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Nonbreeding ecology of the Blackpoll Warbler (*Setophaga striata*) in Colombia

Ecología no reproductiva de la reinita rayada (*Setophaga striata*) en Colombia

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Universidad Nacional de Colombia
Doctorado en Estudios Amazónicos
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A mi familia

En especial a mis Teresas, estrellas que desde el cielo me guían

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Resumen

Ecología no reproductiva de la reinita rayada (*Setophaga striata*) en Colombia:

La reinita rayada (*Setophaga striata*) es un ave migratoria Neártica-Neotropical que está declinando rápidamente, que se reproduce en el bosque boreal de Norte América y migra a Sur América durante su época no reproductiva. Similar a otras especies de migratorias, diferentes factores contribuyen a la disminución de sus poblaciones, como la pérdida de hábitat en los sitios no reproductivos. Actualmente, la información sobre la ecología de *S. striata* en los sitios no reproductivos es escasa, no hay información demográfica, ni de uso para diferentes hábitats en los sitios no reproductivos. En este estudio, queremos contribuir al conocimiento del nicho ecológico y ecología no reproductiva de *S. striata* en Colombia a través de las siguientes preguntas: 1) ¿Cómo varían las tasas de ocupación de *S. striata* a escala regional y local a través del rango no reproductivo en Colombia? 2) ¿Cuáles son las características de la vegetación (estructura del hábitat a escala fina) asociadas con la ocupación de *S. striata* en sistemas agroforestales (cítricos, cacao y silvopastoril y bosque? 3) ¿Cuál paisaje (exurbano vs rural) y hábitat (cítricos vs cacao con sombrío) tiene mejor calidad usando fidelidad al sitio, supervivencia y uso de hábitat para *S. striata* en la región del Orinoco? Es la primera investigación a escala múltiple sobre *S. striata* en las regiones de la Orinoquia y la Amazonia de Colombia, y que podría contribuir a posibles acciones de conservación.

Palabras clave: *Setophaga striata*, ocupación, demografía, hábitat, sitios no reproductivos, rangos de hogar, Amazonia, Orinoquia

Abstract

Nonbreeding ecology of the Blackpoll Warbler (*Setophaga striata*) in Colombia

The Blackpoll Warbler (*Setophaga striata*) is a rapidly declining Nearctic-Neotropical migratory bird that breeds across the boreal forest of North America and migrates to South America during its non-breeding period. Similar to other migratory species, several factors may be contributing to population declines, including habitat loss and degradation on the non-breeding grounds. Currently, information about the ecology of Blackpoll Warblers on their non-breeding grounds is scarce and no demographic information for different non-breeding habitats exists to date. In this study, we will contribute to the knowledge of the ecological niche and non-breeding ecology of the Blackpoll Warbler in Colombia, by addressing the following questions: 1) How do occupancy rates and abundance vary at multiple scales (i.e., regional, landscape, and local) across the Blackpoll Warblers over-wintering range in Colombia?, 2) How does space use and home range size of Blackpoll Warblers vary across different scales?, 3) Do exurban or rural landscapes represent habitats of higher quality for Blackpoll Warblers based on estimations of apparent survival in the Orinoco region? This is the first multi-scale investigation of Blackpoll Warbler in Colombia's Orinoco and Northern Amazon regions, and that could contribute to potential conservation actions.

Keywords: Blackpoll Warbler, occupancy, demography, habitat, home-range, non-breeding areas, Amazon, Orinoco

CONTENIDO

Introduction

The niche concept, which describes the adaptations, interactions of a species with its environment for population maintenance, and how species' distributions are constrained, is a fundamental topic in ecology, and is especially relevant in a time of rapid climate and landcover change (Grinnell, 1917; Hutchinson, 1991; Pausas & Bond, 2021). The study of these subjects contributes to the knowledge of which environmental and biotic factors affect species' distributions (Holt, 2009; Khaliq et al., 2015; Scheele et al., 2017; Soberón, 2007). There are several distinct interpretations of the ecological niche (Freckleton & Jetz, 2009; Grinnell, 1917; Hutchinson, 1991; MacArthur, 1984; Peterson, 2001; Wiens & Graham, 2005). All of them, however, attempt to understand how changes in the multidimensional environmental space and geographic space act as determinants of species' distributions. Several approaches have been used to model species' fundamental ecological niches, including artificial-intelligence algorithms. However, their interpretation must consider the effects of scale, absence o information and model validation (Peterson, 2001; Qiao et al., 2016; Soberón & Peterson, 2005).

The ecological niche of Nearctic-Neotropical migratory birds refers to the range of environmental conditions and resources that these species use during their life cycle, which includes conditions on their temperate breeding grounds, at stopover sites, and on their Neotropical non-breeding grounds (Greenberg & Marra, 2005; Newton, 2007). As they move from one region to another, species can develop wider or narrower niche breadths, and the impact of this variation on geographic distributions, connectivity, or other factors can be evaluated (Nakazawa, 2013).

Migratory birds, with their seasonal movements, encounter a variety of conditions and threats on their breeding grounds, non-breeding grounds and stopover areas (Holmes 2007). In both the Nearctic-Neotropical and Palearctic-Paleotropical systems, declines in the populations of migratory species are widespread (Newton 2007; Rosenberg et al 2016, 2019), which has prompted research on the factors limiting migratory bird populations. Nearctic-Neotropical migrants spend at least half of their life cycle in

Neotropical ecosystems, and events occurring during the annual cycle, in breeding and non-breeding periods, can have an effect on their population dynamics and regional abundances (Bayly et al., 2018; Céspedes & Bayly, 2018; Rushing et al., 2017; Sherry & Holmes, 1996).

Historically, research on Nearctic-Neotropical migratory birds has largely focused on the breeding grounds (e.g. predation, parasitism, suitable breeding habitat; Robbins et al., 1989; Böhning-Gaese et al., 1993), while more recently there has been a greater focus on migration ecology (Bayly et al., 2018; Rosenberg et al 2016; Drake, et al., 2018; Holmes, 2007; Wilson et al., 2011), winter habitat use (Céspedes & Bayly, 2018; Colorado et al., 2018; González et al., 2020; Valdez-Juárez, Drake, Hobson, et al., 2018), and understanding the connectivity between breeding and wintering grounds (Gómez et al., 2021; Hobson & Kardynal, 2015; Hobson & Wassenaar, 1996). Studies on the wintering grounds have shown that habitat quality can affect survival and, ultimately, it can influence reproductive success (Cooper et al., 2015; Harrison et al., 2011; Marra et al., 1998; Norris et al., 2004; Norris & Marra, 2007; Rockwell et al., 2012), highlighting the importance of winter habitats and seasonal interactions.

The main threat to Neotropical migratory bird populations on both breeding and non-breeding grounds is the destruction and transformation of their habitat (Albert et al., 2020; Rosenberg et al., 2016). This transformation is mainly promoted by agricultural intensification and urbanization (Rosenberg et al., 2019), as well as the use of toxic pesticides that is related with declines in insect diversity and cascade impacts on birds and biodiversity (Rosenberg et al., 2019; Sánchez-Bayo & Wyckhuys, 2019; van der Sluijs, 2020). Despite the availability of information regarding the local responses of Nearctic-Neotropical migratory birds to habitat transformations, less is known about landscape level responses to changes in the environment (Albert et al., 2020; Bayly et al., 2018). Changes in land use have impacted the composition and spatial distribution of vegetation at the landscape level (Fahrig et al., 2011). Subsequently, population ecology and dynamics (e.g., abundance, and fidelity) of migrants may be adversely affected by a lack of landscape connectivity (e.g. between natural covers and shade coffee plantations) (Alvarez-Alvarez et al., 2022) Nearctic-Neotropical migratory birds may occupy a variety of habitats in the non-breeding grounds, and the spatial patchiness of habitats as well as the ability to find suitable habitat in a landscape, also influences regional abundance (Sherry & Holmes, 1996).

Integrating the landscape with local features should be a primary objective in preserving both migrating birds and year-round residents (Sherry & Holmes, 1996). Within these local features, habitat quality plays a crucial role. Assessments of habitat quality have traditionally focused on proxies such as survival and other demographic metrics, and habitat use as reflected in occupancy and abundance (Brown & Sherry, 2006; Holmes, 2007; Hostetler et al., 2015; Johnson, 2007; Sherry & Holmes, 1996; Standley et al., 2021).

Numerous studies exploring habitat quality for different species of migrating warblers on their wintering grounds have highlighted the significance of native forests as well as agroforestry systems (Wunderle & Latta, 2000; Johnson et al., 2006; Bakermans et al., 2009, 2012; McDermott & Rodewald, 2014; Ruiz-Sánchez et al., 2017). The studies that have been conducted on agroforestry systems such as shade-grown coffee and cocoa (Colorado & Rodewald, 2017; De Beenhouwer et al., 2013; González, 2018; Johnson et al., 2006), showed that stratification in vertical structure could resemble that of natural forests, which has been considered as a proxy of habitat quality for biodiversity (Brunner et al., 2022; Vergara et al., 2019). Other arboreal agricultural habitats such as citrus plantations can also provide suitable winter habitat for migratory songbirds (Jonhson et al 2006; Valdez-Juarez et al 2018). However, there are gaps in our knowledge of habitat characteristics that promote use by these migratory species, including assemblage configuration in natural ecosystems and in transformed landscapes (e.g., farms, agroecosystems) (Díaz-Bohórquez et al., 2014).

In North America, there are 24 species classified as Common Birds in steep decline that have lost more than 50% of their populations over the past 40 years (Rosenberg et al., 2016). The Blackpoll Warbler (*Setophaga striata*) is one of those species, with the majority of the breeding population occupying the Canadian and Alaskan boreal forests, and being considered an ecological indicator for the boreal migratory bird community (Ralston et al., 2015). Estimated population decreases of 92% (Rosenberg et al., 2016; Sauer et al., 2017) have led to the listing of this species by the IUCN as Near Threatened (IUCN, 2023), and the recognition that Blackpoll Warbler conservation depends on maintaining healthy habitats throughout its annual cycle (e.g., breeding, stopover and winter grounds), Blackpoll Warbler is one of the few migratory warblers that a good portion of its population spends their winter in Amazonia, another highly threatened bioregion (North American Bird Conservation Initiative Canada, 2012).

The ecological niche and winter habitat use by Blackpoll Warblers is poorly understood and demographic information for different habitats is virtually absent. There are a few studies that examine their autumn stopover ecology in the Caribbean (Boal, 2014), as well as on the Guajira peninsula (Bayly et al., 2021). However, no studies to date have examined habitat use and quality in the stationary non-breeding grounds. This research aims to fill these gaps, by assessing the ecological niche and non-breeding ecology of Blackpoll Warbler in Colombia.

In Chapter 1, I investigated how occupancy rates varied at multiple scales, including the regional, landscape and local scales across the Blackpoll Warblers over-wintering range in Colombia, running single-species, single-season hierarchical occupancy models and N-mixture models. At the regional scale, I assessed the effects of elevation, net primary productivity, and climate variables on Blackpoll Warbler occupancy in a region where the species is predicted to be abundant (Fink et al., 2022). Then, at the landscape scale, I evaluated landscape characteristics such as how the amount of native forest and habitat type influence occupancy rates. Finally, I evaluated how local characteristics related to vegetation structure (tree density, shrub density, canopy cover, canopy height, and basal area) influence occupancy at the local scale.

In Chapter 2, I evaluated how space use and home range size of Blackpoll Warblers varied across different scales and agroforestry systems based on complementary methods (i.e., capture-recapture, and manual telemetry). I used a 4-year mark-resighting dataset (2018-2022) to estimate home-range sizes for a comparison between exurban and a rural landscapes, using minimum convex polygons estimators. Additionally, I used radiotelemetry data from 20 individuals fitted with Lotek NTQB-2 Nanotags between January to February 2021 to evaluate home range size in a comparison of a two habitats, shade-grown cocoa and citrus plantations, using kernel density estimators.

Lastly, in Chapter 3, I explored whether exurban or rural landscapes represent habitats of higher quality for Blackpoll Warblers based on estimations of apparent survival in the Orinoco region. I used a 6-year mark-resighting dataset to estimate apparent survival in two contrasting landscapes. I fitted a Cormack-Jolly-Seber (CJS) capture-recapture model to estimate the probabilities of apparent annual and overwinter survival resighting probability based on live-encounter banding records. The estimates of overwinter survival for Blackpoll Warblers on their non-breeding grounds represent an important advance for informing full life cycle models and planning.

This is one of the first studies to assess occupancy rates, habitat use and habitat quality of the Blackpoll Warbler in different landscapes and habitats in the Amazon and Orinoco regions of Colombia. The research provides new knowledge on the species' niche, as well as on its habitat use and habitat quality, and leads to recommendations for future research and conservation actions that could tackle Blackpoll population declines.

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Warblers: a multiscale analysis in Eastern Colombia reveals climate, landscape and vegetation as key variables

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1.1 Abstract

The Blackpoll Warbler (*Setophaga striata*), one of the few boreal-breeding migratory birds that overwinters in the Orinoco and Amazon, is experiencing steep population declines. However, information on the species' distribution and habitat use during the non-breeding season is limited. Here we explore how occupancy probabilities for Blackpoll Warblers in Eastern Colombia during the non-breeding season vary across regional, landscape, and local scales. By running single-species, single-season hierarchical occupancy models and N-mixture models, we evaluated how regional level variables, including precipitation, elevation, energy (Net Primary Productivity), landcover (e.g., agroforestry systems), amount of forest in the landscape, and local variables (e.g., tree density) influence the occupancy of Blackpoll Warblers across this region. We identified factors influencing single-species occupancy probabilities at multiple scales, and highlight the importance of landscapes that include agroforestry systems as wintering habitats for the Blackpoll Warbler in Colombia. Occupancy was positively influenced primarily by net primary productivity but also by non-breeding precipitation. Occupancy and abundance were higher in agroforestry systems (citrus plantations, shade-grown cocoa, and silvopastures) than in forested habitats. Occupancy was negatively correlated with the amount of forest at the landscape scale, as well as with tree density at the local scale. Within the Orinoco region, a spatial prediction based on our results supported high occupancy rates in moister agroforestry systems for the conservation of this and other species. Our findings demonstrate the impact of multi-scale variables encompassing regional, landscape, and local on Blackpoll Warbler occupancy in the Orinoco and Amazon regions.

Key words: Amazon, citrus plantations, Nearctic-Neotropical migrant, non-breeding ecology, Orinoco, Parulidae, shade-grown cacao, silvopasture

1.2 Resumen

La reinita rayada (*Setophaga striata*), una de las pocas aves migratorias que se reproducen en las zonas boreales y pasan el invierno en el Orinoco y el Amazonas, está experimentando un fuerte descenso de su población. Sin embargo, la información sobre la distribución de la especie y el uso del hábitat durante la temporada no reproductiva es limitada. Aquí exploramos cómo las probabilidades de ocupación de la reinita rayada en el este de Colombia durante la época no reproductiva varían a escala regional, de paisaje y local. Ejecutando modelos jerárquicos de ocupación de una sola especie y una sola estación y modelos N-mixture, evaluamos cómo las variables regionales, incluynedo precipitación, elevación, energía (Productividad Primaria Neta), cobertura (p. ej., sistemas agroforestales), cantidad de bosque en el paisaje y variables locales (p. ej., densidad de árboles) influyen en la ocupación de la reinita rayada en esta región. Identificamos los factores que influyen en las probabilidades de ocupación de una sola especie a múltiples escalas, y resaltamos la importancia de los paisajes que incluyen sistemas agroforestales como hábitats de invernada para la reinita rayada en Colombia. La ocupación estuvo positivamente influenciada principalmente por la productividad primaria neta, pero tmbien por la precipitación. La ocupación y abundancia en los sistemas agroforestales (plantaciones de cítricos, cacao bajo sombra y silvopasturas) fue mayor que en los hábitats boscosos. La ocupación también se correlacionó negativamente con la cantidad de bosque a escala de paisaje, así como negativamente con la densidad de árboles a escala local. Dentro de la región del Orinoco, las predicciones espaciales basadas en nuestros resultados apoyan que la alta ocupación ocurre en áreas más húmedas a lo largo y cerca de las estribaciones de los Andes y donde los pastizales del Orinoco hacen la transición al bosque Amazónico. Nuestros resultados revelan la importancia de mantener sistemas agroforestales para la conservación de esta y otras especies.

Orinoco y el Amazonas.

Key words: Amazonas, plantaciones de cítricos, migrantes nearticas-neotropicales, ecología no reproductiva, Orinoco, Parulidae, cacao con sombrío, silvopastoril

1.3 Introduction

Long-distance migratory birds are declining faster than other avian groups, and major stressors such as climate change (Dossman et al., 2023) and the rapid transformation of breeding and non-breeding grounds are affecting them throughout their annual cycle (Rosenberg et al., 2016, Albert et al., 2020, Blount et al., 2021). Deteriorating non-breeding habitat quality has also been shown to affect survival and have carry-over effects that ultimately influence reproductive success (Rockwell et al., 2017, Cooper & Marra 2020). Although it is commonly recognized that non-breeding ground climate and habitat conditions may have significant impacts on population trends, most studies to date have focused on the breeding grounds (Marra et al., 2015). To better understand the reasons for declines and provide effective directions for migratory bird conservation, it is important to improve our knowledge of habitat use and the factors shaping distributions across the entire annual cycle.

The distribution of Neotropical-Nearctic migratory landbirds on their non-breeding grounds is influenced by factors operating at regional, landscape and local scales. Regional-scale factors known to influence distribution patterns and abundance include precipitation (Rockwell et al., 2017, Céspedes & Bayly 2018), elevation (Céspedes et al., 2021; Gómez et al., 2015; Colorado et al., 2012), and net primary productivity (NPP; Somveille et al., 2015, 2018; Ponti et al., 2018, Ng et al., 2022). At the landscape scale, the amount of forest on the landscape and its structure (Johnson et al., 2006, Ruiz-Sánchez et al., 2017, Céspedes & Bayly 2018, Albert et al., 2020, González et al., 2021), as well as the availability of various natural and anthropogenic habitats (Bakermans et al., 2009, Colorado & Rodewald 2017, Valdez-Juarez et al., 2019, Céspedes et al., 2021, Bennett et al., 2022), have been shown to influence the presence and distribution of migrants (Albert et al., 2020). Finally, at local scales, aspects of vegetation structure such as canopy cover, Céspedes & Bayly 2018, Bulluck et al., 2019, Bennett et al., 2022). Knowledge of how regional scale-factors, as well as fine- scale habitat characteristics, drive occupancy and abundance processes in migratory landbirds on their non-breeding grounds, is essential for the design of conservation strategies whose goal is to stabilize and reverse populations declines (Bennett et al., 2016).

The Blackpoll Warbler (*Setophaga striata*) is a long-distance migratory landbird experiencing steep population declines, with an estimated global population decline of 92% over the last 50 years (Rosenberg et al., 2016, Sauer et al., 2017). As a result, the species was recently listed as Near Threatened (IUCN 2023). Current distribution models based on eBird observations suggest that Blackpoll Warblers are abundant in Venezuela, Colombia, and Ecuador during the stationary non-breeding period, mainly along the eastern foothills of the Andes and the adjacent Orinoco and Amazon lowlands (Fink et al., 2022). Notably, these same regions are being rapidly and extensively transformed by large-scale agricultural activities (Lozano Rodríguez 2020). For example, in the Orinoco-Amazon region of Colombia, ~50,000 ha of forest are being lost annually in the Caquetá and Meta departments (IDEAM 2019, 2020), to be replaced by habitats generally considered of lower quality for forest-dwelling migratory landbirds, such as cattle pastures.

Here, we aimed to understand how the occupancy and abundance of Blackpoll Warblers in eastern Colombia varied across regional, landscape, and local scales. Given their relationship with the distribution of other migratory landbirds (Cespedes et al., 2021), we first evaluated how precipitation, elevation and net primary productivity influenced occupancy across the Orinoco region of Colombia, where Blackpoll Warblers are abundant (Fink et al., 2022). We predicted that occupancy would be positively influenced by precipitation and Net Primary Productivity (NPP), based on previous studies of Neotropical-Nearctic migratory landbirds (Wilson et al., 2011, Céspedes et al., 2021, Bennett et al., 2022). Given that the timing of precipitation may be key to creating optimal conditions for Blackpoll Warblers, we evaluated whether annual rainfall, non-breeding season rainfall or rainfall in the driest month best described occupancy patterns.

Next, we evaluated how landscape characteristics such as the amount of native forest and habitat type determined occupancy at the landscape scale. Past studies have found varying responses by birds to forest cover on the landscape (Flather & Sauer 1996, Given current deforestation rates within the non-breeding distribution of the Blackpoll Warbler and its declining status, we hypothesized that the species is forest-dependent and predicted that occupancy and abundance would be higher in landscapes with a higher proportion of forest and would decrease along a gradient of forested to less forested habitats including native forest, shade-grown cocoa, citrus plantations and silvopastures. Finally, at the local or fine scale, we assessed how vegetation structure (tree density, shrub density, canopy cover, canopy height, and basal area) influenced occupancy, with the expectation that occupancy would be positively correlated with canopy cover and tree density (Colorado et al., 2018; Johnson et al., 2006). To our knowledge, this is the first multi-scale investigation of Blackpoll Warbler occupancy, abundance and habitat use within the species' non-breeding grounds.

