratory season, B-Breeding season.

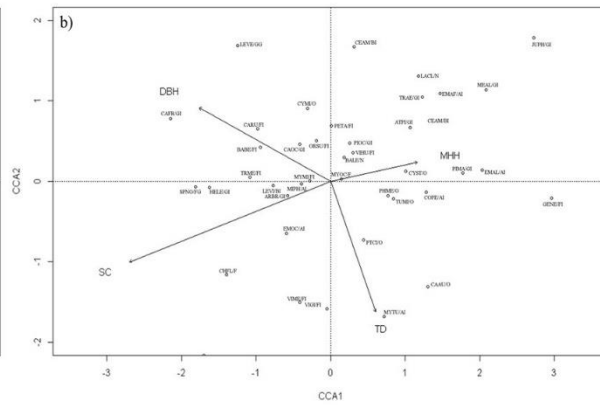
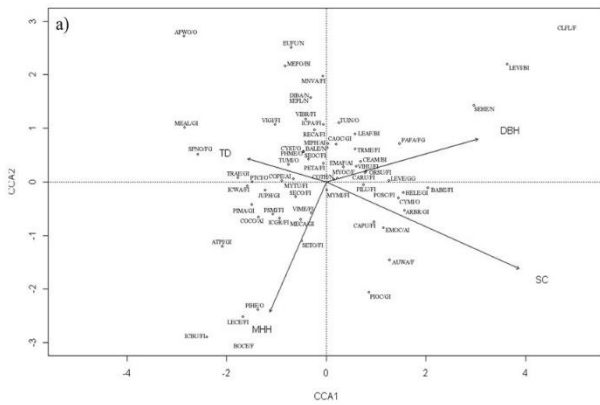
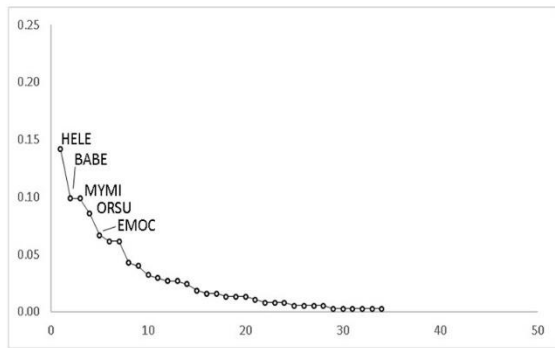
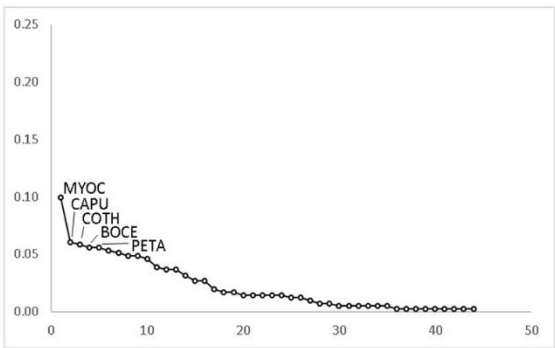
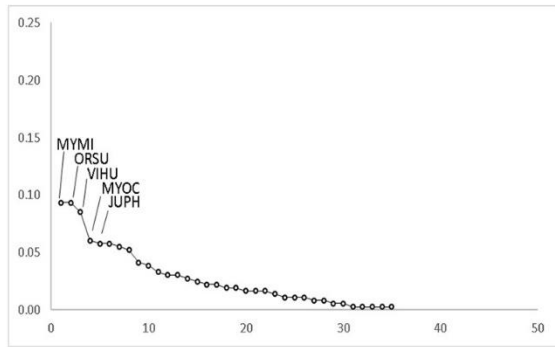
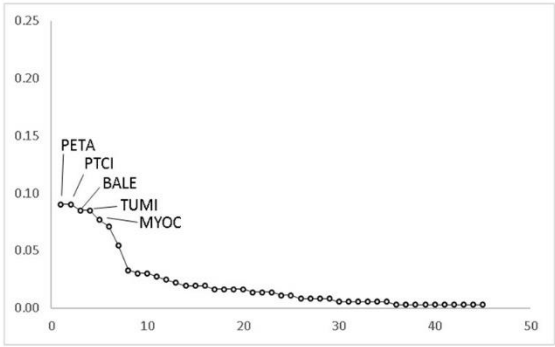
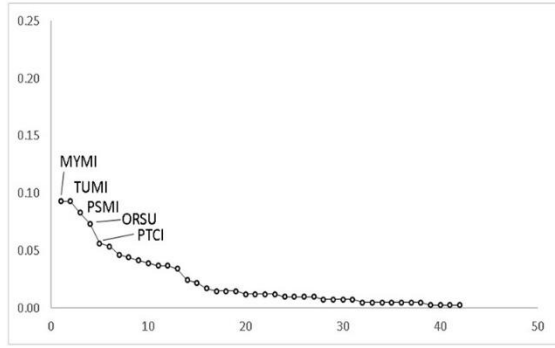
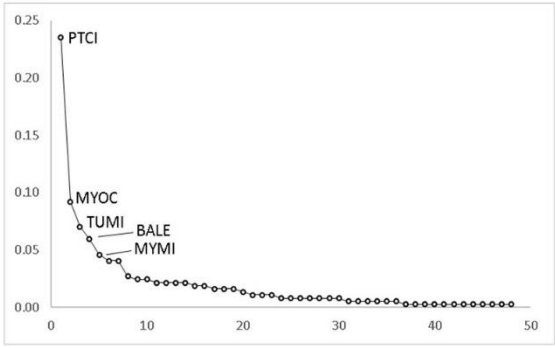


