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CONSERVATION VALUE OF WORKING LANDSCAPES IN MESOAMERICA FOR NEARCTIC-NEOTROPICAL MIGRATORY BIRDS

By

Samuel L. Oliveira

A DISSERTATION

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This dissertation has been approved in partial fulfillment of the requirements for the Degree of DOCTOR OF PHILOSOPHY in Forest Science.

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Author Contribution Statement

Chapter 1 is an overview to introduce the main subjects of this dissertation. This chapter is aimed to conceptualize to the reader by summarizing the major subjects needed to develop the following research chapters.

Chapter 2 was published in *Journal of Field Ornithology*, which currently has the copyright for this chapter. David Flaspohler, Jessie Knowlton and Samuel Oliveira formulated the main idea, Samuel Oliveira, David Flaspohler and Jared Wolfe developed the study design for the bird sampling. Samuel Oliveira and Christopher Webster developed the study design for the vegetation sampling. Samuel Oliveira collected the data. Samuel Oliveira and Jared Wolfe analyzed the data, and Samuel Oliveira was responsible to write the manuscript, with support from the co-authors.

Chapter 3 was published in *Ecological Indicators*, which currently has the copyright of this chapter. Samuel Oliveira, David Flaspohler and Jessie Knowlton were responsible for the conceptualization. Samuel Oliveira, David Flaspohler, Jessie Knowlton and Jared Wolfe developed the methodology. Samuel Oliveira and David Flaspohler were responsible for the project administration. David Flaspohler, Jessie Knowlton and Jared Wolfe reviewed and edited the manuscript. David Flaspohler and Jessie Knowlton acquired funding. Jared Wolfe contributed with the data analysis. Samuel Oliveira was responsible for investigation, data curation, data analysis, write the original manuscript and editing.

Chapter 4 is intended to be submitted as a Short Communication in *Wilson Journal of Ornithology*. David Flaspohler and Samuel Oliveira formulated the main idea. Samuel Oliveira, David Flaspohler and Jared Wolfe developed the study design for the bird sampling. Samuel Oliveira collected the data. Samuel Oliveira and Jared Wolfe analyzed the data, and Samuel Oliveira was responsible to write the manuscript, with support from the co-authors.

Chapter 5 is intended to be submitted in *Ornithological Applications* as a Research Article. Author contributions: Samuel Oliveira and Jared Wolfe conceived the idea and formulated the hypothesis; Samuel Oliveira collected the data; Samuel Oliveira, David Flaspohler and Jared Wolfe wrote the paper; Samuel Oliveira, Jared Wolfe and Christopher Webster designed methods; Samuel Oliveira and Rafael Sühs analyzed the data.

Chapters 4 and 5 are presented in the format defined by *Wilson Journal of Ornithology* and *Ornithological Applications* instructions for authors, respectively.

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Abstract

Populations of many of Nearctic-neotropical migratory birds have declined in the past several decades, recent estimates suggested a dramatic loss of 2.5 billion birds over the past 50 years in North America. Habitat loss and degradation represent a major threat in the tropics. Managed agroecosystems have the potential to mitigate some impacts of land conversion, however, little is known regarding the habitat quality provided by working landscapes in the overwintering range. In this research, we surveyed the migratory bird community in the rapidly expanding oil palm plantations in southern Mexico; and also the declining population of the Wood Thrush (*Hylocichla mustelina*) inhabiting forest fragments in an agricultural matrix in Costa Rica. We assessed the value of both human-modified habitats by using a combination of demographic, distributional, and individual habitat quality indicators, as well as the relationship of these indicators with environmental characteristics. In the Mexican oil palm plantations, we found that species richness of migratory birds tended to be higher in forest patches than in oil palm, that community assemblages of migratory birds differed between habitats, and that differences in migratory bird abundance were driven by vegetative structure. Specifically, when differences in indicators occurred between oil palm and native forest, most migratory species exhibited indicators of better habitat quality in the native forest. Lastly, we observed, for the first time, territoriality in oil palm plantations and estimated home range sizes for the American Redstart (*Setophaga ruticilla*), which tended to be smaller than in the native forest. The Wood Thrush population in Costa Rica exhibited an average territory size estimated of 0.71 ha. We were able to determine associations between fragments' characteristics and body conditions, whereby birds in young and more humid fragments exhibited better fitness. Additionally, fragment size alone is probably not the best indicator of habitat quality for Wood Thrushes in Costa Rica. Our results suggest that most species of migratory birds assessed responded positively to forest structure complexity, and that age and sex ratios combined with measures of the physiological conditions, environmental moisture and home range sizes can be used to assess habitat quality for migratory birds overwintering in working landscapes. Importantly, determining a species' territoriality dynamics, is key when selecting a given indicator of habitat quality for each species due to distributional behavior. Our results also suggest that management strategies that promote forest-like conditions in oil palm plantations can improve the habitat quality in this agroecosystem for declining populations of migratory birds. Additionally, these findings support potential value in variable-sized forest fragments within agricultural areas for the conservation of the Wood Thrushes, and soil humidity could be used as a proximate cue for food availability and ultimately as a habitat quality indicator. Lastly, our results emphasize the importance of determining territoriality dynamics, assessing various habitat indicators, and long-term monitoring, in order to develop effective management measures to improve the conservation value of working landscapes in the Neotropics to mitigate the high rate of habitat loss and degradation, especially considering that habitat availability in the tropics could be limiting migratory bird populations.

1 An overview

1.1 The need to study the value of modified landscapes in the Neotropics

Like most tropical regions, Latin America has experienced dramatic losses of native forest cover to agriculture over the last two centuries (Aide et al. 2013), and, particularly, since the Green Revolution of 1960 (Graesser et al. 2015). Expansion of pasture and agriculture coupled with replacement of native plant communities with those dominated by a single commodity have reduced the available native habitat for forest-dwelling birds and has led to questions regarding the value of different human-modified landscapes for wildlife (Pimentel et al. 1992; Foley et al. 2007). Agricultural demand will only increase over time, making the integration of efficient agricultural production with biodiversity conservation an essential area of research (Tilman et al. 2011; Tscharntke et al. 2012; Railsback and Johnson 2014). Other important questions relate to how such ecosystems could be managed to increase their value for biodiversity and other ecosystem services (Mas and Dietsch 2004; Marja et al. 2014). Some ecologists have gone so far as to suggest that the long-term future of most terrestrial biodiversity may depend largely on the answers to these questions (Balvanera et al. 2001; Rosenzweig 2003; Armsworth et al. 2007). These concerns gave rise to the field of countryside biogeography, a framework that aims to increase the ecological value of human-dominated landscapes for wildlife (Daily et al. 2001).

As an example, coffee-growing (*Coffea sp.*) systems vary greatly in their value to native wildlife, especially birds (Greenberg et al. 1997; Philpott et al. 2008; Bakermans et al. 2012; Perfecto et al. 2014; Colorado et al. 2018). Realization that shade-grown coffee management systems are demonstrably better for bird communities, biodiversity, and ecosystem services than sun-grown coffee led to the creation of a whole new market where economic incentives are driven by consumer preference for bird-friendly agriculture demonstrably better for biodiversity (Greenberg et al. 2008; Tscharntke et al.

2014). Shaded cacao (*Theobroma cacao*) farms also support a greater diversity of migratory and resident birds than non-shaded cacao in Costa Rica, Panama, and Colombia (Parrish et al. 1998; Power and Flecker 1998; Reitsma et al. 2001; Van Bael et al. 2007; Díaz-Bohórquez et al. 2014). Perfecto et al. (1996) found that greater structural and floral complexity in shaded plantations provided a variety of foliage layers and more food resources for a greater diversity of organisms, resulting in bird diversity and density sometimes comparable to native forests in many parts of Latin America (Gonzales et al. 2020). Coffee and cacao agroecosystems are relatively well-studied with regard to their value for birds and other wildlife, and also the benefits provided by the migratory birds, that, when present in coffee and cacao agrosystems, significantly reduced the number of large arthropods and provide valuable pest control services (Van Bael et al. 2008; Johnson et al. 2010; Karp et al. 2013; Spidal and Johnson 2016).

1.2 The influence of wintering ground habitats on Nearctic-neotropical migratory birds

Populations of many species of Nearctic-neotropical migratory birds have declined in the past several decades, recent estimates suggested a dramatic loss of 3 billion birds in the past 50 years in North America, most of them, 2.5 billion, Nearctic-neotropical migratory birds, prompting a search for the causes of these declines on their breeding and wintering grounds and migration routes (Robbins et al. 1989; Faaborg 2002; Newton 2004; Spidal and Johnson 2016; Rosenberg et al. 2019). Although our knowledge about the influence of the wintering grounds on the population limitation is still relatively poor when compared with the breeding grounds (Runge and Marra 2005; Marra et al. 2015; Sherry et al. 2015), the degradation of wintering ground habitat has been implicated to play a critical role in the annual dynamics and in the population declines of several species, especially of forest-dwelling migratory birds (Robbins et al. 1989; Marra and Holmes 2001; Faaborg 2002; Newton 2004; Latta et al. 2016; Kramer et al. 2018; Wilson et al.

2018). For example, forest loss in the neotropics is associated with the decline of the Golden-winged Warbler (Vermivora chrysoptera), the Wood Thrush (Hylocichla mustelina), and the Canada Warbler (Cardellina canadensis) (Rushing et al. 2016; Taylor and Stutchbury 2016; Wilson et al. 2018). Such relationship should be expected, especially when considering that Nearctic-neotropical migratory birds can overwinter from six to eight months in the tropics (Runge et al., 2015). Thus, more attention needs to be focused on the impacts of land cover change on the wintering grounds (Latta and Faaborg 2002; Latta et al. 2016).

Today, with new remote sensing and tracking technology and an improved understanding of the distribution and habitat use by overwintering migratory birds, ecologists are able to more easily investigate the non-breeding ecology of the many warblers, thrushes, vireos, and other migratory birds that spend most of their life in the Latin American tropics (Rhodes, et al. 2015; Alonso, et al. 2016; Weidensaul 2017). We can assess how birds are coping in human-modified landscapes in part by using the Sherry and Holmes (1995, 1996) model of winter population limitation of migratory birds, which suggests that differences in food resources between habitats will result in sex and age class segregation and differences in physiological condition and site fidelity resulting from competitive interactions. Only a few studies have assessed habitat quality indicators by examining wintering bird population responses and individual conditions of nonbreeding birds to prevailing ecological conditions across divergent habitats, especially in working landscapes (Strong and Sherry 2000; Latta and Faaborg 2001; Latta and Faaborg 2002; Latta et al. 2016).

1.3 Mesoamerican oil palm plantations and forest fragments

Oil palm (*Elaies guineensis*) is currently one of the most rapidly expanding agroecosystems in the tropics with more than 15 million ha already converted and an average of 270,000 ha converted annually between 2000 and 2011 (Foster et al., 2011; Henders et al. 2015). In Latin America alone, palm oil output has doubled since 2001 (Furumo and Aide 2017). In South America, 31% of the oil palm expansion occurred in forested areas, whereas, in the Mesoamerican region (Central America, Mexico, and Caribbean), most new oil palm is planted on lands previously deforested for crops or pasture, with only 2% of oil palm aerial growth from converted forest (Vijay et al. 2016). Although global markets for palm oil as a food additive and as a feedstock for biodiesel make it difficult to forecast future expansion of this crop, some authors have suggested that it may be the among the major drivers of the next wave of land conversion in the warm, humid tropics (Gutierrez-Velez and DeFries 2013; Lee et al. 2013). Furthermore, although it is clear that oil palm plantations support far less biodiversity of most taxa than primary or secondary forests (Edwards et al. 2010), it remains unclear how the biodiversity value of oil palm compares to other land uses. In fact, there is evidence that in some cases, oil palm may support more biodiversity than other more intensively managed major crops such as soybeans or sugarcane; other evidence suggests that oil palm plantations support even fewer forest species than do most other agricultural options (Fitzherbert et al. 2008). In eastern Amazonia, oil palm plantations were found to have impoverished avian communities similar to other local non-forest land-uses such as cattle pasture (Lees et al. 2015; Almeida et al. 2016), while in Colombia, oil palm plantations supported greater biodiversity than improved (seeded with non-native grasses) cattle pasture (Gilroy et al. 2015). Many species of Nearctic-neotropical migratory birds use forests in their tropical wintering areas and are, therefore, potentially impacted by oil palm expansion in Latin America (Blandón et al. 2016). Few investigators have examined the use of oil palm plantations by this group of birds. In Mesoamerica, Nearctic-neotropical migratory birds were shown to be abundant in oil palm plantations during the northern hemisphere winter (Bennett et al., 2018; Moo-Culebro, 2018), making this group of interest when investigating variation in overwintering habitat quality.

The conversion of Central American forests to human-dominated agricultural landscapes needs to be understood in the context of a changing mosaic of habitat quality (Aide et al. 2013). Nearctic-neotropical migratory bird declines may be influenced by the reduction of forested areas, and consequent isolation of patches (Rappole et al. 1992). Forest fragments embedded within a matrix of agricultural development fosters pronounced edge effects that may benefit some generalist migrant species at the expense of forest-obligates. However, the impact of forest fragmentation on migratory birds on the wintering grounds is poorly studied and unknown for most migratory birds (Rappole et al. 1992; Webster 2005). Such information about the relationship between fragmentation and habitat quality, i.e., what is the minimum fragment size to provide good habitats for migratory birds, is likely to be complex (Taylor and Stutchbury 2016), and of utmost importance to manage habitats and optimize conservation measurements for forest-depended species. On the breeding grounds, migratory birds prefer large fragments due to the higher risk of suffering nest parasitism and predation (Martin and Finch 1995). Such data is unknown for the overwintering areas, nonetheless, the richness and abundance of migratory birds were higher in continuous forests than in small fragments (Askins et al. 1992), and some species can be only found in large forest fragments (Robbins et al. 1987). As an example, the dramatic Wood Thrush (*Hylocichla mustelina*) population decline of 62% between 1966 and 2015 was associated with tropical forest loss, nevertheless, 83% of the Wood Thrush population in Costa Rica overwinters outside of protected areas, mainly in forest fragments in agricultural regions (Roberts 2011; Sauer et al. 2013; Rushing et al. 2016; Taylor and Stutchbury 2016). Individuals were found in fragments as small as 1 ha (Roberts 2011), importantly, the mere presence of Wood Thrush does not indicate ecological value, given that bird density is not always a reliable measure of habitat quality (Johnson 2007). Raising the question: do small forest patches in agricultural landscapes provide high-quality habitat?

1.4 Assessing habitat quality

Ornithologists have developed a variety of approaches to measure relative differences in habitat quality for birds, beyond information on the abundance and richness of bird species in agroecosystems, more rigorous studies are needed that compare variation in the condition of individual birds by recording, for example, changes in mass, fat levels and muscle mass size (Holmes et al. 1989; Wunderle and Latta 2000). Indices of habitat quality are numerous and have been used with varying degrees of success; they include measuring the habitat itself (e.g., food and nesting resources, vegetative structure and diversity, microclimates, presence of predators, competitors, and mates) as well as directly sampling birds (survival, recruitment, abundance, population growth, reproductive success, stress hormones, triglycerides, molt speed, territory size, and physiological condition) (Grubb 1989; Halpern et al. 2005; Johnson 2007). The appropriateness of a particular index will depend on the specific behaviors and life history strategies exhibited by the study species in question (Johnson 2007). The use of indices has helped researchers distinguish between poor- and high-quality habitats; an important prerequisite towards understanding how environmental change affects avian fitness, and subsequent patterns of population growth (Knutson et al. 2006). Identifying an appropriate measure of habitat quality depends on several factors, including how variation in habitat quality affects bird attributes such as territorial behaviors, which can decouple patterns of density from habitat quality (Fretwell and Lucas, 1969; Van Horne, 1983; Johnson, 2007).

Although not comprehensively studied, many species of sexually dimorphic migratory birds display behaviorally mediated habitat segregation on the wintering grounds, with older males often occupying higher quality habitats compared to females and younger males, a characteristic of the ideal despotic distribution model (Fretwell and Lucas, 1969; Lynch et al. 1985; Ornat and Greenberg, 1990; Marra et al., 1993; Wunderle, 1995; Marra and Holmes, 2001). For such species, assessing habitat quality by comparing density can be misleading since high-quality habitats are often occupied and defended by dominant individuals, which exclude conspecifics, meaning that high-quality habitats may, in theory, have lower densities. A prediction arising from this pattern is that the age and sex ratios of warblers and other migratory groups should vary along a gradient of habitat quality (Spidal and Johnson 2016), potentially allowing us to use these ratios to infer wintering habitat quality. Variation in body condition, fat deposition, and pectoral muscle mass across habitats may also provide valuable insights into relative measures of habitat quality for migratory birds (Holmes et al., 1989; Wunderle and Latta, 2000; Brown et al., 2002; Johnson, 2007; Cooper et al., 2015). Additionally, the degree of within-site persistence and inter-annual return rates of wintering birds is expected to be highest where food is most abundant and predictable, thus offering a measure of habitat quality (Marra et al. 1998; Johnson and Sherry 2001; Latta and Faaborg 2002; Wunderle et al. 2014). Understanding these habitat selection decisions can provide insights into the value of working landscapes to wintering birds, and such information is vital to predict the long-term viability of populations in these human-modified landscapes (Hostetler et al. 2015).

The overall objective of this research was to assess the conservation value of working landscapes for Nearctic-neotropical migratory birds on the wintering grounds, more specifically, 1) determine species richness, community structure, and the vegetation structures that influence these aspects in oil palm plantations, as well as using distributional and individual indicators to analyze the habitat quality compared with native forest; 2) evaluate the habitat quality provided by variable-sized forest fragments to the territorial overwintering population of the Wood Thrush, using indicators and environmental cues to attempt to determine good habitat characteristics.

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2 Migratory bird community structure in oil palm (*Elaies guineensis*) plantations and native forest fragments in southern Mexico[1]

2.1 Abstract

Oil palm (*Elaies guineensis*) plantations are among the fastest growing agroecosystems in the Neotropics, but little is known about how Neotropical birds use oil palm habitats. To better understand the potential value of oil palm as an overwintering habitat for migratory birds, we surveyed birds in oil palm and native forest remnants in Tabasco, Mexico, from 19 December 2017 to 27 March 2018. We collected data on bird abundance and vegetative structure and used generalized linear models and multivariate analysis to assess how oil palm development influenced migrant bird diversity, community assemblages, and abundance. We found that species richness of migratory birds tended to be higher in forest patches than in oil palm, that community assemblages of migratory birds differed between native forest and oil palm plantations, and that differences in migratory bird abundance, and subsequent changes in community assemblages were driven by differences between native forest and oil palm plantations in vegetative structure. The bird community of native forest was characterized by migrant species sensitive to forest loss that forage low in the understory and in the leaf litter, whereas the bird community of oil palm plantations was represented by generalist species that occupy a wider range of foraging niches. Our results suggest that most species of migrant birds responded positively to several forest structural features and that integrating more native

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trees and increasing the amount of understory vegetation in oil palm plantations may increase the value of working landscapes for migratory birds.

2.2 Introduction

Like most tropical regions, Latin America has experienced a dramatic loss of native forest cover to agriculture over the last two centuries (Aide et al. 2013) and, particularly, since the Green Revolution of the 1960s (Graesser et al. 2015). Expansion of pasture and agriculture coupled with replacement of native plant communities with those dominated by a single commodity have reduced the available native habitat for forest-dwelling migrant birds and has led to questions regarding the value of different agroecosystems for wildlife (Pimentel et al. 1992, Foley et al. 2007). Agricultural demand is projected to increase over time, making the integration of biodiversity conservation into agricultural pro-duction an important area of research (Tilman et al. 2011, Tscharntke et al. 2012, Railsback and Johnson 2014). These concerns gave rise to the field of countryside biogeography, a framework that aims to increase the ecological value of human-dominated landscapes for wildlife (Daily et al. 2001). As an example, coffee-growing systems vary greatly in their value for native wildlife, especially birds (Greenberg et al. 1997, Philpott et al. 2008, Bakermans et al. 2012, Perfecto et al. 2014, Colorado et al. 2018). Realization that shade-grown coffee management systems are demonstrably better for bird communities, biodiversity, and ecosystem services than sun- grown coffee led to the creation of a whole new market where economic incentives are driven by consumer preference for bird-friendly agriculture (Greenberg et al. 2008, Tscharntke et al. 2014). Shaded cacao farms also support a greater diversity of migratory and resident birds than non-shaded cacao in Costa Rica, Panama, and Colombia (Parrish et al. 1998, Power and Flecker 1998, Reitsma et al. 2001, Van Bael et al. 2007, Díaz- Bohórquez et al. 2014). Perfecto et al. (1996) found that greater structural and floral complexity in shaded plantations provided a variety of foliage layers and more food resources for a greater diversity of organisms, resulting in bird diversity and density sometimes comparable to native forests in many parts of Latin America (e.g., Gonzales et al. 2020).

Coffee (*Coffea sp.*) and cacao (*Theobroma cacao*) agroecosystems are relatively well-studied with regard to their value for birds and other wildlife. Less is known about how biodiversity responds to oil palm (*Elaies guineensis*) plantation management, even though oil palm is among the most rapidly expanding agroecosystems in the tropics, with more than 15 million hectares already converted and an average of 270,000 ha converted annually between 2000 and 2011 (Foster et al. 2011, Henders et al. 2015). Forecasting the future expansion of this crop is difficult, but some authors have suggested that it may be among the major drivers of future land conversion in the warm, humid tropics (Gutierrez-Velez and DeFries 2013, Lee et al. 2013). In Latin America alone, palm oil output has doubled since 2001 (Furumo and Aide 2017). In South America, 31% of the oil palm expansion occurred in forested areas, whereas, in the Mesoamerican region (Central America, Mexico, and Caribbean), most new oil palm is planted on lands previously deforested for crops or pasture, with only 2% of oil palm aerial growth from converted forest (Vijay et al. 2016). Importantly, although there is strong evidence that oil palm plantations support less biodiversity of most taxa than primary or secondary forests (Aratrakorn et al. 2006, Edwards et al. 2010, 2013, Lees et al. 2015, Almeida et al. 2016, Srinivas and Koh 2016), the ecological value of oil palm compared to other land uses remains unclear, with different studies providing conflicting results.For example, Sayer et al. (2012) found that oil palm may support more biodiversity than other more intensively managed crops such as soybeans (*Glycine max*) or sugarcane (Saccharum sp.), whereas Fitzherbert et al. (2008) found that oil palm plantations supported fewer forest species than other agricultural crops. In Colombia, Gilroy et al. (2014) found that oil palm plantations supported greater biodiversity than cattle pasture, whereas, in eastern Amazonia, oil palm plantations were found to host depauperate avian communities similar to other non-forest habitats, such as cattle pastures (Lees et al. 2015, Almeida et al. 2016).