1.4 Methods

Bird census

In order to understand the factors that drive occupancy patterns of Blackpoll Warbler in Eastern Colombia, we employed a multi-scale approach based on surveys conducted at regional, landscape and local scales, as follows.

Regional scale

At the regional scale, we conducted line-transects in the Orinoco and Amazon basins at 17 sites in the departments of Casanare, Boyacá, Meta, Guaviare, and Amazonas (Figure 1a, Table S1), between January and March 2017 and 2018. Surveys were carried out along 145 transects (between 6 and 11 transects per site), each 100 m long and 50 m wide, and separated by at least 200 m to avoid pseudoreplication (Bibby et al., 2000). Surveys were conducted by four different observers trained in species identification by sight and sound. At least half of the transects (72) were located in blocks of uniform habitats, mainly foothill tropical rainforest (Boyacá-Casanare-Meta) and terra firma tropical humid forest (Guaviare-Amazonas), while the remaining transects were placed in transitional habitats (e.g. forest edge, shade-cocoa, mixed habitats; Table S1). Coordinates for each transect were recorded using a handheld GPS Garmin Map64s unit at the mid-point of each transect with a precision of ±3 m.

transect and registering the number of Blackpoll Warblers encountered. All observations were carried out between 06:00 and 10:00 h. Each site was visited at least twice during the same season, with two repetitions of each transect per day, per visit, for a total of 8 repetitions per transect between January-February 2017 and 4 repetitions for transects in Boyacá and Amazonas between February and March 2018 (Table S1).

Landscape and local scale

The study sites and field methods for both landscape and local-scale occupancy surveys were the same and were designed to equally sample four habitats identified during regional surveys as being used by Blackpoll Warblers: shade-grown cocoa plantations, citrus plantations, silvopastures (i.e. cattle pastures with trees) and native forest. We selected 26 sites within the departments of Meta and Guaviare that included one or more of the focal habitat types and established 160, 30-m fixed radius, point counts (Ortega-Álvarez et al. 2018), divided equally in 40 points per habitat (Fig. 1b) and separated by at least 200 m (Bibby et al., 2000). Points were surveyed during 10 minutes on six occasions between January and March 2020 by three different observers. Repetitions were carried out over a two-day period, to ensure population closure, surveying each point three times a day between 6:00 h and 11:00 h (local time). Observers, as well as the order in which points were visited, were randomized to minimize temporal or observer-based biases.

Study sites were located in two distinct geographic clusters, which were accounted for in subsequent analyses: 1) Guaviare (29 points), and B) Meta (131 points; Fig. 1b, Table S2). The four habitat types were defined by the following characteristics. Shade-grown cocoa plantations (elevation ~190 to 770 m) were between 4 and 8 ha and consisted of two strata: an understory of cocoa plants (*Theobroma cacao*) and a canopy dominated by trees such as *Mimosa trianae*, *Cecropia* sp., *Inga* sp., *Cedrela* sp., *Schefflera* sp., *Musa* sp., and trees from the Fabaceae and Melastomataceae families. Cocoa plants were typically organized in grids of 3 x 3 m or 4 x 4 m. Citrus plantations covered 10 to 40 ha (elevation ~200 to 520 m) and consisted of one stratum of either Valencia oranges *(Citrus sinensis),* Arrayana tangerine *(Citrus reticulata Blanco),* Tahití lime *(Citrus latifolia L.),* Minneola tangerine *(Citrus reticulata* Blanco *x Citrus paradisi* Macfad*).* Citrus trees were planted in 8 x 7 m or 9 x 15 m grids. Silvopastures (elevation ~210 to 540 m) consisted of pastures containing dispersed trees mainly of *Mimosa trianae, Cecropia* sp*., Inga* sp*.,* variable. Finally, native forest corresponded to forest remnants and gallery forests (elevation 180 to 800 m), with a canopy height between 10 and 20 m and an average tree density of 1750 trees/ha (Table S2, Fig. S1).

Occupancy and abundance estimation

To estimate Blackpoll Warbler occupancy at the three geographic scales, we used single-species, single-season hierarchical occupancy models (MacKenzie et al., 2002). In this framework, observations may be influenced by an observer's ability or intrinsic properties of vegetation structure, for example, that determine the probability of detection of an individual, allowing models to account for potential biases in detection probability by assuming that an absence can be a true absence or a failure to detect an individual. Models therefore include covariates for estimating detection probability and occupancy probability.

In habitats where occupancy probability is close to 1, occupancy models are not suitable for inferring differences in abundance/density between habitats. As we were interested in understanding how the abundance of Blackpoll Warblers varied between non-breeding habitats, we employed single species N-mixture models to compare abundance between the four focal habitats surveyed at the landscape scale (see above). N-mixture models assume that a species is detected with probability p_{it} in a point count i at a time t. Counts x_{it} may be viewed as independent realizations of a binomial random variable with parameters N_i, defined as the true abundance of the species in site i and p_{it}, the probability of detecting an individual at a site i at a time t (Kéry et al., 2013). We assumed N_i to be Poisson distributed with parameter λ, the mean abundance of the species per point count. As in occupancy models, N-mixture models account for covariates in abundance and detection. Parameter estimation for occupancy and abundance was performed using the R statistical software (version 4.2.0, R Core Team 2021) and the "unmarked" package (Fiske & Chandler 2011).

Detection probability variables

For regional-scale models, we considered observer as the main detection covariate. We raw detections and occupancy covariates and computed Moran´s I index (Tillé et al., 2018). Significance of the index was assessed based on 1000 randomizations of the occurrence data. The resulting correlation was not higher than expected by chance, corroborating the independence of transects (Moran´s I = -0.02, Expected = -0.008, SD = 0.01, p = 0.8).

For the landscape and local scale models, we evaluated canopy cover (%), canopy height (m), and tree density (number of stems ≥ 7.6 cm dbh per ha), in addition to observer, as detection covariates, based on the hypothesis that increasing canopy cover, canopy height and tree density could directly reduce an observer's probability of seeing a bird that is present. A test of independence of detection histories across point counts revealed a degree of spatial correlation, albeit low (Moran´s I = 0.08, Expected = -0.006, SD = 0.04, p = 0.01).

Covariables for occupancy and abundance analyses

At the regional scale, we were interested in evaluating the relationship between occupancy probability and precipitation, elevation and Net Primary Productivity (NPP). We obtained mean monthly precipitation data for each transect location from the Worldclim 2.0 database at a resolution of 1 km2 (Fick & Hijmans 2017) and then summed data across months to create three new variables hypothesized to influence site selection by Blackpoll Warblers: A) annual rainfall; B) non-breeding season rainfall (December-April); C) rainfall for the driest month. Elevation for each transect was obtained from a handheld GPS unit (GPSMaps 64s). NPP values for each transect were extracted from a MODIS layer (MOD17A2_M_PSN_2016-11-01_rgb_3600x1800) at a 1 km2 spatial resolution based on the Moderate Resolution Imaging Spectroradiometer (MODIS) aboard NASA's Terra satellites (downloaded from National Aeronautics and Space Administration's Earth Observatory 2020).

At the landscape scale, we evaluated two covariates: (1) habitat type as a four-level categorical variable: native forest, citrus plantations, shade-grown cacao and silvopasture, and (2) the % forest cover around each survey point at a radius of 100, 500 and 1000 m. To estimate % forest cover, we first classified Normalized Difference Vegetation Index (NDVI) values as forest or non-forest using the Jenks Natural Breaks algorithm in ArcGIS, resolution between 10 and 20 m for the year 2020 (Samarawickrama et al., 2017, Vrieling et al., 2018).

At the local scale, vegetation variables for each point were based on 0.04 ha circular plots (11.3 m radius), where we recorded tree density (number of stems ≥ 7.6 cm dbh per 0.04 ha), shrub density (< 7.6 cm at dbh), canopy cover (%), canopy height (m), and basal area (m2 per 0.04 ha) (modified from James & Shugart 1970).

Modeling procedure and selection

We performed an independent model selection process for each scale of analysis but adopted the same modeling procedure for each as follows: 1) First, all covariates were standardized by subtracting the mean from each observation and dividing by the standard deviation; 2) We calculated Pearson's correlation coefficients for all possible pairs of covariates and for pairs with a coefficient >0.6 we only included one of each pair in a given model to avoid collinearity; 3) We ran models with detection covariates only, keeping occupancy or abundance constant, and selected the best model using Bayesian Information Criterion (BIC) (Dennis et al., 2019, Yates et al., 2021) based on a difference >2 in the value of BIC between models; 4) We created a model set to test the hypotheses outlined in the introduction for each scale (see below), including the detection covariates from stage 2 in detection and the covariates of interest in the occupancy or abundance side of the model. Support for individual models was assessed using BIC as described above.

Regional scale: We hypothesized that occupancy probability would vary with elevation and show a positive relationship with precipitation and NPP. We also hypothesized that the timing of rainfall could explain occupancy. We therefore created a model set containing a null model and linear and non-linear (quadratic and polynomial) relationships for the following variables (see Table 1): elevation, annual rainfall, non-breeding season rainfall, rainfall driest month and NPP (N.B. additive models containing one or more of the above variables were not contemplated due to correlations >0.6 between variables).

Landscape scale: We hypothesized that occupancy would increase with % forest in the landscape and would decrease in increasingly open habitats. To evaluate these hypotheses, we created a model set including three variables describing the % forest at variable for the four focal habitats in which points counts were conducted. We also hypothesized that abundance would decrease in increasingly open habitats and we compare and contrast N-mixture models with and without the categorical variable habitat.

Local scale: All vegetation structure variables except basal area were highly correlated (Fig. S2). Therefore, we ran a principal component analysis and used the resulting two components in occupancy models. The first component (PC1) explained 58% of the variation and included tree density, shrub density, canopy cover and canopy height. PC2 explained an additional 20% of the variation and included only basal area (Table S3).

Spatial prediction

In order to visualize the results from the regional scale analysis, we selected the model with the greatest support from BIC and the raster for NPP which was clipped to the Orinoco region containing our sampling sites. Next, using the “coef” function in the *stats* package for R, we generated model coefficients and using the “calc” function in the *raster* package computed the predicted occupancy probability for each pixel in the NPP raster. Finally, we overlaid the predicted occupancy surface on a map of Colombia.

1.5 Results

Regional scale occupancy probability

Blackpoll Warblers were detected at 52 of 128 transects surveyed (Naïve occupancy = 0.41), distributed in 140 detections in 837 visits. 66% of detections consisted of one individual, 26% of two individuals, 4% of three individuals, 2% of four individuals, and 1% of five individuals.

In the detection component of occupancy models, observer was an important source of detection heterogeneity and was included in all subsequent models (Table 1). Relative to the null model, there was support for an effect of precipitation, elevation and NPP on occupancy probability. Of the precipitation variables evaluated, “non-breeding season rainfall” ($\beta = 0.65 \pm 0.23$) and “rainfall driest month” ($\beta = 0.66 \pm 0.24$) received equal support and both were positively correlated with occupancy (Table 1, Fig. 2). For elevation, (β = 1.55 ± 0.38), and was the highest ranked model (Table 1, Fig. 2).

Landscape scale occupancy and abundance

Blackpoll Warblers were detected at 116 of 160 surveyed points (Naïve occupancy = 0.72), distributed in 333 detections in 960 visits. 60% detections were of one individual, 24% of two, 9% of three, 3% of four, 2% of five and 0.3% of six individuals. For occupancy, the detection model with strongest support included constant detection, and there was clear support for an effect of % forest in the landscape and habitat type. However, the direction of effects was contrary to our hypotheses. Occupancy was negatively correlated with the % forest at a 1000 m radius around points (FO1000; β = -0.69 ± 0.18) and was higher in the three agroforestry systems evaluated relative to native forest (Fig. 3, Table S4).

Between agroforestry systems there was no clear difference in occupancy probability (Fig. 3), however, the raw number of detections varied markedly, in spite of equal survey effort: native forest (36 detections), silvopasture (75), citrus plantations (104) and shade-grown cocoa (117). An N-mixture model containing PC1 in detection and the categorical variable habitat in abundance received strong support and predicted high abundance in shade-grown cacao, followed by citrus plantations and silvopasture, and low abundance in forest (Fig. 4, Table S5). The wide confidence intervals for cacao and citrus plantations, suggest that abundance varied considerably among points, with some points harboring abundances up to seven times the mean abundance in forest (Fig. 4).

Local scale occupancy probability and abundance

At the local scale (vegetation structure), the best supported model included a negative effect for PC1 on occupancy (PC1 consisted of tree density, shrub density, canopy height, and canopy cover; Fig. S3) for both occupancy and abundance (N-mixture model).

Spatial prediction

A spatial prediction for the Orinoco basin of Colombia based on the highest-ranked regional model (occupancy = ~observer ~NPP), predicted high occupancy at the base of the eastern slope of the Eastern Andes in Meta, Cundinamarca and Boyacá, and in the occupancy in Casanare and across the central Orinoco plains (Fig. 5).

1.6 Discussion

Blackpoll Warbler occupancy was well explained by environmental factors at multiple scales. At the regional scale, models provided support for the hypotheses that elevation, precipitation and net primary productivity are all driving occupancy in the Orinoco region of Colombia. A spatial prediction of the model containing NPP, that captures responses to both elevation and precipitation, indicated that birds were selecting moister areas in or close to the foothills of the Eastern Andes and in transition zones between the Orinoco plains and Amazonian forests. At the landscape scale, contrary to our expectations, Blackpoll Warblers had lower occupancy rates and abundance in forested landscapes/habitats. Occupancy and abundance were higher in agroforestry systems compared to native forest, with some support that shade-grown cacao held the highest abundance. Overall, our findings contribute to our knowledge of how migratory landbirds respond to environmental gradients on their non-breeding grounds, and emphasize the crucial role that agroforestry systems can play in the conservation of certain species (Bakermans et al., 2009, De Beenhouwer et al., 2013, González 2018, Valdez-Juarez et al., 2019).

Regional scale occupancy

We found a positive relationship between non-breeding season rainfall and occupancy and between NPP and occupancy, as we had predicted based on findings from previous studies. Both factors are known to influence the spatial distribution of energy/food resources in tropical ecosystems (Thorup et al., 2017, Somveille et al., 2018, Boyle et al., 2020) and it is notable that there was a stronger relationship between non-breeding season rainfall and occupancy than with annual rainfall, highlighting the importance of seasonality in resource availability on the distribution of Blackpoll Warblers. Precipitation during the driest month (typically January or February) also influenced occupancy probabilities, suggesting that a threshold for rainfall during the dry season may exist, below which the distribution of Blackpoll Warblers is limited.

For elevation, a quadratic relationship with occupancy received the greatest support, primary productivity relative to the adjacent Orinoco plains. The direct correlation between elevation, rainfall and NPP, explains why NPP better explained occupancy probabilities than either elevation or rainfall alone (Table 1). The spatial prediction based on a model with NPP illustrates this clearly, with higher occupancy predicted along the Andean foothills but also in moister areas away from the Andes at the interface between the Orinoco and Amazon regions. Similarly strong relationships with precipitation and elevation have been found for several long-distance migratory warblers on the non-breeding grounds (Céspedes & Bayly 2018, Bennett et al., 2019), however, not all species (e.g. Tennessee Warbler) show a positive linear relationship with precipitation (and by extension NPP; Cespedes et al., 2021).

Landscape-scale occupancy and abundance

Contrary to our expectations at the landscape scale, we found that Blackpoll Warblers had lower occupancy rates and abundance in forested habitats compared to agroforestry systems. In contrast to other species, such as Cerulean Warbler (*Setophaga cerulea*) and Canada Warbler (*Cardellina canadensis*) (Colorado et al., 2012, Céspedes & Bayly 2018, González et al., 2020), Blackpoll Warblers did not exhibit the anticipated preference for forested habitats. Indeed, they are more similar to Mourning Warbler (*Geothlypis philadelphia*), Yellow Warbler (*Setophaga petechia*) and other Neotropical-Nearctic migrants that regularly use semi-open agricultural landcovers (Bakermans et al., 2009, Valdez-Juarez et al., 2019, Céspedes et al., 2021). They can "adapt" to disturbed habitats.

Given that our findings imply that Blackpoll Warblers generally avoid closed forest on the non-breeding grounds, it is important to understand the natural factors that could generate suitable habitats for the species in the Orinoco region. Rivers in this region, especially those close to the base of the Andes, are highly dynamic, with flood cycles consistently resulting in changes in course, extensive floodplains and the regular creation of edges and secondary vegetation (Lewis et al., 2000, Montoya et al., 2011). Additional factors, including landslides, fires and falling trees, contribute to these successional processes, generating dynamic landscapes, which are more similar to agroforestry systems than to closed-canopy forests. The historical presence of these natural successional habitats may explain the habitat preferences found here.

2022) emphasizing the role of agroforestry systems such as shade-grown cocoa, citrus plantations and silvopastures as non-breeding habitats for Neotropical-Nearctic migrants, including several Parulids in Colombia and elsewhere (Wunderle & Latta 2000, Johnson et al., 2006, Bakermans et al., 2009, 2012; McDermott & Rodewald 2014, Ruiz-Sánchez et al., 2017). Shade-grown cocoa plantations are similar to shade-grown coffee plantations in terms of their structural properties and retention of native trees in the shade (Nájera & Simonetti 2010, Sekercioglu 2012, Bennett et al., 2022), which likely explains why they held a higher abundance of Blackpoll Warblers relative to citrus plantations or silvopastures. While there are relatively few studies on the use of citrus plantations by migratory birds, evidence from Central America suggests that they can support a diverse community of non-breeding migratory birds (Mills & Rogers 1992, Brown & Sherry 2006).

Previous work on silvopasture systems in Colombia, found a positive relationship between increasing vegetation structure and the richness and abundance of migratory and resident forest species (McDermott & Rodewald 2014, Colorado et al., 2018, Morales-Rozo et al., 2021, Lentijo et al., 2022). While mean occupancy and abundance for Blackpoll Warblers was lower in silvopastures relative to cacao or citrus plantations, the differences were slight and there was considerable overlap in 95% confidence intervals. These results highlight a potential role for silvopastures in providing habitat for Blackpoll Warblers. Most silvopastures in our study area were managed as monocultures dominated by legumes such as *Mimosa trianae*, therefore, actions aimed at increasing vegetation structure and tree diversity in these systems, have the potential to enhance silvopastures for the species. Combined, our results at the landscape scale provide evidence for the importance of maintaining diverse landscapes containing both agroforestry systems and native forest.

Local-scale occupancy

At the local scale, habitat characteristics such as tree density, shrub density, canopy height, and canopy cover had a negative effect on Blackpoll Warbler occupancy and abundance. This result appears to be driven primarily by the low use of closed forest and is in contrast with other studies, which have found that basal area (a metric of tree abundance), canopy height and canopy cover are positively related to the occupancy and abundance of forest-dwelling migratory birds at local scales (Colorado & Rodewald 2017, Cespedes & Bayly 2018, Colorado et al., 2018, Tarbox et al., 2018).

Given the declining status of the Blackpoll Warbler, our findings have important implications for where to direct conservation efforts on the species' stationary non-breeding grounds. At the scale of our study area, we found strong evidence for birds selecting areas with higher non-breeding season rainfall and NPP, and our spatial prediction of these results suggest that habitat protection/creation activities should be focused along the foothills of the Andes in Meta, Cundinamarca and Boyacá, as well as transition zones between the Orinoco plains and Amazonian forests. The finding that Blackpoll Warblers tend to have lower occupancy and abundance in forest relative to agroforestry systems must be interpreted carefully. Agroforestry systems can provide benefits for biodiversity and rural economies, and generate environmental sustainability and resilience (Jha et al., 2014, Alvarez-Alvarez et al., 2022), but patches of forest should also be conserved (McNeely & Schroth 2006, Jose 2012), as total forest loss in a landscape could result in unexpected cascade effects at different trophic levels. Nonetheless, promoting diverse agroforestry systems, especially silvopastures, given the extensive areas of cattle pastures in our study region, could provide connectivity between forest patches and increase the available habitat for Blackpoll Warblers, with the potential to combat further population declines.

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Authors' contributions

N.B. and A.M.R. conceived the study; N.B., A.M.R. and G.C. designed the study. A.M.R. led the data collection, J.G., N.B. and A.M.R designed and carried out the analysis. A.M.R version.