Fig. S3. A) Rank abundance plot of bird communities at each landscape scenario. 1) Fragmented Non-Breeding; 2) Variegated Non-Breeding; 3) Intact Non-Breeding; 4) Fragmented Breeding; 5) Variegated Breeding; 6) Intact Breeding; B) Canonical correspondence analysis biplot of bird species. Each species is depicted with the first two letters of the genus and the first two letters of the specific epithet, followed by an abbreviation of their nesting substrate and an abbreviation of the feeding guild after diagonal bar. Codes are depicted in Table 1. a) Migratory; b) Breeding. Vegetation variables codes are depicted at the tip of each vector. DBH: Diameter at Breast Height; TD: Tree Density; SC: Shrub Cover; MHH: Maximum Herb Height

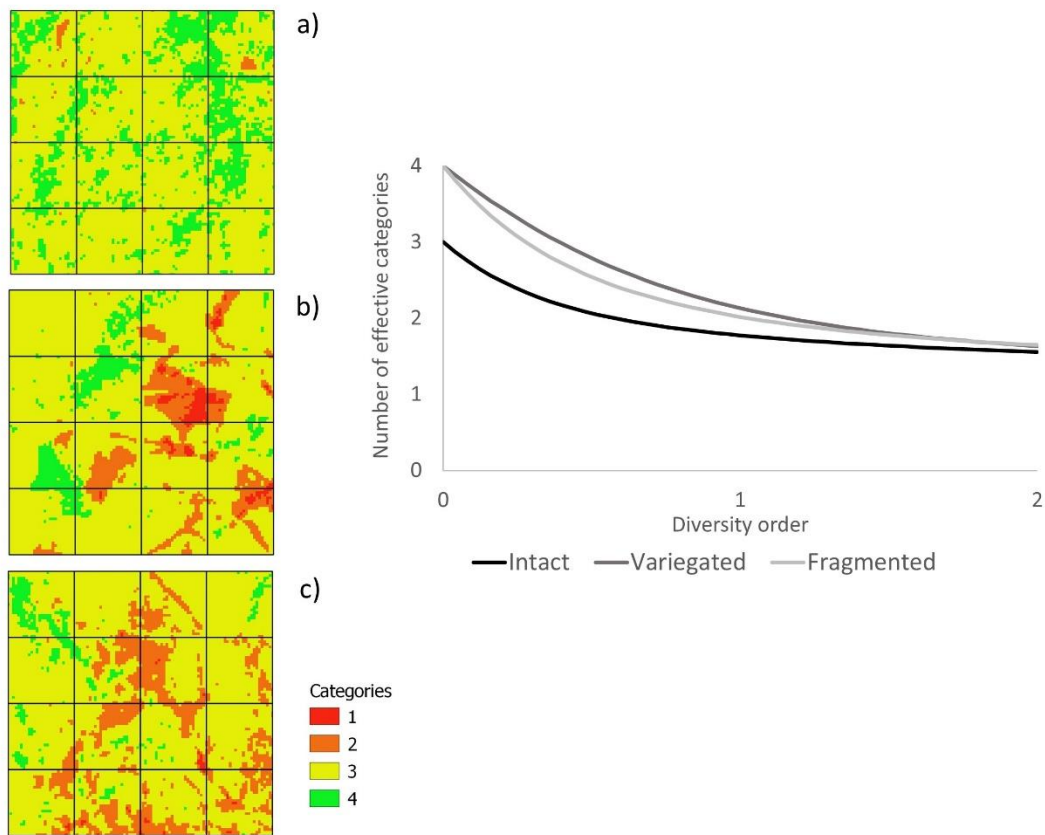


Fig. S4. Land categorization of the studied sampling windows. Left: Categories were defined according to NDVI values of each pixel as follows: Category 1: 0-0.25; Category 2: 0.25-0.5; Category 3: 0.5-0.75; Category 4: 0.75-1. a) Intact scenario; b) Variegated scenario; c) Fragmented scenario. Right: NDVI diversity profiles from $q=0$ to $q=2$.