Many species of Neotropical migrant birds use forests in their tropical wintering areas and are, therefore, potentially impacted by oil palm expansion in Latin America. Additionally, degradation of wintering ground habitat has been implicated in the population declines of several species of forest-dwelling migratory birds (Robbins et al. 1989, Faaborg 2002, Newton 2004, Kramer et al. 2018, Wilson et al. 2018). More specifically, Kramer et al. (2018) associated forest loss in northern South America with declines in populations of Golden-winged Warblers (*Vermivora chrysoptera*), a species currently being petitioned for protection under the U.S. Endangered Species Act. Furthermore, deforestation in their wintering areas was shown to be a significant driver of Wood Thrush (*Hylocichla mustelina*) population trends, a species that suffered a population decrease of 62% between 1966 and 2015 (Rushing et al. 2016, Taylor and Stutchbury 2016). Few investigators have examined the use of oil palm plantations by migrant birds in the Neotropics. In Guatemala, Bennet et al. (2018) compared migratory bird communities in oil palm and secondary forest and found a similar species richness, but a greater abundance of migratory birds in oil palm than in secondary forest. Conversely, in Tabasco, Mexico, Moo-Culebro (2018) found greater species richness of migratory birds in oil palm than in secondary forest and pasture. These conflicting observations, coupled with the high potential for future expansion of oil palm and forest loss in southern Mexico and Latin America, where avifaunal studies in oil palm are scarce compared to southeast Asia, highlight the need for an improved under- standing of Neotropical bird communities in oil palm plantations.

We identified the species of migratory birds found in oil palm plantations in Tabasco, Mexico, and assessed the structural features that may drive dissimilar responses of migrant birds to oil palm development using comparisons with remnant native forest patches. Specifically, we examined the influence of oil palm plantation and secondary forest structure on the composition of migrant bird communities. In addition to community-scale differences, we examined the relationships between vegetative structure and densities of migrant birds to identify drivers of habitat selection across native forest and oil palm plantations for each species of migrant bird. We developed two non-mutually exclusive hypotheses: (1) habitats characterized by structural homogeneity will support fewer migratory bird species and fewer individuals of each species, and (2) certain habitat features (e.g., canopy cover, understory density, and tree diversity) will influence species-specific patterns of habitat selection. Given our hypotheses, we predicted that we would find: (1) greater species richness and bird abundance in native forests with more structural heterogeneity than in structurally simplistic oil palm plantations, and (2) that differences in migratory bird densities in oil palm plantation and native forest would be correlated with specific vegetative attributes. To test our hypotheses and predictions, we compared migrant bird communities in oil palm farms and adjacent forest patches in Tabasco, Mexico. Given the rapid increase in the number of oil palm plantations in areas important for migratory birds, understanding how these species cope with this relatively new agroecosystem is imperative and can point to effective conservation management.

2.3 Methods

2.3.1 Study area

Located in southeast Mexico, the state of Tabasco has lost all but a few small fragments of what was once extensive moist lowland rainforest (Arriaga-Weiss et al. 2008). As in most of Latin America, Tabascan forests were cleared for pasture and agriculture, a process driven by a combination of federal government policy and population growth (Tudela 1989). Beginning about 25 years ago, global demand and government incentives encouraged many farmers to begin planting oil palm, primarily in areas that had previously been cleared for cattle or other row crops. Currently, remnants of undisturbed forest are only found in areas with very rugged relief and steep slopes, like the Sierra de Tabasco, which is considered an Important Bird Area (Birdlife International 2020). Today, oil palm plantations are expanding rapidly in southern Mexico, with ~ 76,000 ha already planted (SAGARPA 2016) and close to 8.9 million ha deemed suitable for oil palm cultivation (INIFAP 2016). We conducted our surveys at five sites in two patches of native forest (17.6495°N, -92.8146°W; 17.6198°N, -92.8565°W) and six sites in two oil palm plantations (17.5788°N, -92.8526°W; 17.6992°N, -92.9488°W) in the municipalities of Tacotalpa, Jalapa, and Teapa (Fig. 2.1). The landscape is mostly pasture with scattered trees (potreros) and small secondary-growth forest fragments surrounded by plantations of banana and cacao, as well as annual crops like corn.

2.3.2 Avifaunal survey

To capture migratory songbirds, we randomly selected six plots in oil palm plantations and five plots in native forest patches; each plot was at least 50 m from an edge and at least 250 m from another plot. We selected oil palm plantations of similar ages (~ 12 year) to minimize variation in vegetation structure due to the palm growth. In each plot, we placed a line of 10 mist-nets (12 9 3 m, 36-mm mesh). We chose mist-netting over audio-visual surveys due to the low acoustic detectability of Neotropical migratory birds during the non-breeding season (Robbins 1981), especially in the dense understory of native forests. We operated nets at least two times per plot, where nets were opened shortly after sunrise for four hours. We completed 1160 mist-net hours, including 520 hours in native forest and 640 hours in oil palm plantation (mini-mum of 80 mist-net hours per plot). All captured migratory birds were marked with aluminum bands (United States Geological Survey), measured (tarsus and tail length, wing chord, and exposed culmen), aged, and sexed (following Pyle 1997), and weighed. Captured resident birds were excluded from subsequent analyses.

2.3.3 Vegetation structure sample

Vegetation structure at each plot was sampled by selecting three equidistant points along the net line, including the beginning (0 m), middle (60 m), and end (120 m) of the line using a 10-m radius. Within this radius, we measured six structural features: (1) diameter at breast height (DBH; we only considered trees with DBH ≥ 10 cm), (2) tree density, (3) tree species richness, (4) tree height, (5) understory density, and (6) canopy cover. Variables were chosen based on the results of previous studies relating bird communities with vegetation complexity in plantations (Greenberg et al. 1997, 2000, Philpott et al. 2008, Bakermans et al. 2012, Bennet et al. 2018, Colorado et al. 2018). Tree height was measured using an electronic clinometer. For understory density and canopy cover, we collected measurements at four cardinal points placed 10 m from the center of the vegetation sampling point, and then calculated the average. We used a vegetation cover board to assess understory density between 0 and 2 m, and a spherical densiometer for canopy cover. Because each plot had three vegetation structure sampling points, we used mean values from each net line in subsequent analyses. Fieldwork was conducted during the overwintering season from 19 December 2017 to 27 March 2018.

2.3.4 Statistical analysis

To compare vegetative structure and generate an environmental gradient, we used Principal Component Analysis (PCA) to ordinate each site by vegetation structure (tree height, canopy cover, understory density, tree density, tree richness, DBH, and tallest tree), followed by a PERMANOVA test to identify differences between habitats. Migrant bird community assemblages of oil palm and native forest were analyzed using non-metric multidimensional scaling (NMDS) with Bray–Curtis dissimilarity metric to ordinate each site by density (capture rate) of migrant species. The secondary matrix for each ordination contained a categorical variable for habitat type. We included “tallest tree” in the vegetative structure PCA based on recommendations from Bennet et al. (2018), where the tallest tree was found to be an important predictor of migratory bird abundance, richness, and diversity. Prior to our ordination analysis, we used ANOVA to assess homogeneity of multivariate dispersion (Anderson 2005). To test for possible differences between migrant bird community assemblages in native forest and oil palm plantations, we used ANOSIM with Bray–Curtis dissimilarities between the habitats. To identify the migrant species responsible for differences between habitats, we used vector fitting analysis, where the direction and length of the arrow represents the correlation between the NMDS ordination and the bird species (Oksanen 2015). Ordinations, PERMANOVA, and ANOSIM analyses were conducted using the package "vegan" (Oksanen et al. 2018) in program R (R Core Team 2020).

We used *t*-tests to examine possible differences in species-specific capture rates between native forest and oil palm plantations (only for species with more than five captures per habitat). Before performing *t*-tests, we checked dataset distributions for normality, which is an assumption of *t*-tests (Hogg and Craig 1978). When distributions were not normal, we used a non-parametric Wilcoxon test. To deal with a higher probability for type I error due to multiple comparisons, we applied Holm–Bonferroni corrections for multiple capture rate tests because it is less conservative than the original Bonferroni correction, and better for small sample sizes (Rice 1989). Rarefaction estimates of species richness were generated using EstimateS (Colwell 2013), where we extrapolated the sample size to double the effort. Generalized linear modeling was used to determine which habitat features influenced the density of migratory bird species (based on capture rates) in native forest and oil palm plantations. We used the number of individuals captured and net hours to generate capture rates (a measure of density based on number of birds per net hour). Additionally, we constructed rank abundance curves to assess patterns of evenness between native forest and oil palm plantations. We built linear models for overall migratory bird community and species-specific capture rates (species with at least five individuals captured in both habitats) as response variables. Explanatory variables were habitat features (tree height, canopy cover, understory density, tree density, tree richness, diameter at breast height [DBH], and height of the tallest tree) and PC1 axis scores from the vegetation structure variables ordination as a structural gradient of habitat heterogeneity (Tews et al. 2004), with more positive values indicating forest-like conditions (vegetation complexity). We included this last variable by examining the proportion of variability each axis explained (McCune et al. 2002). All explanatory variables were checked for collinearity. For each species, we developed, a priori, 17 competitive models, including a null model. Of these 17 models, we included eight models with quadratic effects associated with habitat features. We tested for heteroscedasticity of residuals using Breusch–Pagan test. All models were evaluated and compared to the null model using Akaike's Information Criterion corrected for small samples sizes (AICc) and changes in model deviance. Analyses were completed in program R (R Core Team 2020) using the R package "AICcmodavg" (Mazerolle 2019).

2.4 Results

We captured 341 migratory birds, including 233 in native forest and 108 in oil palm, representing 24 Neotropical species, with 19 captured in native forest and 14 in oil palm. The two habitats shared nine species, including Gray Catbirds (*Dumetella carolinensis*), Wood Thrushes (*Hylocichla mustelina*), Northern Waterthrushes (*Parkesia noveboracensis*), Ovenbirds (*Seiurus aurocapilla*), Hooded Warblers (*Setophaga citrina*), Magnolia Warblers (*Setophaga magnolia*), American Redstarts (*Setophaga ruticilla*), Worm-eating Warblers (*Helmitheros vermivorum*), and Indigo Buntings (*Passerina cyanea*). Gray Catbirds were the most common species in native forest, and Northern Waterthrushes were the most common species in oil palm (Fig. 2.2).

2.4.1 Ordinations for vegetation and bird communities

Our results from the vegetation structure ordination demonstrated stark, but not unexpected, differences in habitat features between native forest and oil palm plantations, resulting in distinct and significant clustering in multivariate space (PERMANOVA, P = 0.001 for 999 permutations; Fig. 3). Axis 1 (PC1) is a better representation in variation of the gradient of vegetation structural heterogeneity between the habitats (R^2 = 0.94). Results of a permutation test suggested that differences in habitat features were significantly correlated with differences in vegetation structure (Fig. 2.3). Thus, we included PC1 as an explanatory variable for linear modeling, considering it to represent the vegetation complexity gradient.

Our NMDS ordination analyses also suggested that migrant bird communities in oil palm plantations and native forest differed (Fig. 2.4). To determine statistical significance, we used an ANOSIM test and found that the composition of migrant bird communities differed between oil palm plantations and native forest (R = 0.997, P = 0.003 for 999 permutations). Using vector fitting analysis, we observed which species of migratory birds were most associated with changes in community composition across both habitats based on correlations between changes in community assemblage and changes in capture rates of migrant birds. Our analyses showed that nine of 24 species strongly influenced community differences between the two habitats (Fig. 2.4). The results of our *t*-tests and Wilcoxon tests, based on differences in species-specific capture rates in native forest and palm oil plantations, suggested that, of nine species found in both habitats, only the capture rates of Magnolia Warblers did not differ between habitats (Fig. 2.2).

2.4.2 Species richness and evenness

Observed species richness showed that native forest hosted a richer migratory bird community (N= 19) than oil palm plantations (N= 14). However, our species richness analysis, where we extrapolated sample sizes using rarefaction to estimate richness, suggested no statistically significant difference between habitats in overall bird richness (Table 2.1, Figs. 2.5 and 2.6). Rank abundance curves suggested similar evenness between native forest fragments and oil palm plantation migrant bird communities (Fig. 2.7).

2.4.3 Linear modeling

To model migrant bird density in relation to vegetative features, we included PC1 scores from the vegetation structure ordination as an explanatory variable called vegetation complexity. Additive and interactive models were not built because all explanatory variables were collinear. No model residuals were heteroscedastic. Our modeling results identified habitat complexity (as indicated by vegetation ordination PC1) as a driver of overall community density (Table 2.2), meaning that habitat complexity associated with remnant native forest patches was positively correlated with migratory bird density (β = 0.024, SE = 0.004, 95% CI = 0.015, 0.35). Tree species richness (β = 0.57, SE = 0.1, 95% CI = 0.34, 0.8), DBH (β = -0.06, SE = 0.01, 95% CI = -0.09, -0.04) and understory density (β = 0.03, SE = 0.004, 95% CI = 0.016, 0.038) were ranked as competitive models (within 2 AICc units of the top model; Burnham and Anderson 2002) because they influenced migrant density as well. Vegetation complexity was positively correlated with a higher capture rate of Hooded Warblers in native forest (β = 0.041 SE = 0.002, 95% CI = 0.036, 0.046), whereas understory density was positively correlated with a higher capture rate of Ovenbirds in forest (β = 0.033, SE = 0.008, 95% CI = 0.016, 0.051) and negatively correlated with a higher capture rate of American Redstarts in oil palm plantations (β = -0.027, SE = 0.006, 95% CI = -0.042, -0.013). Tree species richness was positively correlated with the capture rate of Gray Catbirds (β = 1.62, SE = 0.21, 95% CI = 1.14, 2.1) and DBH was positively correlated with the capture rates of Northern Waterthrushes (β = 0.054, SE = 0.017, 95% CI = 0.016, 0.091). Magnolia Warblers were the only species where the null model ranked as the most competitive model (β = 2.18, SE = 0.32, 95% CI = 1.45, 2.9). Presence of collinearity between all the explanatory variables made it difficult to extract the relative importance of each variable from the models.

2.5 Discussion

Our results suggest that, although species richness of migratory birds in native forest and oil palm plantations did not differ significantly, the community assemblages of migrant birds differed significantly between the two habitats. These results partially corroborate the findings of Bennett et al. (2018) in Guatemala, where species richness and diversity of migratory birds were similar in oil palm and secondary forest. The community assemblage in native forest was characterized by species with narrower habitat tolerances and less plasticity in habitat use and foraging behavior (e.g., Kentucky Warblers, Worm-eating Warblers, Wood Thrushes, Blue-winged Warblers, and Swainson's Warblers) (Forbush 1929, Ficken and Ficken 1968, Lack and Lack 1972, Greenberg 1987, Holmes and Robinson 1988, Graves 1998). Specifically, this group of sensitive birds includes species that tend to forage on arthropods lower in the forest understory (i.e., below 2 m) and leaf litter, representing a predominantly terrestrial insectivore guild (DeGraaf et al. 1985). Of these sensitive species, both Wood Thrushes and Kentucky Warblers have experienced substantial population declines over the past 50 years (DeGraaf and Rappole 1995, Sauer et al. 2017).

Mexican oil palm plantations in our study hosted a migrant bird community characterized by generalist species capable of using a diversity of habitats, including forest edge, disturbed forest, shrub, cultivated areas, and thickets (e.g., Magnolia Warblers, American Redstarts, Common Yellowthroats, Yellow Warblers, and Northern Waterthrushes) (DeGraaf and Rappole 1995). In addition, these species are insectivores that forage in lower canopy leaves and were the most represented feeding guild in the oil palm plantations (DeGraaf et al. 1985). Nevertheless, the presence of some forest-associated species in oil palm plantations (e.g., Wood Thrushes, Hooded Warblers, Ovenbirds, and Worm-eating Warblers) warrants further investigation. Native forest accounted for more than two thirds of the birds captured in our study, despite a similar number of net hours in both habitats. The greater abundance of migratory birds in oil palm plantations relative to native forest or hardwood plantations as reported by Bennett et al. (2018) and Moo-Culebro (2018) using point counts may, in part, be explained by differences in visual detectability in each habitat. Many species of migratory birds inhabit dense understory and vocalizations are infrequent during the winter (Robbins 1981). Lack and Lack (1972) noted that point counts were not effective in sampling Worm-eating Warblers in their wintering areas and, although not frequently observed, they were the fifth most common species captured using mist-nets in Jamaica. This pattern may hold for other species that do not sing or commonly vocalize in their wintering areas.

Differences in overall migratory bird density were explained by vegetation structural complexity (PC1). Greater complexity of vegetation was positively correlated with higher bird densities, suggesting that retaining or restoring structural complexity can benefit many migratory birds. Habitat value for migrant birds is directly related to vegetation complexity in shade coffee plantations (Gordon et al. 2007, Bakermans et al. 2009, Bakermans et al. 2012, Philpott and Bichier 2012, Colorado et al. 2018) and shade cacao farms (Greenberg et al. 2000, Reitsma et al. 2001, Van Bael et al. 2007). Unlike native forest and forest-like cultivars, oil palm plantations typically have uniform tree spacing and age structure, a lower canopy, sparse understory development, patchy or absent leaf litter, unstable microclimate, and a higher level of disturbance (Peh et al. 2006, Luskin and Potts 2011). These characteristics may contribute to a reduced density or absence of forest specialists like Wood Thrushes, Hooded Warblers, Ovenbirds, Worm-eating Warblers, and Kentucky Warblers.

We found that most species of migrant birds responded positively to several forest structural features. For example, in species-specific models, vegetation complexity was positively correlated with the density of Hooded Warblers. Given that Hooded Warblers are forest specialists (Greenberg et al. 2000), our results suggest that vegetation complexity plays a key role in winter habitat selection. Our results agree with those of previous studies where investigators found that understory vegetation below 0.7 m, including more sapling and shrub foliage, pro-vided high-quality foraging habitat for Hooded Warblers in their wintering areas (Keast and Morton 1980, Morton et al. 1987). We found that understory density influenced capture rates of Ovenbirds and American Redstarts across our study sites. Dense understory vegetation provides more heterogeneous habitat and more surface area for herbivorous insects that make up a large part of the diet of these two species. Hooded Warblers and Ovenbirds are classified as forest birds in Mexico (Greenberg 1992, Lynch 1992, Rappole et al. 1992, Greenberg et al. 2000) and prefer to forage in the lower understory near the forest floor (Rappole and Warner 1980), especially in leaf litter (Strong 2000). Most oil palm plantations are managed to maintain a low understory density of living plants or fallen leaf litter (Luskin and Potts 2011). However, the common practice of stacking pruned palm fronds between oil palm trees may provide foraging habitat and cover for some species of migratory birds. Other migratory species were observed foraging in dead frond vegetation (S. L. Oliveira, pers. comm.), including Hooded Warblers and Ovenbirds. For American Redstarts, capture rates were negatively associated with understory density, which may be a sampling artifact because they commonly forage in midstory vegetation and this stratum can vary in height in different habitats (Bennett 1980). Thus, higher capture rates in oil palm likely reflect the shorter vertical profile than that of native forest and the consequent limited reach of the mist-nets (3 m).

Additionally, DBH was a significant predictor of capture rates of Northern Waterthrushes in oil palm plantations. A larger DBH is usually associated with more mature forest and structural heterogeneity because larger trees can have more epiphytes. Although epiphytes probably benefit Northern Waterthrushes by providing microhabitats for arthropods that they can prey on in low vegetation, the main habitat feature for this species, presence of water (Smith et al. 2011, Whitaker and Eaton 2020), was not quantified and may be a latent variable. Oil palm plantations in our study had numerous water channels (built to prevent flooding during the wet season) where we commonly observed foraging Northern Waterthrushes. These plantations also have exposed soil with standing water throughout most of the winter season which likely attracts Northern Waterthrushes.

Tree species richness was positively correlated with our capture rate of Gray Catbirds. This species is known for its fruit-rich diet, especially in the fall and winter (Martin et al. 1951), and a greater diversity of tree species likely provides more diverse fruit resources, especially considering that Gray Catbirds will select habitat based on fruit availability (Martin 1985). Interestingly, oil palm fruits can also be a resource for Gray Catbirds because they were observed consuming oil palm fruits at our study site (S. L. Oliveira, pers. comm.). Additional study is needed to determine if oil palm fruits can influence the presence of Gray Catbirds in these plantations and if they benefit from the high fat content of oil palm fruits when preparing for spring migration. Determining if fruit consumption affects productivity of oil palms is also important. If so, identifying strategies to mitigate the consumption of oil palm fruits by birds to prevent persecution by farmers will be equally important.

Magnolia Warblers were the only species in our study with similar densities in oil palm plantations and patches of native forest, with no habitat element performing better than the null. Similarly, Johnson and Sherry (2001) found no correlation between vegetative characteristics and abundance of Magnolia Warblers in Jamaica. Instead, food availability positively affected the abundance of Magnolia Warblers and five other species of forest-canopy insectivorous warblers. Importantly, five of the six species in that study are considered habitat generalists, including Magnolia Warblers (DeGraaf and Rappole 1995) and, by definition, are not associated with particular habitat features. For example, in their wintering areas, Magnolia Warblers have been found in a diversity of habitats ranging from scrub and orchards to forest, with cleared fields being among the only unused habitats (Dunn and Hall 2020). Thus, structural elements may be less important in habitat selection by these warblers. We suggest that investigators in future studies in oil palm plantations address food availability as an explanatory variable and its interactions with habitat heterogeneity.

Although our sampling effort was constrained to one season, resulting in a small dataset, we were able to access important patterns of habitat selection by Neotropical migratory birds in native forest patches and oil palm plantations. Longer-term studies are needed to fully understand how the rapid expansion of oil palm agroecosystem impacts wintering populations of Neotropical migratory bird. In particular, how long-term climatic variability influence food resource abundance and subsequent habitat value for migratory birds in oil palm plantations. Another limitation of our study stems from the extensive deforestation in the study region, thereby preventing us from sampling primary forest as a baseline for comparisons. Overall, primary forests are expected to have richer bird communities, but this pattern may not hold true when considering only Neotropical migratory birds because secondary forests have been found to support more migrants than primary forests in wintering areas (Terborgh 1989, Petit et al. 1995, Rappole 1995, Stotz et al. 1996, Robinson and Terborgh 1997, Blake and Loiselle 2001, Chandler et al. 2013).