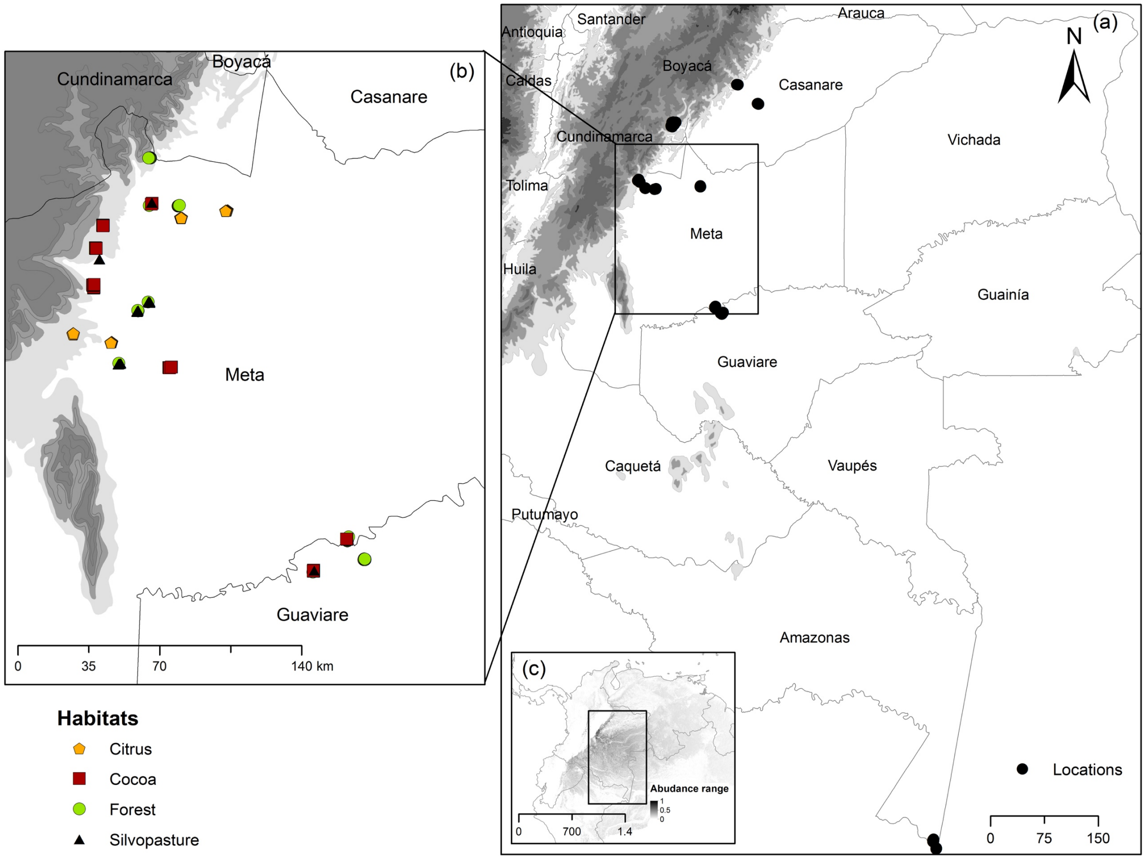
Tables

Table 1. Model set for the analyses of regional scale factors influencing the occupancy of Blackpoll Warblers in the Orinoco region of Colombia. Models are ordered based on Bayesian Information Criteria (BIC), where a difference >2 (ΔBIC) between models is considered as support for one model over another.

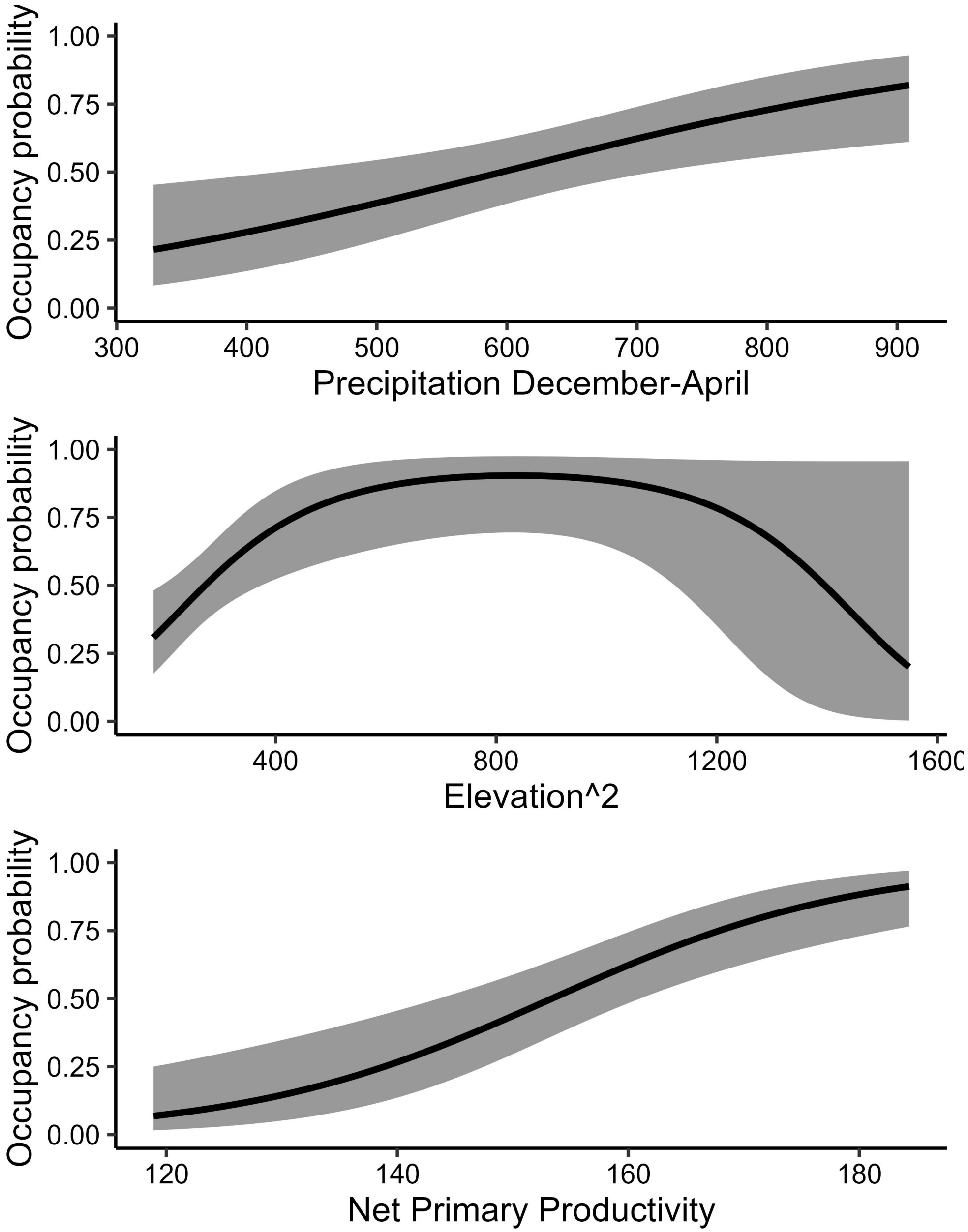
Model	df	logLik	BIC	ΔBIC	Weight
~Observer ~ Net Primary Productivity	6	-319.2	667.6	0	1.0
~Observer ~ Elevation	6	-326.3	681.8	14.2	0.0

~Observer ~ Rainfall driest month	6	-327.3	683.8	16.2	0.0
~Observer ~1	5	-331.6	687.5	19.9	0.0
~Observer ~ Elev + Elev^2 + Elev^3	8	-324.6	688.0	20.4	0.0
~Observer ~ Annual rainfall	6	-329.5	688.2	20.6	0.0

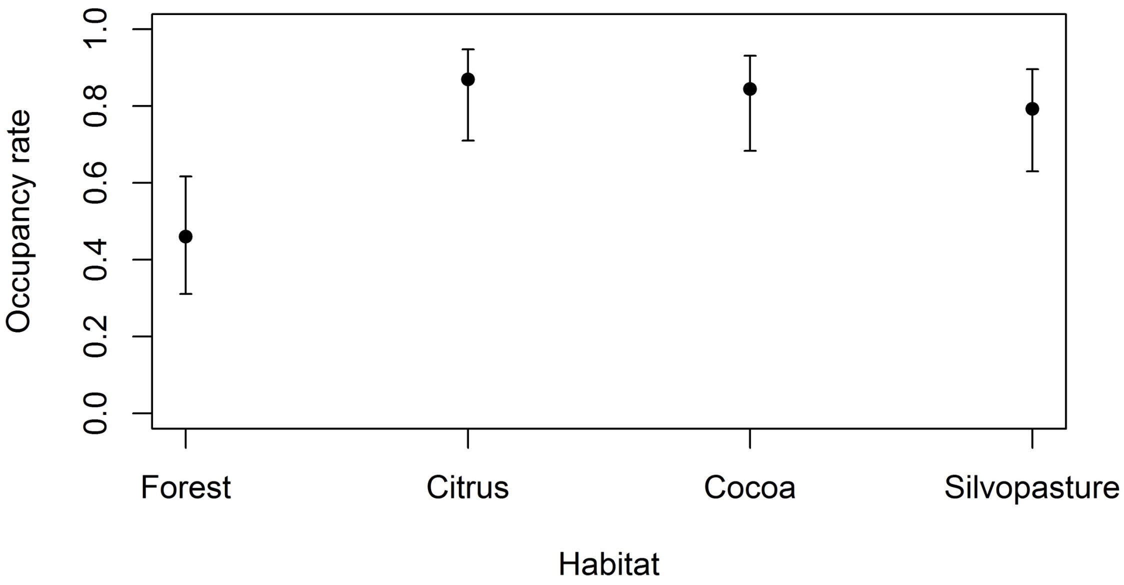
Figure 1. (a) Study sites in the Orinoco and Amazon basins in Colombia for evaluating regional scale occupancy patterns of Blackpoll Warblers in 2017 and 2018. See Supplementary 1 and 2 for the names of sites. (b) Location of study sites (color-coded by habitat) for examining landscape scale (habitat and % forest in the landscape) and fine-scale (vegetation structure) occupancy in the departments of Meta and Guaviare, between January and March 2020. (c) Abundance surface for the non-breeding distribution of the Blackpoll Warbler (from eBird 2021).



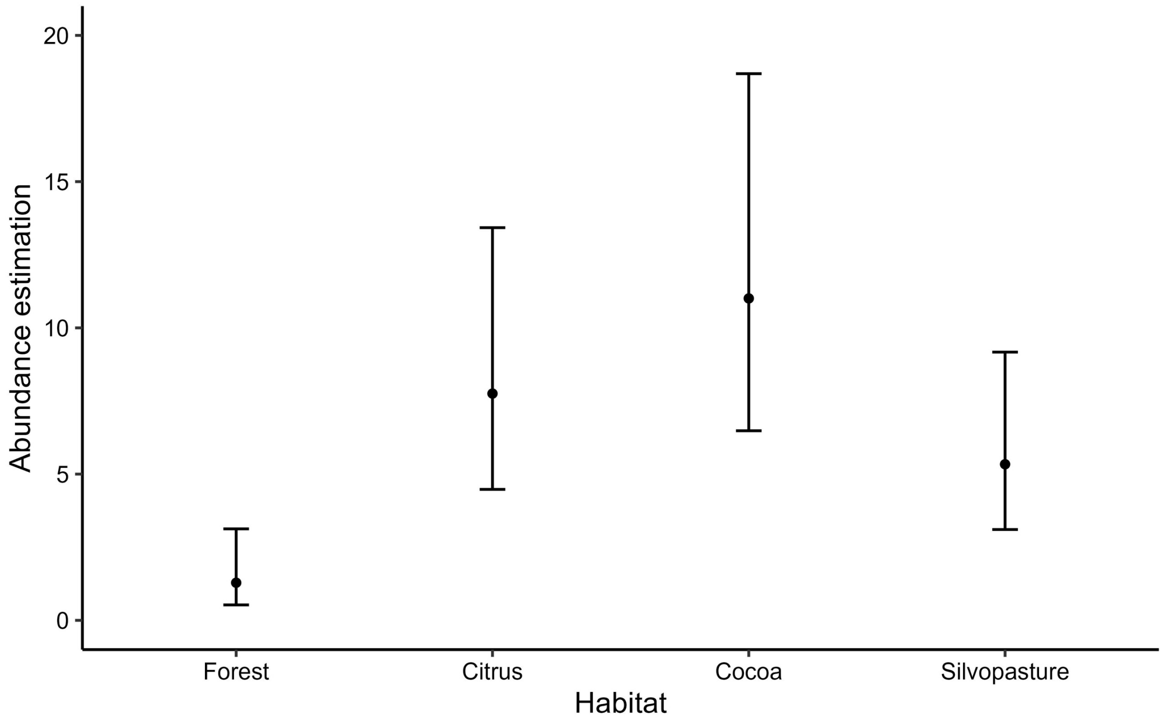
Blackpoll Warblers in the Orinoco region of Colombia and non-breeding season precipitation (mm; December-April), elevation (m) and Net Primary Productivity (gC/m2/year).



breeding habitats in the Orinoco region of Colombia: Native forest, citrus plantations, shade-grown cocoa and silvopasture.



Blackpoll Warblers across four habitat types in the Orinoco region of Colombia based on N-mixture models: native forest, citrus plantations, shade-grown cocoa and silvopasture.



Colombia based on the best global model with Net Primary Productivity (gC/m2/year).

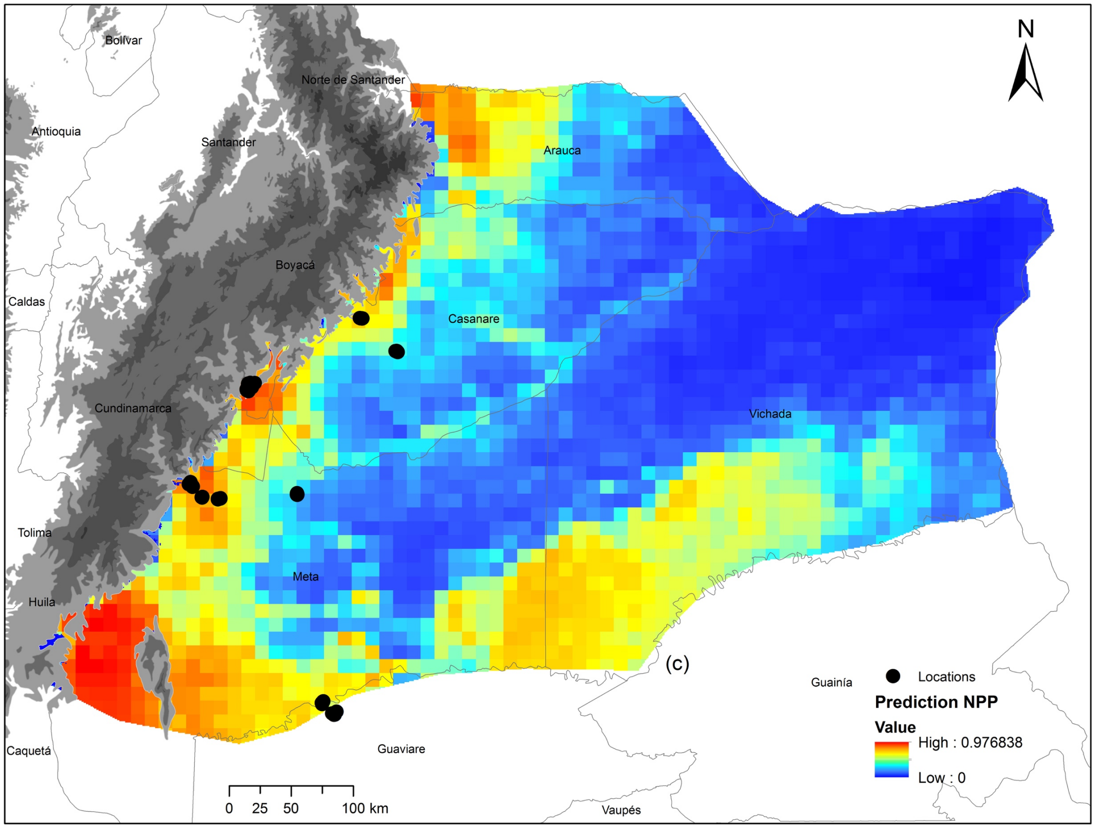


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Table S1. Location, number of transects, number of repetitions and average elevation for 17 sites surveyed for Blackpoll Warblers during 2017 and 2018.

Department	Habitat	Average elevation (m)	No. Transects	Repetitions	No. Detections
Casanare	Forest and open areas	492	10	8	13
Casanare	Forest and open areas	194	10	8	0
Boyacá	Forest	1243	8	4	0
Boyacá	Forest	803	7	4	1
Boyacá	Cocoa	787	12	4	5
Boyacá	Forest	1520	2	4	0
Boyacá	Forest and Cocoa	913	8	4	3
Boyacá	Forest and open areas	1092	7	4	0
Meta	Forest	1166	10	8	21
Meta	Forest	638	6	8	19
Meta	Mixed habitats	390	7	8	26
Meta	Forest	328	10	8	23
Meta	Forest and open areas	207	10	8	2
Guaviare	Forest and open areas	227	11	7	7
Guaviare	Forest	191	10	8	20
Amazonas	Forest	76	6	4	0
Amazonas	Forest	83	5	4	1
Amazonas	Forest and open areas	60	6	4	0
	Total		145	107	141

surveyed for Blackpoll Warblers during 2020. b) Images of the study habitats for a comparison of occupancy by Blackpolls Warbler occupying forest, citrus and shade cocoa and silvopasture in Meta, Colombia.

Department	Habitat	Average elevation m	No. Points	Repetitions	No. Detections
Guaviare	Forest	211	20	6	6
Guaviare	Cocoa	216	7	6	6
Guaviare	Silvopasture	213	2	6	4
Meta	Forest	499	20	6	30
Meta	Cocoa	568	33	6	111
Meta	Silvopasture	371	38	6	71
Meta	Citrus	345	40	6	104
	Total		160	42	328

tree density; ShruDen: shrub density; CanopyCov: canopy cover; CanopyH: canopy height; BasalA: basal area.

	Comp.1	**Comp.2**	**Comp.3**	**Comp.4**	**Comp.5**
Standard deviation	1,69	1.0.0	0,82	0,53	0,38
Proportion of Variance	0,58	0,2	0,14	0,06	0,03
Cumulative Proportion	0,58	0,78	0,91	0,97	1.0.0

Loadings	**Comp.1**	**Comp.2**	**Comp.3**	**Comp.4**	**Comp.5**
TreeDen	0,5		0,42	0,69	0,31
ShruDen	0,48		0,54	-0,69	
CanopyCov	0,52	-0,32	-0,26	0,11	-0,75
CanopyH	0,47		-0,67	-0,18	0,54
BasalA	-0,16	-0,95	0,14		0,24

Colombia in 2020. F1000: proportion of forest at 1000 meters radius around any given point, F100: proportion of forest at 100 meters radius around any given point, Habitat (habitat type was considered to have four levels: native forest, citrus plantations, shade cacao and silvopastures),); number of model parameters (df), log-likelihood (logLik), ΔBIC scores, and model weight, are shown for each model.

Model	ρ(Int)	ψ(Int)	ψ(F100)	ψ(F1000)	ψ(Habitat)	df	logLik	BIC	ΔBIC	weight
~1~FO1000	-0,13	1,14		-0,7		3	-565,7	1146,6	0,0	0,9
~1~Habitat	-0,13	1,89			+	5	-563,6	1152,5	5,9	0,0
~1~1	-0,13	1,056				2	-573,4	1156,9	10,3	0,0
~1~FO100	-0,13	1,066	-0,2188			3	-572,6	1160,4	13,8	0,0

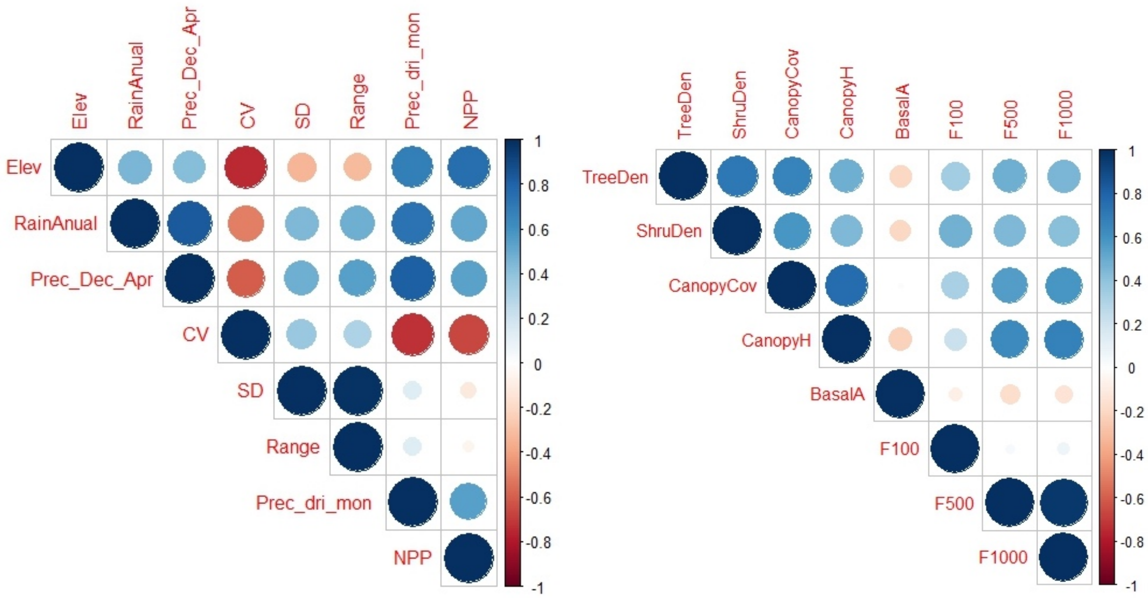
PC1: TreeDen: tree density; ShruDen: shrub density; CanopyCov: canopy cover; CanopyH: canopy height; F1000: proportion of forest at 1000 meters radius around any given point, F100: proportion of forest at 100 meters radius around any given point, Habitat (habitat type was considered to have four levels: native forest, citrus plantations, shade cacao and silvopastures); number of model parameters (df), loglikelihood (logLik), Δ BIC scores, and model weight, are shown for each model.