Tables

Table S1. Summary of sampling measures of bird communities at each landscape in two different seasons. Sample completeness was assessed as 1) Sampling efficiency, the ratio (expressed as a

percentage) between the observed and estimated number of species according to Chao 1 richness estimator, and 2) Sample coverage, the probability that a newly sampled individual belongs to any species already represented at the sample. S_{obs} -Observed number of species, Cov-Sample coverage, E-Sampling efficiency, B: Breeding Season; NB: Non-breeding Season, $IF_{0,q}$: Inequality Factor

	Individuals	S_{obs}	Chao 1	E (%)	Cov	Singletons	Doubletons	$IF_{(0,1)}$	$IF_{(0,2)}$
NB	1147	67	76.4	87.7	0.9895	12	6	1.99	1.73
B	1147	52	55.8	93.3	0.9948	6	3	2.94	2.26

Table S2. Mean, lower and upper values of true diversity at the landscape level. NB-Non-breeding season; B-Breeding season

	Mean	Lower	Upper
0D NB	74.6	65.5	83.6
0D B	53.1	48.5	57.8
1D NB	34.5	32.3	36.7
1D B	30.2	28.6	31.8
2D NB	23.0	21.1	24.9
2D B	23.0	21.5	24.6

Table S3. Wilcoxon test summary of paired comparisons of estimated richness (according to Chao 1 richness estimator) between seasons at frame and cell scales. N-Number of paired samples

FRAMES	CELLS
N	12 N 48
Non-Breeding	34.4 Non-Breeding 19.2
Breeding	26.6 Breeding 14.5
WILCOXON TEST	
W	73 W 921
p	0.008 p 3.2E-05

Table S4. Spearman correlation coefficients between percentage of forest cover and diversities of order 0, 1 and 2 at the frame and cell scales. *Significant correlations

	% Forest Cover	
	Frames	Cells
⁰ D NB	0.27	0.46*
¹ D NB	0.90*	0.62*
² D NB	0.91*	0.65*
⁰ D B	-0.39	0.02
¹ D B	-0.41	0.07
² D B	-0.43	0.08

Table S5. Paired comparisons (t test) between the similarity values at two contrasting seasons at two different scales. NB-Non Breeding; B-Breeding

FRAMES		CELLS	
N		N	
Jaccard NB	0.42	Jaccard NB	0.26
Jaccard B	0.48	Jaccard B	0.29
Morisita NB	0.56	Morisita NB	0.37
Morisita B	0.59	Morisita B	0.37
T TEST			
Jaccard			
t value	-6.04	t value	-8.26
p value	<0.001	p value	<0.001
Morisita			
t value	-2.01	t value	-0.62
p value	<0.01	p value	0.37

Chapter 3

Breeding in the cold? A White-eared Hummingbird (*Basilinna leucotis*) winter nest record from the mountains of Oaxaca, Mexico

The Wilson Journal of Ornithology 132(3):755–761, 2020

Breeding in the cold? A White-eared Hummingbird (*Basilinna leucotis*) winter nest record from the mountains of Southern Oaxaca, Mexico

Omar Suárez-García,^{1*} Erwin López-Osorio,¹ and Matthias Rös²

ABSTRACT—We report the finding of a White-eared Hummingbird (*Basilinna leucotis*) nest during the winter. The observation took place on 9 February 2019 in San José del Pacífico, Oaxaca, Mexico, in the Sierra Madre del Sur. The hummingbird nest was located in the understory, 115 cm above the ground. The nest was placed within a plot of a pine-oak forest at 2,857 m a.s.l. and had 2 nestlings with complete juvenile plumage. Floral phenology is known to be a key factor that determines the biological cycles of hummingbirds, which rely heavily on nectar resources to fulfill their nutritional needs in the breeding season. Around the nest, we observed *Salvia pusillae* Epling, a plant that blossoms during the winter months in the Mexican mountains and is visited by White-eared Hummingbirds. Previous winter nest records in Southern Oaxaca date from more than 50 years ago. We briefly discuss the implications of winter reproduction for the species and the potential commonness of this event. Received 9 February 2020. Accepted 4 November 2020.

Key words: breeding season, Endemic Bird Area, Mexican Transition Zone, nestling, pine forest, *Salvia pusillae* Epling, Sierra Madre del Sur.

¿Criando en el frío? Un registro de anidación invernal de Zafiro Oreja Blanca (*Basilinna leucotis*) en las montañas de Oaxaca, México

RESUMEN (Spanish)—Reportamos el hallazgo de un nido invernal de Zafiro Orejas Blancas (*Basilinna leucotis*). La observación del nido tuvo lugar el 9 de febrero del 2019 en San José del Pacífico, Oaxaca, México, en la Sierra Madre del Sur. El nido estaba entre unos arbustos a 115 cm del suelo, en una parcela de bosque de pino-encino a 2,857 metros, y tenía en su interior dos polluelos con el plumaje juvenil completo. Se sabe que la fenología floral es un factor clave que determina los ciclos biológicos de los colibríes, los cuales dependen en gran medida del néctar para cumplir con sus requerimientos nutricionales en la temporada reproductiva. Alrededor del nido observamos a *Salvia pusillae* Epling, una planta que florece durante los meses invernales en las montañas mexicanas y que es visitada por el Zafiro Orejas Blancas. Los registros previos de anidación invernal en el sur de Oaxaca datan de hace más de 50 años. Discutimos brevemente las implicaciones de

la reproducción invernal de esta especie y la posible regularidad de este evento.