As expected, our results suggest that secondary forest patches are preferable to oil palm plantations for most Neotropical migratory birds. Native forests harbor a more abundant community of migrants, especially forest-dependent species that suffer from population declines and were found to be absent or nearly absent in oil palm plantations (e.g., Kentucky Warblers, Swainson's Warblers, Wood Thrushes, and Worm-eating Warblers). Therefore, retention of forest patches should be prioritized as a meaningful conservation strategy for migratory birds in southern Mexico. Our observed pattern of species richness between oil palm plantations and native forest patches suggests that oil palm does provide habitat, although of yet unknown value, for certain species of migratory birds in southern Mexico. The value of oil palm as habitat compared with other land uses and native forest patches requires further study. Differences in community assemblages and species-specific density were strongly influenced by habitat heterogeneity, similar to shade coffee and cacao farms in Latin America (Nájera and Simonetti 2010a). Results from previous studies suggest that understory vegetation is a key feature in structuring migratory bird communities in agroecosystems, and studies conducted in oil palm plantations have revealed higher bird richness and abundance where management practices allowed undergrowth (Aratrakorn et al. 2006, Bennett et al.

2018). In addition, Nájera and Simonetti (2010a,b) cleared understory vegetation in oil palm plantations to test its impact on resident and migrant bird communities in Guatemala, and found significant declines in avian abundance and richness when understory vegetation was removed. Specifically, only one of nine species of migratory birds remained in plantations after understory removal.

Although agroecosystems appear to differ in their capacity to provide the food or structural resources found in native forests, management aimed at enhancing forest-like conditions may increase the value of these agroecosystems for native biodiversity, including migrant bird communities (Brockerhoff et al. 2008). One approach would be management focused on increasing vegetative structure complexity and decreasing disturbance. More directly, based on our model results, key habitat features that should be targeted for maintenance or enhancement through management are under-story density and tree richness. Managing these characteristics by maintaining a denser understory, not removing sparse native trees from the already deforested “potreros” before planting oil palms, and including another tree species (e.g., native hardwood) could favor the migratory bird community and contribute to a more sustainable practice in oil palm production.

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2.8 Tables

Table 2.1. Results from the rarefaction analysis based on capture of migratory birds in native forest and oil palm plantations in Tabasco, Mexico. CI is 95% confidence interval and SD is standard deviation.

Habitat	**Observed richness**	**Estimated richness**	**CI**	**SD**
Native forest	19	19.81	2.79	1.42
Oil palm plantation	14	16.82	5.85	2.99

Table 2.2. Summary of the top models for predicting the density of migratory birds based on elements of forest structure in native forest and oil palm plantations in Tabasco, Mexico. wi = AICc weight, k = number of parameters, DBH = diameter at breast height.

Species	**Model**	**ΔAIC$_c$**	***wi***	***k***
Overall capture rate	Vegetation complexity^{+}	-	0.23	3
	Null	12.84	0	2
Northern Waterthrush	DBH^{+}	-	0.21	3
	Null	4.49	0.02	2
Gray Catbird	Tree richness^{+}	-	0.57	3
	Null	18.29	0	2
Ovenbird	Understory density^{+}	-	0.44	3
	Null	8.38	0.01	2
Hooded Warbler	Vegetation complexity^{+}	-	0.55	3
	Null	31.51	0	2
Magnolia Warbler				
	Null	-	0.47	2
American Redstart	Understory density^{-}	-	0.33	3
	Null	8.27	0.01	2

2.9 Figures

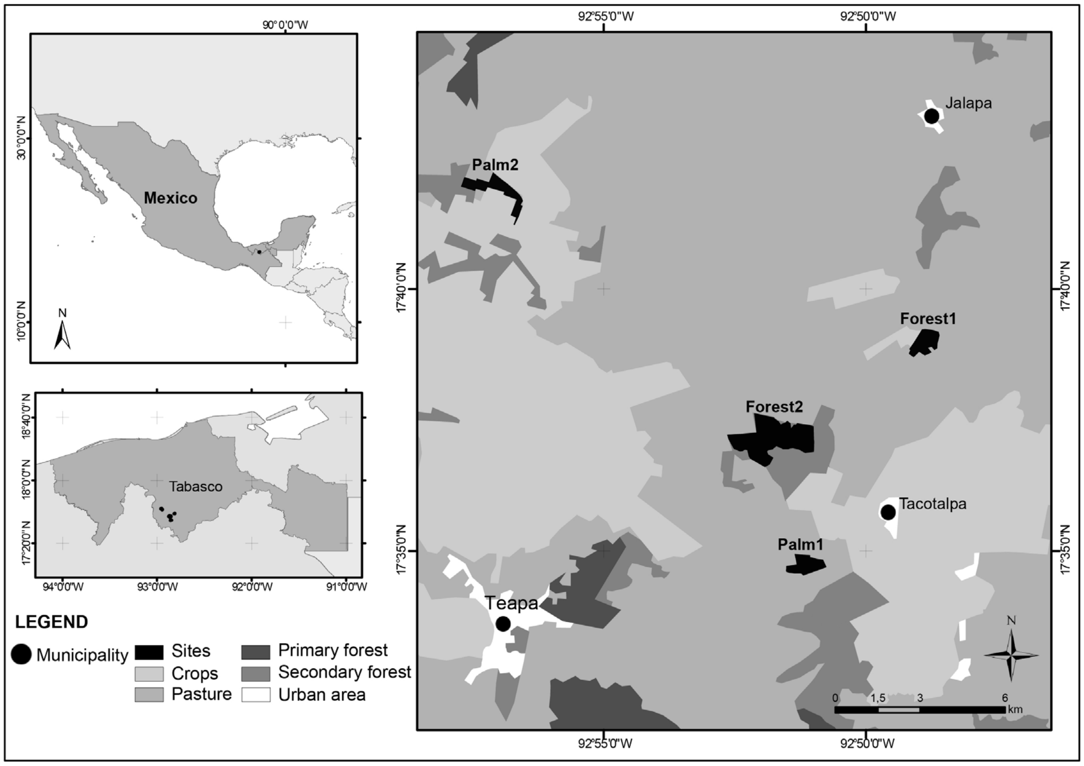

Figure 2.1. Study area, land characteristics and location of the two native forest fragments and two oil palm plantations where we sampled Neotropical migratory birds during the 2017-2018 winter season.

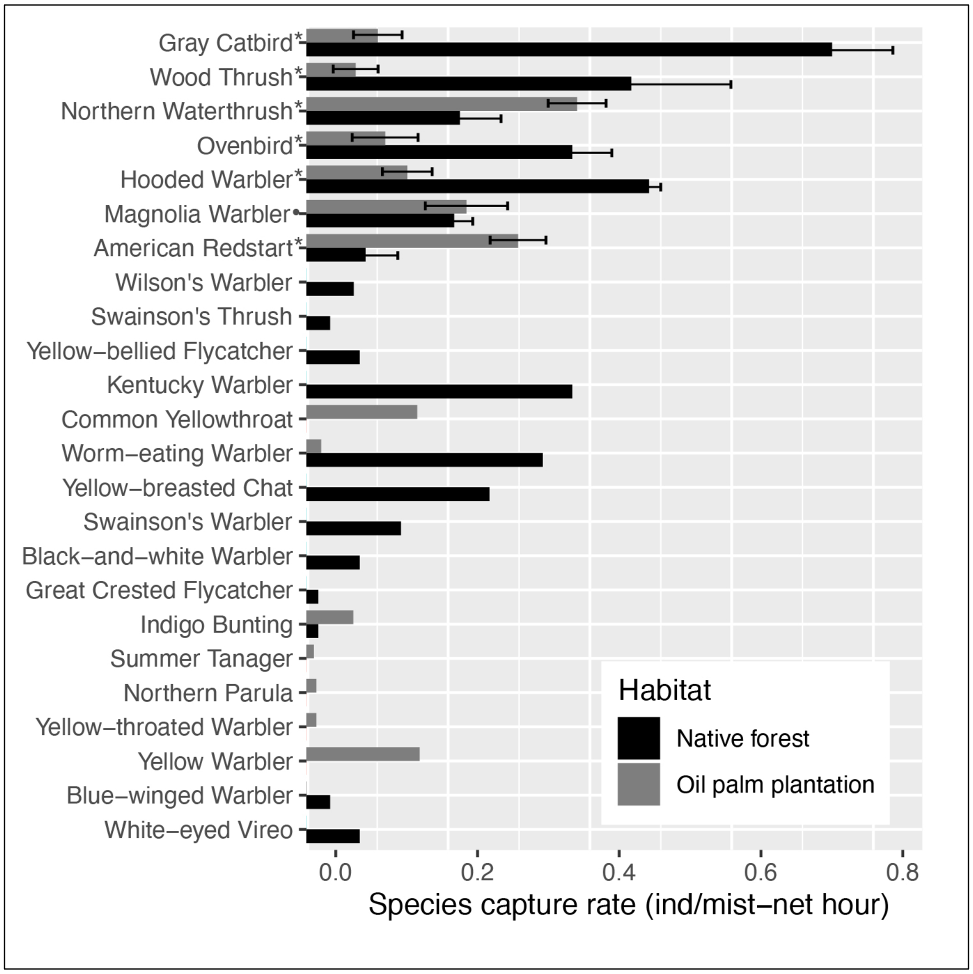

Figure 2.2. Mean capture rates (± SE) of migratory birds in Tabasco, Mexico. Note that we did have enough data to conduct t-tests or Wilcoxon tests for seven of the 24 species. * represents $P < 0.05$ and · is $P > 0.05$.

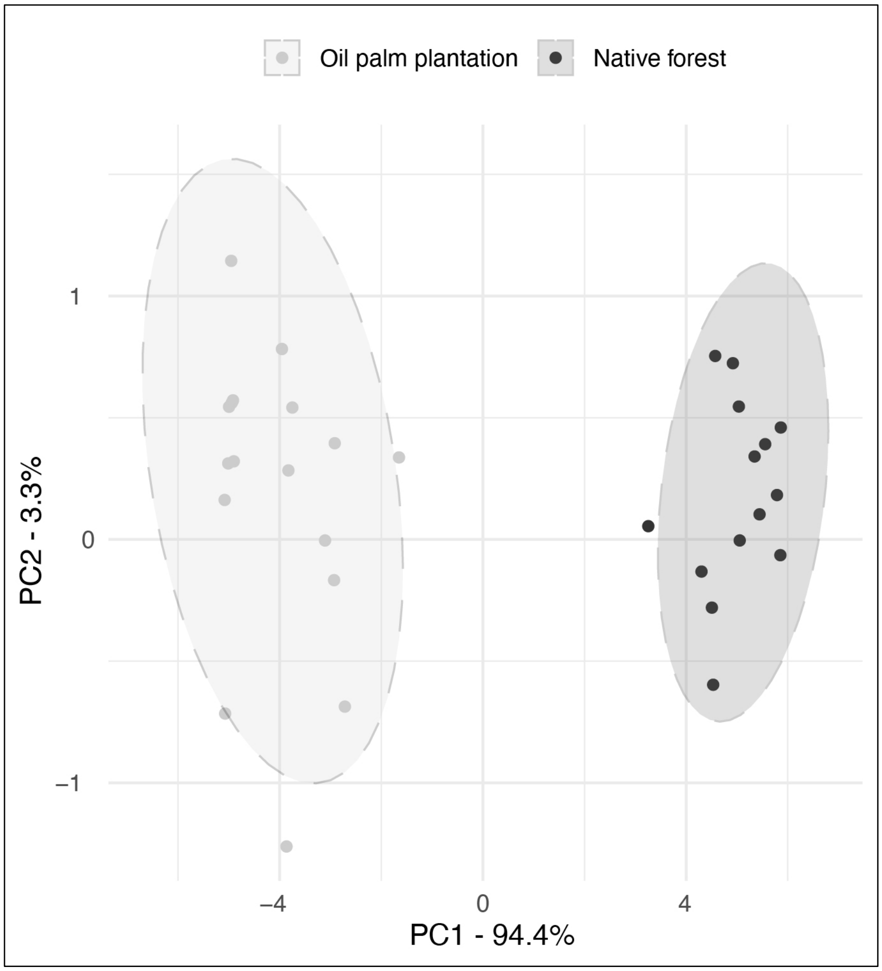

Figure 2.3. Visualization of the Principal Component Analysis (PCA) ordination of the difference in vegetation structure between oil palm plantations and native forest fragments where we included tree height, understory density, tree density, tree richness, canopy cover, mean DBH (diameter at breast height), and height of the tallest tree. Data were collected from six oil palm plantation sites and five native forest site in 2017-2018 in Tabasco, Mexico. Ellipses represent 95% confidence intervals around the centroid.

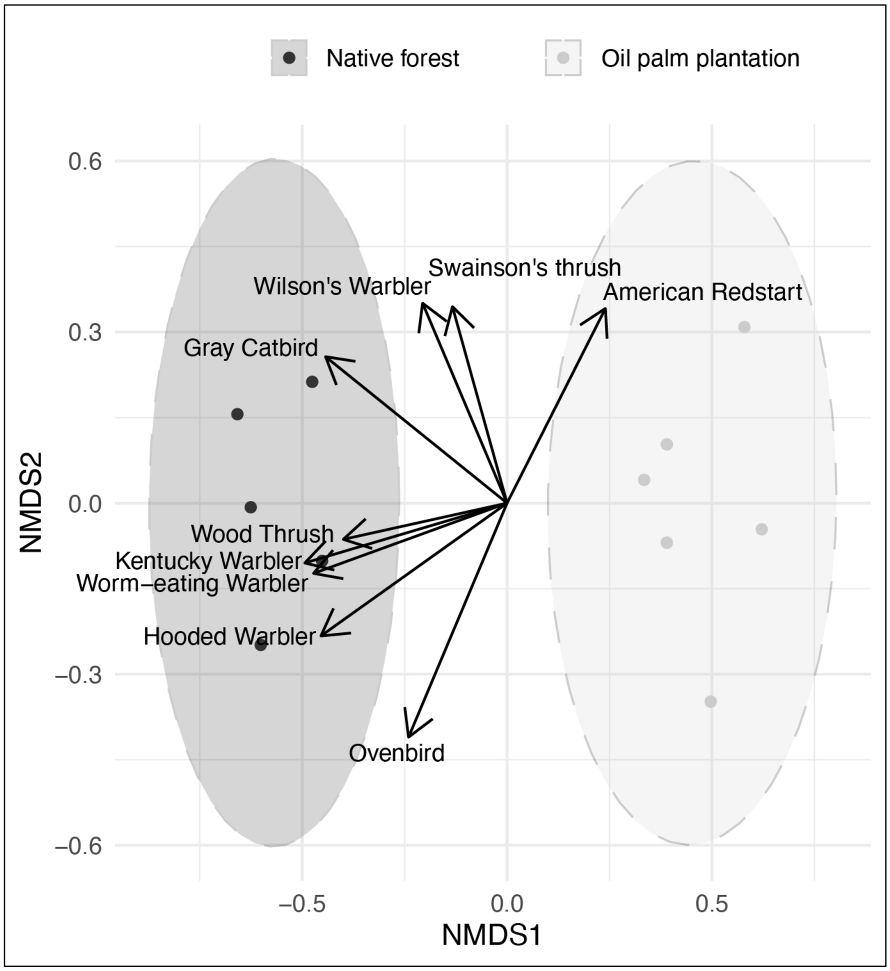

Figure 2.4. Visualization of the Non-metric Multidimensional Scaling (NMDS) ordination and vector fitting analysis where we included capture rates of 24 species of migratory birds captured in oil palm plantation and native forest. For vector fitting, we included only the nine migrant bird species that strongly influenced community differences between the two habitats ($P < 0.05$). Data were collected from six oil palm plantation sites and five native forest sites in 2017-2018 in Tabasco, Mexico. The ellipses represent 95% confidence intervals around centroids. Stress value = 0.071.

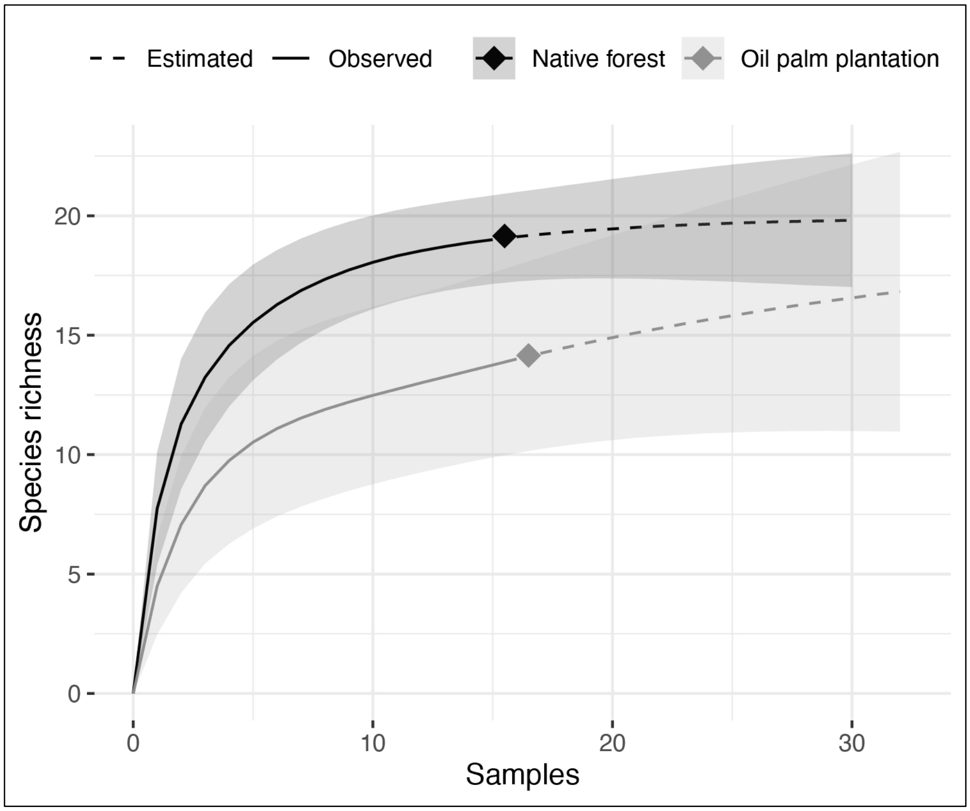

Figure 2.5. Rarefaction curve of estimated migratory bird species richness in native forest and oil palm plantation in Tabasco, México. Each sample represents one day of mist-netting in native forest and oil palm sites. Shaded areas represent 95% confidence intervals.

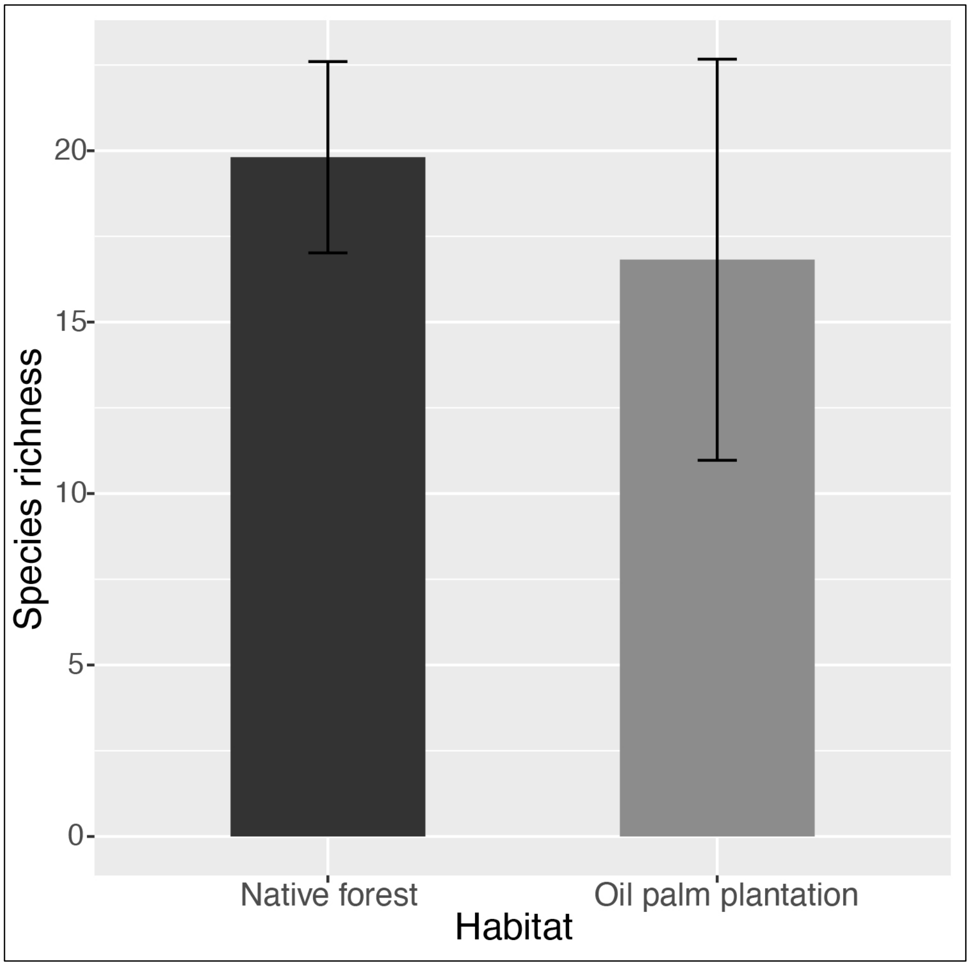

Figure 2.6. Estimated migratory bird species richness in native forest and oil palm plantation in Tabasco, México. Bars represent 95% confidence intervals.