Model	p(Int)	λ(Int)	p(PC1)	λ(F1000)	λ(F100)	λ(Habitat)	df	logLik	BIC	deltaBIC	weight
~PC1~F1000	-2,51	1,84	-0,09	-0,58			5	-838,6	1702,5	0	0,952
~PC1~Habitat	-2,24	2,05	0,15			+	7	-836,5	1708,5	5,98	0,048
~PC1~F100	-2,59	2,02	-0,29		0,09		5	-846,7	1718,8	16,24	0,0
~PC1~1	-2,44	1,94					3	-854,3	1723,8	21,25	0,0

Warbler occupying forest, citrus and shade cocoa and silvopasture in Meta, Colombia.

 Forest	 Citrus
 Shade cocoa	 Silvopasture

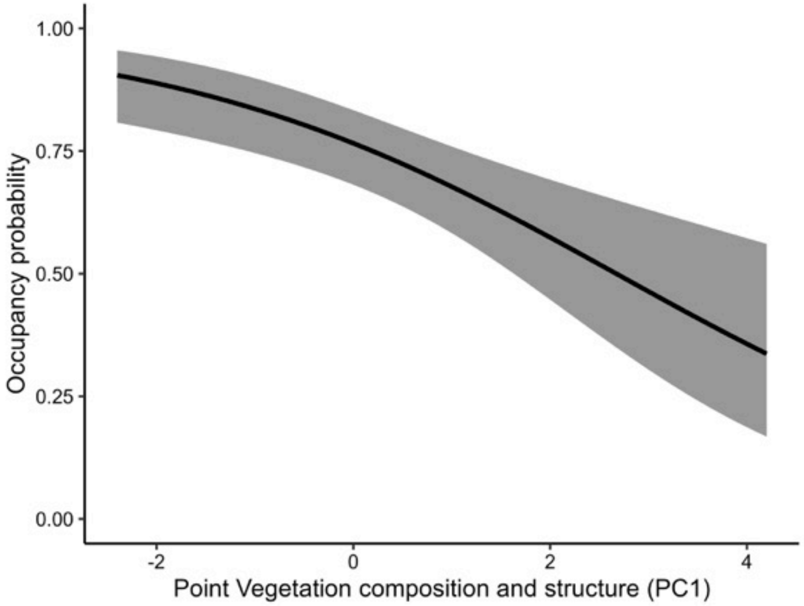
scale to avoid collinearity. We then selected one variable from each pair of variables with a coefficient greater than |0.6|. a) Regional scale: Elevation: Elev; RainAnual: Annual Precipitation; Prec_Dec_Apr: range for the precipitation from December to April (“winter precipitation”); CV: coefficient of variation; SD: standard deviation; Prec_dri_mon: precipitation of the driest month; NPP: Net Primary Productivity. b) Landscape and local scale: TreeDen: tree density; ShruDen: shrub density; CanopyCov: canopy cover; CanopyH: canopy height; BasalA: basal area; F100, F500, F1000: 100, 500 and 1000 m radius buffers around the location of each point count.



a) Regional scale

b) Landscape and local

vegetation structure where PC1 included tree density, shrub density, canopy cover and canopy height. Gray lines correspond to 95% confidence intervals.



Chapter 2: Home range size, space use, and site fidelity in Blackpoll Warblers on their non-breeding grounds in Colombia

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2.1 Abstract

The Blackpoll Warbler is one of the few Neotropical-Nearctic migrants that overwinters in the Orinoco and Amazonian bioregions throughout the non-breeding season that is in steep decline. However, there is little information available on their home ranges and space use. We evaluated how home range size and space use by Blackpoll Warblers varied across different landscapes (exurban and rural) based on captured, color banded and resighted individuals during four non-breeding seasons from December to April between 2018 and 2022 in Villavicencio, Meta. Additionally, we evaluate how home range size varied across different agroforestry systems (shade-grown cocoa and citrus plantations) based on manual telemetry, between January and February 2021 in Villavicencio, Acacias, and Guamal, Meta. We estimated home-range sizes for the landscape and habitat scales using minimum convex polygons and kernel density estimators respectively. At the landscape scale Blackpoll Warblers exhibited home ranges <1 ha based on minimum convex polygons (95% and 50%) and we found variation in home range estimates between years in exurban and rural landscapes, with larger home ranges between 2018-2019 when rainfall was diminished by a weak El Niño event, and smaller home ranges between 2020-2022 when rainfall increased with a moderate La Niña. At the habitat scale we found differences using kernel density estimators, finding as well as spatial and site fidelity across the study sites at different scales are proxies of habitat quality. Our study contributes novel insights into the non-breeding ecology of the Blackpoll Warbler in Colombia, and reveal that diverse modified landscapes and diverse agroforestry systems (e.g., shade-grown cocoa and citrus plantations) could help to combat population declines of Blackpoll Warbler.

Key words: Habitat, radiotelemetry, agroforestry, shade-grown cocoa, citrus plantations

2.2 Resumen

La reinita rayada (*Setophaga striata*) es uno de los pocos migrantes neotropicales-neárticos que pasan el invierno en las biorregiones del Orinoco y la Amazonia durante la época no reproductiva y que se encuentra en franco declive. Sin embargo, hay poca información disponible sobre su área de distribución y uso del espacio. Evaluamos cómo el tamaño del rango de hogar y el uso del espacio por parte de *Setophaga striata* varió a través de diferentes paisajes (exurbano y rural) con base en individuos capturados, anillados con anillos de color y reavistados durante cuatro temporadas no reproductivas de diciembre a abril entre 2018 y 2022 en Villavicencio, Meta. Adicionalmente, evaluamos cómo varió el tamaño del rango de hogar a través de diferentes sistemas agroforestales (plantaciones de cacao y cítricos bajo sombra) con base en telemetría manual, entre enero y febrero de 2021 en Villavicencio, Acacias y Guamal, Meta. Se estimaron los tamaños de los rangos de hogar para las escalas de paisaje y hábitat utilizando polígonos convexos mínimos y estimadores de densidad kernel respectivamente. A escala de paisaje, las currucas capirotadas exhibieron rangos de hogar <1 ha, encontramos que las estimaciones de rango de hogar usando polígonos convexos mínimos (95% y 50%) mostraron diferencias entre años en paisajes exurbanos y rurales, con rangos de hogar más grandes entre 2018-2019 cuando la precipitación es afectada por un débil El Niño-Oscilación del Sur (ENSO), y rangos de hogar más pequeños entre 2020-2022 cuando la precipitación aumenta por un moderado La Niña. A escala de hábitat, encontramos diferencias utilizando estimadores de densidad kernel, encontrando áreas de campeo más pequeñas en el cacao cultivado a la sombra en relación con las plantaciones de cítricos. Los territorios pequeños, así como la fidelidad espacial y al emplazamiento entre los capirotada en Colombia, y revela que diversos paisajes modificados y diversos sistemas agroforestales (por ejemplo, cacao bajo sombra y plantaciones de cítricos) podrían ayudar a combatir la disminución de la población de la *Setophaga striata*.

Palabras clave: Hábitat, radiotelemetría, agroforestal, cacao son sombrío, plantaciones de cítricos.

2.3 Introduction

In Nearctic-Neotropical migratory birds, population dynamics are known to be influenced by habitat quality (Johnson, 2007; Rushing et al., 2016; Sherry & Holmes, 1996), particularly in their non-breeding areas where it has been recognized as a primary driver of population fluctuations (Faaborg et al., 2010; Sherry & Holmes, 1996). Habitat quality can impact various aspects of a migratory birds´ life cycle, including body condition, timing of migration, breeding success and survival, which, ultimately, can result in long-term carry-over effects (Albert et al., 2020; Bayly et al., 2018; Norris & Taylor, 2006; O'Connor & Cooke, 2015). Additionally, habitat quality is closely tied to attributes such as territorial behavior (Marra, 2000; Marra et al., 1993; Winker et al., 1995), and resource availability (Johnson & Sherry, 2001; Pulliam, 2000).

Resource availability influences territory size on the non-breeding grounds and, therefore, territory or home range size can be an useful proxy for exploring habitat quality (Latta & Faaborg, 2001; Marra & Holmes, 2001; Winker et al., 1995). For example, changes in food availability have knock-on effects on territory size, as demonstrated through experiments with Ovenbirds (*Seiurus aurocapilla*), which showed that sedentary birds adjust their home range in response to food availability at a small scale without significant changes in size, while floater birds adjust their spatial utilization to the availability of resources on a broader scale (Brown & Sherry, 2008a). In other species, such as American Redstarts (*Setophaga ruticilla*), males abandoned their territories in response to significant food losses in food-reduced territories (Brown & Sherry, 2008a). Some males may change their behavior from being territorial to being a floater when food availability decreases and this behavior may influence population dynamics (Brown & Sherry, 2008a; Cooper et al., 2015). In addition, territories and habitats supporting a higher density of birds can be indicative of higher habitat quality (Albert et al., 2020; González, 2018; Ruiz-Sánchez et al., 2017; T. M. Smith & Shugart, 1987). Conversely, larger territories have been reported in both transformed habitats (e.g. pastures, agricultural matrices; Chandler et al., 2016; Rappole, 1995) and when food supplies are reduced and birds became non-territorial (Brown & Sherry, 2008a).

Space use responses may also be influenced by habitat availability in migratory birds. For instance, when habitat is limited, birds can be forced to occupy the available habitats (including those of low quality) but, due to density dependent effects, their home ranges may be smaller than the optimal, leading birds to experience reduced fitness by not having access to sufficient resources (e.g., ecological trap; Anich et al., 2010; Boves et al., 2013; Robertson et al., 2013; Schlaepfer et al., 2002). Another observed pattern is when birds make large modifications to their space use. Swainson's Warblers (*Limnothlypis swainsonii*) in open habitats exhibit more pronounced shifts in their home ranges, adapting their home ranges in response to variations in precipitation and the associated increases in food availability following rainfall (Brunner et al., 2022). Rappole (2013) noted that obligate insectivores, like warblers and flycatchers, usually establish and defend small, stable territories during his research in Panama and other Neotropical regions. On the other hand, species that consume fruit and nectar that is only available during certain seasons cover greater distances in order to take advantage of dispersed food sources.

Based on the above, variation between habitats, their availability and quality, generates diverse territorial behaviors on the non-breeding grounds, also individual variation, with some migratory species typically defending territories (e.g., Kirtland’s Warbler (*Setophaga kirtlandii*); Cooper et al., 2017; Kramer et al., 2018), while others do not seem to exhibit territoriality (e.g., Prothonotary Warbler *Protonotaria citrea*; Lefebvre et al., 1992; Wolfe & Johnson, 2015). These changes in territorial behavior are often believed to be associated with the availability of resources (e.g., fruits or insects; Albert et al., 2020).

Some studies have linked territoriality to site fidelity and habitat quality. There is extensive evidence in the literature indicating that migratory birds often display fidelity to their wintering areas, returning to the same locations from year to year (Holmes & Sherry, 1989; Latta & Faaborg, 2001; Bulluck et al., 2019; Wunderle et al., 2014; Bayly et al., 2020). The advantages of site fidelity include increased efficiency in food acquisition, familiarity with

with a high degree of site fidelity to their wintering grounds may be particularly vulnerable to declines resulting from habitat transformation (Warkentin & Hernández, 1996; Wunderle & Latta, 2000). This is particularly relevant considering that habitat transformation is a primary threat to Neotropical-Nearctic migratory populations on both the breeding and non-breeding grounds (Banks-Leite et al., 2020; DeSante et al., 2018; Wilson et al., 2018). Forest loss and land use change have been identified as drivers of declines in the availability of high quality non-breeding habitats (Colorado & Rodewald, 2017; Petit et al., 1995; Rushing et al., 2016; Wilson et al., 2018). This is believed to be the case for 24 common migratory birds in steep decline that have lost more than 50% of their populations over the past 40 years due to numerous anthropogenic stressors (Rosenberg et al., 2016). The Blackpoll Warbler (*Setophaga striata*) is one of those species, a long-distance migratory landbird that has recently been listed by the IUCN as Near Threatened (IUCN, 2023) and whose populations have been estimated to have declined by more than 90%. Thus, competition for optimal winter territories may be an important factor limiting populations of Neotropical–Nearctic migrant songbirds (Sherry & Holmes, 1996), with implications for the conservation and management of non-breeding ground habitats.

The Blackpoll Warbler is one of the few Neotropical-Nearctic migrants that spends the stationary non-breeding period in the Orinoco and Amazonia region (Fink et al., 2022). These bioregions are being rapidly and extensively transformed by large-scale agricultural activities and land grabbing (Lozano Rodríguez, 2020), potentially affecting Blackpoll Warbler habitat. Despite being one of the steepest declining landbirds in the Americas, virtually no information is available on the species' non-breeding ecology (Bayly et al., 2020; Gómez et al., 2021). Unexpectedly, a recent study examining Blackpoll Warbler occupancy patterns found higher occupancy rates in agroforestry systems (e.g., shade-grown cacao and citrus plantations) compared to natural forests in Colombia (Morales-Rozo et al. *in prep*), contrasting with other declining warblers on the non-breeding grounds that showed similar or higher use of native forest relative to agroforestry systems, e.g., Cerulean Warbler (*Setophaga cerulea*) and Canada Warbler (*Cardellina canadensis*) (Bakermans et al., 2009; Céspedes & Bayly, 2018; González et al., 2021; McDermott & Rodewald, 2014; Ruiz-Sánchez et al., 2017; Wunderle & Latta, 2000). These differences in Blackpoll Warbler occupancy by habitat are likely driven by habitat quality, which, in turn, can be assessed through different proxies, including home range analysis (Johnson, agroforestry systems can shed light on the value of these habitats to Blackpoll Warblers.

In this study, we provide novel information on the non-breeding ecology of the Blackpoll Warbler in Colombia by estimating and comparing home range size, space use and site fidelity across different landscapes and between different agroforestry systems in the Orinoco region of Colombia based on complementary methods (i.e., resightings of color-banded birds, and manual telemetry). We first evaluated how home range size and space use varied across exurban and rural landscapes. Since species space use behavior can vary in response to landscape structure (natural vs anthropogenic; Leonard et al., 2008; Taylor & Krawchuk, 2005), we expected home range and space use size to be smaller (higher quality) in a rural landscape with extensive monocultures and polycultures, relative to an exurban landscape with a diverse mosaic of landcover types. We then focused on two agroforestry systems regularly used by the species in the Orinoco-Amazonia region, shade-grown cocoa and citrus plantations, estimating and comparing territories and home ranges between these two habitats. We expected that territories and home ranges would be larger in lower-quality habitats (i.e., monocultures such as citrus plantations, less resources) compared to a more taxonomically and structurally diverse habitat such as shade-grown cocoa, which maintain a shade of native trees that generates vertical stratification in structure similar to natural forests: a characteristic that has been considered a proxy of habitat quality for biodiversity (Brunner et al., 2022; Vergara et al., 2019). Finally, we examined site fidelity of Blackpoll Warblers between and within winters, expecting a high degree of site fidelity in the rural landscape and monocultures related to exurban (e.g., citrus plantations) as described for others migratory birds (Holmes & Sherry, 1989; Latta & Faaborg, 2001, Wunderle & Latta, 2000). To our knowledge, this is the first study to assess non-breeding ground habitat quality in Blackpoll Warblers in different landscapes and agroforestry systems.

2.4 Methods

Study area

We studied Blackpoll Warblers along the eastern foothills of the Eastern Andes in the Meta department of Colombia. The climate in the region is characterized by a temperature that ranges from 25 to 32°C, and an annual average precipitation of 4,383 mm distributed in an

April to November (IDEAM, 2017) (Figure 1).

Landscape comparison

To examine space use and territory size in Blackpoll Warblers, we worked in two contrasting landscapes in the municipality of Villavicencio, Meta department: A) Barcelona campus of the Universidad de los Llanos at 12 km from Villavicencio (4.073118N, -73.580857W; 390 masl), exurban landscape of approximately 45 hectares, the study took place in 16 hectares containing a diverse mosaic of fishponds, pastures, open areas, riparian strips, live fences, small experimental plots of citrus and shade-grown cocoa plantations (~1 hectares), small fragments of native forest, buildings (11% urban area) and roads (Avendaño et al 2018; Bayly et al 2020; Yantén et al 2022, Figure 1, Figure S1). B) Libertad-Agrosavia Research Center at 17 km from Villavicencio (4.058914N, -73.464356W; 330 masl), rural landscape with a total extension of 1,332 hectares. The study took place in 40 hectares of experimental plots dominated by monocultures of citrus crops (14.16 hectares) and African oil palm (4.45 hectares), bordered b y smaller areas of agroforestry systems (3.55 hectares), only 4% of urban area and native forest (5.2 hectares; Figure 1, Figure S1).

Habitat comparison

To compare space use and territory size of Blackpoll Warblers between two contrasting agroforestry systems, we selected Citrus plantations and shade-grown cacao plantations. The former had just one stratum dominated by either Valencia oranges (*Citrus sinensis*), Arrayana tangerine (*Citrus reticulata* Blanco), Tahití lime (*Citrus latifolia* L.), Minneola tangerine (*Citrus reticulata* Blanco x *Citrus paradisi* Macfad), or Mandarine orange (*Citrus reticulata* Blanco). Shade-grown cocoa plantations consisted of two strata: an understory of cocoa plants (*Theobroma cacao*) and a canopy dominated by trees such as *Mimosa trianae*, *Cecropia* sp., *Inga* sp., *Cedrela* sp., *Scheflera* sp., and *Musa* sp., as well as other legumes and trees from the Melastomataceae family. Citrus plantations cover ~7000 hectares in the Meta department, while cocoa plantations cover ~7023 hectares in 2020

(Benavides, 2008). Two sites were selected for each habitat. Citrus plantations were located in the municipality of Villavicencio at: 1) Libertad-Agrosavia Research Center, in a ~15 hectares citrus plantation, ~20 years old, surrounded by tropical fruit trees, agroforestry systems, rubber and African palm experimental plots (Figures 2, 2A); and 2) Santa Rosa (4.009970 N; -73.453580 W; 301 masl), a citrus farm covering ~40 hectares with an average age of ~40 years, surrounded by riparian forest and live fences (Figures 1, 2B). The distance between the two sites was 6 km.

Cocoa plantations were located at: 1) Finca El Triunfo in the municipality of Acacias (3.974170 N; -73.797500 W; 691 masl), a ~6 hectares farm with cocoa trees of different ages (1, 4 and 7 years), with a shade dominated by Fabaceae trees (mostly *Mimosa trianae*), surrounded by riparian strips and live fences and adjacent areas that included native forest patches, fish farms and pastures (Figures 1, 2C); and 2) Finca Villatatiana in the municipality of Guamal (3.871650 N; -73.830660 W; 657 masl), ~8 hectares with cocoa trees of different ages (3 to 6 years), and a shade dominated by Fabaceae trees (mostly *Mimosa trianae*) (Figures 1, 2D), surrounded by forest patches and riparian strips. The distance between the sites was 12 km.

Capture and resightings for landscape comparison

To study the home range and space use of Blackpoll Warblers in the Barcelona campus of the Universidad de los Llanos (exurban landscape) and the Libertad-Agrosavia Research Center (rural landscape), we captured, color banded and resighted individuals during four non-breeding seasons from December to April between 2018 and 2022. Captures took place during 10 days in December and 10 days in January in each season, using mist-nets (6 nets of 12 m x 2.5 m x 30 mm mesh and 1 of 18 m x 2.5 m x 30 mm mesh), in combination with playback of Blackpoll Warbler calls and songs. For all mist-netted warblers, we determined age and sex by plumage characteristics (Johnson et al., 2011; Ryder & Wolfe, 2009; Wolfe et al., 2010). Blackpoll Warblers were banded with standard numbered aluminum bands and a unique combination of plastic color bands to facilitate subsequent identification in the field. Nets were operated under good weather conditions and were closed in the event of rain, strong winds or direct sunlight. All birds were released in good condition after processing.

December through April of 2018-2022 covering the entire non-breeding period. In each period, we spent two days per site, giving rise to 28 days of effort per season per site. In each landscape, observations were carried out between 6:00 hr and 9:30 hr with passive walks around the study area and between 15:30 hr to 17:30 hr using playback of Blackpoll Warbler calls in the same area (Figure S1). Resightings were conducted along pre-established paths, each 2 km in length, walked slowly at least twice during the morning and once during the afternoon. In addition, when we heard an individual, we left the paths to check if it corresponded to a banded bird. We identified each bird encountered by its unique color-band combination and recorded the exact position using a GPS Garmin64s (accuracy of <3m), as well as time of day and date.

Manual radiotelemetry for habitat comparison

In order to compare home range and space use of Blackpoll Warblers in cocoa and citrus plantations, we used radiotelemetry. Between the 4th and 14th of January 2021, we captured birds in the four study sites (two for each agroforestry system) using mist-nets and playback of Blackpoll Warbler calls and songs. In total, we fitted 20 individuals with Lotek NTQB-2 Nanotags (Lotek Wireless Inc., Newmarket, ON, Canada), five individuals per site (2 agroforestry systems x 2 sites x 5 individuals per site). Nanotag weight was 0.32 g for all birds (<2.9% of the lean weight of birds), while pulse rates and expected lifespans varied but did not affect our ability to manually track and locate birds (see Table S1). For all radio-tagged birds, we determined age and sex by plumage characteristics (Johnson et al., 2011; Ryder & Wolfe, 2009; Wolfe et al., 2010). Each individual was banded with a standard numbered aluminum band and a unique combination of plastic color bands to facilitate subsequent identification in the field. Transmitters were attached to birds using a leg-loop harness (Rappole & Tipton, 1991) made of elastic nylon thread and with a total length (straightened chord) between 76 mm and 86 mm.