Palabras clave: Temporada reproductiva, Área de Aves Endémicas, Zona de Transición Mexicana, polluelo, bosque de pino, *Salvia pusillae* Epling, Sierra Madre del Sur.

Reproduction is a critical event at the organismal level that defines population dynamics (Stiling 2012). For birds, breeding implies a high investment of energy and nutrients to accomplish activities such as mating displays, nest construction, territorial defense, and parental care (Hainsworth 1977). Therefore, according to the food availability hypothesis (Lack 1950), breeding can only be carried out when food resources are abundant.

In temperate regions, bird reproduction generally takes place between spring and summer, mainly due to the high primary productivity rates in such seasons (Lack 1950). In contrast, birds from the tropics have a suite of breeding strategies, including reproduction that starts in both dry and wet seasons and breeding seasons that can last 6–8 months (Stutchbury and Morton 2001). Since photoperiods remain relatively constant across the year in the tropics, it seems that other variables—such as water availability—are factors that trigger food abundance, which in turn potentially increase nesting success (Stiles 1992).

Although Oaxacan pine-oak forests lie within tropical latitudes, they can be considered as a temperate vegetation type, due to their plant composition and biogeographic history, mainly dominated by Holarctic tree species (e.g., *Pinus* spp., *Quercus* spp., and *Abies* spp.; Velazquez et al. 2000). However, such highland forests also have well-developed shrubby and herbaceous strata dominated by tropical species (Cortés-Flores et al. 2013) whose phenology influences biological cycles of understory animal species (Santos-Moreno et al. 2019). In addition, the minimum

¹ Programa de Posgrado-CIDER Oaxaca, Instituto Politécnico Nacional, Santa Cruz Xoxocotlán, Oaxaca, Mexico

² CONACYT, CIDER Oaxaca, Instituto Politécnico Nacional, Santa Cruz Xoxocotlán, Oaxaca, Mexico

* Corresponding author: osuarezg1500@alumno.ipn.mx

temperatures during winter in those vegetation types can reach values as low as the freezing point, preventing most of the birds from breeding during this season because of the high mortality risks due to cold conditions (Skutch 1985).

The White-eared Hummingbird (*Basilinna leucotis*) is endemic to the highlands of Mexico and northern Central America. It inhabits mountainous ecosystems between 1,200 and 3,500 m a.s.l. in both the Atlantic and Pacific slopes, from northwestern and eastern Mexico south to the highlands of southern Mexico, Guatemala, Honduras, and Nicaragua (Howell and Webb 1995, Arizmendi and Berlanga 2014). Its northern populations (north and central Mexico) have been reported to breed exclusively in the boreal spring and summer months (Mar–Aug), with a few reports of southern Mexico populations breeding in May–August and occasionally between November and February, and in Guatemala and El Salvador between October and December (Arizmendi et al. 2015). In Oaxaca, Rowley (1966, 1984) reported 3 instances of winter nest activity between December 1964 and February 1965 with no further published records of nesting in this season.

The objective of this short communication is to describe and document a White-eared Hummingbird nest and 2 nestlings that we found during the winter of 2019 in the southern mountains of Oaxaca, Mexico. We also discuss the implications of winter reproduction for this species.

Methods

The study site was located in the municipality of San Mateo Río Hondo, in the state of Oaxaca, Mexico (Fig. 1). We used climate data recorded from 1979 to 2014 by a meteorological station (property of CONAGUA-SMN) in San José del Pacífico, at an altitude of 2,500 m, to describe temperature and precipitation at the study site. The mean annual temperature was 14 °C (SD = 0.4 °C), mean minimum temperature 7.6 °C (SD = 0.3 °C), mean minimum extreme temperature 5.4 °C (SD = 0.4 °C), with extreme minima of 3 °C and 2 °C in December and January, respectively (CONAGUA-SMN 2020; Fig. 2). Mean annual precipitation was 1,500 mm (Fick and Hijmans 2017) with a dry season between November and April. Scattered

rains during the winter months are caused by the influence of cold fronts (<10% of the total annual precipitation; Fig. 2).

For the purpose of this report, we refer to the period between December and February as winter, although temperature differences between months in our region are of only a few degrees Celsius (Fig. 2). The main vegetation type is pine forest (Fig. 1). Our study site is situated within the Endemic Bird Area Sierra Madre del Sur (Birdlife International 2020), which lies within the boundaries of the Mexican Transition Zone, a large area of Mexico and Central America where Nearctic and Neotropical biotas overlap (Halffter and Morrone 2017).

While carrying out bird surveys for a project describing bird diversity, we found a White-eared Hummingbird nest with 2 live nestlings. We recorded the following data: (1) number of nestlings, (2) nest characteristics, (3) altitude, and (4) vegetation type. We further visited the nesting site in order to assess the status of the nestlings and collect additional observations.

Results

On the morning of 8 February 2019, while surveying birds in a pine-oak forest plot at an elevation of 2,857 m, we found one nest of White-eared Hummingbird in the understory, 115 cm above the ground. The nest was occupied by 2 nestlings; both asleep with only their upperparts visible (Fig. 3A). We noted that one of them had a whitish postocular stripe. Soon after we discovered the nest, we heard the typical alarm calls of this hummingbird and spotted 2 adults: one male and a second individual that could not be visually sexed. Both hummingbirds made aerial displays and perched about 3 m away from the nest. We took pictures of the nest and georeferenced the location.