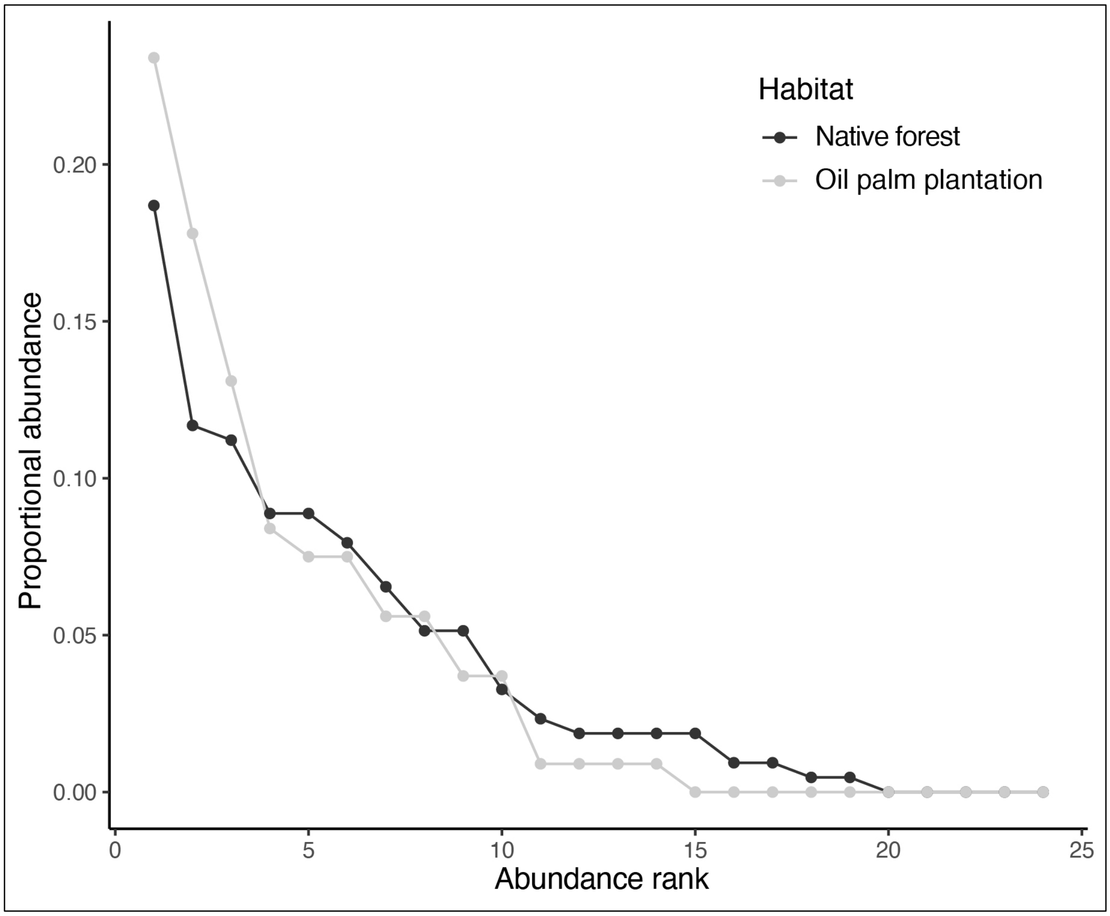

Figure 2.7. Rank abundance curves for the Neotropical migratory bird communities in native forest fragments and oil palm plantations in Tabasco, Mexico.

3 Do oil palm plantations provide quality habitat for migratory birds? A case study from Mexico[2]

3.1 Abstract

Habitat loss and degradation represent a major threat to Nearctic-neotropical migratory birds in the tropics. Managed agroecosystems have the potential to mitigate some impacts of land conversion, however, we know little regarding the quality of expanding oil palm plantation habitat for migratory birds in the neotropics. In this study, we used sex and age ratios, body condition, fat deposition, and muscle mass to assess oil palm habitat quality for seven species of migratory songbirds. Specifically, we captured individuals in native forest fragments and oil palm plantations in the state of Tabasco, Mexico, during two winter seasons (2017-2018, 2018-2019), and compared differences in age and sex ratios, and condition indices between habitats. We found that, when differences occurred, most species exhibited indicators of better habitat quality in native forest (older males with higher body condition indices) when compared to oil palm. Our results suggest that age and sex ratios combined with measures of physiological condition can be used to assess habitat quality for Nearctic-neotropical migratory birds overwintering in modified landscapes. Importantly, determining a species' territorial behavior is key when selecting a given indicator of habitat quality for each species, and in certain cases, more intensive approaches such as estimates of survival, territory size, and food availability may be needed. Our results suggest that management strategies that promote forest-like

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[2] The material containing in this chapter was previously published in the *Ecological Indicators*. See Oliveira, S. L., Flaspohler, D. J., Knowlton, J. L., and Wolfe, J. D. 2022. Do oil palm plantations provide quality habitat for migratory birds? A case study from Mexico. Ecological Indicators 139: 108964.

conditions in oil palm plantations will improve habitat quality for declining populations of Nearctic-neotropical migratory birds.

3.2 Introduction

Migratory bird demography is influenced by multiple and disparate habitats, often distributed across hemispheres, challenging conservation and management efforts (Greenberg and Marra, 2005). Populations of many species of Nearctic-Neotropical migratory birds have declined in recent decades (Robbins et al., 1989; Butcher and Niven, 2007), with estimates suggesting a dramatic loss of 2.5 billion birds over the past 50 years (Rosenberg et al., 2019). According to Johnson (2007), habitat loss and degradation represent the greatest threat to bird populations. Still, other factors such as building and window collisions, outdoor domestic cats, and reduced populations of arthropods contribute to widespread declines (Klem 1990; Erickson et al., 2005; Loss et al., 2012; Tallamy and Shriver, 2021). Identifying causal factors responsible for population declines among migratory species is often complicated given that experiences in distinct habitats, spread across hemispheres, can interact to dynamically affect an individual bird's fitness (Sherry and Holmes, 1995; Norris and Marra, 2007).

Broadly, bird populations may be limited by one or more discrete and identifiable factors, such as Brown-headed Cowbird (*Molothrus ater*) parasitism and jack pine (*Pinus banksiana*) mismanagement diminishing populations of Kirtland's Warbler (*Setophaga kirtlandii*) (Walkinshaw, 1983). Conversely, fitness of individual birds may be affected by carry-over effects, or interacting events experienced during different phases of the annual cycle. Carry-over effects have been best described in American Redstarts (*Setophaga ruticilla*) whereby subordinate individuals can be excluded from high quality winter habitats by dominant individuals, resulting in worse body condition, later departure dates, and lower reproductive success months later on the breeding grounds (Marra et al., 1998; Cooper et al., 2015). Irrespective of whether bird populations are regulated by discrete limiting factors, carry-over effects, or a combination of both, winter habitat quality often plays a key role in promoting or limiting population growth (Norris et al., 2004; Newton, 2007; Latta et al., 2016). Such relationship should be expected, especially when considering that Nearctic-neotropical migratory birds can overwinter from six to eight months in the tropics (Runge et al. 2015).

In the neotropics, deforestation and land conversion for pasture and row crops have been widespread for the last two centuries, with higher rates since the middle of the twentieth century (Aide et al., 2013; Graesser et al., 2015). Continued loss of winter habitat to agricultural expansion may prevent population level recovery of several migratory species (Faaborg, 2002; Rosenberg et al., 2016), like Wood Thrush (*Hylocichla mustelina*), Golden-winged Warbler (*Vermivora chrysoptera*) and Canada Warbler (*Cardellina canadensis*) whose population declines have been linked to land conversion and deforestation in Central and northern South America (Taylor and Stutchbury, 2016; Kramer et al., 2018; Wilson et al., 2018). However, certain agroecosystems, such as coffee plantations, can be managed to provide overwintering habitat for some species (Tejada-Cruz and Sutherland, 2004; Bakermans et al., 2009), resulting in the creation of bird-friendly coffee certifications that promote specific management guidelines to enhance bird habitat. Measures vary depending on the certification, but in all standards, canopy height and cover as well as structural and floristic complexity are part of the guidance to increase habitat quality (González-Prieto, 2018). Due to their economic importance, coffee and cacao have received the majority of attention from researchers seeking to understand the value of tropical agroecosystems for migratory birds. Additionally, the traditional or rustic coffee system used in warmer and drier environments, known as shade-grown, can host similar communities of migratory birds as those found in the native forest (Greenberg et al., 2000; Reitsma et al., 2001; Gordon et al., 2007; Van Bael et al., 2007; Bakermans et al., 2009; Bakermans et al., 2012; Philpott and Bichier, 2012; Colorado et al., 2018; Gonzáles et al., 2020). Shade-grown plantations are characterized by multistoried vegetation that mimics the structural complexity of natural forest.

One of the most rapidly expanding crops in the global tropics is oil palm (*Elaies guineensis*), which is grown for food and cosmetics (Foster et al., 2011). Palm oil is the most widely used cooking oil on earth, with global annual production rising from two million tons in 1970 to 71 million tons in 2018 (FAOSTAT, 2021). Overall, the majority of research focused on the impacts of oil palm agriculture on biodiversity has been conducted in Southeast Asia, where most of the global production is located, and presented a considerable negative impact on the bird richness and abundance following the conversion from native forest (Donald 2004; Aratrakorn et al. 2006, Edwards et al. 2010, Azhat et al. 2011, Savilaakso et al. 2014). Bird richness and foraging guild diversity also vary depending on farming systems, whereby smallholdings - especially those practicing polyculture - exhibit better indicators of habitat quality than plantation estates (Azhar et al. 2011, 2013,2014). Additionally, bird diversity was shown to be lower in oil palm when compared to other agricultural habitats like shaded cacao, rubber, and pasture (Donald 2004, Fitzherbert et al. 2008, Foster et al. 2011, Lees et al. 2015).

In Mesoamerica, Nearctic-neotropical migratory birds were shown to be abundant in oil palm plantations in Southeast Mexico during the northern hemisphere winter (Bennett et al. 2018, Moo-Culebro 2018), making this group of interest when investigating variation in overwintering habitat quality. Oil palm trees in this region are typically grown on previously deforested areas formerly used as pasture for cattle farming, in plantations with varying amounts of ground, understory, and epiphytic plants permitted to share the plantation, which likely facilitate the use of these plantations by some migratory birds (Bennett et al., 2018; Oliveira et al., 2021). To date, only a few studies in Latin America have assessed the value of oil palm plantations for migratory birds by comparing patterns of richness and demographic measures of habitat quality, such as overall and species-specific density in oil palm plantation, native forest, and other agricultural systems (Nájera and Simonetti, 2010; Bennet, 2018; Moo-Culebro, 2018; Oliveira et al., 2021). Results from these studies suggest that compared with pasture and other agricultural crops, oil palm plantations contain a relatively rich diversity of migratory birds. Still, the important question of whether oil palm plantations serve as demographic sources or sinks remains poorly understood.

Ornithologists have developed a variety of approaches to measure relative differences in habitat quality for birds. Broadly, these fall into two categories: 1) let the birds reveal habitat quality themselves by using indices of fitness (demographic measures, physiological condition, and others), and densities, or 2) directly measuring the habitat itself (food resources, vegetation, etc.) (Johnson 2007). Identifying an appropriate measure of habitat quality depends on several factors, including how variation in habitat quality affects bird attributes such as weight gain and territorial behaviors, which can decouple patterns of density from habitat quality (Fretwell and Lucas, 1969; Van Horne, 1983; Johnson, 2007). Although not comprehensively studied, many species of sexually dimorphic migratory birds display behaviorally mediated habitat segregation on the wintering grounds, with older males often occupying higher quality habitats compared to females and younger males, a characteristic of the *ideal despotic distribution* model (Fretwell and Lucas, 1969; Lynch et al., 1985; Ornat and Greenberg, 1990; Marra et al., 1993; Wunderle, 1995; Marra and Holmes, 2001). For such species, assessing habitat quality by comparing density can be misleading since high quality habitats are often occupied and defended by dominant individuals, which exclude conspecifics, meaning that high quality habitats may, in theory, have lower densities. Thus, among territorial migratory species, using age and sex classifications may serve as a meaningful index of hierarchical structures across a gradient of habitat quality. Additionally, variation in body condition, fat deposition and pectoral muscle mass across habitats may also provide valuable insights into relative measures of habitat quality for migratory birds (Holmes et al., 1989; Wunderle and Latta, 2000; Brown et al., 2002; Johnson, 2007; Cooper et al., 2015).

Here, we assessed migratory bird habitat quality in oil palm plantations and native forest using sex and age ratios and condition indices. Given that native forest is characterized by higher structural and floristic complexity relative to oil palm plantations (Oliveira et al., 2021), we hypothesized that native forest would provide concordantly higher habitat quality to migratory birds when compared to lower quality oil palm plantations. Given our hypotheses, we predicted that we would find: 1) among territorial species, adult males will be over-represented in higher quality native forest, while females and young males will be over-represented in presumed poorer quality oil palm plantations; 2) territorial species in higher quality native forest will show better physiological condition than individuals inhabiting oil palm plantations; and 3) non-territorial species will exhibit equal age and sex ratios, as well as equal physiological condition, across the native forest and oil palm plantation habitats.

3.3 Methods

3.3.1 Study area

The state of Tabasco, in southeast Mexico, was covered by moist lowland forest until the mid-1900s, when extensive deforestation and the expansion of pasture and agriculture transformed much of the region into a mosaic of second growth semi-deciduous forest, annual crops, hardwood plantations, and pasture (Tudela, 1989; Salazar-Conde et al., 2004; Sánchez-Munguía, 2005; Arriaga-Weiss et al., 2008). Agriculture and livestock account for about 65% of the Tabascan territory, including 20,000 ha of oil palm plantations (Briones-Salas et al., 2015; SIAP, 2017). Government incentives fueled the expansion of oil palm farming in the region about 25 years ago, primarily converting pasture for cattle to oil palm plantations (Tudela 1989). The average temperature in the region is 24º to 28ºC, and precipitation ranges from 2,500 to 4,000 mm (INEGI, 2015). Most of our fieldwork occurred during the cold front season (November—February). We conducted our samples in four native forest patches (17.7478ºN, -92.7986ºW; 17.6495ºN, -92.8146ºW; 17.6198ºN, -92.8565ºW; 17.7936ºN, -92.850456ºW) and seven oil palm plantations or estates (17.6133ºN, -92.8513ºW; 17.5788ºN, -92.8526ºW; 17.7667ºN, -92.7760ºW; 17.6473ºN, -92.8304ºW; 17.5714ºN, -92.8394ºW; 17.6992ºN, -92.9488ºW; 17.7652ºN, -92.7915ºW) in the municipalities of Jalapa, Tacotalpa and Teapa (Figure 3.1). All the forest patches were isolated, and not connected with continuous primary forests which are confined to mountainous areas. Native forest sites ranged from 11 to 276 hectares (98.5 ± 60.09 SE) and oil palm plantations ranged from 15 to 84 hectares (55.43 ± 10.37 SE). Due to logistical constraints, we focused our effort on similar ages of oil palm plantations (~ 12 years) to control for variation in vegetation structure due to oil palm growth. Plantations were managed similarly to the smallholding farms in Southeast Asia, characterized by medium to small sizes, independent owners, low use of mechanical harvest, and presence of different age stands (Azhar et al. 2011, 2014). Weed management was done manually by workers using machetes, with no herbicides used, differently than the common practices in Southeast Asia (Tohiran et al. 2017). Additionally, no oil palm site sampled was certified by the Roundtable on Sustainable Palm Oil (RSPO).

3.3.2 Field methods

We used 36 mm mist-nets (12 x 3 m) to capture migratory songbirds in nine native forest plots and 21 oil palm plots within the aforementioned sites, with one to ten mist-nets opened in each of the plots. The number of mist-nets opened was constrained by the number of trained banders available and capture rates. Nets were opened shortly after sunrise for four hours, except during rain. Fieldwork was conducted during two winter seasons, the first between 19 December 2017 and 27 March 2018, and the second between 16 October 2018 and 28 March 2019. The total sampling effort for the two seasons was 2,926 mist-net hours, 1,140 hours in native forest and 1,787 hours in oil palm plantations. In both seasons, we allocated more mist-netting hours to oil palm plantations to increase our capture numbers in this relatively understudied habitat. In the second season, we used playback to increase our capture rate. The playback used was a 5 min owl-mobbing (developed by Kenneth Rosenberg and Ruth E. Bennet, Cornell Lab of Ornithology, 2015) that proved to be effective in Guatemala (Bennet et al., 2018). It contains the song of two owl species, Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) and Eastern Screech-Owl (*Megascops asio*), and alarm calls from ten common migratory species. We broadcasted the recording for 15 min after opening mist-nets and repeated it each hour for another 15 min. On occasions when we caught high numbers of birds in the first net check, we did not repeat the owl broadcast to allow us to band and process all the birds safely. All captured migratory birds were marked with aluminum bands (United States Geological Survey), measured (tarsus and tail length, wing chord, exposed culmen), weighed (± 0.01 g), aged and sexed (following Pyle, 2007). We classified birds as either adults, AHY (after hatch year) and ASY (after second year), or as young HY (hatch year) and SY (second year). Fat deposition score was based on a modified scale from Holmes et al. (1989), where we observed the furcular fat and assigned a classification: N = no visible fat, L = 1-3 strands of fat, S = strands of fat merging into a continuous sheet in some places, H = fat nearly forming a continuous sheet but with some holes, F = continuous sheet of fat filling the furcula and G = continuous sheet of fat filling the furcula and spreading to other body parts. For pectoral muscle classification we followed Tonra et al. (2013), where 0 = muscle concave and keel prominent; 1 = muscle neither concave nor convex and keel prominent; 2 = muscle slightly convex and keel still visible; 3 = muscle convex and keel recessed.

3.3.3 Data analysis

3.3.3.1 Age and sex ratios

Previous research indicated that among territorial songbird species, females and young males may be subordinate to older males and are subsequently excluded from high-quality habitats (Marra, 2000). We assessed species-specific social dominance by grouping young males and females, irrespective of age class, as subordinates to compare with the adult male (dominant) group between habitats using a Chi-square test, or

Fisher's exact test when at least one cell in the contingency table of the expected frequencies was below five (Bower, 2003). Segregation patterns by dominants over subordinates are expected among species that follow an ideal despotic distribution (Fretwell and Lucas, 1969). However, for most overwintering migratory birds, it is unknown whether this behavior exists, especially for non-dimorphic species (Albert et al. 2020). Thus, we evaluated evidence for dominance hierarchies for species with enough captures, including those species in which territorial behaviors on the wintering grounds is not yet known.

3.3.3.2 Condition index

We generated a body condition index (mass corrected by body size), where correlations between body size (wing chord) and body mass was determined using a simple linear regression, where the residuals represent variation in body condition (Marra and Holmes, 2001; Labocha and Hayes, 2012). We tested the residuals for normality and homogeneity of variance and then used a one-way ANOVA to determine differences in body condition between forest and oil palm plantation. To ensure we were using data only from the stationary wintering period, excluding recent arrivals and birds preparing for spring migration, we used Pearson's correlation analysis to test the relationship between day of capture and body mass. Fat storage and muscle scores were analyzed using the Wilcoxon rank sum test.

3.4 Results

Over two winter field seasons we captured a total of 683 individuals, 242 in oil palm plantations representing 17 species of migratory birds, and 441 individuals in native forest representing 21 species of migratory birds (Table 3.1). Most of the sampled species did not have enough captures in both habitats to allow for statistical inference. Thus, we decided to focus on species with at least nine individuals captured in both habitats: American Redstart (*Setophaga ruticilla*), Hooded Warbler (*Setophaga citrina*), Magnolia Warbler (*Setophaga magnolia*), Gray Catbird (*Dumetella carolinensis*), Northern Waterthrush (*Parkesia noveboracensis*), Ovenbird (*Seiurus aurocapilla*), and Wood Thrush. Sex and age class segregation were analyzed for those species with sexual dimorphism: American Redstart, Hooded Warbler, and Magnolia Warbler. For non-dimorphic species, only age segregation was analyzed: Gray Catbird, Northern Waterthrush, Ovenbird, and Wood Thrush. Other than the Gray Catbird, all the assessed species are classified as insectivorous during the winter (DeGraaf et al., 1985; Martin, 1985). From the seven species assessed, five of the species have exhibited population declines in some part of their distribution, except for the Hooded Warbler and the Northern Waterthrush (Sauer et al., 2017; Rosenberg et al., 2016; Dunn and Hall, 2020, Smith et al., 2020). We were unable to assess habitat quality of oil palm and native forest for resident birds due to few captures.

American Redstart age and sex class distributions indicated a dominance hierarchy where adult males were over-represented in native forest (Fisher's Exact Test, $P = 0.033$, Figure 3.2). Our analysis suggested that the Hooded Warbler also exhibited a dominance hierarchy with adult males found most frequently in native forest (Fisher's Exact Test, $P = 0.029$, Figure 3.2). Conversely, Magnolia Warbler did not show a significant difference in sex or age class distribution between habitats (Chi-squared test, $P = 1$, Figure 3.3). We were only able to assess age distribution in non-dimorphic species; for the Gray Catbird, there was no detectable dominance hierarchy by age class (Chi-squared test, $P = 0.809$, Figure 3.4). Northern Waterthrush also did not show age segregation (Chi-squared test, $P = 1$, Figure 3.4). Ovenbird and Wood Thrush distribution did tend to exhibit a higher proportion of adults in native forest (Figure 3.5), although we found no significant difference between habitats (Fisher's Exact Test, $P = 0.378$ and $P = 0.324$, respectively). Both Ovenbird and Wood Thrush may exhibit age or class segregation, but the small number of individuals captured in oil palm plantations and the impossibility to determine the sex in the field could mask this pattern.

3.4.1 Body condition index

Three species differed in body condition between habitats (Table 3.2; Figure 3.6). American Redstart (ANOVA, $F_{(1,56)} = 8.455$, $P = 0.005$) and Gray Catbird (ANOVA, $F_{(1,101)} = 4.883$, $P = 0.029$) showed higher body condition in native forest. In contrast, Magnolia Warbler had significantly higher body condition in the oil palm plantations (ANOVA, $F_{(1,46)} = 4.222$, $P = 0.046$). Wood Thrush body condition tended to be higher in native forest, but the difference was not statistically significant (ANOVA, $F_{(1,59)} = 1.1$, $P = 0.299$). The small sample size for Wood Thrush in the oil palm plantation likely contributed to high variation, hindering a more accurate assessment of Wood Thrush.

3.4.2 Fat storage and pectoral muscle scores

Two species differed significantly with regards to the amount of deposited fat between habitats, the Gray Catbird was the only species that showed higher fat storage in the native forest (Wilcoxon rank sum test, W = 1131.3, $P = 0.037$, Figure 3.7); and, contrary to our prediction, American Redstart had higher fat deposits in oil palm plantations (Wilcoxon rank sum test, W = 147, $P = 0.049$). Our analysis found no species with significantly higher pectoral muscle scores in native forest (Figure 3.8).
Conversely, Magnolia Warbler showed higher muscle scores in oil palm plantations (Wilcoxon rank sum test, W = 181, $P = 0.029$).

3.5 Discussion

Habitat quality in the neotropics has been linked to demographic changes in migratory bird populations (Albert et al., 2020). Expanding oil palm agriculture in the neotropics, together with a high rate of deforestation and land conversion threatens migratory bird populations. While most researchers use audiovisual methods and estimates of density to assess habitat quality in the neotropics, we successfully used age and sex ratios coupled with condition indices to assess relative differences in migratory bird habitat quality between native forest and oil palm plantations.