Birds were manually radio-tracked during at least 15 days after initial capture between January and February 2021, between 06:00–12:00 hr and 14:00–18:00 hr, using a Lotek handheld receiver (LOTEK SRX600) with a 3-element Yagi antenna. At least three points were collected per individual per day. Data collection was rotated between the sites, and each day the recording schedule was changed to collect points from individuals at different times of day. We tracked tagged birds either until we could achieve visual confirmation or of each other in order to perform triangulation, with gain values between 50-80 in the direction of the strongest signal. We calculated the centroid from triangulated points with the function gCentroid in the R package rgeos (Bivand et al., 2021).

Each time a radio-tracked bird was detected, we recorded coordinates using a handheld GPS Gamin64s with an accuracy of <3m, date, hour, tag number, elevation, signal strength, gain, direction in degrees, land cover (e.g. citrus, cocoa and other), tree species (when possible), vertical stratification of the bird in a tree (e.g. canopy, midstory and understory), presence of conspecifics, and social behavior when possible (e.g., solitary, with other Blackpoll Warblers and with other species).

Spatial analyses for landscape comparison

We estimated home-range sizes of Blackpoll Warblers using minimum convex polygons (MCP), since the number of records for each subset of our data was small (10-20 registers per individual), MCP represented the most appropriate method (Hansteen et al., 1997). The landscape dataset was organized by year and season, and each season was divided into early (December and January) and late (February to April). We assessed the 95% (maximum) as well as the 50% (core area) home range isopleths of each individual. The 50% isopleth is used to describe the core area or area of intensive use (Barg et al., 2005; Castaño et al., 2019; Howell & Chapman, 1997; Townsend et al., 2010), and is useful for defining conservation and habitat management strategies (Leonard et al., 2008). MCP was calculated using the "mcp" function of the R package adehabitatHR (Calenge, 2006). We employed generalized linear models (GLM) to explore the relationship between home-range size (both 95% and 50%) and site, year, season, and potential interactions (e.g., season:landscape and year:landscape). Because the data had a positively skewed distribution, we used the logarithmic transformation using the "glm" function in "lme4" package in R (Bates et al., 2015). Model selection was carried out using AICc for small sample sizes. Models with delta AICc < 2 (AICc differences) were considered equally plausible (Burnham & Anderson, 2004).

Spatial analyses for habitat comparison

Home ranges for Blackpoll Warblers for the habitat comparison were estimated using a kernel density estimator (KDE). Since we collected >30 registers per individual, KDE habitat dataset was organized by site and habitat. KDE are considered the most accurate and robust estimates of an individual´s space use (Leonard et al., 2008; Marzluff et al., 2004; Worton, 1989), and is commonly used for habitat selection studies where size estimation is crucial (Barg et al., 2005). We used a reference smoother (h_{ref}) that provides the required information about the utilization distribution (Worton 1989, Leonard et al 2008). We assessed the 95% (maximum) as well as the 50% (core area) kernel home range isopleths of each individual. KDE was calculated using the “kud” function of the R package. We calculated the percentage overlap of kernel home ranges for all individuals sharing a site using the “kerneloverlaphr” function in the “adehabitatHR” package in R (Fieberg & Kochanny, 2005).

We used generalized linear mixed-effects models (GLMM) to evaluate the association of the KDE home-ranges (both 95% and 50%) with independent variables such as habitat, sex and age, with site as a random effect. We built GLMMs with a Gamma distribution because the data were not normally distributed. We used the “glmer” function in “lme4” package in R (Bates et al., 2015). Initially, in order to assess whether site or habitat had an effect on home range sizes, GLMMs were constructed by setting site as a random variable. The resulting GLMM null model was indistinguishable from other models in their respective pool, implying that site had little or no effect on home range ($p>0.1$). In subsequent models, we therefore grouped sites by habitat and used generalized linear models (GLM) to evaluate the effect of habitat, sex and age on our dependent variable, the KDE home range (both 95% and 50%), using the “glm” function in “lme4” package in R (Bates et al., 2015). Model selection was carried out using AICc for small sample sizes. Models with delta AICc < 2 (AICc differences) were considered equally plausible (Burnham & Anderson, 2004).

Site fidelity for all scales

We describe both within-year (overwinter site persistence) and between-year (annual return rate) site fidelity. The former is defined as those birds banded in December and subsequently recaptured or resighted in January or April of the same field season. We quantify overwinter site persistence during the entire December–April winter period. The annual return rate was defined as the percentage of within-year site persistent birds (from a previous field season), which were captured or resighted in a subsequent field season.

2.5 Results

We captured 177 Blackpoll Warblers across the four non-breeding seasons between 2018-2022: 101 individuals in the Libertad-Agrosavia Research Center (mean per season: 15 individuals), and 76 individuals in the Barcelona Campus of Universidad de los Llanos (mean per season: 8 individuals). Based on individuals with more than 10 georeferenced locations, we obtained 1501 location records for 48 individuals across both localities, with 26 individuals (663 records) at the Libertad-Agrosavia Research Center (17 males and 9 females), and 22 individuals (838 records) at the Barcelona Campus (15 males and 7 females; Table S2). Blackpoll Warblers were consistently observed throughout the resighting period between December and April.

Raw return rates between seasons varied such that 65% of individuals captured in 2017-2018 non-breeding season in Agrosavia returned, 45% during the second season, and 37% during the third season. In Unillanos, 63% of individuals from the first season returned, 33% from the second season, and 22% from the third season. Notably, at least three individuals were consistently documented across all four seasons at each site (Figure S2).

We found no clear difference in our minimum convex polygon estimates for overwintering Blackpoll Warblers in an exurban and a rural landscape (GLM = 0.11, p = 0.91). The mean minimum convex polygons estimate (95%) in the Barcelona campus (exurban landscape) was (mean ± SD) 0.124 ± 0.198 hectares (N = 22, range = 0.007 - 0.908 hectares; Table S3), whereas the core area (50%) was 0.018 ± 0.029 (N = 22, range = 0.001 - 0.137 hectares; Table S4). For the Libertad-Agrosavia Research Center (rural landscape), the mean minimum convex polygon estimates (95%) was 0.129 ± 0.071 ha (N = 26, range = 0.019 - 0.437 hectares; Table S3), whereas the average core area (50%) for all individuals was 0.028 ± 0.029 (N = 26, range = 0.002 - 0.130 hectares; Table S4).

No differences in home range (95% and 50%) were found between seasons (GLM=-0.41, p=0.68) or during a season, e.g., dividing the season into early (December and January) and late (February to April), although there was a tendency for larger home ranges later in the season (Fig. 4). However, home ranges did vary between seasons (e.g., 2020: GLM =

consistent pattern of home range size variation between sexes and ages ($p > 0.1$).

Habitat comparison

Among the 20 individuals captured for the habitat comparison, there was a sex ratio of ~1:1.3 males:females, with a total of 7 males and 13 females across all sites. The sample consisted of 11 immature/first year (FCF: first cycle formative) birds and 9 adult birds (DCB: definitive cycle basic; Table S1). We could only calculate home range for 9 individuals in citrus plantations since we excluded one individual that lost its radio transmitter at day 9. Blackpoll Warblers exhibited high site fidelity throughout the entire tracking period (i.e., January to February 2021) in both citrus and cocoa plantations, with no evidence for birds leaving sites or moving between sites.

In the citrus plantations, the average height at which individuals was observed was (mean ± SD) 3.1 ± 1.2 m, with 73% of the records located in the canopy, 20% in the midstory, and 7% in the understory (branches on the ground from cut citrus trees). Conversely, in the shade-grown cocoa plantations, average foraging height was 6.0 ± 3.8 m, with 63% of the records in the canopy, 30% in the midstory, and 6% in the understory (cocoa plants). Of the 94 records in citrus plantations, 73% were for solitary birds, 26% with conspecifics, and 1% in presence of other species. For the 380 records in cocoa plantations, 73% of the records were for solitary birds, 27% in the presence of conspecifics, and 2% in the presence of other species.

We found variation in kernel home range estimates for Blackpoll Warblers between the two agroforestry systems, with birds using significantly larger areas in citrus plantations compared to shade-grown cocoa plantations (GLM = 2.16 hectares, $p = 0.05$ for the 95% estimate and GLM = 1.79 hectares, $p = 0.05$ for the 50% estimate). The mean of Kernel home range estimates (the maximum area using the 95% percentile) for birds in citrus plantations was 5.81 ± 4.96 hectares ($N = 9$, range = 1.30-16.39 hectares), whereas the core area (the maximum area using the 50%) was 1.53 ± 1.44 hectares ($N = 9$ range = 0.12-4.33 hectares; Table 3). In turn, the mean of Kernel home range estimates (95%) in shade-grown plantations was 2.22 ± 1.76 hectares ($N = 10$, range = 0.73-6.64 hectares), whereas the core area (50%) was estimated at 0.62 ± 0.49 hectares ($N = 10$, range = 0.18-1.87 hectares; Tables 3, 4, 5; Fig. 5, 6). Moreover, GLM models supported larger hectares, cocoa N = 7, mean 1.6 hectares).

Home ranges for all radio-tracked Blackpoll Warblers overlapped, except for one male in Guamal, which did not overlap with the others having been captured away from the other birds (Table S5). In citrus plantations, the mean overlap was 33%, with females overlapping ~31% of their home ranges, and males ~41%. In shade-grown cocoa plantations, the mean overlap was 53%, with females overlapping ~50% and males ~58%.

2.5 Discussion

Our study contributes novel information on the non-breeding ecology of the Blackpoll Warbler by examining how home range, space and habitat use, and site fidelity are shaped by landscape and habitat characteristics. At the landscape scale, we found that home range estimates (95% and 50% minimum convex polygons) did not exhibit differences either by landscapes or by season. However, home range sizes varied across years being larger in the 2018-2019 non-breeding season and apparently decreasing in each successive year in the Agrosavia study site. Blackpoll Warblers were registered in the same landscapes throughout the entire non-breeding season (season was divided into early - December and January - and late - February to April), as well as between years. At the habitat scale, home range estimates (95% and 50% Kernel estimate) varied by habitat (i.e., larger in citrus plantations) and sex (i.e., larger for males). Individuals overlapped in their home ranges at all the study sites and within and between sexes, implying that the species does not defend exclusive territories. Blackpoll Warblers were registered throughout the entire tracking period in both citrus and shade-grown cocoa plantations.

Our study suggests that the size of Blackpoll Warbler´s territories could be scale-dependent, there were no differences between landscapes, but differences were found at the habitat level. We showed evidence that Blackpoll Warbler´s territories were maintained and enable them to overwinter through the December to April in the Orinoco region. In terms of social structure, our observations indicate that both males and females share the same space and they use non-exclusive areas with a high degree of fidelity. The small territories and fidelity could be indicative of high habitat quality. Thus, agricultural habitats such as shade-grown cocoa and citrus plantations played a crucial role for the Blackpoll Warblers studied, and may contribute to population maintance in the Orinoco region.

Blackpoll Warblers exhibited small home ranges (<1 ha) based on our analysis of observations of color-banded birds. Other studies have reported small territory sizes for warblers on their non-breeding grounds. For instance, in Mexico, mean territory size for Yellow Warblers was 0.05 ha in isolated patches of tress in cattle pastures (Greenberg & Salgado-Ortiz, 1994), while territory size reported for Wilson´s Warbler was 0.09 ha in an agricultural landscape in Mexico (Ruiz-Sánchez et al., 2017). Moreover, recent estimates of territory size for American Redstarts in oil palm plantations in an agricultural landscape gave rise to mean of 0.29 ha (Oliveira et al., 2022). Small territories at landscape scale may be is a response to food and habitat availability (Marra & Holmes, 2001; Winker et al., 1995). In our study sites, changes in the landscape occurred throughout the years. For example, between 2020-2021, we observed the elimination of experimental plots of citrus in rural landscapes (<3.5 hectares), and between 2021-2022 in the cocoa experimental plot in our exurban landscape, some trees of *Mimosa trianae* were cut, and the *Acacia* trees died apparently because an herbicide was applied to them. Some species have been found to modify their space use behavior in response to structural changes in the landscape caused by productive systems or anthropogenic activities (Leonard et al., 2008).

We did not observe significant differences in home range size between exurban and rural landscapes, and there was considerable amount of variation among individual birds occupaying these landscapes (e.g., rural range = 0.007 - 0.908 hectares). This outcome is likely attributable to the migratory birds' capacity to locate suitable habitat patches in a landscape, which also impacts their home range size (Sherry & Holmes, 1996). Our findings indicated that home range sizes tend to be small (<1 hectare) in both landscapes, which mainly were agricultural matrix with a diverse mosaic of landcover types, and they both also have experienced changes in the landscape structure between 2020-2022 and could have an influence on the size of the home range, less habitat available, the home range is limited to the few habitats left. Some studies suggest that migratory birds make initial decisions upon reaching their wintering sites by assessing the landscape, but their final decisions may be influenced by finer-scale factors, ranging from patches to microhabitats (Deppe & Rotenberry, 2008; Faaborg et al 2010), as suggested by our results.

landscapes. This variation may be linked to climatic conditions affected by a weak El Niño-Southern Oscillation (ENSO) between 2018 and 2019, which had a significant impact on the amount of rainfall and temperature patterns in our study region. During this period, there was a reduction in rainfall relative to the historical monthly averages and an increase in air temperatures (source: Golden Gate Weather 2023; Ministerio de Agricultura y Desarrollo Rural 2023). Notably, in 2018-2019, home range sizes were larger compared to other years. It is likely that the El Niño-Southern Oscillation reduced rainfall and resulted in decreased food supplies, prompting birds to expand their home ranges (Brown & Sherry, 2008a). The 2019-2020 non-breeding season was accompanied by a transition from El Niño to La Niña conditions, while the 2020-2021 and 2021-2022 seasons were affected by a moderate La Niña associated with an increase in rainfall and decrease in air temperatures (source: Golden Gate Weather 2023; Ministerio de Agricultura y Desarrollo Rural 2023). Correspondinly, we found that home ranges size were smaller in three seasons following the El Niño event.

Changes in climatic conditions may have impacted resource availability as reported for other migratory birds in the Neotropics (González et al., 2021; Wunderle et al., 2014). For instance, a recent study of Swainson's Warblers indicated that individuals may decrease their home range size in response to increased rainfall, a change likely associated with an increase in food availability (Brunner et al., 2022; Studds & Marra, 2007). There is one important exception to the ENSO pattern described above, likely related to changes in landscape structure. In our rural landscape, home ranges seemed to increase in the 2020-2021 season. This may be related to the elimination of experimental plots of citrus trees (<3.5 ha) at the Agrosavia site during the same season.

Although we did not find clear differences in home range within a season, there was a tendency for smaller home ranges during the early season (December to February) compared to the later part of the season (February to April). Furthermore, the increase in home ranges appeared to be more pronounced in Agrosavia (rural), which experiences lower rainfall in general when compared to Unillanos (exurban). The wet season in our study region typically ends in late November, and as such, we can expect a decrease in available resources from December to March, leading to a concurrent increase in home range size, as birds require more space to find sufficient food (Janzen & Hallwachs, 2019).

Blackpoll Warblers had smaller home ranges in shade-grown cocoa compared to citrus plantations. Non-breeding territories of migrant passerines tend to be smaller where food abundance is higher (Sherry & Holmes, 1996; Wunderle & Latta, 2000), and can be indicative of higher habitat quality under certain conditions (Albert et al., 2020; González, 2018; Ruiz-Sánchez et al., 2017; Smith & Shugart, 1987). Shade-grown cocoa plantations with a shade of native trees generate stratification structurally similar to forests (Bennett et al., 2022; Faria et al., 2007; Greenberg et al., 2000) and also more structural complexity, and both factors may contribute to their apparently higher quality. Additionally, shade trees are likely key to shaping the diversity and abundance of food resources and ties in with our observation that most birds in cacao plantations foraged in the canopy and not in the cacao itself. In contrast, citrus plantations are monocultures in which the diversity of potential prey items is most likely lower (Mills & Rogers, 1992).

Home range size in Blackpoll Warblers in shade-grown cocoa and citrus plantations also varied between males and females. Our results suggest that males utilized larger home ranges than females. However, we only have data on six males of different ages, and not all of them had large home ranges. In other species, such as Golden-Winged Warblers in Nicaragua y Costa Rica, home ranges are similar between males and females, but in general males did not overlap their territories with other individuals (Chandler et al., 2016). Strikingly, we found that males and females in shade-grown cocoa and citrus plantations overlapped in space use with several individuals of both sexes. Our findings suggest that Blackpoll Warblers tolerate space sharing with other conspecifics (~20% of records), including those of the same sex, as well as with other *Setophaga* species. This finding contrasts with several migratory landbirds, including warblers in the *Setophaga* genus, which have despotic non-breeding distributions with competitive exclusion and sexual segregation by habitat (Albert et al., 2020; Bennett et al., 2019; Marra & Holmes, 2001; Sherry & Holmes, 1996).

Blackpoll Warblers exhibited strong intra- and inter-seasonal spatial and site fidelity at both the landscape and habitat scales along the eastern foothills of the Eastern Andes, with ~ 65% of individuals returning to their territories in the following year. Site fidelity to non-breeding grounds by migratory birds has been well described, and evidence from the literature suggests that most species return to the same winter location from year to year habitat patches in agricultural matrixes (Latta & Faaborg, 2001; Wunderle & Latta, 2000), similar to our results. High levels of site fidelity are predicted to be associated with areas with predictable interannual food resources (Johnson & Sherry 2001; Latta & Faaborg 2001).

Conclusions

Our study is the first to examine space and habitat use by Blackpoll Warblers in diverse modified landscapes and diverse agroforestry systems (e.g., shade-grown cocoa and citrus plantations) during the non-breeding season, increasing our awareness of the variety of habitats and space use strategies adopted by Nearctic-Neotropical migratory passerines on their non-breeding grounds. Small territories, as well as spatial and site fidelity across the study sites at different scales, are most likely influenced by resource availability, and these attributes are proxies of habitat quality (Latta & Faaborg, 2001; Winker et al., 1995). However, the high degree of site fidelity exhibited by Blackpoll Warblers on their non-breeding grounds may increase their vulnerability to habitat transformation (Wunderle & Latta, 2000). This is especially relevant, considering the high rates of deforestation and continuing expansion of intensive agriculture and livestock in the region (Álvarez et al., 2023). Our findings support the idea that landscapes with natural and agricultural elements (working landscapes) could help to combat population declines of Blackpoll Warblers along the eastern foothills of the Eastern Andes in the Meta department of Colombia.

We found that home range was scale-dependent, with no clear differences at the landscape scale but with variation in home range size at the local or habitat scales, apparently reflecting the properties of specific landcover types, as opposed to the wider matrix. Our results indicated that shade-grown cocoa plantations were of higher quality than citrus plantations for the species and further research aimed at comparing different agroforestry systems are warranted. Additionally, conducting long-term studies on space utilization patterns, as well as habitat preferences, would be valuable in addressing the challenges associated with the steep population declines occurring in Blackpoll Warblers.

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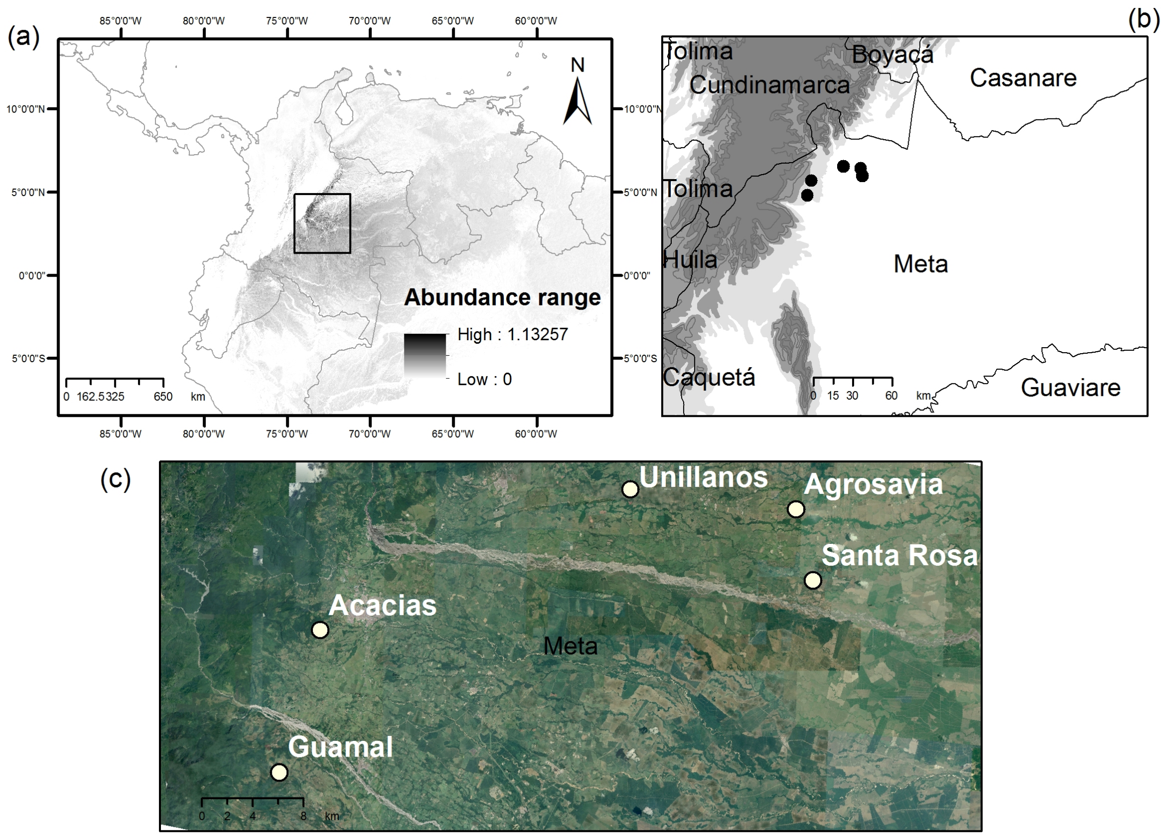
Authors' contributions

N.B. and A.M.R. conceived the study; N.B., A.M.R. and G.C. designed the study. A.M.R. led the data collection, G.C, N.B., P.T., and A.M.R designed and carried out the analyses. A.M.R led the manuscript writing, and all authors contributed to text editing and approved the final version.

on eBird Status and Trends models (Fink et al., 2022), indicating the location of our study region in Colombia (square); b) Location of study sites in and near to the eastern foothills of the Eastern Andes in the Meta Department, Colombia (black dots); and c) the location of study sites (white dots) in the municipalities of Villavicencio for Landscape: Unillanos, Agrosavia. For Habitat scale: Citrus (Agrosavia, Santa Rosa), Shadow cocoa (Acacias and Guamal) over a satellite image from Google Earth.