On 9 February, we observed the nestlings inside the nest (Fig. 3B). The nest was a cuplike structure made of vegetal tissue (mainly pine needles and moss covered with lichens) and spiderwebs (Fig. 3C). We determined that both nestlings were males by the red coloration in the basal section of their bill and the presence of iridescent blue frontlet (Guayar and Galles 2017). We noticed the ground surrounding the nest covered with *Salvia patriciana*

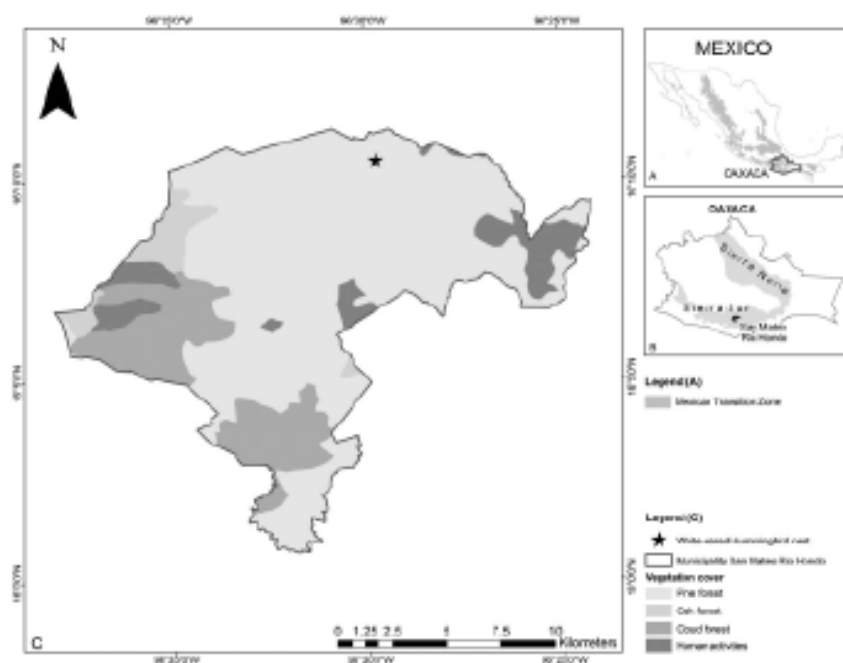


Figure 1. Location of a White-eared Hummingbird winter nest in the municipality of San Mateo Rio Hondo, Oaxaca. Mexican Transition Zone (A) provided by Morrone et al. (2017). Sierra Norte and Sierra Sur physiographic subprovinces (B) according to Ortiz-Pérez et al. (2004). Vegetation cover categories (C) are according to INEGI (2015). Human activities include agriculture, cattle ranching, and forestry.

Epling, an herb endemic to Guerrero and Oaxaca, Mexico (Fig. 3D).

Finally, on 14 February, we visited the nest and found it empty. We saw one individual (probably one of the fledglings, as we observed it in the dusky plumage typical of juveniles) perched atop a 2 m pine branch for a while, and then it flew away. In a subsequent visit to the site (February 2020) we observed an adult White-eared Hummingbird defending and feeding on a *Salvia patricans* patch.

Discussion

In his pioneer work, Rowley (1966) documented for the first time the winter nesting activity of White-eared Hummingbird in southern Oaxaca. He reported the finding of one nest near Río Jalatenango (Sierra Sur), a place 20 km south from

San José del Pacífico, in February 1965. The nest was abandoned and had 2 eggs in its interior, and was placed over a bush in a creek, where he also found several empty nests of the same species.

Two months before, in December 1964, he found 2 nests with eggs at the Cerro San Felipe (Sierra Norte; Rowley 1984). To our knowledge, these are the only 2 known records of winter nesting White-eared Hummingbirds, with no further published reports in the state, although it is acknowledged that this species may breed in 2 different seasons of the year in southern Mexico (Arizmendi et al. 2015). Skutch (1945) reported that White-eared Hummingbirds have a 23–26 d nestling period. According to our estimations, the eggs of the single nest we report may have been laid within the first 2 weeks of January.