Due to more complex vegetative structure in native forest when compared to oil palm (Oliveira et al., 2021, Figure 3.9), we hypothesized that each study species would exhibit indicators of higher quality (older birds in better condition) in native forest. Although most species adhered to our predictions, surprisingly, a few exhibited elevated physiological condition in oil palm plantations compared to native forest or showed no significant difference between the two habitats. American Redstarts, as expected, exhibited a pattern consistent with adult male dominance in native forest patches. The same pattern was found when comparing populations in mangrove and shrub habitats in Jamaica (Marra et al., 1993; Marra et al., 1998; Marra, 2000; Studds and Marra, 2008; Peele et al. 2015), forest and shrub habitats in southern Mexico (Ornat and Greenberg, 1990), and in primary forest in Venezuela (Bakermans et al., 2009). Dominant adult males exclude young males and females of any age class from high quality habitat, forcing them into suboptimal habitats (Newton, 2008). In such situations, subordinate individuals may adopt transient behavior, where individuals defend no territories and exhibit longer distance movements compared with territorial birds (Brown and Long, 2007). In the Dominican Republic and Jamaica, females and young males comprised most of the transient individuals of American Redstart (Wunderle and Latta, 2000; Peele et al., 2015). Overall, male-biased habitats are forested sites with wetter understories

(Sherry et al., 2020), likely reflecting more stable invertebrate food resources. Our results also suggested better body condition in American Redstarts using native forest than in oil palm plantation. Such differences in body condition may reflect sex and age segregation, and subsequent cascading effects of segregation on fitness during the nonbreeding season (Marra and Holberton, 1998; Marra and Holmes, 2001; Studds and Marra, 2005). Interestingly, we documented redstarts with higher fat loads in the oil palm when compared to native forest. In some species, elevated fat stores may serve as insurance when faced with unpredictable food resources in suboptimal habitat (Cooper et al., 2015).

Likewise, Hooded Warbler showed adult male-biased segregation in native forest patches. This result corroborates previous findings where males occupy mature forests and females are more commonly found in shrub and disturbed habitats (Lynch et al., 1985; Morton et al., 1987; Ornat and Greenberg, 1990; Stutchbury, 1994). Nevertheless, physiological condition did not vary between forest and oil palm habitats. Similarly, Conway et al. (1995) found no difference in Hooded Warbler survival rates between mature and early successional habitats. Furthermore, after experimental removal of territorial males from forests, no females using adjacent shrub areas moved to the purportedly higher quality vacant territories. This could indicate dissimilar habitat selection across the sexes and/or non-exclusion by males. It may be that females are adapted to select secondary forest and shrub habitats during the winter, reducing competition for territories and food resources with males (Morton et al., 1987).

Our results suggested no dominance hierarchy among Magnolia Warblers across native forest and oil palm at our study sites. Populations of this species exhibited a tendency for females to select drier shrubby habitats in Quintana Roo, Mexico (Ornat and Greenberg, 1990). Since oil palm plantations have continuous canopy cover throughout the winter, it is possible that changes in humidity are not as pronounced as in the subdeciduous forests of the Yucatan Peninsula, resulting in similar food resource distributions for Magnolia Warblers across habitats. Additionally, among the Parulidae family, the Magnolia Warblers are regarded as an adaptable bird, being found overwintering in a broad range of habitats except recently cleared fields (Dunn and Hall, 2020); as such, this species likely does not exhibit a strong aversion to degraded forest habitats (Reed, 1992; Robbins and Esterla, 1992). In fact, populations in oil palm plantations had better body conditions and higher pectoral muscle scores than those found in native forest. Food availability has been shown to drive Magnolia Warbler abundance (Johnson and Sherry, 2001); thus, we hypothesize that Magnolia Warblers may benefit from less interspecific competition for food resources due to the overall lower density of migratory birds in oil palm plantations (Oliveira et al., 2021).

The Gray Catbird was the only non-sexually dimorphic species assessed that exhibited dissimilar condition indices in native forests when compared to oil palm plantations. Birds in native forest had better body conditions and higher subcutaneous fat storage. Gray Catbirds tend to select more forested sites during the winter compared to the breeding grounds (Smith et al., 2020), likely due to habitat selection associated with fruit availability (Martin, 1995). Gray Catbirds are known to have a fruit-rich diet in the winter (Martin et al., 1961), and tree species richness is correlated with higher Gray Catbird density in native forest patches (Oliveira et al., 2021). Fat deposition was also correlated with habitat quality for Gray Catbirds during spring migration (Dunn, 2001), showing that physiological condition may serve as a good indicator of habitat quality for the species.

For Northern Waterthrush, no differences in age ratios or condition indices were found between native forest patches and oil palm plantations. Although this species has been shown to exhibit territorial mediated dominance hierarchies on the wintering grounds (Smith el al., 2010; 2011), we found no evidence of age segregation. Our results may reflect oil palm management at our study sites: high precipitation in the wet part of the winter season is mitigated by digging channels crossing the entire plantation to drain water and decrease flooding. Considering that Northern Waterthrushes have preference for foraging on the ground near wet soils, mud, water surfaces and pools (Smith et al., 2011; Rappole and Warner, 1980), individuals may find suitable habitats with enough food during the winter months in these plantations (Smith et al., 2010; 2011).

On the wintering grounds, Ovenbirds are known to prefer forested sites, but can also use a variety of non-forested habitats (Rappole et al., 1992; Porneluzi et al., 2020). The ability to pray on ants opportunistically, the main food item in the winter, may be related to their use of a variety of habitats during the nonbreeding season (Strong, 2000), and could explain their generalist behavior (Wunderle and Waide, 1993). For example, in the Bahamas, Ovenbirds exhibited similar capture rates and body mass in different habitats including shrub, mangrove, early successional and secondary forest (Murphy et al., 2001). Sex and age ratios were also similar among sedentary and floater individuals in Jamaica (Brown and Sherry, 2008). Our study was the first to assess age ratios and condition indices of Ovenbirds in oil palm plantations. Similarly, we found no significant differences in age ratios or condition indices between habitats. Without the possibility of sexing individuals in the field, density and food availability seem to perform better as habitat quality indicators for wintering Ovenbirds (Strong and Sherry, 2000; Brown and Sherry, 2006; Oliveira et al., 2021).

Lastly, although Wood Thrushes tended to have higher body condition and an over representation of adults in native forest patches, we failed to find a significant difference. The small sample size in oil palm plantations (*n* = 10) likely resulted in elevated variance and hindered statistical inference. Also, wandering behavior is more common in poor quality habitats (Winker, 1989), and this group can have higher fat depositions than sedentary birds (Winker, 1990), which can complicate the use of condition indices when territoriality cannot be determined. McKinnon et al. (2015) monitored Wood Thrushes throughout the winter and found faster declines in body condition, fat deposition, and muscle mass among individuals using disturbed forest and shrubby areas by the end of the season, when compared with mature forest. Additionally, females were more abundant in dry habitats in Belize and in small fragments in Costa Rica, suggesting male mediated dominance (Roberts, 2007; McKinnon, 2017). Considering that Wood Thrush select forested habitats during the winter, territory densities may be much lower in oil palm plantations than in native forest patches (Graham and Blake, 2001; Oliveira et al., 2021; Stanley et al., 2021), and individual Wood Thrushes in oil palm may represent floaters occupying a suboptimal habitat.

For species that did not exhibit a difference in age or sex class, or physiological condition between native forest and oil palm plantations, more intensive approaches such as mark-recapture for survival estimates, territory mapping, or genetic markers for sex determination should be used to assess habitat quality. For example, with knowledge of sex, researchers found that Northern Waterthrushes increased and decreased body condition in wet habitats and drier habitats, respectively, when monitored through the entire winter; territoriality was more common in wetter habitats and males showed more positive mass changes than females (Smith et al., 2010; 2011a; 2011b). Ovenbird body condition was positively related to food abundance during the winter (Brown and Sherry, 2006). Similar to Northern Waterthrush, Wood Thrush body condition declined throughout the winter in suboptimal habitats (McKinnon et al., 2015). Moreover, sedentary individuals had lower mortality rates than wanderers, which are more commonly found in poor quality habitats (Winker et al., 1990).

Conversion of native tropical forest into oil palm has notable and negative impact on avian diversity (Fitzherbert et al. 2008; Edwards et al., 2010). Studies focused on the effect of oil palm plantations on migrant birds in the Neotropics are scarce. As expected, our study suggested that the native forest provides better habitat quality for most of our study species. Nevertheless, some species can apparently adapt to this recently introduced agroecosystem in the Americas, primarily generalists like Magnolia Warbler, Northern Waterthrush, Common Yellowthroat, and Yellow Warbler (Nájera and Simonetti, 2010; Bennett et al., 2018; Oliveira et al. 2021). Species that forage low in understory and leaf litter for arthropods are considered vulnerable to deforestation and habitat degradation (DeGraaf and Rappole, 1995), including loss of structural complexity caused by oil palm cultivation (Oliveira et al., 2021). Wood Thrush and Ovenbird are part of this group in our study and tended to present better indicators in the native forest, although not significantly so.

According to Azhar et al. (2015, 2017), the most widely used oil palm certification (RSPO) does not account for important managements that benefit bird diversity, like habitat heterogeneity and understory vegetative complexity. Studies conducted in shaded coffee plantations highlighted the importance of structural and floristic complexity (González-Prieto, 2018), mostly based on birds' richness and abundance, and could be used as a baseline for the oil palm certification in the Neotropics. However, it is recommended that requirements for certifications include further steps to increase the sustainability of oil palm cultivation. A combination of demographic, distributional, and individual indicators, accounting for each species' life history, could be adopted to assess the value of the oil palm agroecosystems for birds and provide a tool to support certification programs for bird-friendly oil palm.

3.6 Conclusion

Based on our findings, we recommend several additional steps to advance our understanding of anthropogenic habitat quality for Nearctic-neotropical migratory birds in the tropics: 1) identify territorial behaviors to determine if densities (for non-territorial species) or demographics, age ratios, sex ratios, territory size should be used (for territorial species); 2) sex and age segregation appears to be a useful indicator of habitat quality for sexually dimorphic species where dominant birds exclude individuals from good quality habitats; 3) densities or direct measures of important resources (e.g., food abundance) can be used for both territorial and non-territorial species. Identifying why some working landscapes appear to provide higher quality habitats relative to others represents an important line of inquiry with potential to benefits for declining populations of species that use oil palm plantations such as Wood Thrush, American Redstart and Gray Catbird (Rosenberg et al. 2016; Rushing et al., 2016; Smith et al., 2020). Lastly, given that our results indicate that native forest provides higher quality habitat than oil palm plantations, we should develop management strategies that create forest-like conditions in oil palm plantations, including increased floristic and structural complexity.

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3.9 Tables

Table 3.1. Neotropical migratory birds captured in native forest and oil palm plantation in Tabasco, Mexico.

Species	**Native forest**	**Oil palm**
Cardellina pusilla	5	
Catharus ustulatus	3	
Dumetella carolinensis	91	20
Empidonax flaviventris	5	1
Geothlypis formosa	32	
Geothlypis trichas	4	28
Helmitheros vermivorum	29	1
Hylocichla mustelina	52	10
Icteria virens	17	2
Limnothlypis swainsonii	12	
Mniotilta varia	7	1
Myiarchus crinitus	1	
Parkesia noveboracensis	31	50
Passerina cyanea	1	11
Piranga rubra		1
Seiurus aurocapilla	40	9
Setophaga americana	1	2
Setophaga citrina	65	15
Setophaga dominica		2
Setophaga magnolia	28	23
Setophaga petechia		17
Setophaga ruticilla	9	49
Vermivora cyanoptera	2	
Vireo griceus	6	

Table 3.2. Means and standard errors of body condition indices from Neotropical migratory birds captured in native forest and oil palm plantation in Tabasco, Mexico.

Species	**Native forest**	**Oil palm**
Setophaga ruticilla	0.233 ± 0.11	-0.043 ± 0.04
Setophaga citrina	0.012 ± 0.08	-0.048 ± 0.16
Setophaga magnolia	-0.093 ± 0.07	0.120 ± 0.08
Dumetella carolinensis	0.268 ± 0.28	-1.112 ± 0.51
Parkesia noveboracensis	-0.151 ± 0.13	0.092 ± 0.13
Seiurus aurocapilla	-0.017 ± 0.18	0.077 ± 0.3
Hylocichla mustelina	0.203 ± 0.48	-1.037 ± 1.08

3.10 Figures

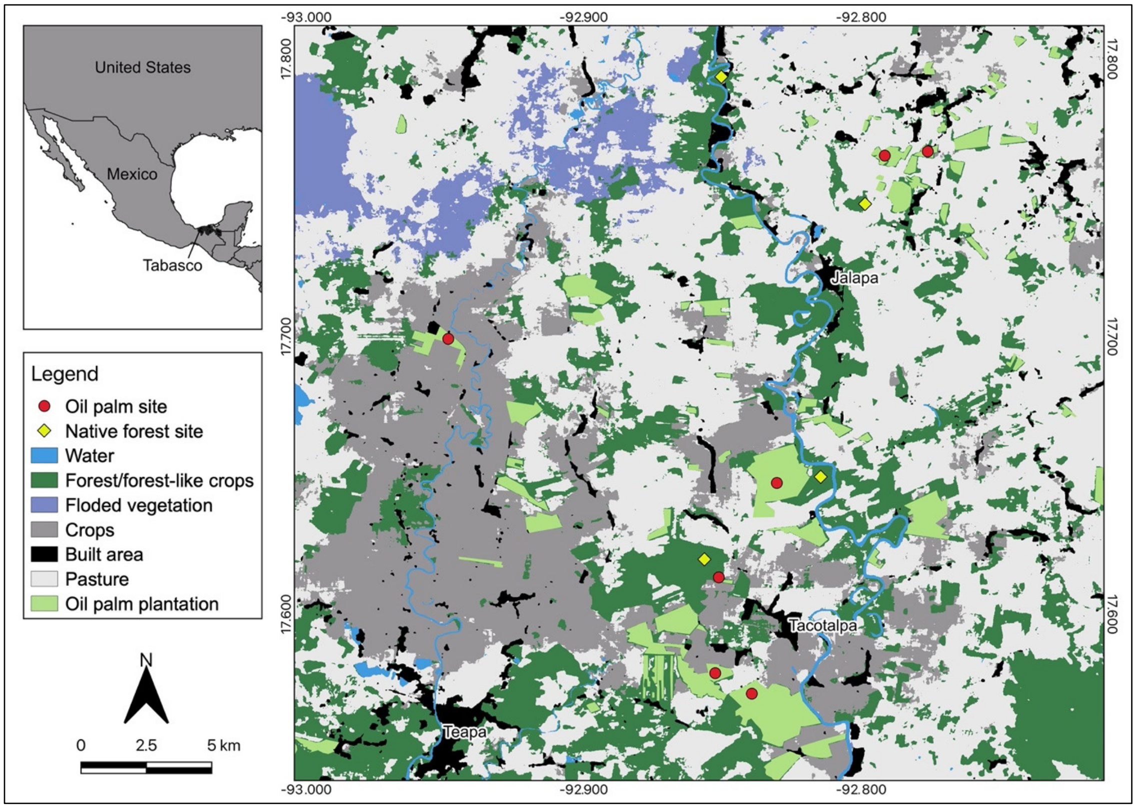

Figure 3.1. Location of the native forest and oil palm plantations where Neotropical migratory birds were captured in Tabasco, Mexico.

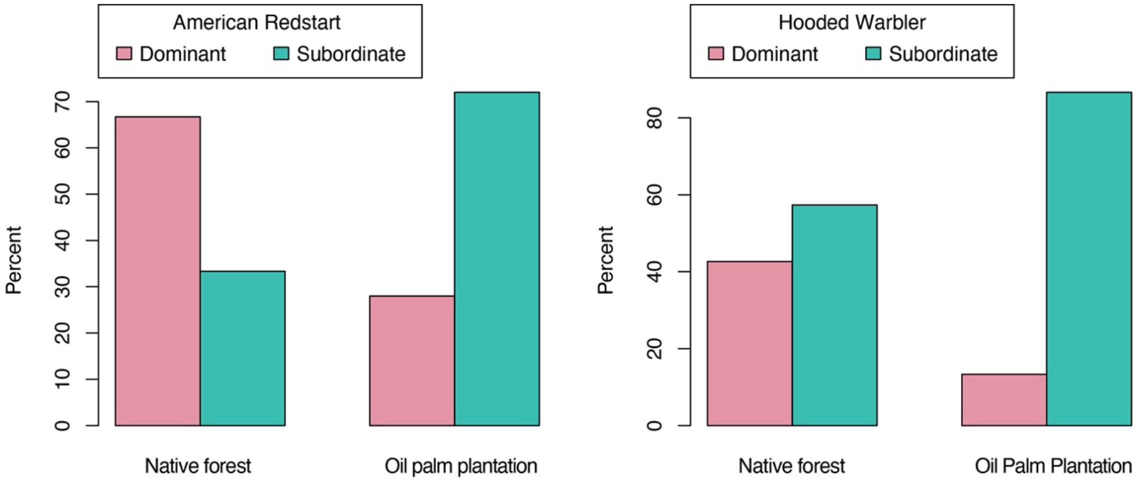

Figure 3.2. Age and sex class distributions of American Redstart (*Setophaga ruticilla*) and Hooded Warbler (*Setophaga citrina*) in native forest and oil palm plantation in Tabasco, Mexico. Dominant = adult males. Subordinate = adult and young females and young males.

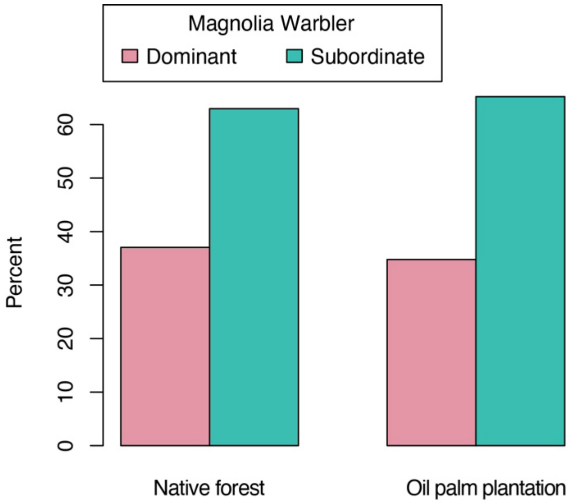

Figure 3.3. Age and sex class distributions of Magnolia Warbler (*Setophaga magnolia*) in native forest and oil palm plantation in Tabasco, Mexico. Dominant = adult males. Subordinate = adult and young females and young males.

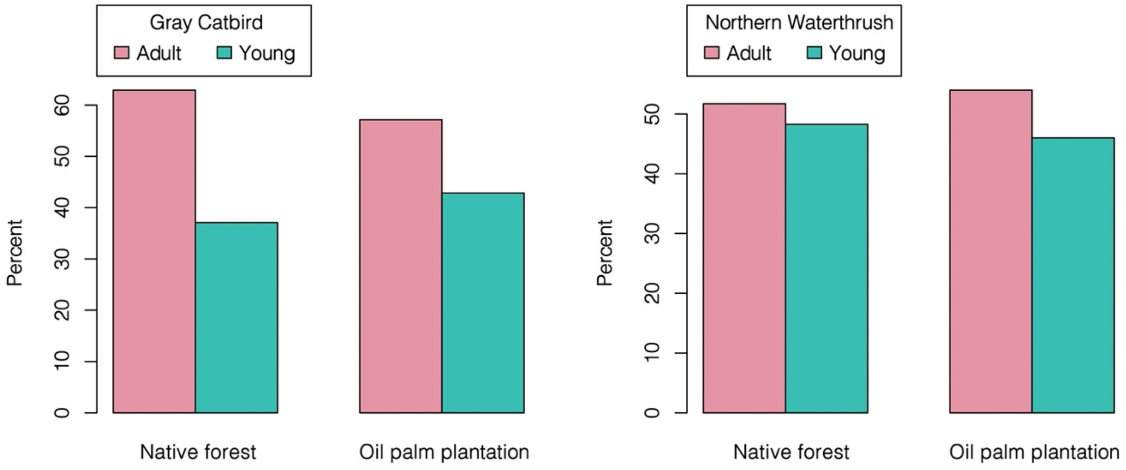

Figure 3.4. Age class distributions of Gray Catbird (*Dumetella carolinensis*) and Northern Waterthrush (*Parkesia noveboracensis*) in native forest and oil palm plantation in Tabasco, Mexico.

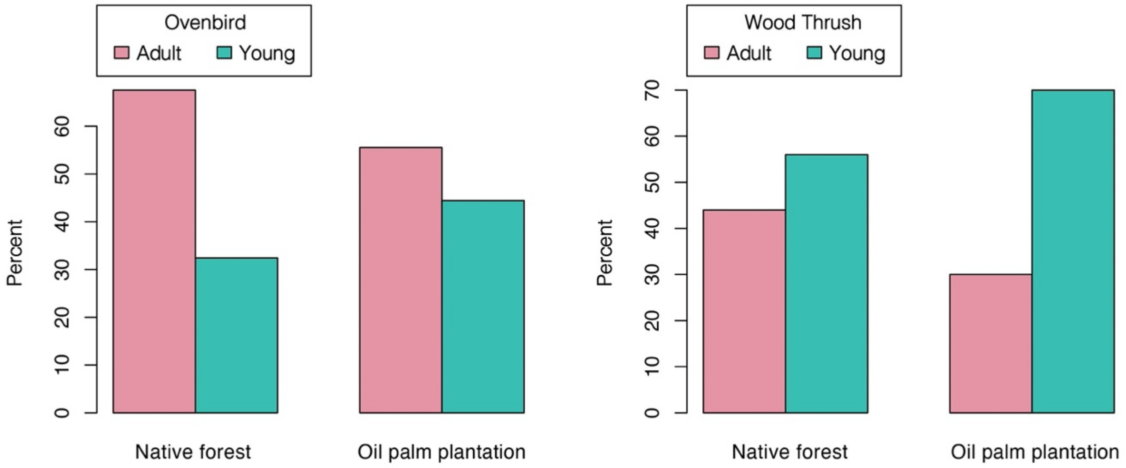

Figure 3.5. Age class distributions of Ovenbird (*Seiurus aurocapilla*) and Wood Thrush (*Hylocichla mustelina*) in native forest and oil palm plantation in Tabasco, Mexico.