Warblers occupying citrus and shade-grown cocoa plantations was undertaken in the Meta department, Colombia.

A. Agrosavia- Citrus plantation

B. Santa Rosa- Citrus plantation

C. Acacias- Shade-grown cocoa

D. Guamal- Shade-grown cocoa

polygons for Blackpoll Warblers in two contrasting landscapes in Colombia: Agrosavia – rural landscape, N=26 individuals; Unillanos Barcelona Campus – exurban landscape, N=22 individuals, across four non-breeding seasons between 2018-2022 (Dec-Apr).

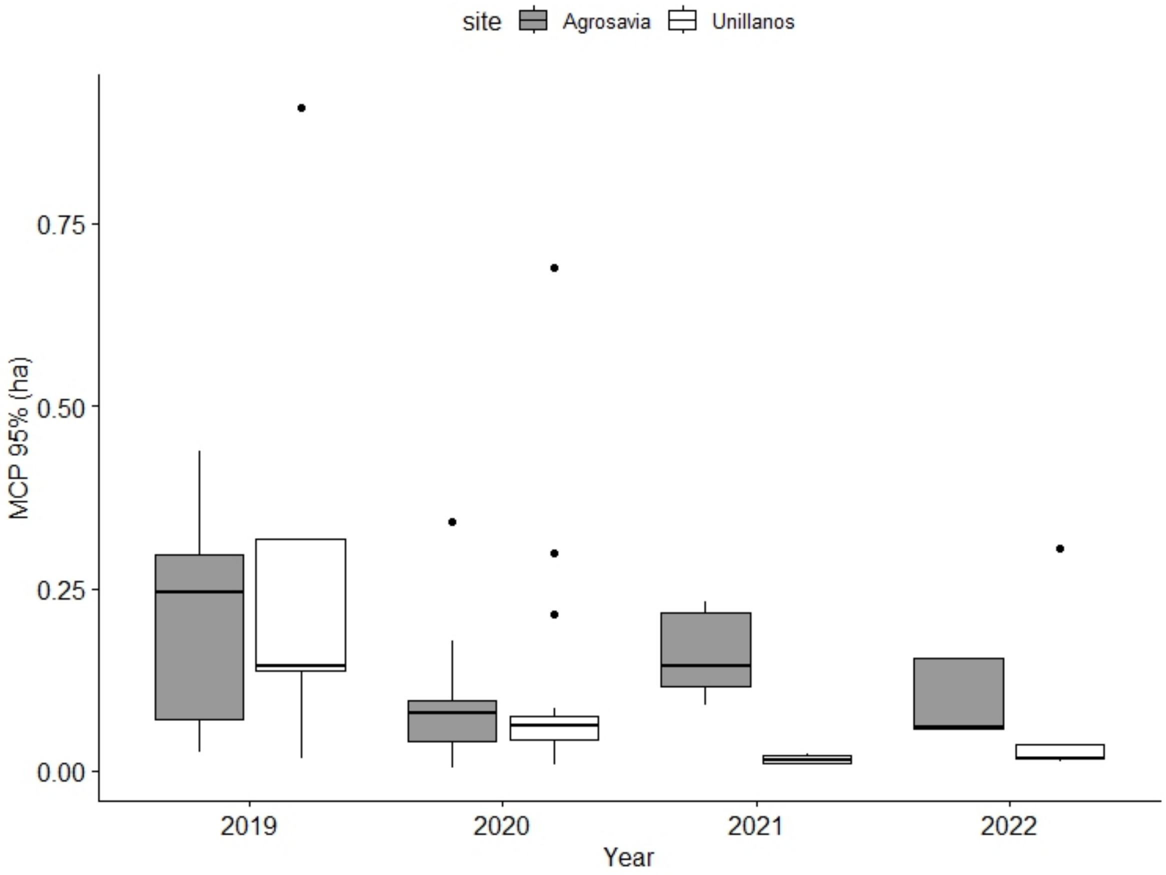
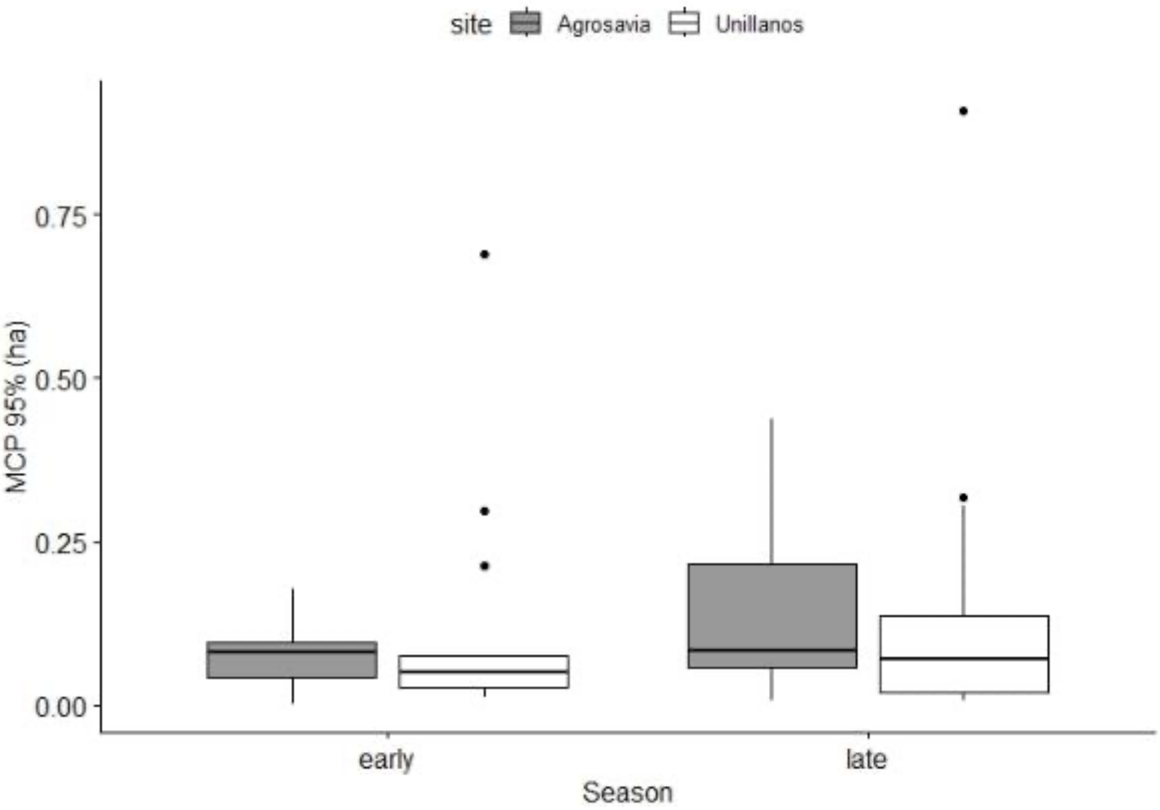
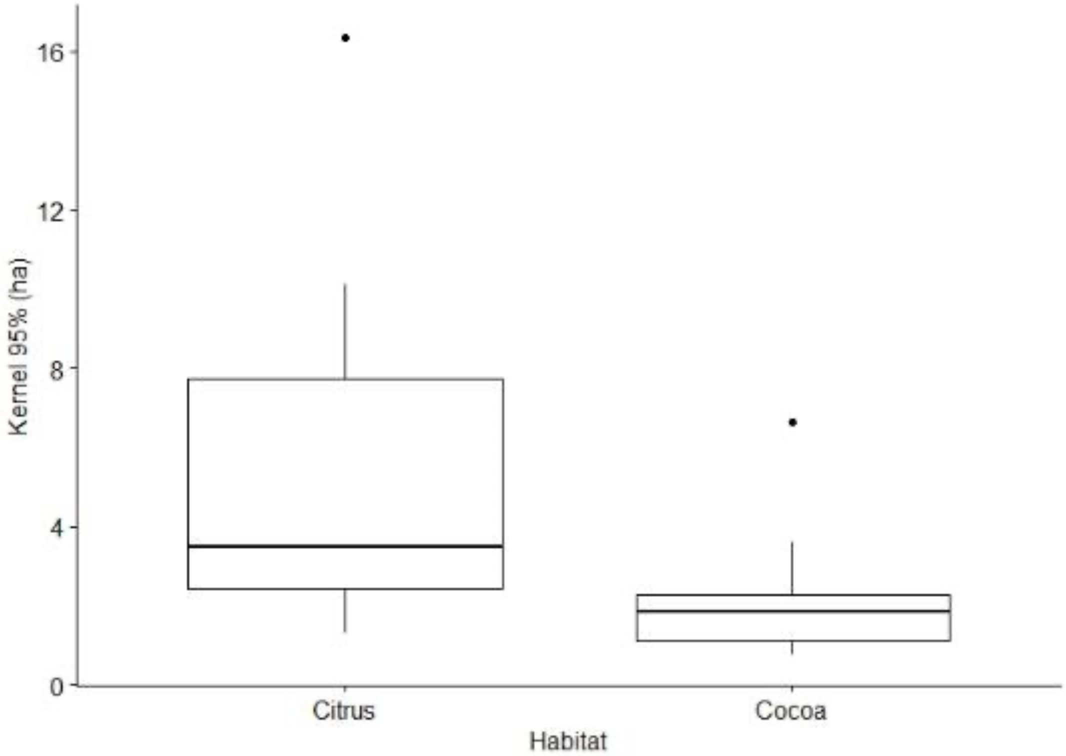


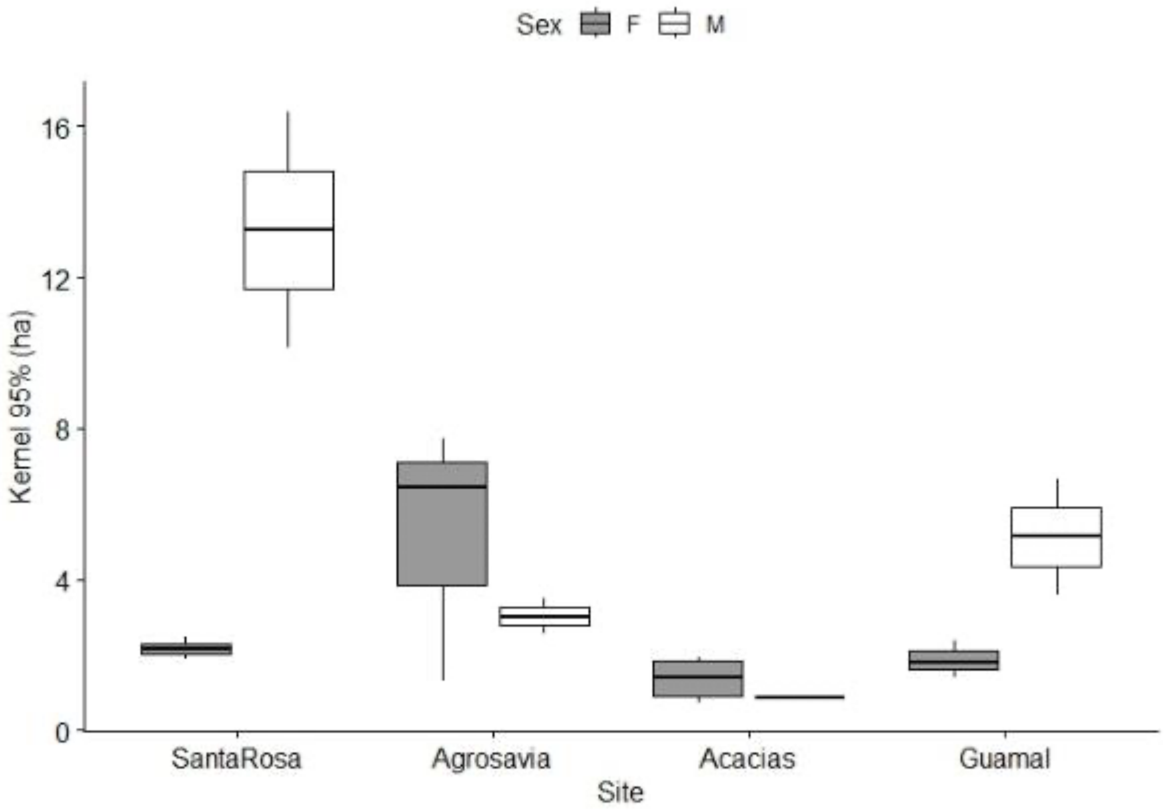
Figure 4. Mean home range estimates (in hectares) based on 95% minimum convex polygons for Blackpoll Warblers during the early (Dec-Jan) and later (Feb-Mar) part of the non-breeding period (years 2018–2022) in two contrasting landscapes in Colombia: Agrosavia – rural landscape, N=26 individuals; Unillanos Barcelona Campus – exurban landscape, N=22 individuals.



estimators for Blackpoll Warblers spending the stationary non-breeding period in shade-grown cocoa (N = 10) and citrus plantations (N = 9) in Meta department, Colombia, during January-February 2021.



Blackpoll Warblers occupying citrus (Santa Rosa: 2 males, 3 females, Agrosavia: 2 males, 3 females) and shade-grown cocoa plantations (Acacias: 1 male, 3 females, Guamal: 2 males, 3 females) during the non-breeding season in Meta department, Colombia. January-February 2021.



(season was divided into early: December and January and late: February to April) between 2018-2022 on estimates of 95%, and 50% of minimum convex polygons estimators of Blackpoll Warbler.

Model structure	**K**	**AICc**	**ΔAICc**	**AICcWt**
log10(MCP 95%)~site+bioyear+season+season:site + bioyear1:site	11	1595.17	0.00	1.000
log10(MCP 95%)~site+bioyear+season+season:site	8	1774.42	179.25	0.000
log10(MCP 95%)~site+bioyear+season	7	1802.39	207.21	0.000
log10(MCP 50%)~site+bioyear+season+season:site + bioyear1:site	11	1770.47	0.00	1.000
log10(MCP 50%)~site+bioyear+season+season:site	8	1987.45	216.98	0.000
log10(MCP 50%)~site+bioyear+season	7	2036.68	266.21	0.000

evaluate the role of site, year and time of season on estimates of 95% and 50% minimum convex polygons estimators of Blackpoll Warbler in 2019-2022.

Measurement	Factor	Estimate	Std. error	Statistic
MCP 95%	(Intercept)	-0.80	0.06	**-13.88**
	siteUnillanos	0.01	0.07	0.11
	bioyear12020	-0.40	0.05	**-7.72**
	bioyear12021	-0.01	0.06	-0.21
	bioyear12022	-0.29	0.07	**-4.05**
	seasonlate	-0.02	0.04	-0.41
	siteUnillanos:seasonlate	-0.02	0.05	-0.41
	siteUnillanos:bioyear12020	0.02	0.07	0.25
	siteUnillanos:bioyear12021	-1.00	0.09	**-11.68**
	siteUnillanos:bioyear12022	-0.42	0.09	**-4.46**
MCP 50%	(Intercept)	-1.77	0.06	**-29.17**
	siteUnillanos	-0.10	0.08	-1.36
	bioyear12020	-0.13	0.05	**-2.36**
	bioyear12021	0.34	0.07	**5.08**
	bioyear12022	0.17	0.08	**2.26**
	seasonlate	-0.04	0.04	-1.05
	siteUnillanos:seasonlate	-0.01	0.05	-0.15
	siteUnillanos:bioyear12020	0.25	0.07	**3.50**
	siteUnillanos:bioyear12021	-0.81	0.09	**-8.93**
	siteUnillanos:bioyear12022	-0.76	0.10	**-7.56**

Signif. codes: bold: 0 '***'; bold and underline: 0.01 '*' core area for 19 Blackpoll Warblers followed using manual telemetry in two citrus and two shade-grown cocoa plantations between January and March 2021 in Meta, Colombia. M: male, F: female; FCF: first cycle formative; DCB: definitive cycle basic).

Place/ Habitat	ID-Sex-Age	Points Seen	Points Triangulate	Total points	90% KDE (ha)	50% Core area (ha)
Santa Rosa-Citrus	17-M-FCF	37	6	43	16.37	4.33
	19-M-DCB	35	11	46	10.12	3.07
	231-F-DCB	30	12	46	2.44	0.47
	142-F-DCB	2	2	4		
	137-F-FCF	9	16	25	1.89	0.43
Agrosavia-Citrus	11-F-DCB	36	5	41	1.30	0.13
	125-F-DCB	39	9	48	6.43	1.28
	135-M-FCF	30	5	35	3.49	0.99
	143-F-DCB	28	16	44	7.74	2.44
	248-M-FCF	42	12	54	2.53	0.59
	Average	28.80	9.40	38.60	5.81	1.53
	SD	13.12	4.81	14.47	4.97	1.44
Acacias-Cocoa	6-F-FCF	42	3	45	0.74	0.18
	8-M-DCB	43	0	43	0.88	0.23
	112-F-FCF	40	5	45	0.99	0.27
	138-F-FCF	28	7	35	1.94	0.67
	243-F-DCB	34	9	43	1.83	0.57
Guamal-Cocoa	7-M-FCF	32	8	40	3.59	0.81
	9-M-DCB	32	8	41	6.65	1.87
	18-F-FCF	42	4	46	1.41	0.40
	118-F-FCF	46	3	49	1.82	0.46
	130-F-FCF	32	11	43	2.40	0.69
	Average	37.10	5.80	43.00	2.22	0.62
	SD	6.15	3.36	3.80	1.77	0.49

estimates of 95% Kernel density estimators (KDE), and 50% Core area of Blackpoll Warbler in 2021.

Model family	Model structure	K	AICc	ΔAICc	AICcWt
GLMM	KDE~Habitat+Sex+(1|Site)	5	92.51	0.00	0.46
	KDE~1+(1|Site)-Null	3	93.76	1.25	0.25
	KDE~Habitat+(1|Site)	4	93.76	1.25	0.25
	KDE~Habitat+Age+(1|Site)	5	97.40	4.89	0.04
GLMM	Core.area~Habitat+Sex+(1|Site)	5	45.57	0.00	0.45
	Core.area~Habitat+(1|Site)	4	46.60	1.03	0.27
	Core.area~1+(1|Site)-Null	3	46.77	1.20	0.24
	Core.area~Habitat+Age+(1|Site)	5	50.24	4.67	0.04
GLM	KDE~Habitat+Sex	4	86.80	0.00	0.67
	KDE~Habitat	3	88.71	1.91	0.26
	KDE~Habitat+Age	4	91.90	5.10	0.05
	KDE~1-Null	2	93.29	6.49	0.03
GLM	Core.area~Habitat+Sex	4	39.81	0.00	0.60
	Core.area~Habitat	3	41.36	1.55	0.27
	Core.area~1-Null	2	44.02	4.20	0.07
	Core.area~Habitat+Age	4	44.52	4.71	0.06

effect given by our fixed factors: habitat type (Citrus and Cocoa platations) and sex of Blackpoll Warbler in 2021.