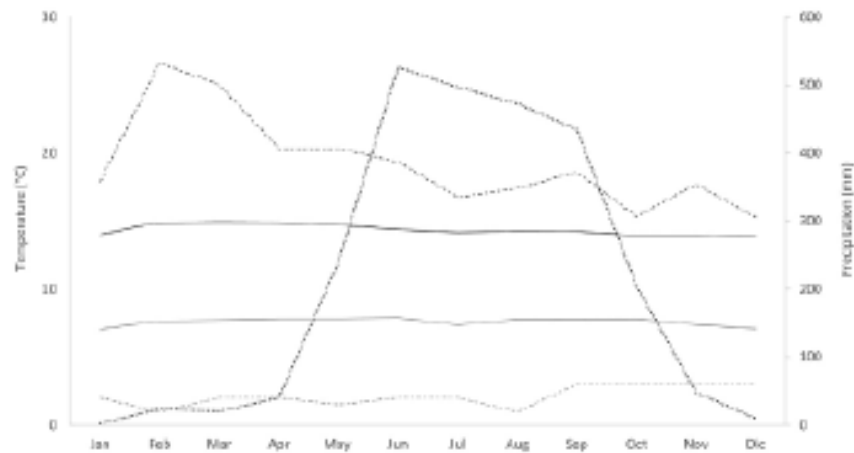


Figure 2. Monthly mean temperatures and precipitation at the study site. Solid black line: mean daily temperature; solid gray line: minimum mean daily temperature. Dashed lines indicate mean maxima (black) and extreme minima (gray) recorded, respectively. Dotted black line: mean precipitation. Data from CONAGUA-SMN (2020).

Surprisingly, when we inspected temperature data at our study site, we found that there were no important differences between the mean and minimum values recorded during winter months (Dec–Feb). Minimum temperatures can reach values below 5 °C throughout the year and this means that White-eared Hummingbirds (and other bird species) must deal with low temperatures at any time of the year. In the Sierra Norte of Oaxaca, where White-eared Hummingbird winter breeding activity also takes place, temperature regimes are colder than in our study site. For instance, mean winter temperatures in Cuajimuloyas (a place in Sierra Norte, located at 2,800 m) range between 8 and 9 °C, compared to mean temperatures between 13 and 14 °C at our study site (CONAGUA-SMN 2020). This means that White-eared Hummingbirds are capable of breeding under harsher conditions than those of the Sierra Sur, still above the physiological limits known for hummingbirds (Calder and Booser 1973, Carpenter 1974, Wolf et al. 2020).

Recently, Ortega-Álvarez et al. (2018) documented Bumblebee Hummingbird (*Selasphorus helotis*) breeding in winter at the Sierra Norte of Oaxaca. Although this hummingbird has a more restricted distribution, it shares most of its range with White-eared Hummingbird. Both occupy pine-oak and

pine forests in the mountains of both the Atlantic and Pacific slopes of Mexico (Howell and Webb 1995). Although different in their ecology, both rely on nectar as the main food source. The availability of this resource may determine breeding phenology in the southern mountains of Oaxaca, where it is possible to find the 2 species coexisting (Arizmendi and Berlanga 2014).

Hummingbird occurrence is thought to be mainly influenced by distribution and abundance of floral resources (Wagner 1946, Wolf et al. 1976, Partida et al. 2012). In temperate forests in the tropics, some herbaceous plants flower during the winter months, in response to sporadic winter rains (Cortés-Flores et al. 2013). *Salvia panicans*, for example, blooms from October to January (Gonzalez-Gallegos 2014). Its tubular and magenta corollas make it especially suitable for being visited by hummingbirds (Espino-Espino et al. 2014). It is well known that White-eared Hummingbirds establish territories where floral resources are abundant (Marquez-Luna et al. 2015) and confers them competitive advantages over trap-lining hummingbirds (Feinsinger 1976).

Researchers have suggested that winter reproduction is a strategy to avoid competition or have competitive advantages over similar species that breed later in the year (Pitelka 1951, Lyon 1976).

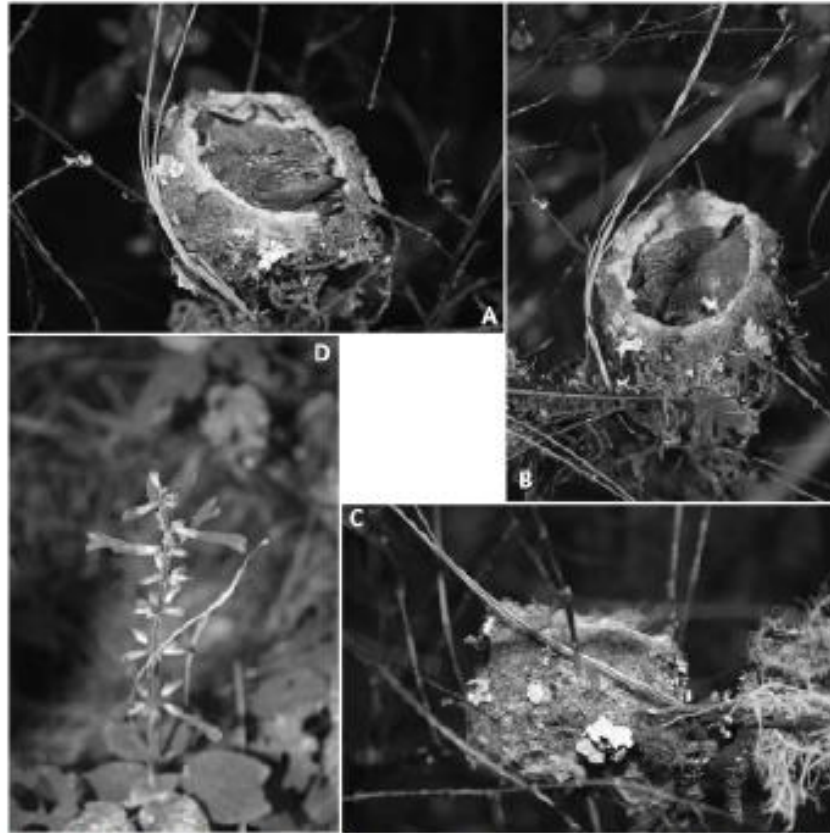


Figure 3. Photographic details of the White-eared Hummingbird winter nest observed in the municipality of San Marcos Río Honda, Oaxaca. (A) Upper view of the nest on day 1. (B) Frontal view of the nest on day 2. (C) Outer view of the nest. (D) Close-up of the inflorescences of *Salvia patriciana* Epling.