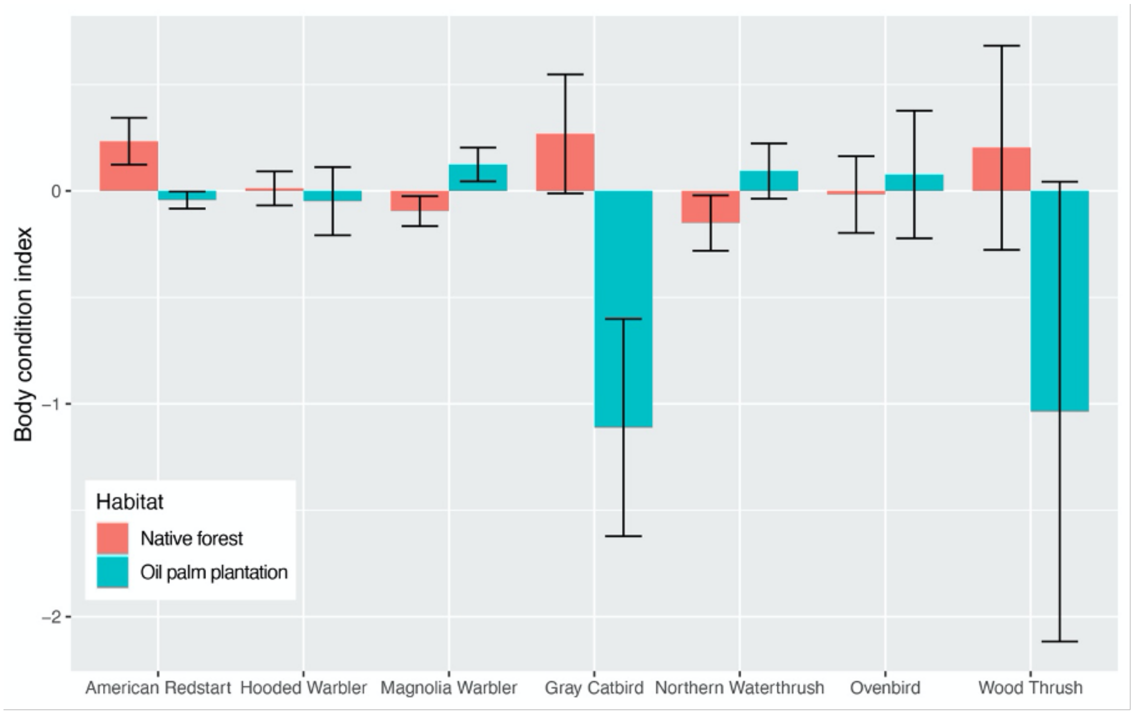

Figure 3.6. Body condition index for Nearctic-Neotropical migratory birds in native forest and oil palm plantations in the state of Tabasco, southeast Mexico. Bars represent standard error.

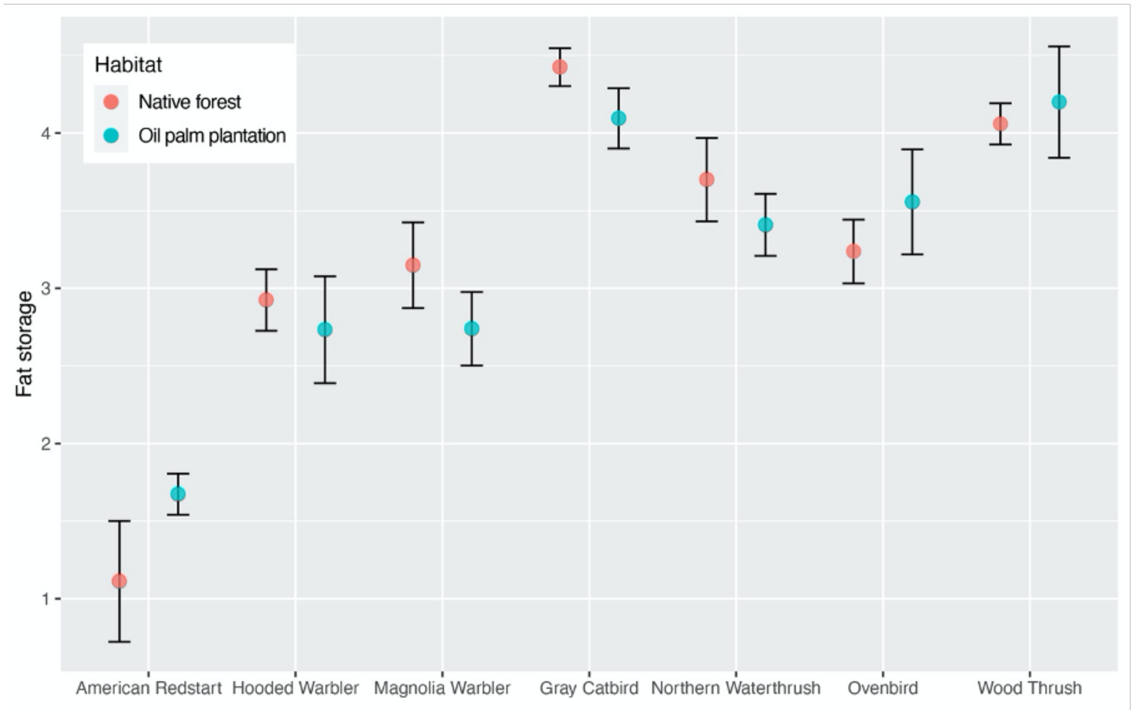

Figure 3.7. Fat storage for Nearctic-Neotropical migratory birds in native forest and oil palm plantations in the state of Tabasco, southeast Mexico. Bars represent standard error.

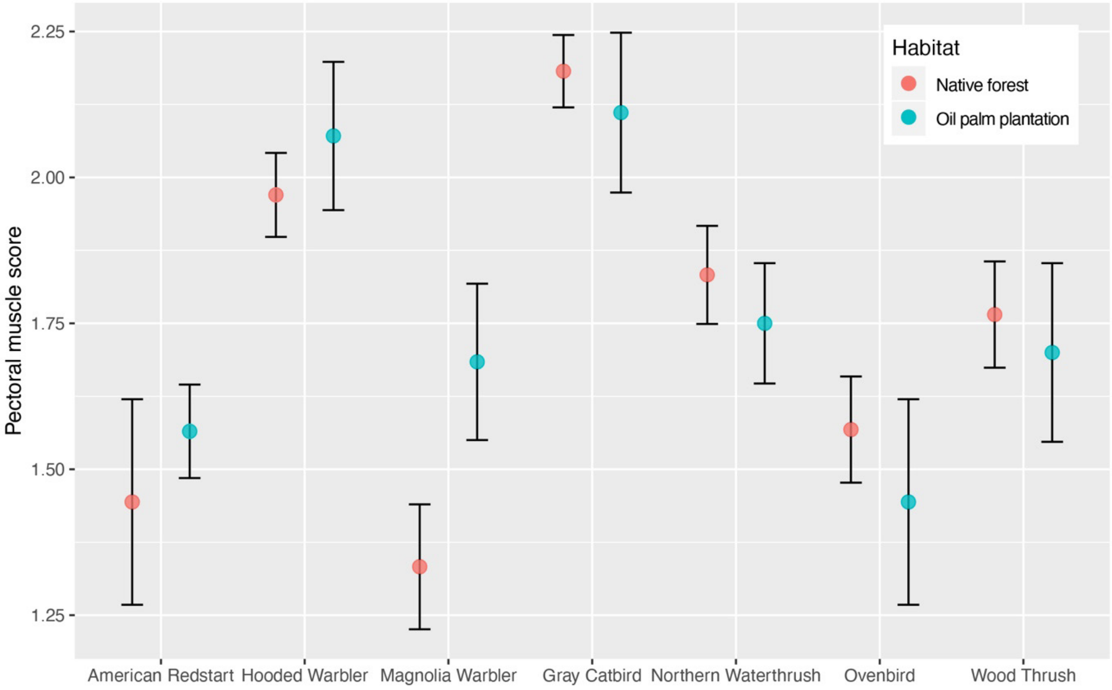

Figure 3.8. Pectoral muscle scores for Nearctic-Neotropical migratory birds in native forest and oil palm plantations in the state of Tabasco, southeast Mexico. Bars represent standard error.

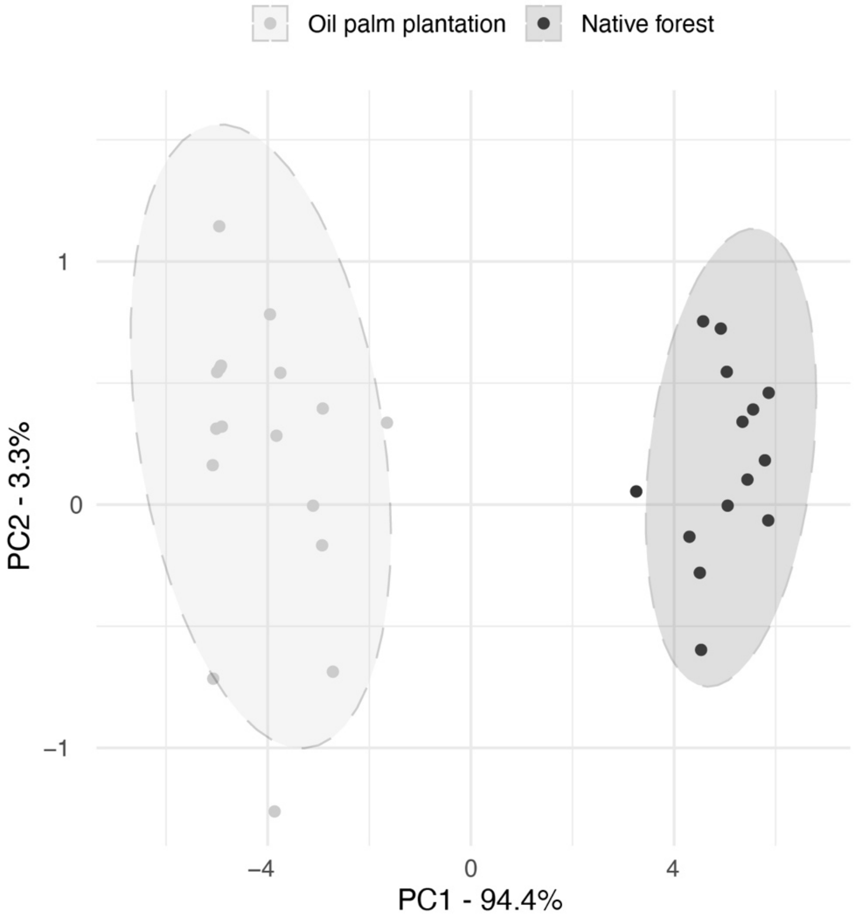

Figure 3.9. Visualization of the Principal Component Analysis (PCA) ordination of the difference in vegetation structure between oil palm plantations and native forest fragments where we included tree height, understory density, tree density, tree richness, canopy cover, mean DBH (diameter at breast height), and height of the tallest tree. Data were collected from six oil palm plantation sites and five native forest sites during the winter season of 2017-2018 in Tabasco, Mexico. Ellipses represent 95% confidence intervals around the centroid. Reprinted from "Migratory bird community structure in oil palm (*Elaies guineensis*) plantations and native forest fragments in southern Mexico," by S. L. Oliveira, D. J. Flaspohler, J. L. Knowlton, C. R. Webster and J. D. Wolfe, 2021, Journal of Field Ornithology, 92.

4 Winter territoriality of the American Redstart in oil palm plantations[3]

4.1 Abstract

Aspects of territorial behavior of Nearctic-neotropical migratory birds during the non-breeding period are poorly studied. Information about territoriality, site persistence, between-year site fidelity, and home range size is not available for most birds, especially in working landscapes. The American Redstart (*Setophaga ruticilla*) is considered a model for population dynamics in the tropics; however, territoriality behavior was only assessed in disparate native habitats. In this work, we determined territorial aspects of the American Redstart in oil palm plantations in the State of Tabasco, Mexico. Although rapidly expanding in the Neotropics, studies of the value of this agroecosystem for migratory birds are scarce. We assessed territorial behavior and home range size using radio tags for individual relocation in two winter seasons. We were able to estimate ten home ranges, seven in oil palm plantations and three in native forest patches. The average home range size was 0.25 ha. When considering the habitats separated, we estimated 0.29 ha in oil palm plantations and 0.17 ha in native forest. Albeit presenting larger home range size in oil palm plantations, which could indicate poor habitat quality, the difference in both habitats was not statistically significant. Our results suggest that the American Redstart is highly territorial in oil palm plantations. Additionally, home range size could be an important indicator of habitat quality for American Redstarts in the tropics. Our results emphasize the importance to determine territoriality dynamics, especially in working landscapes, since good habitat availability in the tropics could be limiting migratory bird populations.

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[3] The material contained in this chapter is in preparation for submission to *Wilson Journal of Ornithology*.

4.2 Introduction

Most Nearctic-neotropical migratory birds tend to adopt territorial behavior during the breeding season, even returning to the same site after the winter season, known as between-year site fidelity (Gauthreaux 1982). Using the same site likely provides energetic advantages due to the previous knowledge of the area and increased foraging success (Greenwood et al. 1982). Such territorial behavior is also believed to be common among such migrants on the wintering grounds (Rappole and Wagner 1980, McNeil 1982, Greenberg 1984), however, ecological information is highly skewed toward the breeding season (Marra et al. 2015).

One of the Neotropical migrants with the most information available during the non-breeding season is the American Redstart (*Setophaga ruticilla*). This species is considered a model for population dynamics studies in the tropics, including one of the earliest studies to demonstrate carry-over effects on migratory birds, showing that habitat quality in the winter can influence reproductive success in the summer (Marra et al. 1998, Norris et al. 2004). Redstarts display territoriality and adult male dominance in the tropics, whereby adult males exclude females and young males from high-quality habitats like mangroves (Marra et al. 1993, Marra et al. 1998, Marra 2000, Studds and Marra 2005, Peele et al. 2015) and primary and secondary forests (Ornat and Greenberg 1990, Bakermans et al. 2009, Oliveira et al. 2022). Subordinate groups are forced into suboptimal habitats (Newton 2008), characteristic of the ideal despotic distribution model (Fretwell and Lucas 1969).

Demographic indicators of habitat quality, like species density, could be misleading where dominance behavior occurs (Johnson 2007). Alternative indicators include distributional and individual measures, such as sex and age ratios, fitness variation (e.g., body condition index, fat and muscle scores), spring departure date, seasonal survival rate, site persistence, rate of transient behavior, and territory size. Specifically, transient behavior occurs when otherwise territorial birds do not hold territories and frequently undergo long-distance displacement (Brown and Long 2007). Transient American Redstarts tended to be females and young individuals of both sexes (Wunderle and Latta 2000, Peele 2015, Peele et al. 2015) and are more common in poor habitats (Lefebvre et al. 1994, Toms 2011, Toms 2013). Additionally, resource availability can be assessed by estimating territory size. Birds in good quality territories do not need to forage long distances when compared to individuals in poor habitats, and thus territory size is inversely correlated with habitat quality (Stenger 1958, Brown 1964, Wilson 1975). Previous studies assessed American Redstart home range size in different types of native vegetation, such as mangrove, dry forest, second-growth dry limestone shrub forest, wet limestone forest, and lowland coastal forest (Holmes et al. 1989, Toms 2011, Cooper et al. 2014).

Although the American Redstarts exhibit a skewed preference for undisturbed forests during the winter (Sherry and Holmes 1996), populations also use a diversity of habitats, from forest edges, young secondary forests, and regenerating pasture (Reid et al. 2008, Sherry et al. 2020), as well as working landscapes, like shade coffee plantations in Puerto Rico and Venezuela (Wunderle and Latta 2000, Bakermans et al. 2009), and cacao plantations in Mexico (Greenberg et al. 2000). Furthermore, recent surveys showed that American Redstarts are fairly common in oil palm plantations (*Elaies guineensis*) in southern Mexico (Moo-Culebro 2018, Oliveira et al. 2021). This agroecosystem is expanding rapidly in the Neotropics where it often replaces secondary forests or pasture (Foster et al. 2011). For this reason, understanding the role of oil palm as winter habitat for Nearctic-neotropical migratory birds is of utmost importance. To our knowledge, no information is available about the territoriality and home range size of American Redstarts in oil palm plantations. Understanding these habitat selection decisions can provide insight into the value of oil palm to wintering birds, and such information is vital to predicting the long-term viability of populations in these human-modified landscapes (Hostetler et al. 2015). Our objectives were: 1) determine if American Redstart held territories in oil palm plantations, 2) estimate the territory size, and 3) compare territory size between oil palm and native secondary forests. Given the high territoriality and dominance behavior exhibited by the American Redstart in other parts of their winter range, we hypothesized that birds would maintain territories in both habitats and that individuals using the lower quality habitat (i.e., oil palm plantations) would have larger territories due to lower resource availability.

4.3 Methods

4.3.1 Study area

This study took place in southeast Mexico in the state of Tabasco where the original moist tropical forest has largely been converted to cattle pasture, known as “potreros”, as well as crops like banana, corn, hardwood, and most recently oil palm plantations (Tudela 1989, Arriaga-Weiss et al. 2008). This process resulted in just a few secondary forest remnants remaining in lower elevations. The climate in the region is characterized by an average temperature of 24° to 28°C and precipitation ranging from 2,500 to 4,000 mm (INEGI 2015). We collected data during two winter seasons, 2017-2018 and 2018-2019, and most of the fieldwork took place during the stationary migratory period (November - February), in the municipalities of Jalapa, Tacotalpa, and Teapa. Study areas included one secondary native forest site (17.6495°N, -92.8146°W) and three oil palm plantations (17.5788°N, -92.8526°W; 17.6992°N, -92.9488°W; 17.6473°N, -92.8304°W). The secondary forest patch included 60 ha and was isolated from other woodlands, and the oil palm plantations ranged from 46 to 84 ha (mean 63.3), were characterized by similar age (~ 12 years), and presented no adjacent contact with native forest.

4.3.2 Field methods

This work is part of a project focused on the use of oil palm plantations by Nearctic-neotropical migratory birds. Mist-netting was used to capture birds to assess habitat quality through various indicators, including species abundance, community composition, fitness indices, and age and sex segregation (Oliveira et al. 2021, 2022). Concurrently with the bird captures (see Oliveira et al. 2022), we outfitted 16 American Redstarts with 0.3 g radio telemetry transmitters (Advanced Telemetry Systems model no. 2414) attached using eyelash glue on the trimmed lower back of the birds. To increase the chance that we were putting transmitters on territorial individuals, we only attached the tags on birds recaptured at least once on the same mist-net line. Tracked individuals were also color banded with a unique color combination to facilitate identification by resighting.

4.3.2.1 Tracking

After release, birds were relocated using handheld radio receivers (ATS model 410) and a three-element Yagi antenna (ATS model 148-152). Because American Redstart relocation methodology was mainly constrained by the 14-day battery life of the transmitter, we based our tracking on burst sampling (Barg et al. 2005). However, we spaced the interval between relocations every 5-min to guarantee that the individuals would have enough time to move to any point in their home range. Cooper et al. (2015), have suggested that because American Redstarts have relatively small territories in the winter, 30-sec between locations is sufficient for sampling independence. Observers tracked the birds until they could confirm a location visually or until the signal strength was sufficient that we were confidently within 10 meters of the bird and recorded a GPS point (Universal Transverse Mercator). We relocated the individuals no less than three days apart and collected no more than five points per day. We stopped tracking the individuals when the transmitter battery died, when the transmitter accidentally fell from the bird's back, or when no signal was not located in the territory or within a 150 meters radius from the last location.

4.3.3 Data analysis

We estimated home range size for individuals with at least 20 GPS relocations using the minimum convex polygon calculated by the package "adehabitatHR" (Calenge 2006) in program R (R Core Team 2020). The difference in home range size between oil palm plantations and native forest was compared using a one-way ANOVA. Normality of residuals and homogeneity of variance were checked prior to the test.

4.4 Results

We attached 16 radio transmitters on American Redstarts, from these individuals we were able to collect the minimum of 20 GPS point relocations (mean 30.7) for 10 birds. We estimated the home range size for seven individuals in oil palm plantations and three individuals in the native forest patch. Overall mean home range size, including both native forest and oil palm plantations, was 0.25 ha (± 0.03 SE). Home range size ranged from 0.18 to 0.42 ha (mean 0.29 ± 0.04 SE) in oil palm plantations, and from 0.07 to 0.24 ha (mean 0.17 ± 0.05 SE) in native forest (Table 4.1). Our results suggest that, on average, American Redstarts have larger territories in oil palm plantations than in the native forest (Fig. 4.1). However, the difference was not significant (ANOVA, $F_{(1,8)} = 3.72$, $P = 0.09$). Two individuals captured during the first season were recovered in the second season, both in oil palm plantations. The rate of inter-annual site fidelity could not be assessed with the relatively small sample size; however, we did estimate the home range size of one individual in both seasons. The bird was a juvenile male during the first season and held a 0.34 ha territory, while in our second field season the territory size was very similar at 0.29 ha (Fig. 4.2). Additionally, although a year apart, the two home ranges included significant spatial overlap based on the minimum convex polygons (Fig. 4.3).

4.5 Discussion

Although considered a suboptimal habitat for the American Redstarts in the wintering grounds (Oliveira et al. 2021, 2022), the oil palm plantations were still used by the species, which also exhibited territorial behavior in our sites in southern Mexico. Winter territoriality and sexual segregation have been shown to exist in American Redstarts overwintering in more natural forest habitats in the Neotropics (Marra et al. 1993, Parrish and Sherry 1994). Our study is the first to identify territorial behavior in a monoculture surrounded by other human-modified land covers, broadening our understanding of the way migrants sort and distribute themselves across a wide gradient of habitat quality on the wintering grounds.

Because they have been shown to arrange themselves according to the ideal despotic distribution, the presence or abundance of an American Redstart at a given site does not indicate that the individuals are in their preferred habitat. This is a common misconception, especially for generalist birds with broader habitat tolerances (Peele 2015). In the case of the American Redstart, prey availability, influenced in part by humidity, play an important role in determining habitat quality for individuals inhabiting different classes of native vegetation areas (Studds and Marra 2007, Cooper et al. 2015). In Venezuelan shade coffee (Bakersman et al. 2009), citrus orchards in Jamaica (Johnson et al. 2006), and oil palm plantations in Mexico (Bennett et al. 2018, Oliveira et al. 2021), the observed higher densities of Redstarts, when compared with native vegetation could lead one to believe that these agroecosystems provide similar or higher quality habitats. Further assessments in citrus and oil palm plantations, using distributional and individual indicators, showed that these monocultures are likely to represent poor habitats for American Redstarts (Johnson et al. 2006, Oliveira et al. 2022), due to significant lower body condition, sex and age segregation, and between-winter survival.