Measurement	Factor	Estimate	Std. error	Statistic
	(Intercept)	0.29	0.08	3.58**
KDE	HabitatCocoa	0.23	0.11	2.16*
	SexM	-0.17	0.09	**-2.01**
KDE	(Intercept)	0.17	0.05	3.65**
	HabitatCocoa	0.28	0.13	2.20*
	(Intercept)	1.15	0.35	3.27**
Core area	HabitatCocoa	0.77	0.43	1.79
	SexM	-0.72	0.37	**-1.95**
Core area	(Intercept)	0.66	0.19	3.45**
	HabitatCocoa	0.97	0.49	**2.00**

Signif. codes: 0.001 '**' 0.01 '*' **0.05 '.'**

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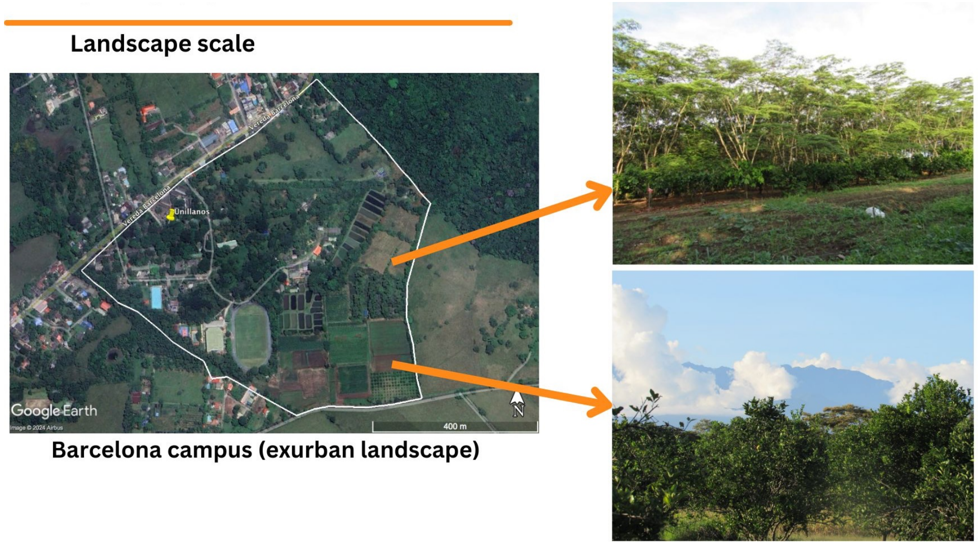
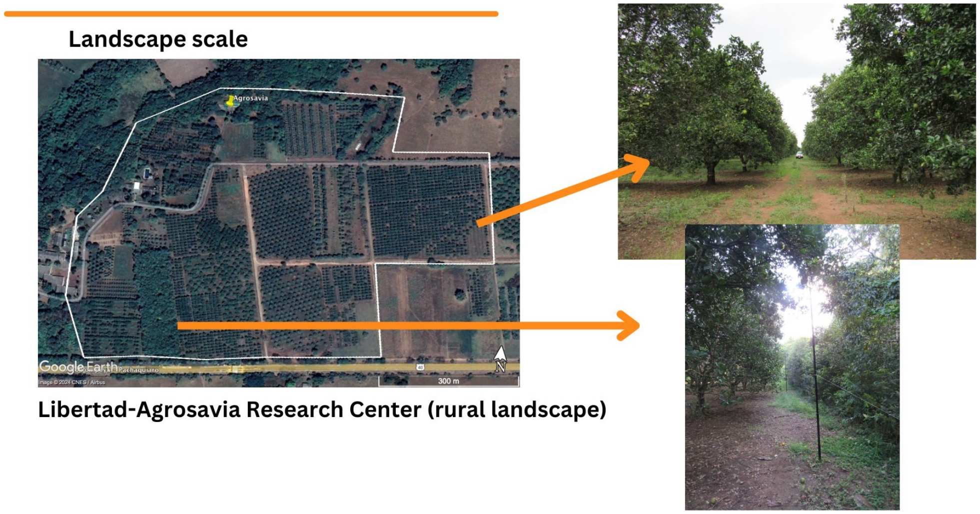
Figure S1. Landscape comparison: rural=Agrosavia (Libertad-Agrosavia Research Center) and exurban=Unillanos (Barcelona campus Universidad de los Llanos) in the municipality of Villavicencio, Meta, Colombia.

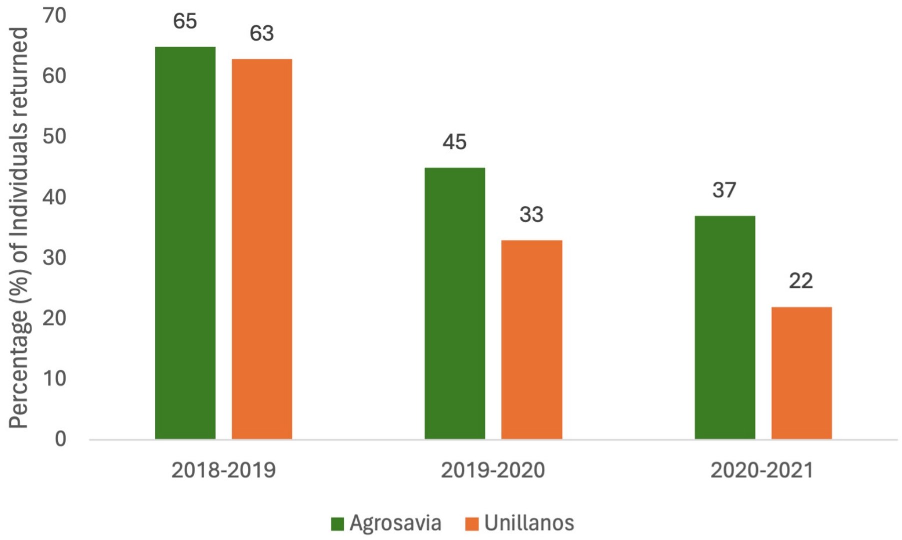


Barcelona campus (exurban landscape)



Libertad-Agrosavia Research Center (rural landscape)

in two landscpaes rural=Agrosavia (Libertad-Agrosavia Research Center), N=26 and exurban=Unillanos (Barcelona campus Universidad de los Llanos), N=22 in the municipality of Villavicencio, Meta, Colombia



in shade-grown cocoa and citrus plantations in Meta department, Colombia, during January-February 2021.

Place	Band	Sex	Age	Taq	TaqInterval (s)	TaqExpected life (days)	Weight (gr)	Wing (mm)	First register	Last register	Days of Mapping	Telemetry type
Santa Rosa	AA7394	M	FCF	17	4.9	30	10.5	73	7-Jan	13-Feb	15	Manual Telemetry
Santa Rosa	AA7396	M	DCB	19	4.9	30	11.2	76	7-Jan	13-Feb	15	Manual Telemetry
Santa Rosa	AA7398	F	FCF	137	29.3	159	10.8	68	7-Jan	2-Feb	9	Manual Telemetry
Santa Rosa	AA7399	F	DCB	142	29.3	159	11	72	12-Jan	27-Jan	3	Manual Telemetry
Santa Rosa	AA7400	F	DCB	231	19.9	100	10.4	67	7-Jan	13-Feb	15	Manual Telemetry
Agrosavia	AA8703	F	DCB	125	5.1	40	11.5	70	8-Jan	10-Feb	16	Manual Telemetry
Agrosavia	AA7380	F	DCB	11	4.9	30	10.8	70	8-Jan	5-Feb	14	Manual Telemetry
Agrosavia	AA8708	F	FCF	5	4.9	30	10.9	71	7-Jan	5-Feb	0	Manual Telemetry
Agrosavia	AA7371	M	FCF	135	29.3	159	10.3	71	8-Jan	5-Feb	13	Manual Telemetry
Agrosavia	AA8074	F	DCB	143	29.3	159	10.2	68	10-Jan	12-Feb	15	Manual Telemetry
Agrosavia	AA7388	M	FCF	248	19.9	100	11.5	71	23-Jan	12-Feb	12	Autamate Telemetry
Agrosavia	AA8732	F	FCF	140	29.3	159	10.4	72	21-Jan	1-Mar	40	Autamate Telemetry
Agrosavia	AA8735	M	FCF	247	19.9	100	11	74	22-Jan	1-Mar	40	Autamate Telemetry
Agrosavia	AA8734	M	FCF	136	29.3	159	10.3	70	22-Jan	1-Mar	40	Autamate Telemetry
Agrosavia	AA8736	M	FCF	144	29.3	159	11.8	76	24-Jan	1-Mar	40	Autamate Telemetry
Guamal	AA8713	F	FCF	118	5.1	40	10.1	66	12-Jan	13-Feb	15	Manual Telemetry
Guamal	AA8714	M	FCF	18	4.9	30	12.5	76	12-Jan	13-Feb	15	Manual Telemetry
Guamal	AA8715	F	FCF	130	5.1	40	10.7	69	12-Jan	13-Feb	16	Manual Telemetry
Guamal	AA8716	M	FCF	7	4.9	30	10.7	71	12-Jan	13-Feb	15	Manual Telemetry
Guamal	AA8718	M	DCB	9	4.9	30	11	73	16-Jan	13-Feb	13	Manual Telemetry
Acacias	AA8724	M	DCB	8	4.9	30	11.5	76	15-Jan	15-Feb	15	Manual Telemetry
Acacias	AA8726	F	FCF	6	4.9	30	10.1	72	15-Jan	15-Feb	14	Manual Telemetry
Acacias	AA8728	F	FCF	112	5.1	40	10.8	70	17-Jan	18-Feb	15	Manual Telemetry
Acacias	AA8729	F	FCF	138	29.3	159	10.4	71	17-Jan	18-Feb	15	Manual Telemetry
Acacias	AA8730	F	DCB	243	19.3	100	11.4	71	15-Jan	18-Feb	16	Manual Telemetry

across 2019 to 2022. M: male, F: female; FCF: first cycle formative; DCB: definitive cycle basic): Early: December, January; Late: February, March, April.

				2019		2020		2021	2022		
Site	**Band**	**Sex**	**Age**	**Early**	**Late**	**Early**	**Late**	**Late**	**Early**	**Late**	**Total**
Agrosavia	AA7368	F	FCF					15			15
	AA7387	M	FCF					14		14	28
	AA7388	M	FCF					15			15
	AA8036	M	DCB		11	22	16				49
	AA8039	F	DCB		11						11
	AA8043	M	SCB		13						13
	AA8044	M	DCB		16						16
	AA8046	M	DCB		12	11					23
	AA8065	F	DCB					11			11
	AA8068	M	DCB		12						12
	AA8069	F	DCB		24						24
	AA8735	M	FCF					16			16
	AA9501	M	DCB			52	20				72
	AA9504	M	DCB			20					20
	AA9505	M	DCB			28					28
	AA9506	M	DCB			36	20				56
	AA9507	F	DCB			11					11
	AA9509	M	DCB			27	15				42
	AA9510	F	DCB			26	14				40
	AA9512	M	DCB			25	18				43
	AA9514	F	FCF			13	14				27
	AA9515	M	DCB				22				22
	AA9534	F	FCF				23				23
	AA9536	F	DCB				11				11
	AB0321	M	FCF							15	15
	AB0325	M	FCF							20	20
Unillanos	AA4753	M	FCF		18	12					30
	AA7361	M	DCB					11			11
	AA7363	M	FCF					13			13
	AA7365	F	FCF					23			23
	AA8024	M	DCB	12	20	26	33	11	14	27	143
	AA8030	F	DCB	13	23						36
	AA8032	M	FCF		19						19
	AA8077	M	FCF		29						29
	AA8091	F	FCF				12	11			23
	AA9516	M	DCB			55	13				68
	AA9518	F	DCB			20				11	31
	AA9521	M	DCB			24					24
	AA9522	M	DCB			24	24				48
	AA9524	F	DCB			12					12
	AA9526	M	DCB			66	22				88
	AA9527	M	DCB			17					17
	AA9528	M	DCB			36	17	13			66
	AA9529	M	FCF			21	24				45
	AA9537	F	DCB				24				24
	AA9538	M	FCF			15	45				60
	AA9540	F	DCB				14				14

wintering at Agrosavia and Barcelona Campus, in the Meta, Colombia, 2019–2022 M: male, F: female; FCF: first cycle formative; DCB: definitive cycle basic): Early: December, January; Late: February, March, April.

				2019		2020		2021	2022		
Site	**Band**	**Sex**	**Age**	**Early**	**Late**	**Early**	**Late**	**Late**	**Early**	**Late**	**Average**
Agrosavia	AA7368	F	FCF					0.23			0.23
	AA7387	M	FCF					0.12		0.06	0.09
	AA7388	M	FCF					0.22			0.22
	AA8036	M	DCB		0.03	0.02	0.01				0.02
	AA8039	F	DCB		0.07						0.07
	AA8043	M	SCB		0.07						0.07
	AA8044	M	DCB		0.24						0.24
	AA8046	M	DCB		0.21	0.003					0.11
	AA8065	F	DCB					0.14			0.14
	AA8068	M	DCB		0.44						0.44
	AA8069	F	DCB		0.30						0.30
	AA8735	M	FCF					0.09			0.09
	AA9501	M	DCB			0.10	0.34				0.22
	AA9504	M	DCB			0.07					0.07
	AA9505	M	DCB			0.18					0.18
	AA9506	M	DCB			0.10	0.14				0.12
	AA9507	F	DCB			0.16					0.16
	AA9509	M	DCB			0.08	0.08				0.08
	AA9510	F	DCB			0.03	0.02				0.03
	AA9512	M	DCB			0.04	0.04				0.04
	AA9514	F	FCF			0.05	0.08				0.06
	AA9515	M	DCB				0.07				0.07
	AA9534	F	FCF				0.06				0.06
	AA9536	F	DCB				0.04				0.04
	AB0321	M	FCF							0.15	0.15
	AB0325	M	FCF							0.06	0.06
Unillanos	AA4753	M	FCF		0.14	0.21					0.18
	AA7361	M	DCB					0.02			0.02
	AA7363	M	FCF					0.01			0.01
	AA7365	F	FCF					0.01			0.01
	AA8024	M	DCB	0.02	0.21	0.02	0.04	0.02	0.01	0.02	0.05
	AA8030	F	DCB	0.02	0.32						0.17
	AA8032	M	FCF		0.91						0.91
	AA8077	M	FCF		0.14						0.14
	AA8091	F	FCF				0.07	0.02			0.04
	AA9516	M	DCB			0.69	0.02				0.36
	AA9518	F	DCB			0.30				0.31	0.30
	AA9521	M	DCB			0.06					0.06
	AA9522	M	DCB			0.02	0.02				0.02
	AA9524	F	DCB			0.03					0.03
	AA9526	M	DCB			0.05	0.07				0.06
	AA9527	M	DCB			0.06					0.06
	AA9528	M	DCB			0.05	0.02	0.01			0.02
	AA9529	M	FCF			0.07	0.08				0.08
	AA9537	F	DCB				0.08				0.08
	AA9538	M	FCF			0.06	0.08				0.07
	AA9540	F	DCB				0.01				0.01

wintering at Agrosavia and Barcelona Campus, in the Meta, Colombia, 2019–2022 M: male, F: female; FCF: first cycle formative; DCB: definitive cycle basic): Early: December, January; Late: February, March, April.

				2019		2020		2021	2022		
Site	**Band**	**Sex**	**Age**	**Early**	**Late**	**Early**	**Late**	**Late**	**Early**	**Late**	**Average**
Agrosavia	AA7368	F	FCF					0.06			0.06
	AA7387	M	FCF					0.03		0.02	0.02
	AA7388	M	FCF					0.06			0.06
	AA8036	M	DCB		0.003	0.003	0.002				0.00
	AA8039	F	DCB		0.03						0.03
	AA8043	M	SCB		0.01						0.01
	AA8044	M	DCB		0.02						0.02
	AA8046	M	DCB		0.01	0.003					0.00
	AA8065	F	DCB					0.07			0.07
	AA8068	M	DCB		0.03						0.03
	AA8069	F	DCB		0.03						0.03
	AA8735	M	FCF					0.01			0.01
	AA9501	M	DCB			0.01	0.02				0.02
	AA9504	M	DCB			0.01					0.01
	AA9505	M	DCB			0.02					0.02
	AA9506	M	DCB			0.05	0.07				0.06
	AA9507	F	DCB			0.13					0.13
	AA9509	M	DCB			0.01	0.05				0.03
	AA9510	F	DCB			0.01	0.00				0.01
	AA9512	M	DCB			0.01	0.01				0.01
	AA9514	F	FCF			0.02	0.01				0.01
	AA9515	M	DCB				0.01				0.01
	AA9534	F	FCF				0.01				0.01
	AA9536	F	DCB				0.01				0.01
	AB0321	M	FCF							0.06	0.06
	AB0325	M	FCF							0.01	0.01
Unillanos	AA4753	M	FCF		0.005	0.004					0.004
	AA7361	M	DCB					0.003			0.003
	AA7363	M	FCF					0.001			0.001
	AA7365	F	FCF					0.003			0.003
	AA8024	M	DCB	0.004	0.01	0.003	0.021	0.010	0.003	0.003	0.01
	AA8030	F	DCB	0.01	0.01						0.01
	AA8032	M	FCF		0.02						0.02
	AA8077	M	FCF		0.03						0.03
	AA8091	F	FCF				0.003	0.01			0.01
	AA9516	M	DCB			0.27	0.01				0.14
	AA9518	F	DCB			0.01				0.01	0.01
	AA9521	M	DCB			0.02					0.02
	AA9522	M	DCB			0.01	0.01				0.01
	AA9524	F	DCB			0.01					0.01
	AA9526	M	DCB			0.01	0.05				0.03
	AA9527	M	DCB			0.01					0.01
	AA9528	M	DCB			0.02	0.01	0.004			0.01
	AA9529	M	FCF			0.04	0.02				0.03
	AA9537	F	DCB				0.04				0.04
	AA9538	M	FCF			0.01	0.02				0.01
	AA9540	F	DCB				0.00				0.002
	AA9955	M	FCF							0.001	0.001

sexes in 2021. F=female, M=male.

Acacias	6_F	8_M	112_F	138_F	243_F
6	1.00	0.73	0.52	0.31	0.09
8	0.59	1.00	0.71	0.56	0.28
112	0.34	0.58	1.00	0.74	0.62
138	0.12	0.26	0.43	1.00	0.44
243	0.04	0.13	0.36	0.45	1.00
mean	**0.27**	**0.43**	**0.50**	**0.52**	**0.36**

Guamal	7_M	9_M	18_M	118_F	130_F
7	1.00	0.00	0.33	0.44	0.53
9	0.00	1.00	0.00	0.00	0.00
18	0.88	0.00	1.00	0.75	0.96
118	0.88	0.00	0.56	1.00	0.75
130	0.77	0.00	0.52	0.55	1.00
mean	**0.84**		**0.47**	**0.58**	**0.75**

Agrosavia	11_F	125_F	135_M	143_F	248_M
11	1.00	0.00	0.08	0.00	0.00
125	0.00	1.00	0.00	0.41	0.04
135	0.03	0.00	1.00	0.66	0.00
143	0.00	0.39	0.28	1.00	0.03
248	0.00	0.11	0.00	0.07	1.00
mean	**0.03**	**0.25**	**0.18**	**0.38**	**0.03**

Santa Rosa	17_M	19_M	137_F	231_F
17	1.00	0.31	0.12	0.16
19	0.52	1.00	0.18	0.16
137	1.00	0.88	1.00	0.08
231	1.00	0.59	0.06	1.00
mean	**0.84**	**0.59**	**0.12**	**0.44**

Chapter 3. Overwinter and annual survival of Blackpoll Warbler from non-breeding sites in Colombia

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3.1 Abstract

Migratory species in decline are in urgent need of vital-rates data from their entire annual cycle. There are only a handful of species for which we have annual, or within non-breeding period survival data, and this considerably hinders our ability to design effective conservation measures where species need them most. Blackpoll Warbler populations have declined drastically, and until recently, data on their non-breeding ecology and survival were scarce. Using Cormack–Jolly–Seber models to analyze mark-resighting data collected over six years (2017 to 2022) at Blackpoll Warbler wintering sites in Colombia, we estimated inter and intra annual apparent survival and examined variation in survival by site, age, and sex. Our results indicate large annual variation in survival during our 6 years of study (0.4-0.7), where 2018 had the lowest annual survival that could be linked to climatic conditions influenced by El Niño-Southern Oscillation (ENSO). We found differences in annual survival between landscapes and sexes, but we found no differences between age groups. Monthly apparent survival probability varied within (0.96) and between (0.92) periods. The high monthly survival estimate we found is similar to rates found in other species, suggesting that survival in non-breeding sites may not be a limiting factor for Blackpoll Warblers.

Key words: agricultural landscape, habitat quality, *Setophaga striata*, migratory birds, wintering habitat.

Las especies migratorias en declive necesitan urgentemente datos sobre las tasas vitales de todo su ciclo anual. Sólo disponemos de datos sobre la supervivencia anual o durante el periodo no reproductor de unas pocas de especies, lo que dificulta considerablemente nuestra capacidad para diseñar medidas de conservación eficaces allí donde las especies más las necesitan. Las poblaciones de la reinita rayada (*Setophaga striata*) han disminuido drásticamente y, hasta hace poco, los datos sobre su ecología y supervivencia fuera del periodo reproductor eran escasos. Utilizando modelos de Cormack-Jolly-Seber para analizar los datos de avistamiento de marcas recopilados durante seis años (2017 a 2022) en los sitios de invernada de *Setophaga striata* en Colombia, estimamos la supervivencia aparente interanual e intraanual y examinamos la variación en la supervivencia por sitio, edad y sexo. Nuestros resultados indican una gran variación anual en la supervivencia durante nuestros 6 años de estudio (0.4-0.7), donde 2018 tuvo la supervivencia anual más baja, probablemente atribuido a las condiciones climáticas influenciadas por El Niño (ENSO). Encontramos diferencias en la supervivencia anual entre paisajes y sexos, pero no encontramos diferencias entre grupos de edad. La probabilidad de supervivencia aparente mensual varió dentro (0.96) y entre (0.92) periodos. La alta supervivencia mensual estimada que encontramos es similar a las tasas encontradas en otras especies, lo que sugiere que la supervivencia en lugares no reproductivos podría no se un factor limitante para la población.