Additionally, it has been documented that during the reproductive season, hummingbird species rely on insect availability to feed the nestlings both in the Nearctic and the Neotropical regions (Montgomery and Redsell 1980, Jacomassa 2014) and on honeydew produced by oak-parasitic insects in highland forests (Greenberg et al. 1993, Lara et al. 2011).

The nest record reported here and those of Rowley (1966, 1984) and Binford (1989) make us speculate whether these White-eared Humming-

bird reproductive activities during the winter months are not isolated incidents but are part of the regular yearly cycle of the species. Rowley (1966) hypothesized White-eared Hummingbird breeding periods may be intimately related to the blooming of plants of the Family Lamiaceae (i.e., *Salvia* and *Peustemon* spp.), abundant in the understory of the highland forests of Oaxaca.

We found a remarkable gap in published nesting data on the birds of southern Oaxaca. Follow-up questions derived from our work are: (1) Why are

there not more species breeding in winter at our study site? and (2) What strategies allow hummingbirds to breed in winter at the highlands of Oaxaca?

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General Discussion

Throughout this work, I have demonstrated that it is possible to make landscape ecology without invoking the common places of concepts derived from the mainstream binary approach, such as fragmentation, matrix, and connectivity, among others. I have worked with a different paradigm in mind: the variegated landscape framework (Lindenmayer and Fisher 2006). There are still few works on landscape ecology that use this innovative (although not understood at all by the most of ecologists), and I hope that the contribution of this work, as well as those from some of my teammates (Rös et al. 2012; Martínez-López et al. 2017), and others around the world (González-Varo et al. 2012; Costa et al. 2017; Correa et al. 2019) can be best known and useful to go one step forward in the understanding of the effects of spatial patterns in ecological processes.

The Mexican tropic is a complex region with a suite of climatic and topographic conditions that have influenced biogeographic and ecological processes (Morrone 2019). The ecological knowledge of the Mexican tropical landscapes has mainly come from well-studied regions such as the lowlands of Veracruz (Arroyo-Rodríguez et al. 2008; García-Aguirre et al. 2010; Cadavid et al. 2020) and the rainforests in Chiapas (Arroyo-Rodríguez et al. 2013; Carrara et al. 2015; Sánchez de Jesús et al. 2015; Rivera et al. 2020), and recently from urban environments (Ortega-Álvarez and MacGregor Fors 2009; Cázares et al. 2019; Lemoine-Rodríguez et al. 2019). The fieldwork of my thesis was carried out in two understudied ecosystems, not only at the national scale, but also at the regional one: the tropical dry forest (although in its relictual form) and the mountains dominated by pine-oak forests, which are also locally endangered by human actions (Cervantes et al. 1996; Almazán-Núñez et al. 2016). There are other works carried out in mountain landscapes, but mainly focused on Tropical Cloud Forests (Martínez-Morales 2005; Rueda-Hernández et al. 2015). From my own perspective, one

of the main contributions of my work was to address two understudied vegetation types using a different conceptual model, contrasting to the formerly mentioned works, which mostly used the fragmentation approach even when some of the studied regions showed spatial patterns not suitable for assessing under the binary approach. A human-modified landscape is the interaction between biotic factors and human communities, so the development or impoverishment of one of these components may cause the same effect on the other. In Oaxaca, these interactions date from several centuries (if not millenia) ago, and have allowed both parts to develop and persist together (Robson et al. 2018).

My thesis supports the idea that management schemes that are carried out by locals in Oaxaca (i. e. low-intensity agriculture, selective logging) can support high biological diversity in comparison to more intensive land uses (i. e. urban environments and landscape scenarios that have suffered severe vegetation losses). The trend may not be evident when alpha diversity is analysed, but when beta diversity is considered, there are noticeable differences between those scenarios and landscapes. Beta diversity can increase or decrease (heterogeneization vs homogeneization) by different ecological processes (species addition vs subtraction, Socolar et al. 2016) and from the findings of this work, I can conclude that intensive human activities can negatively affect species composition either when species abundances are considered or not.