Our overall home range estimates, including native forest and oil palm plantations, was 0.25 ha, similar to the values reported for native vegetation in Jamaica, 0.25 and 0.3 ha (Holmes et al. 1989, Cooper et al. 2014) and Puerto Rico, 0.39 ha (Toms 2011). The mean home range size in the Tabascan native forest (0.17 ha) was also close to the value reported by Cooper et al. (2015) in Jamaica, 0.16 ha. The area defended by territorial birds can be used as a proximate cue to assess food availability (Stenger 1958, Smith and Shugart 1987), and ultimately habitat quality. Our results suggest that, although not statistically significant, American Redstart home range size tended to be larger in oil palm plantations than in native forests. Despite a small sample size, we observed a pattern that suggests that home range size varies with the habitat quality for this species in this landscape. This pattern was shown in overwintering Wilson's Warblers (*Cardellina pusilla*) in Veracruz, Mexico, where individuals defended smaller territories in conserved forests than in disturbed lowland forest-covered sites (Ruiz-Sánchez et al. 2017). On the breeding grounds, Red-eyed Vireos in West Virginia defended smaller territories in areas with more caterpillars (Marshal and Cooper 2004). Likewise, Ovenbirds in eastern Tennessee, held smaller territories in sites with higher prey abundance (Smith and Shugart 1987). Conversely, sedentary Ovenbirds did not change to floater behavior, expand territory size, or move their home ranges when their food supply was experimentally reduced in Jamaica. This suggests that other mechanisms may be influencing home range size in the wintering grounds, such as agonistic interactions with also sedentary adjacent individuals (Brown and Sherry 2008).

Inter-season winter site fidelity has been observed among American Redstarts (McNeil 1982, Faaborg and Arendt 1984, Holmes et al. 1989, Holmes and Sherry 1992, Johnson et al. 2006b, Sherry and Holmes 1996, Wunderle and Latta 2000, Peele 2015).

Our work is the first to describe this behavior in oil palm plantations with the recovery of two individuals captured in the first winter season. Furthermore, the home range overlap exhibited by one individual monitored in both seasons suggests that the American Redstart exhibits high site fidelity even in poor-quality homogenous habitats like the oil palm plantations. Between-year site fidelity is considered advantageous as a result of individuals returning to a familiar site (Gauthreaux 1982, Greenwood and Harvey 1982, Stamps et al. 2005). The rate of between-year return of wintering birds is expected to be highly correlated with food abundance and predictability, thus serving as an index of habitat quality (Marra et al. 1998, Johnson and Sherry 2001, Latta and Faaborg 2002, Wunderle et al. 2014). However, this pattern could be detrimental, specifically in highly territorial species, since the individuals can continue using poor-quality habitat that they were able to occupy in the previous season, even if high-quality habitat is available (Warkentin and Hernández 1996). This could explain why American Redstarts, excluded from high-quality habitats, would return, and defend the same poor-quality territory in the next season. Further long-term studies monitoring populations using oil palm plantations would be helpful in estimating the between-year return rate, the proportion of sedentary and floaters, site persistence, survival, and the variation of these indicators over the years. Such understanding could be used to assess the viability of the populations using this and other human-modified landscapes.

According to Sherry and Holmes (1996), the American Redstart's preference for less disturbed forested habitats in most of its winter distribution suggests that human land use change in the wintering range has contributed to the population decline in recent decades, a decline of 12% in the breeding population over the last 45 years (1970-2014) (Rosenberg et al. 2016). Because Nearctic-neotropical migratory birds overwinter in a region much smaller than the breeding grounds (Terborgh 1989), the loss of quality habitat during the winter is especially troubling. Evidence indicates that some habitats occupied by Redstarts in the Neotropics seem to be saturated due to elevated density (Marra et al. 1993, Sherry and Holmes 1996, Cooper et al. 2015, Marra et al. 2015). Rushing et al. (2016) have suggested that reproductive success may ultimately be limited by the quality of the winter habitat. This emphasizes the importance of home range estimates, especially in non-natural vegetations, since good habitat availability could be limiting the population. Lastly, determining territoriality and the average home range sizes in human-modified landscapes in the tropics could help to assess the wintering population size, which is often unavailable for Nearctic-neotropical migratory birds. Such estimates could be used to compare with the breeding population estimates and better monitoring the declining trend.

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4.8 Tables

Table 4.1. Home range estimates of territorial American Redstarts (Setophaga ruticilla) during the non-breeding season in Tabasco, Mexico. Two estimates for the individual SR6 are reported, each one for a different season.

Bird	**Home range (ha)**	**Vegetation**	**Sex**	**Age**
SR1	0.421	Oil palm	Male	Adult
SR2	0.181	Oil palm	Male	Young
SR3	0.071	Native forest	Male	Adult
SR4	0.248	Native forest	Male	Adult
SR5	0.182	Native forest	Male	Adult
SR6	0.344	Oil palm	Male	Young
SR7	0.360	Oil palm	Male	Young
SR8	0.241	Oil palm	Male	Adult
SR6	0.292	Oil palm	Male	Adult
SR14	0.182	Oil palm	Male	Young

4.9 Figures

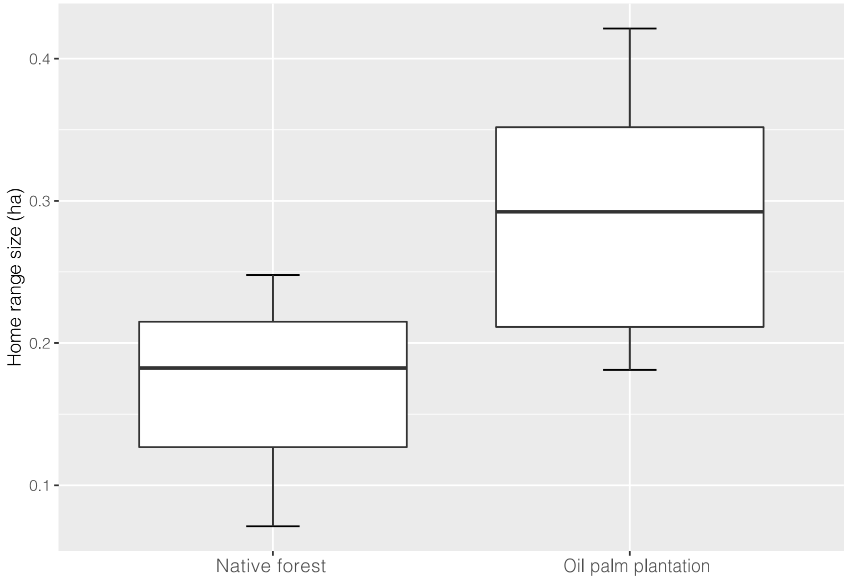

Figure 4.1. Boxplot of mean home range size of American Redstarts (*Setophaga ruticilla*) in oil palm plantations (*Elaies guineensis*) and in native forest in Tabasco, Mexico. Lines represent, in bottom-up order: minimum, first quartile, median, third quartile, and maximum.

Figure 4.2. Pictures of the American Redstart (Setophaga ruticilla) (SR6) captures in the first (left) and the second (right) wintering season, in oil palm plantations (*Elaies guineensis*), Tabasco, Mexico.

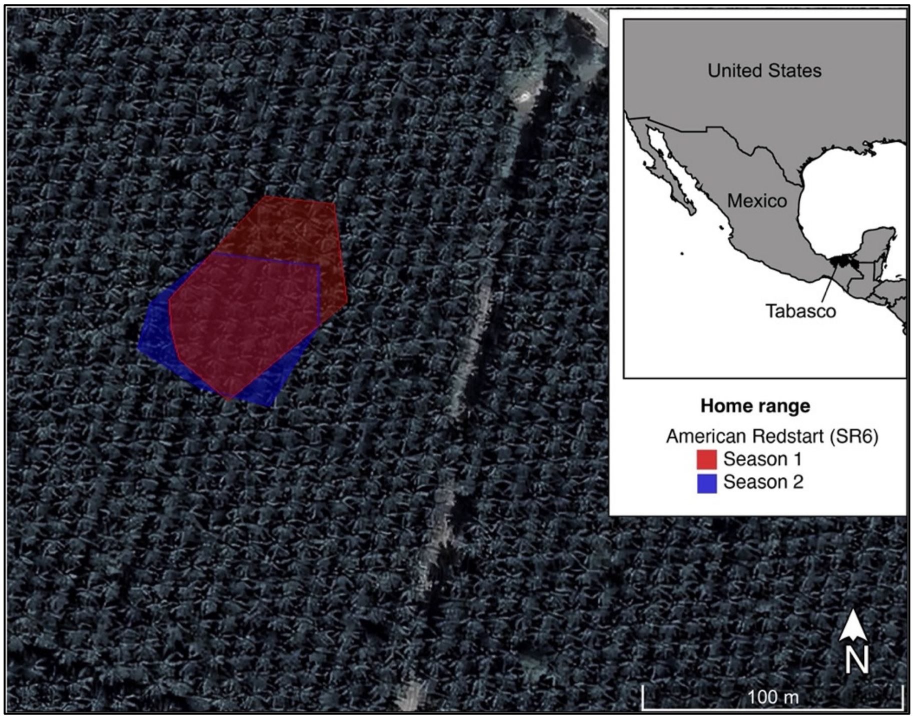

Figure 4.3. Oil palm plantation (*Elaies guineensis*) home range of the same American Redstart (*Setophaga ruticilla*) (SR6) on two consecutive wintering seasons, in the state of Tabasco, Mexico. The first season is represented by the transparent red polygon (0.34 ha) and the second season by transparent blue (0.29 ha).

5 The role of forest fragments in the conservation of Wood Thrush (*Hylocichla mustelina*) in Costa Rica[4]

5.1 Abstract

The Wood Thrush (*Hylocichla mustelina*) population decline of 62% during the past five decades has been associated with forest loss on the wintering grounds. Nevertheless, most of its population (83%) in the core winter range is found in unprotected secondary forest fragments in agricultural regions. The conservation value of these forest patches surrounded by a working landscape matrix is poorly studied, especially for declining migratory birds. We used indices of physiological conditions, estimates of territory size, and forest structure and physical characteristics, to determine how Wood Thrush habitat quality varied across a diversity of forest fragment sizes in Costa Rica. We used target mist-netting to capture Wood Thrushes in 12 forest patches ranging from 3 to 500 hectares in the Sarapiquí county, during the winters of 2019-2020 and 2020-2021. A total of 52 individuals were captured; additionally, 23 Wood Thrushes had their territory sizes estimated via attached radio transmitters. The average territory size estimated was 0.71 hectares. Using mixed effects models, we were able to determine associations between fragments' characteristics and body conditions, whereby birds in young fragments exhibited better fitness, which is also positively correlated with soil humidity. Additionally, young birds tended to have smaller home ranges. Our results suggest that Wood Thrushes inhabiting young fragments could be dealing with the uncertain food availability by increasing fat deposition, thus the unexpected higher mass in young fragments. Additionally, soil humidity could be used as a proximate cue for food availability and ultimately as a habitat quality indicator. Lastly, solely forest fragment size is probably not the best indicator for habitat quality for Wood Thrushes in Costa

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[4] The material contained in this chapter is in preparation for submission to *Ornithological Applications*.

Rica, supporting potential value in conservation of native forest fragments of variable sizes in working landscapes.

5.2 Introduction

Determining drivers of habitat quality represents an important step towards effectual conservation planning for migratory songbirds (Albert et al. 2020). Variation in abiotic and biotic characteristics - such as microclimates, predators, food resources, and cover - manifest as changes in habitat quality which affect patterns of fitness: the capacity of a bird to survive and successfully reproduce (Sæther and Bakke 2000). Given difficulties associated with measuring changes in avian fitness relative to variations in biotic and abiotic characteristics, researchers often rely on a suite of indices that presumably vary with changes in habitat quality. Indices of habitat quality are numerous and have been used with varying degrees of success; they include measuring the habitat itself (e.g., food and nesting resources, vegetative structure and diversity, microclimates, presence of predators, competitors, and mates) as well as directly sampling birds (survival, recruitment, abundance, population growth, reproductive success, stress hormones, triglycerides, molt speed, territory size, and physiological condition) (Grubb 1989, Halpern et al. 2005). The appropriateness of a particular index will depend on the specific behaviors and life history strategies exhibited by the study species in question (Johnson 2007). The use of indices has helped researchers distinguish poor- and high-quality habitats; an important prerequisite towards understanding how environmental change affects avian fitness, and subsequent patterns of population growth (Knutson et al. 2006).

Given that events occurring on the winter grounds play an important role in the population dynamics of migratory species (Holmes et al. 1989, Wunderle 1995, Marra and Holberton 1998, Marra and Holmes 2001, Latta and Faaborg 2002, Latta et al. 2016), the conversion of Central American forests to human-dominated agricultural landscapes needs to be understood in the context of a changing mosaic of habitat quality (Aide et al.

2013). Forest fragments embedded within a matrix of agricultural development fosters pronounced edge effects that may benefit some generalist migrant species at the expense of forest-obligates. In fact, the loss of Mesoamerican forests has already been implicated in the population decline of several forest-dwelling migratory birds (Robbins et al. 1989, Faaborg 2002, Newton 2004, Kramer et al. 2018, Wilson et al. 2018).

One of the most dramatic examples of population decline associated with tropical forest loss is the Wood Thrush (*Hylocichla mustelina*) whereby the species suffered a pervasive population decrease of 62% between 1966 and 2015 (Sauer et al. 2013, Rushing et al. 2016, Taylor and Stutchbury 2016). Given the population decline of Wood Thrush throughout much of its range, the species is fast becoming symbolic of migratory bird conservation throughout the Americas (BirdLife International 2017). In the winter, Wood Thrush inhabits the southeast of Mexico and most of Central America and relies on primary forest, but can also be found in a diversity of forested habitats, such as regenerating forests and forest patches within agroecosystems (Evans et al. 2020). In Costa Rica, Roberts (2011) estimated that 83% of the Wood Thrush population overwinters outside of protected areas, mainly in forest fragments in agricultural regions, raising the question: do small forest patches in agricultural landscapes provide high quality habitat? Importantly, the mere presence of Wood Thrush does not indicate ecological value, given that bird density is not always a reliable measure of habitat quality (Johnson 2007). For example, the density of Wood Thrush in shade coffee farms in Honduras is higher than in forests; however, the probability of survival and exhibiting territorial behavior were lower in shade coffee compared to forested habitats (Bailey and King 2019). These findings suggest that territorial and dominant Wood Thrush occupy high quality forested habitat and competitively exclude subordinates to poorer quality habitats.

Pervasive forest loss and agricultural expansion in Latin America have generated questions regarding the value of remnant forest patches to Wood Thrush (Pimentel et al. 1992, Foley et al. 2007). Given that Wood Thrush are long-distance migrants, forest obligates, and often territorial (DeGraaf et al. 1985, Rappole et al. 1989), we suggest that a combination of indices can adequately distinguish the value of small and large forest fragments to Wood Thrush; specifically, (1) physiological condition, (2) estimates of territory size, and (3) correlations between the core of a bird's territory and variation in forest structural complexity and microclimates. Justification for our three indices reflect several considerations of Wood Thrush natural history. First, Wood Thrushes select habitats with food resources to acquire the fat and muscle tissue necessary to successfully complete their spring migrations (Martin 1985a, Loiselle and Blake 1991). The rate at which fat and muscle is deposited varies relative to food resource availability, and can be readily measured by capturing birds and recording their fat and muscle deposition. Second, variation in habitat quality is inversely correlated with territory size, a phenomenon likely driven by resource availability – such as food – whereby individuals in high-quality habitats do not need to travel as far to forage when compared with individuals moving greater distances in poorer quality habitats (Stenger 1958, Brown 1964, Wilson 1975). Third, forest structure and microclimatic conditions in the core of an individual's territory, where they spend a disproportionate amount of time, reflect higher quality habitats that provide adequate temperature and humidity conditions, food, cover, and water resources (Adams 2001). We suggest that core areas actively being used in greater proportion to their availability will reflect stable understory conditions known to be favored by Wood Thrush like humid understories (Stanley et al. 2021a).

Our objective was to determine how Wood Thrush habitat quality varied across a diversity of forest fragment sizes and ages, within a Costa Rican agricultural system. For this purpose, we developed the following two hypotheses: (1) larger and older forest fragments within an agricultural matrix provide higher quality habitat for Wood Thrush, relative to smaller and younger ones; (2) high quality Wood Thrush habitat is characterized by relatively humid understories and structurally complex forest when compared to drier and less complex forest. Based on our hypotheses, we developed two predictions: (1) Wood Thrush inhabiting larger and older fragments (better quality habitat) will exhibit elevated fitness, and smaller territories relative to individuals in smaller and younger forest fragments; (2) within their territories, individual Wood Thrush will spend disproportionately more time in higher quality habitat, characterized by humid understories (higher quality habitat), relative to forest with drier understories (poorer quality habitat).

Determining relationships between Wood Thrush physiological condition, territory size, habitat use within territories, and habitat quality will provide insight into the ecological value of small forest fragments to declining populations of Wood Thrush. Furthering our understanding of Wood Thrush habitat quality in working landscapes represents a necessary first step towards integrating Wood Thrush conservation into the management planning of tropical agricultural systems.

5.3 Methods

5.3.1 Study Area

The study area was located in northeastern Costa Rica, in Sarapiquí county, province of Heredia. The region is characterized by evergreen tropical wet forests (Holdridge 1947). The annual precipitation mean is 3,710 mm with seldom severe dry seasons and an annual temperature mean of 26º C (Solano and Villalobos 2000). Our work was focused on the Atlantic Caribbean lowlands, characterized by fragmented forest patches surrounded by an agricultural matrix of pasture and cultivation of mostly pineapple, banana, and heart of palm (Roberts 2011). The region also presents a large portion of protected forest comprised of two conservation areas, La Selva Biological Station and Braulio Carrillo National Park, resulting in 47,571 ha (McDade and Hartshorn 1995).

We sampled Wood Thrushes at 14 plots within 12 sites (Figure 5.1; Table 5.1), including fragments ranging in size from 3 to 500 hectares. Aside from the size, fragments were also classified into two age classes, mid-to-late successional forest (mature) with tallest tree average higher than 20 meters, and young successional forest with trees lower than 20 meters, and/or history of exploitation like selective logging. Our classifications resulted in ten mature plots and four young successional plots.

5.3.2 Field Methods

We captured Wood Thrushes using target mist-netting, where we employed a playback broadcasting calls and songs with a speaker. We walked through fragments playing Wood Thrush call vocalizations, and when an individual vocalized back aggressively, we set up one mist-net (12 x 3 m, 36 mm mesh) to capture the individual.

Data were collected in two overwintering seasons, from 30 December 2019 to 13 March 2020 and 7 November 2020 to 19 February 2021. All captured Wood Thrushes were marked with a numbered aluminum band (Costa Rica Bird Observatories - CRBO) on the left leg and a unique combination of two-color bands on the right leg, allowing identification by resighting. We also collected morphological data: mass (± 0.01 g), tarsus, tail, and wing chord length.

To estimate territory size, we attached a 1.7 gram SOBP 2028 Radio Transmitter (Wildlife Materials International, Murphysboro, Illinois, USA) on the bird's back using a leg loop harness (Rappole and Tipton 1991). Birds were relocated with an R410 Radio Receiver (ATS, Isanti, Minnesota, USA) and a three-axis Yagi antenna. We used a combination of homing and triangulation to relocate birds and mark their location with a GPS. During fieldwork, we noticed that the homing method was only possible in areas with less dense understory; otherwise, our movements toward the bird caused enough noise to influence the bird's behavior. Triangulation done by two observers and two sets of radio receivers and antennas was less invasive and likely caused no influence on the bird's behavior. For this method, two observers were separated by a minimum of 15 meters, and GPS coordinates and the compass bearing towards the direction with the strongest radio signal were marked simultaneously. Due to time constraints, the birds were relocated more than once per day, from sunrise until 11 AM, with a minimum interval of 30 min between relocations. To determine the coordinates of the birds in each relocation, we used the package "*sigloc*" (Berg 2015) in the software R (R Core Team 2022).

Kernel density estimations were used to provide approximations of territory size and activity centers. These estimates provided maps of each individual's territory, including the core area (50% isopleth) where the birds concentrate most of their activity and the standard home range area (95% isopleth). We randomly sampled forest structure and microclimates inside and outside the territory, considering a minimum distance of 15 meters among the points. The number of points sampled was constrained by the territory size, with a maximum of 15 sample points (five at each area of the territory and five outside). At each point, we measured canopy density, understory density, leaf litter depth, the tallest tree within a 10 meters radius, temperature, air and soil humidity. Canopy density was measured using a spherical densiometer and calculated based on the mean from four cardinal directions. Understory density was measured using a modified cover pole method (Robel et al. 1970, Toledo et al. 2008); four measures were done from the center point, where a 2 meter pole, with color marks every 10 cm, was placed; a smaller 1 meter pole, for guiding observation angle, was placed 4 meters away from the central pole at four cardinal directions. Vegetation covers were estimated, then the mean was calculated from each sample point. Leaf litter depth was measured with a manual caliper placed one meter from the center point towards each of the four cardinal directions, by using the pin from the back end of the caliper to pierce through leaves until it hit the soil, and then averaged the four values obtained. The tallest tree height was chosen to represent the vertical profile of the vegetation and was measured using a digital clinometer. The tallest tree within the 10 meters radius was determined visually before measurement, when similar height trees were present, we ensure choosing the right one by measuring the height of all visually indistinguishable trees. Air temperature and humidity were obtained with a digital temperature and humidity meter (Model MS6508, Vlike) at 1.5 meter height, and soil humidity with the same equipment placed 1 cm from the soil. We also checked for the presence of running water within a 50 meters radius from the individuals estimated home range, this variable presented a binary response, (presence or absence of running water).

5.3.3 Data Analysis

We used kernel density estimation to calculate the home range sizes based on utilization distribution (Worton 1989). This method provides relative frequency of occurrence in a two-dimensional distribution, whereby the density estimate will be high in areas with many observations (core area) and low in areas with few observations (buffer area), resulting in the home range estimate with 95% of the utilization distribution. The reference bandwidth method (h_{ref}) was used as a smoothing parameter because it performs better with small numbers of relocation points than the least squared cross-validation method (Seaman and Powell 1996). Analyses were conducted with the package "*adehabitatHR*" (Calenge 2006), in program R (R Core Team 2022). To test the hypothesis that habitat selection of territory cores are mediated by microclimates and forest structure, we used Principal Component Analysis (PCA) with all habitat variables collected in the core, buffer and outside of the estimated territory. The ordination included soil humidity, canopy cover, understory density, tallest tree, leaf litter, temperature, and air humidity. We tested the assumption of homogeneity of multivariate dispersion using ANOVA (Anderson 2005), and the PCA was followed by a PERMANOVA test to assess differences among territory areas.

5.3.4 Modeling

We built mixed effects models (GLMM) using either birds' mass or territory size as response variables. For all models, we chose the Gaussian distribution with an identity link function because it visually fitted the residuals better compared to a log link function (Zuur et al., 2009). Model validation was based on a graphical analysis of residuals (Zuur et al., 2009) and residuals diagnostics. Before running the models, we checked for covariate correlations, and outliers were removed through graphical exploratory data analysis (Zuur et al., 2010).

5.3.4.1 Wood Thrush mass and forest fragment models

With individual measures of Wood Thrush mass as a response variable, we used combinations of fragment size, fragment age, and bird age as explanatory variables in a set of six candidate models, plus a null model (low sample size precluded larger and more complex models). As tarsus size influences mass (Figure 5.2), we included tarsus size as an offset term in the models. Since the mass of individuals could vary during daylight hours (e.g., increased weight by feeding in the morning, decreased weight by energy loss in the afternoon), and could be affected by the site where birds were sampled (e.g., food availability could vary among sites), we included day period nested with site as a random intercept term in the models. Captured individuals were divided into six periods of the day, according to the time they have been captured: early morning (from 0600-0800 hours), mid-morning (from 0800-1000 hours), late morning (from 1000-1200 hours), early afternoon (from 1200-1400 hours), mid-afternoon (from 1400-1600 hours) and late afternoon (from 1600-1800 hours).

5.3.4.2 Wood Thrush mass and territory models

We used Wood Thrush mass as a response variable, coupled with measures of habitat characteristics from 23 Wood Thrushes territories as explanatory variables in a series of competitive mixed effects models. Specifically, our explanatory variables included soil humidity, leaf litter, understory density, canopy cover, tallest tree, and bird age in a set of 14 models, plus a null model. As the previous set of models, site was included as random intercept term in all models. Similar to above (see *Wood Thrush mass and forest fragment models*), we included tarsus size as an offset term, and day period nested with site as a random intercept term in the models.

5.3.4.3 Territory size models

We used estimates of territory size as a response variable, coupled with the following explanatory variables: soil humidity, leaf litter, understory, tallest tree (as a proxy for fragment age), fragment size, and bird age; we used site as a random intercept term in all models. We formulated a total of 15 candidate models plus an intercept-only model (null) based on combinations of explanatory variables, including interactions.

Model selection was based on the Akaike information criterion corrected for small samples (AICc - Burnham e Anderson 2002). We assessed model performance through marginal and conditional R^2 for GLMM. All analyses were run in the R environment (R Core Team, 2022) using the following packages: "*glmmTMB*" (Brooks et al., 2017) for GLMMs, "*DHARMa*" (Hartig, 2021) for residuals' diagnostics, "*visreg*" (Breheny & Burchett, 2017) for model visualization and "*MuMIn*" (Barton, 2020) for model performance.

5.4 Results

In total, we captured 52 individual Wood Thrushes over two winter seasons in Costa Rica. Wood Thrush ranged from 45.1 to 55.9 grams (49.44 ± 0.37 SE). We estimated territory size for 23 individuals with a minimum of 20 relocation coordinates (mean of 22.3), and no less than three different sampling days with an interval of at least one week. Wood Thrushes territories across all fragments ranged from 0.08 to 1.57 hectares (0.71 ± 0.1 SE). Four radio-tagged individuals abandoned their territories or presented issues with the transmitters before we reached the threshold to estimate territory size.

Within Wood Thrush territories, we sampled habitat characteristics at a total of 321 points, divided in the core area (91), buffer area (111), and outside the territory (113). The sample size difference among each area was due to the minimum radius of 15 meters among points and the territory size variation among individuals. Seven continuous variables were measured at each point: soil humidity (85.3% ± 0.3 SE), canopy cover (91.48% ± 0.27 SE), understory density (41.8% ± 1.03 SE), tallest tree (23.16 m ± 0.5 SE), leaf litter (25.8 cm ± 0.7 SE), temperature (26.4^o C ± 0.1 SE), and air humidity (80.6% ± 0.4 SE). Furthermore, most of the territories (19) had running water in the area or nearby (50 meters radius). Our results from the Principal Component Analysis with habitat characteristics showed no separation across areas of high use, low use, as well as outside the territory (PERMANOVA, $P = 0.354$ for 999 permutations; Figure 5.3).

In our model selection sets, collinearity was detected with canopy cover and soil humidity and canopy cover and leaf litter, thus we were not able to use these covariates in the same model. No top-ranked models showed heteroscedasticity in the residuals. Our *mass and forest fragment models* analysis identified fragment age as being correlated with Wood Thrush mass variation in forest fragments (Table 5.2), whereby individuals inhabiting young successional areas exhibited higher mass compared with birds in mature forests (β = 1.59, CI = 0.15, 3.06). An interaction model with fragment size and fragment age ranked as the second most competitive model (β = -0.013, CI = -0.03, -0.001), with its associated AIC_c within two units from the top model (Burnham and Anderson 2002). In this model, fragment size exhibited a slightly positive association Wood Thrush mass. For our *Wood Thrush mass and territory models,* we found a top model that included additive effects of fragment age and soil humidity (Table 5.2). These results suggest that fragment age was negatively associated with Wood Thrush mass (β = -0.321, CI = -

0.494, -0.148), while soil humidity exhibited a positive correlation with mass ($\beta = 0.211$, CI = 0.023, 0.399). For our *territory size analysis*, the top model included bird age as an explanatory variable ($\beta = -0.368$, CI = -0.722, -0.001). We found that a birds' home range tended to be smaller for younger birds compared to adults.

5.5 Discussion

Among species that defend territories, variation in habitat quality within the individual's territorial core and periphery can dynamically interact to affect fitness (Johnson 2007). In this study, we aimed to determine if the territorial core of Wood Thrush was associated with particular habitat structures (Adams 2001). Considering that Wood Thrush primarily forage in the forest understory (DeGraaf et al. 1985), we hypothesized that microclimate and territorial core characteristics, such as understory density, soil humidity, and leaf litter depth, would be different from less used parts of a Wood Thrush's territory (Studds and Marra 2011). We failed to find support for our hypothesis that Wood Thrush select unique microhabitats in their territorial core given that we found no discernable difference in structure or microclimate between the core and periphery of their territories. It is possible that we simply failed to measure meaningful differences in microhabitats between the territory core and periphery, such as variation in water or food resources. For example, recent research from Belize demonstrated that Wood Thrush space use was influenced by variation in food availability, whereby home range wetness was positively correlated with fruit and insect abundance, and that individuals are more likely to adopt facultative movements when in wetter habitats (Stanley et al. 2021a).

Forest fragment size and age represent the landscape scale of habitat selection for Wood Thrush (Hutto 1985, Stanley et al. 2021b). Our first set of models assessed if Wood Thrush mass was influenced by the size and age of forest fragments. Contrary to what we expected, young fragments hosted individuals with higher mass than their counterparts in mature forests. However, it is important to consider that the consumption of fruits by Neotropical migratory birds is higher in young forests (Blake and Loiselle 1992), where they are abundant throughout the year (Levey 1988, Loiselle and Blake 1991). For instance, Roberts (2011) often observed Wood Thrushes eating *Miconia* sp. fruits near the edge of fragments in Costa Rica. Furthermore, food resources (arthropods and fruit) are predicted to be more temporally variable in younger forests, and more stable in older forests (Martin 1985b, Wolfe et al 2015). One known strategy for dealing with uncertainty in food availability is increased fat deposition to buffer any future dearth of food availability (Rappole and Warner 1980), as observed in floater Wood Thrushes in Mexico (Winker et al. 1990). The trade-off with this strategy may be slower flight, thereby subjecting heavier birds in poorer habitat to increased predation. Thus, floater Wood Thrush and individuals in poorer quality habitat may be exhibiting a similar strategy of fattening up to mitigate any future uncertainty associated with their winter habitat. Our hypothesis that fragments size would be correlated with Wood Thrush mass was not corroborated, however, our second most competitive model did include fragment size in an additive model with fragment age, with a slightly positive influence on bird's mass. Roberts (2007) did find lower Wood Thrush's body conditions in small fragments in Costa Rica, but only for males. Data about the sex of the birds we captured were not available for our study, which could be important to determine sex-specific variation especially when considering likely sex segregation (Roberts 2007, but see Chin et al. 2014 and Stanley et al. 2021a).

Along with the *mass and forest fragment models*, our second set of models investigating microhabitat characteristics measured within Wood Thrush's territories also had fragment age, represented by tree height, negatively associated with mass. Forest age, together with soil humidity, seems to play an important role in the dynamics that regulate habitat quality for Wood Thrush. The latter exhibited a positive correlation with Wood Thrushes' body mass, corroborating our hypothesis. Moisture influences variation in food availability for migratory birds on the wintering grounds (Studds and Marra 2011), thus soil humidity represented an indirect measurement of resources, and may be an important indicator to assess habitat quality for Wood Thrushes in the tropics. Stanley et al. (2021a) used remote sensing and isotopic analysis to show that wetter territories provided more insects and fruits for Wood Thrushes in Belize, and that individuals in wetter territories consumed more insects and exhibited better body condition.

In territorial individuals, the size of the defended area can also be useful to assess habitat quality, which is inversely correlated with territory size, a phenomenon likely driven by resource availability, whereby individuals in high-quality territories do not need to travel as far to acquire necessary resources when compared with individuals in poorer quality habitats (Wilson 1975, Stenger 1958). Territory size was already shown to be negatively related with food abundance for Neotropical migratory birds in the tropics (Smith and Shugart 1987, Marshal and Cooper 2004, Ruiz-Sánchez et al. 2017, González-Prieto 2018). Wood Thrush often exhibits territorial behavior and active home range defense during the winter (Rappole et al. 1989), and higher insect abundance was associated with smaller home ranges in Belize (Stanley 2021a). Nevertheless, our models showed that bird age was the best predictor for territory size, young birds exhibited smaller territories. Therefore, birds' age category may be important when explaining variation in home range sizes. Habitat characteristics could also be influencing territory size but on a finer spatial scale. The smaller territory size of young individuals could be explained by behavioral adjustment of territory size, considering that territory defense influences territory size, and it is energetic demanding, especially with competitive neighbors (Adams 2001), younger and inexperienced individuals may be avoiding conflicts by defending smaller areas. Additionally, Neotropical migratory birds prioritize foraging opportunities when selecting territories in the tropics (Rappole et al. 1999, Johnson and Sherry 2001), and individuals in their first fall migration with no experience in foraging in the tropics would have less time remaining to defend bigger territories.

Our finding suggested that forest fragment size is probably not the best indicator for habitat quality for Wood Thrushes in Costa Rica. A similar result was reported by Roberts (2011), whereby Wood Thrush density was higher in continuous forest, but not among fragments of different sizes, supporting potential value in conservation of native forest fragments in working landscapes. Additionally, unprotected small fragments also provided good habitats for overwintering Wilson's Warbler (*Cardellina pusilla*), in southern Mexico (Ruiz-Sánchez et al. 2017). The forest fragment successional stage should be considered when assessing habitats, especially for presenting Wood Thrushes with higher body mass than in mature forests. However, this finding must be interpreted with caution since underlying intra-specific interactions could be driving this result, warranting further investigations. Lastly, soil humidity and environment moisture seemed to be a reliable indicator of habitat quality for Wood Thrush, as well as the presence of running water that was prevalent in the mapped territories. We recommend that both understory humidity – likely maintained by increased canopy closure and understory complexity – and proximity to water reflect important climate refugia in lowland tropical forests, and likely serve as indicators of habitat quality for Wood Thrush. Promoting climate refugia in lowland tropical rainforests will likely become a more common management objective given that understory drying has been implicated in the decline of multiple bird species throughout Central and South America (Curtis et al. 2021, Stoufer et al. 2021), and climate projections predict diminished precipitation throughout the Caribbean (Fuentes-Franco et al. 2015). Considering that high quality Wood Thrush habitat may reflect climate refugia in the tropics, managing habitat for Wood Thrush may indirectly provide quality habitat for a multitude of other taxa in human-dominated landscapes.

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5.8 Tables

Table 5.1. Size and coordinates of the sampled fragments where Wood Thrushes (*Hylocichla mustelina*) were captured in Costa Rica.

Site	**Area (ha)**	**Latitude**	**Longitude**
Frag23	3	10.4540ºN	84.0615ºW
Frag58	7.1	10.3791ºN	83.9303ºW
Frag60	7.5	10.4201ºN	84.1422ºW
Frag1	8	10.4292ºN	84.1202ºW
Frag30	9	10.3668ºN	83.9594ºW
Resg	10	10.2879ºN	83.9265ºW
Frag20	49	10.3690ºN	83.9291ºW
Frag13	50	10.3001ºN	83.9343ºW
Frag16	66	10.2460ºN	83.9389ºW
Bijagual	280	10.3632ºN	84.1052ºW
Frag2	380	10.4119ºN	84.1136ºW
CRBO	500	10.1744ºN	83.9301ºW

Table 5.2. Summary of the top models for predicting body mass and territory size of Wood Thrush (*Hylocichla mustelina*) in Costa Rica. wi = AICc weight, k = number of parameters, + = positive correlation and - = negative correlation.

Model set	**Top model**	**ΔAICc**	w_i	***k***
Body mass and forest fragments	Fragment age$^-$	-	0.36	2
	Null	1.7	0.16	1
Body mass and territory	Soil humidity$^+$ + Tallest tree$^-$	-	0.42	3
	Null	7.2	0.01	1
Territory size	Bird age$^-$	-	0.33	2
	Null	1.1	0.19	1

5.9 Figures

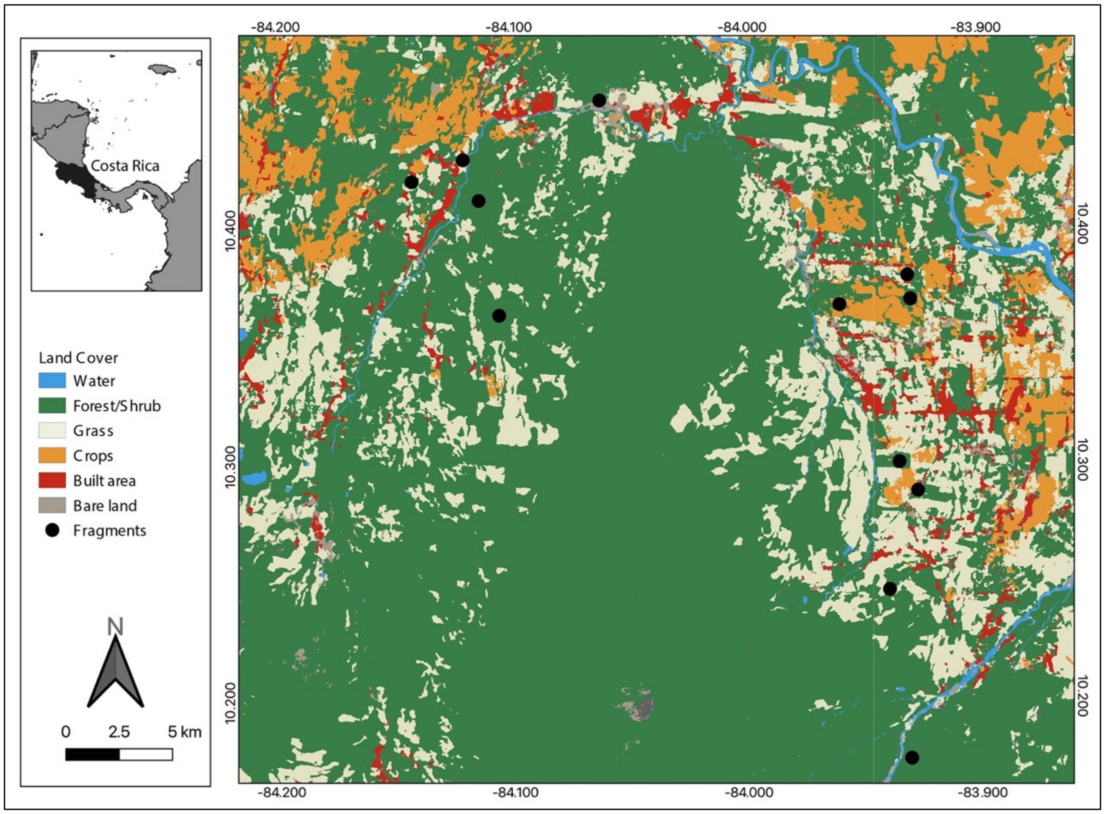

Figure 5.1. Map of the Heredia province in Costa Rica with the location of the fragments where Wood Thrushes (*Hylocichla mustelina*) were captured.

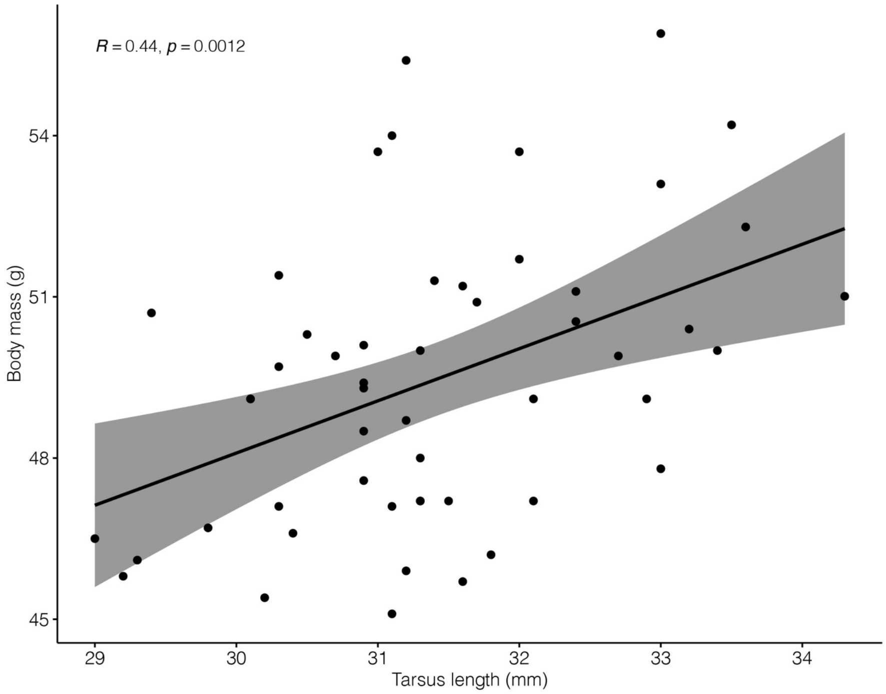

Figure 5.2. Correlation between body mass and tarsus length from Wood Thrushes (*Hylocichla mustelina*) captured in forest fragments in Costa Rica.

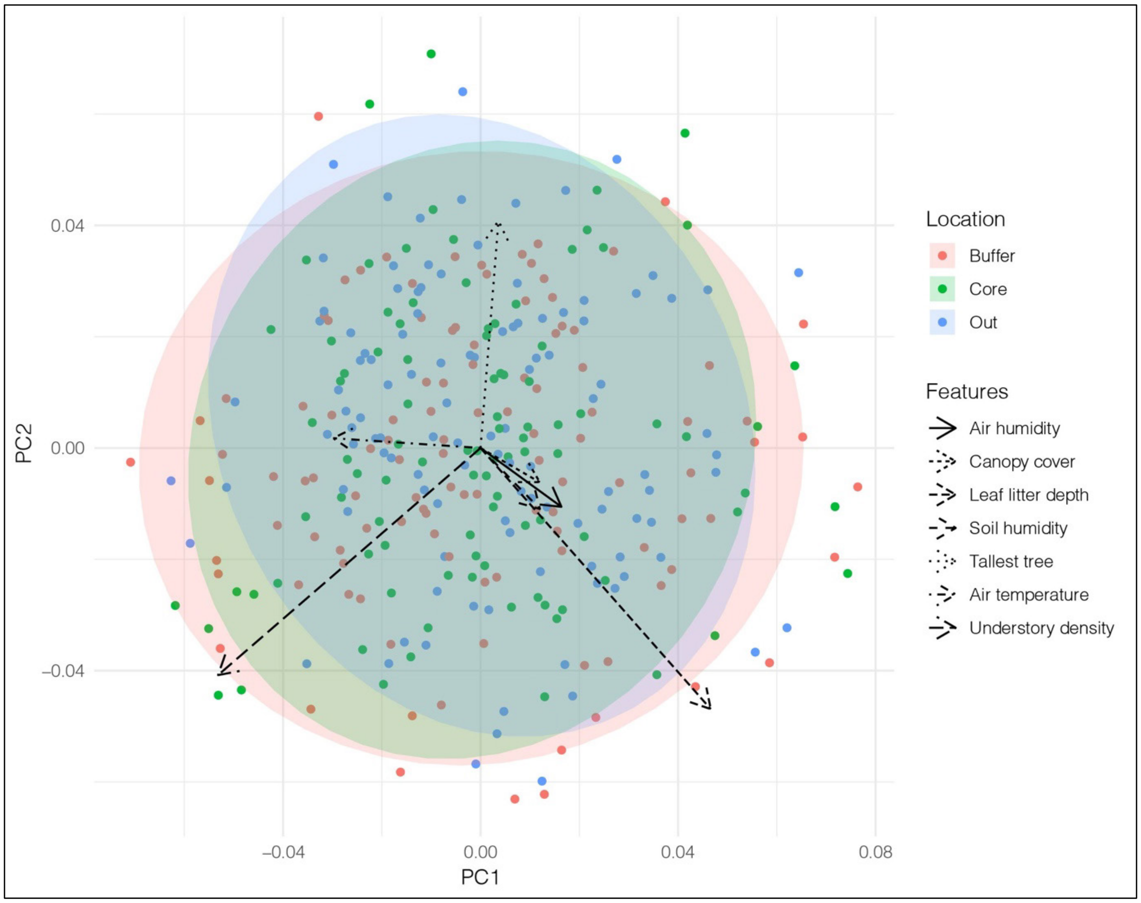

Figure 5.3. Visualization of the Principal Component Analysis (PCA) of the difference in habitat features within Wood Thrushes (*Hylocichla mustelina*) territories (core and buffer) and outside the territory (out). Data were collected in 12 forest fragments during two winter seasons (2020 and 2021) in Costa Rica. Confidence intervals (95%) are represented by the ellipses around the centroid.