The study design (sampling windows, Halffter and Rös 2013) used in this work is an innovative sampling scheme to use in landscape ecology. To my knowledge, the work of Neilan et al. (2018) is the only published research using a similar sampling design studying bird communities. I think that sampling under a windows approach offers several advantages to study bird diversity over traditional designs, which are mainly focused on small-scale environmental features. First, sampling windows do not assume vegetation types or habitat patches *a priori*, but consider the landscape heterogeneity, which is one of the main drivers of ecological patterns

(Anderson et al. 2006). Second, it allows to perform a multi-scale study, which is important because ecological processes at the landscape level are scale dependent (Turner 2001). Third, the sampling windows design allows to optimize the sampling effort, given that it is important to get a reasonable sampling completeness in order to make valid scientific conclusions.

Birds are one of the most studied taxa in landscape ecology, and it is so because their biology is well-known, because there are standardized field methods for estimating their diversity, and because they are sensitive to environmental changes (Ortega-Álvarez and MacGregor-Fors 2009). As said before, the plethora of works about birds and landscape ecology in the American tropics have been done under a binary approach; by counterpart, this thesis and the work of López-Osorio (2020) are the first works focusing on bird diversity by using both sampling windows and the variegated landscape model. In this regard, there are several works that use this approach in the study of dung beetle communities (Rös et al. 2012; Costa et al. 2018; Rivera et al. 2020), which are an important advance in the study of diversity in tropical landscapes.

Although my finding of the winter White-eared Hummingbird nest in the Sierra Sur of Oaxaca could seem an isolated incident and an outlier from the objectives of this thesis, I think that it highlights the importance of the fieldwork in ecology. At the present times, the amount of scientific researches based on data collected without sampling protocols (i. e. eBird) or based on predictive models or historical data is increasing. This trend have advantages (i. e. the possibility of doing broader scale studies, inexpensive and quick assessments, etc.) but also withdraws (i. e. mismatch between the scale of studies and ecological inferences, misidentification issues, etc.). In this regard, I think the major disadvantage of doing research without fieldwork is that we are not updating the natural history of the living species. Surprisingly, the antecedents of our work is the information generated by the early expeditions of brilliant naturalists who made observations

and notes from the end of the XIX century through the middle of the XX century. For Mexico, the most evident case is that the guide of Howell and Webb (1995) is the top source of Mexican bird biology. As said before, there are information gaps of around half a century (if not more) and therefore these information could be out of date (or maybe not, but we have to corroborate the data). The finding of the winter nest is a reminder that we have to put the effort on the direct observations to accurately understand the ecological patterns we found in the field.

The case of Oaxaca is particular: in this place, a combination of human history, social dynamics and biophysical conditions have allowed to either informally or formally implement management schemes that promoted biodiversity conservation and sustainable forest exploitation (Robson and Berkes 2011; Van Vleet et al. 2016). In the Sierra Norte, the most studied region of Oaxaca, forest dynamics has been explored to analyse the historical trends in forest cover during the second half of the XX century and the beginning of the current one (Bray 2005). Contrary to the trends observed in other parts of the world, or even at the national scale in Mexico, there has been observed that forest cover in the region not only have remained constant but has even increased during the last 20 years (Van Vleet et al. 2016), giving place to what is considered as the forest transition (Mather 1992; Bray 2009).

Oaxaca belongs to the Mesoamerican region (Hernández-Baños et al. 2019), a worldwide biodiversity hotspot located in Southeastern Mexico and Central America. Mesoamerica (Myers et al. 2000) also encompasses the ancestral territories of many ethnic groups (Grandia 2007). Indigenous people from Mesoamerica has a long history of interaction with the nature that surrounded them, to the point that it is probable that several forests that currently spread throughout the region (i. e. the Yucatán peninsula) were determined in their composition by people from the precolumbian times (Peters 2018). Therefore, it is crucial to understand and acknowledge that, in this region, forest landscapes and human societies have evolved together

since several millenia ago, and that this interactions have caused the persistence of both biodiversity and human societies in the long term.

Given these circumstances, every formal conservation plan for the mountainous lands of Oaxaca (and maybe Mesoamerica) must consider the historical context, as well as the opinion and expertise of the local communities (Pazos-Almada and Bray 2018). Therefore, the idea of the establishment of Protected Areas via initiatives from the government or any external agent (top-down) without consensus and agreement from the locals could be innapropriate, misleded or even dangerous, and may compromise their correct implementation or viability (Van Vleet t al. 2016). Instead, conservation in Oaxaca should be based on the main idea that human communities are closely related to their physical space and, of course, to the biodiversity that surrounds them: there are multiple examples that have shown that initiatives rooted and developed from within the communities (bottom-up) are the best option to ensure the feasibility of biological conservation not only in Oaxaca but throughtout the Mesoamerican hotspot (Bray et al. 2008), via both land sharing and land sparing strategies (Harvey et al. 2008; Phalan 2011).

As final thought, I want to point out both the potential of Oaxaca to make biological research and the striking lack of information in the most biodiverse state of the country. Oaxaca is a living laboratory, a vast and complex region where we still ignore basic biological issues regarding birds, and I hope that in the near future the governments, NGO´s and funding agencies can support more research projects in a place where more than half of the population is living in poverty but also struggles for the conservation of nature. Research could be a way to bridge the economic and social gaps in Oaxaca, and also a way to dignify and recognize the local communities that know and preserve the nature in their territories day by day.

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