Palabras clave: paisaje agrícola, calidad de hábitat, *Setophaga striata*, hábitat no-reproductivo, Reinita rayada

Migratory songbird populations are influenced by a combination of events throughout the year that, altogether, can affect demographic parameters such as survival (Culp et al., 2017; Hostetler et al., 2015; Webster et al., 2002). While studies on the full life cycle biology (Culp et al., 2017; Marra et al., 2015a) and migratory connectivity (Somveille et al., 2021; Webster et al., 2002) of Nearctic-Neotropical birds have become more common in recent years, there is still a lack of understanding regarding specific factors that limit the populations of those species, particularly the role of non-breeding areas (Albert et al., 2020; Cooper et al., 2015; Runge & Marra, 2005).

In the non-breeding areas, survival rates may be influenced by a series of limiting factors (Rappole & McDonald, 1994), including extrinsic factors like climatic variation (e.g., precipitation, humidity, temperature; (La Sorte et al., 2017; Rosenberg et al., 2019; Woodworth et al., 2017), which are considered to be density-independent factors. In contrast, intrinsic factors such as competition for resources (e.g., food, and territory; (Brown & Sherry, 2006; Hostetler et al., 2015; Studds & Marra, 2007), act as population size regulators and are density-dependent (Marra et al., 2015; Newton, 2004; Norris & Marra, 2007). Resource availability is likely a key limiting factor linked to habitat quality for migratory birds, which can impact survival, body condition, migration timing, and subsequent reproductive success (Albert et al., 2020; Marra et al., 2015b).

Several studies examining non-breeding habitat quality have used indicators of quality such as body condition or the availability of the resources within a specific habitat (Latta & Faaborg, 2001; Marra & Holmes, 2001). However, the ultimate measure of quality is survival, as this has a direct impact on demographic parameters (Johnson et al. 2006). However, obtaining sufficient recaptures or resightings, and adequate sample sizes for estimating survival can be challenging and instead many studies have used proxies of habitat quality including site fidelity, sex and age ratios, changes in body condition, and stress levels, among others (Johnson et al., 2006; Latta & Faaborg, 2001; Marra & Holmes, 2001; Valdez-Juárez et al., 2018; Winker et al., 1995).

Given the above, there are relatively few studies examining overwinter survival of Nearctic-Neotropical migratory birds as indicator of habitat quality on the non-breeding grounds in Central and South America (Albert et al., 2020). Some of these studies have found

(*Setophaga cerulea*) in shade coffee plantations compared to primary forests. In Jamaica, studies have found higher survival probabilities for American Redstart (*Setophaga ruticilla*) in Black mangrove relative to scrub or other habitats types (Johnson et al., 2006; Marra & Holmes, 2001). In contrast, other studies indicate similar survival rates between habitats. In Costa Rica, for example, overwintering Golden-winged Warblers (*Vermivora chrysoptera*) did not exhibit differences in apparent survival or recruitment between secondary forests and agroecosystems (Chandler & King, 2011). Likewise, apparent annual survival rates in Swainson's Thrush (*Catharus ustulatus*) and Canada Warbler (*Cardellina canadensis*) between native forest and shade-coffee plantations in the Colombian Andes was similar in both habitats (González et al., 2020, 2021).

Thus, demographic studies of overwintering Nearctic-Neotropical migrants are urgently needed, considering that many species of this group are experiencing continuous declines (Rosenberg et al., 2019), including the Blackpoll Warbler (*Setophaga striata*). Indeed, this Nearctic-Neotropical migrant was recently listed as Near Threatened (IUCN, 2023). On its non-breeding grounds in Colombia, the species has higher occupancy rates in agroforestry systems compared to natural forest (Morales-Rozo et al *in prep*). Although declines in Blackpoll Warbler populations can be explained in part by changes in distribution related to climate change (Gómez et al., 2021; Finch et al., 2017; Stralberg et al., 2015), a factor contributing to declines could also be the loss and transformation of habitat on the non-breeding grounds and during migration. Despite the extensive habitat transformation, particularly in regions where this species is distributed (e.g., Orinoco and Amazonia regions), there is a significant lack of knowledge regarding survival rates and sex and age ratios in the agricultural/urban matrix that remains and that is extensively used by the species during the non-breeding period.

In this study, we estimated apparent survival of Blackpoll Warblers between and within non-breeding periods, and explore their variation as a means to get at non-breeding habitat quality across exurban and rural landscapes in the Orinoco region of Colombia, an area extensively used to overwinter. We used a 6-year mark-resighting dataset to estimate apparent survival in two contrasting landscapes, which in addition to having undergone different transformation processes, also differed in the number of habitat types present and the degree of heterogeneity in the landscape. We expected higher apparent survival in survival rates in large farm fragments compared with small farm fragments (Bayne & Hobson, 2002). Based on the assumption that the rural landscape is of higher quality than the exurban landscape, we also expected age and sex differential survival at these sites (Marra, 2000; Studds & Marra, 2005; Wunderle et al., 2014). Given that currently no information exists on the demography of Blackpoll Warblers on their non-breeding grounds, our estimates of overwinter survival represent an important advance for informing full life cycle models and planning.

3.4 Methods

Study area

We conducted this study on Blackpoll Warblers in the eastern foothills of the Eastern Andes, in the Meta department of Colombia. The climate of the region is characterized by temperatures ranging from 25 to 32°C, along with an annual average precipitation of 4,383 mm. The area exhibits a unimodal rainfall pattern, with a dry season spanning from December to March and a rainy season from April to November (IDEAM, 2017) (Figure 1).

To investigate survival and sex and age ratios of Blackpoll Warblers, our study was conducted at two sites, both located in the municipality of Villavicencio, Meta department, Colombia. Site A: Barcelona Campus of the Universidad de los Llanos (exurban landscape; from now on Unillanos) (4.073118N, -73.580857W; 390 masl), covering an area of approximately 45 hectares. This campus represents a diverse mosaic comprising fishponds, pastures, open areas, riparian strips, live fences, small experimental plots of citrus and shade cocoa (approximately 1 hectare), small fragments of native secondary forest (~1 hectare), buildings, and roads (Avendaño et al., 2018; Bayly et al., 2020; Yantén et al., 2022, see Figure 1). Site B: Libertad-Agrosavia Research Center (rural landscape; from now on Agrosavia) (4.058914N, -73.464356W; 330 masl), with a total extension of 1332 hectares. Our study was conducted in 40 hectares of experimental plots predominantly featuring monocultures of citrus crops (14.16 hectares), African palm (4.45 hectares), as well as smaller experimental plots with polyculture agroforestry systems (3.55 hectares), and native forest (5.20 hectares; see Figure 1).

To study the survival of Blackpoll Warblers in two landscapes, we color banded and resighted individuals during 6 non-breeding periods from December to April of 2017-2022. Captures occurred over 10 days in December and 10 days in January during each season using mist-nets (6 of 12 m x 2.5 m x 30 mm mesh and 1 of 18 m x 2.5 m x 30 mm mesh). Playback of Blackpoll Warbler calls and songs complemented the mist-netting process. Age and sex were determined for all captured Blackpoll Warblers based on plumage characteristics, following established criteria (Johnson et al., 2011; Ryder & Wolfe, 2009; Wolfe et al., 2010). To facilitate subsequent identification in the field, Blackpoll Warblers were fitted with standard numbered aluminum bands and a unique combination of plastic color bands. Nets were operated under favorable weather conditions, and were closed during heavy rain, strong winds, or direct sunlight. Following processing, all birds were released in good condition.

We conducted resightings of color-banded birds during 14, 2-days periods per site. Resighting periods were separated by 10 days across the entire non-breeding season: birds departed in late April or early May (mean 5th May; Bayly et al., 2020). Within each observation period, we allocated two days of surveys to each study site. Observations took place between 6:00 hr and 9:30 hr, during which time intensive searches were undertaken within the study area. Additional observations were carried out from 15:30 hr to 17:30 hr, during which we broadcasted playback of Blackpoll Warbler calls in the same areas searched in the morning (Figure 1). We conducted resightings along predetermined 2 km paths, walked at least twice in the morning and once in the afternoon. Whenever we heard a Blackpoll Warbler call, we deviated from the paths to verify if it was a banded bird. Identification of each encountered bird was based on its color-band combination. We recorded the exact location, time of day, and date using a Garmin64s GPS device with an accuracy of <3m. Overall, we had 26 sampling occasions in the six years (27 capture events, there are 26 intervals, and all-time intervals are in months).

Data analysis

We estimated apparent survival with fitted Cormack-Jolly-Seber (CJS) capture-recapture models (Cormack, 1964; Jolly, 1965; Seber, 1965; White & Burnham, 1999) using the RMark package in the R software (Laake 2013). We approached our analysis in two ways.

– Birds captured in their formative plumage, or with formative plumage feathers retained in their alternate plumage and aged as FCF (First molt cycle, formative plumage) or HY (Hatch year); and Adults – Birds in basic or alternate plumage and aged as DCB (Definitive molt cycle, basic plumage) or DCA (Definitive molt cycle, alternate plumage), AHY (After hatching year) or ASY (After second year) (Wolfe et al 2010; Pyle et al., 2004). We coded survival so that juveniles would be assigned a differential survival to adults, and individuals initially captured as juveniles, and recaptured in future years were coded as adults (see supplementary R code). We estimated survival (Φ) with multiple models to determine how and where survival varied by year, age, sex and site, and allowed detection probability (ρ) to vary by year (Hill et al., 2019; Lebreton et al., 1992). Model selection was carried out using AICc for small sample sizes. Models with delta AICc < 2 (AICc differences) were considered equally plausible (Burnham & Anderson, 2004).

Our second approach was used to determine differences within and between non-breeding period survival. We used an expanded capture history using the 27 sampling occasions from our capture and resighting surveys (27 capture events comprising 26 intervals, and all-time intervals are in months). Therefore, we had both repeated within period occasions, and between year sampling occasions. We then coded a ‘period’ variable determining whether survival at each period corresponded to within or between non-breeding periods. We then proceeded to estimate survival within and between periods and compared differences by site and sex.

Given that time intervals between sampling occasions were not uniform, we specified the time intervals. Sampling effort was also different by site, so we included an effort variable to assess detectability variations due to sampling effort. We ran models both with temporal variation in detectability and including the effort variable. We used confidence intervals as a criterion for statistical significance.

3.5 Results

We captured and marked 170 Blackpoll Warblers (95 individuals from Agrosavia=rural landscape, and 75 individuals from Unillanos=exurban landscape) across the 6-year period, including 51 immature females, 33 adult females, 48 immature males, and 38 adult throughout December to April, with an average of 65% of individuals recorded at least once during the season in Agrosavia (rural) and 48% at Unillanos (exurban).

We found evidence for large annual variation in survival during our 6 years of study (Figure 2). 2018 had the lowest annual survival, compared to the other three years (mean ± SE: 0.43 ± 0.24 vs 0.71 ± 0.10, respectively; Table 1). The best multiple models included site and sex (Table S1A). Survival in Agrosavia (rural landscape, 0.70 ± 0.06) was higher than in Unillanos (exurban landscape, 0.61 ± 0.05) in line with our expectations (Figure 3). We did not find large differences in survival between age groups (Adults 0.63 ± 0.08; juveniles 0.65 ± 0.05; Figure 4). However, females had slightly lower mean annual survival than males (Females 0.63 ± 0.05; males 0.66 ± 0.06; Figure 5). We found support for variation in detection probability by year and was lower in 2018. The average detectability estimation was 0.64 ± 0.11 (Table 1).

Apparent survival probability varied within and between periods (Table S1B). Monthly apparent survival rate in Colombia during the non-breeding period (December-April) was 0.96 ± 0.05, while the monthly estimate for the months between non-breeding period periods (May-November) was 0.92 ± 0.03 (Table S1B). Survival within and between non-breeding periods maintained the pattern observed in the annual analyses, where Agrosavia (rural) had higher estimates than Unillanos (exurban) (within non-breeding periods: rural 0.96 ± 0.06; exurban 0.91 ± 0.03; Figure 6), and females had slightly lower estimates than males (within non-breeding periods: females 0.95 ± 0.06; males 0.96 ± 0.07; Figure 7). We found temporal variation in detectability in our 27 capture events (26 intervals), being lower between 1 to 16 (2017, 2018) and 27 to 28 (April-May 2019) (Figure 8). The average detectability estimation was 0.5 ± 0.08 (Table S1B). The results with effort were the same, so we present the time variation.

3.6 Discussion

Our study represents the first attempt to estimate apparent survival for Blackpoll Warblers on their non-breeding grounds and in the Orinoco region of Colombia, a region that potentially harbors the largest wintering concentration of the species. Annual survival varied between years, with 2018 as the year with the lowest estimate that could be linked but we did no find differences in annual survival between age groups. Apparent monthly survival was higher during the stationary non-breeding season in Colombia compared to the six month-period covering the two-migration periods and breeding.

Annual survival probabilities for Blackpoll Warbler in this study (0.4-0.7) are similar to other Parulids (Bakerman et al., 2009; DeSante et al., 2015), and, in particular for Nearctic–Neotropical warblers, >0.6 is a remarkable survival rate (Sillett & Holmes, 2002). The observed variation in annual survival probability (with 2018 with the lowest estimate) may be attributed to climatic conditions influenced by El Niño-Southern Oscillation (ENSO) during the period spanning 2018 to 2019. This climatic phenomenon significantly influences precipitation and temperature patterns within our study region. Throughout this timeframe, there was a notable decline in rainfall when compared to historical monthly averages, coupled with an elevation in air temperatures (source: Golden Gate Weather 2023; Ministerio de Agricultura y Desarrollo Rural 2023). Our results suggest that survival of this Neotropical migrant is strongly influenced by ENSO-related weather changes during its annual cycle, similar to information reported for other Nearctic–Neotropical migrants, which influences the availability of the resource and the quality of habitat (González et al., 2020, 2021; Lamanna et al., 2012; Rockwell et al., 2017).

The mean model-averaged estimate of adult year-round survival probability for Blackpoll Warblers based on a breeding ground study was 0.48 in North America (DeSante et al 2015), which is similar to our results (0.45 and 0.47) in Colombia. Annual survival rates for other migratory species are variable. Some species show lower annual survival, such as Black-throated Blue Warblers (*Setophaga caerulescens*) in Jamaica (annual survival = 0·43; Sillett & Holmes, 2002). Others species have higher annual survival such as Kirtland’s Warblers (*Setophaga kirtlandii*) in Bahamas, with a mean annual survival probability of 0.58, and winter rainfall suggested as influencing survival probability (Rockwell et al., 2017). For Golden-winged Warblers (*Vermivora chrysoptera*) in Costa Rica the annual apparent survival probability was 0.539 (Ritterson et al., 2021), our data contribute to the information supporting the idea that given the high survival rates during both breeding and non-breeding periods, the migration period may pose a significant risk to migratory species (Sillett & Holmes 2002).

to other Nearctic–Neotropical warblers (Sillett & Holmes, 2002). For example, monthly survival for Golden-winged Warbler (*Vermivora chrysoptera*) in Costa Rica was 0.967 (Ritterson et al., 2021) in human-dominated landscapes with some forest patches within a matrix of villages and agricultural areas. Similarly, the monthly apparent survival of Yellow Warblers (*Setophaga petechia*) in Mexico was >0.94 in agricultural habitat (Valdez-Juarez et al., 2019). Likewise, Kirtland's Warblers (*Setophaga kirtlandii*) in Bahamas exhibited a high monthly survival probability of 0.97 in evergreen and semi-deciduous vegetation (Rockwelle et al., 2017). Lastly, American redstarts (*Setophaga ruticilla*) in Jamaica demonstrated higher annual survival in high-quality mangrove (>0.9) compared to second-growth scrub habitats (0.5) during the winter period (Marra & Holmes, 2001). The high monthly survival probability during non-breeding period, suggest food supply and habitats available (Brown & Sherry, 2008a; Albert et al., 2020), and given that Blackpoll Warblers in Colombia showed high site fidelity (Morales-Rozo et al in prep), we suggest that our survival probability is a good indicator of high habitat quality.

We found different apparent survival rates between rural and exurban landscapes (0.70 vs 0.61, respectively). This finding aligns with other studies that have reported differences in survival rates for different habitats, such as those for American Redstart (*Setophaga ruticilla*) in Jamaica, that shows higher survival probabilities in black mangrove relative to scrub or other habitats types (Johnson et al., 2006; Marra & Holmes, 2001). In Venezuela, for Cerulea Warbler (*Setophaga cerulea*) within season survival probabilities and between-season return rates were higher in shade coffee (Bakermans et al., 2009). This result is particularly relevant for agricultural landscapes resembling natural habitats, which have been shown to provide high-quality winter habitat for Neotropical migrants (Bakermans et al., 2012; Bennett et al., 2022; Johnson et al., 2006). Our study sites comprised experimental agricultural plots of variable size and included citrus crops and shade-grown cocoa plantations among others, which were in close proximity to native forest fragments. These landscapes show little resemblance to the original landcover or even when compared to a coffee growing landscape, for example, suggesting that Blackpoll Warblers can tolerate considerable levels of transformation. Such tolerance has been found in other Nearctic–Neotropical migratory landbirds, including the Yellow Warbler (Heath et al., 2017; Valdez-Juarez et al., 2019) but is unusual in steeply declining species. For Blackpoll Warblers in our study region, exurban and rural landscapes provided suitable winter habitat mosaics around these landscapes could be essential to ensure the availability of resources, including roosting sites and food. Also, other areas in the low foothills would also be interesting to study.

Our estimates of apparent survival, coupled with our observations that many individuals return to the same non-breeding location from year to year, suggest that Blackpoll Warblers exhibit a high degree of site fidelity. This behavior, which can vary significantly among species during the non-breeding season and throughout the annual cycle (Albert et al., 2020), is measured through metrics such as overwinter site persistence and annual return rates (Albert et al., 2020) (Sherry & Holmes, 1996; Wunderle et al., 2014). For example, Prothonotary Warblers (*Protonotaria citrea*) displayed geographical variation in fidelity, with a negative relationship between latitude and persistence (Ruiz-Gutierrez et al., 2016). In Colombia, this species showed greater persistence in mangrove habitats (Bulluck et al., 2019). In contrast, American Redstarts (*Setophaga ruticilla*) exhibited higher persistence and habitat segregation, with males displaying greater persistence in mangroves than in scrub, while females persisted equally in both habitats during the winter (Marra & Holmes, 2001).

Warblers are expected to exhibit site fidelity in areas with the highest availability of resources (Bayly et al., 2020; Bulluck et al., 2019; Latta & Faaborg, 2001). The benefits of site fidelity involve capacity to avoid predators, heightened efficiency in obtaining food, and familiarity with resource variations (Gauthreaux, 1982; Warkentin & Hernández, 1996; Wunderle & Latta, 2000). However, increased site fidelity to wintering grounds may render migratory birds more vulnerable to reductions caused by habitat change (Warkentin & Hernández, 1996; Wunderle & Latta, 2000) and, therefore, transformation of these habitats in Colombia could have implications for population dynamics.

Additionally, our findings indicate that females had slightly lower survival than males (annual, within and between non-breeding periods). However, we did not find conclusive evidence to support the idea of sexual or age segregation by landscape in our study area. In the same way, Blackpoll Warblers tolerate space sharing with other conspecifics, including those of the same sex, as well as with other *Setophaga* species (Morales-Rozo

(Albert et al., 2020; Bennett et al., 2019; Marra & Holmes, 2001; Sherry & Holmes, 1996). This information is a valuable addition to our understanding of the non-breeding ecology of the species. Apparent survival by sex, can serve as indicators of non-breeding habitat quality, with potential implications for the conservation of this species.

In this research, we present evidence that our monthly survival estimates, exceeding 0.90, are consistent with rates reported for other Nearctic–Neotropical warblers on their non-breeding grounds. Therefore, it seems that survival at stationary non-breeding sites is not a limiting factor for the Blackpoll Warbler population in the Orinoco bioregion of Colombia. Furthermore, our results suggest that Blackpoll Warblers overwintering in exurban and rural landscapes experienced different survival rates. Our study sites are situated within a mosaic of habitats, including agricultural and natural areas, which may provide suitable non-breeding habitat for migratory species like the Blackpoll Warbler.

While this study provides new insights into the non-breeding ecology of Blackpoll Warblers it has some limitations. The variation in time intervals and sampling effort between years, primarily due to restrictions imposed during the COVID-19 pandemic, may have influenced our final estimates. Future research should prioritize the estimation of survival rates and sex-age ratios in contrasting habitats used by the species, including highly occupied productive systems such as citrus and shade-cocoa plantations, as well as forests. In same way, we recommend to integrate these survival studies with evaluations of body condition to determine whether winter survival rates remain consistent across two divergent landscapes. Additionally, establishing a connection between survival rates and variations in body condition will enable an assessment of the performance of individuals in contrasting landscapes. This approach will shed light on whether birds fare better or worse in the more urbanized landscape, providing valuable insights into the interplay between survival, landscape characteristics, and individual body condition. This will allow for a better understanding of how these habitats contribute to demographic processes and the conservation of this species.

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Authors' contributions

N.B. and A.M.R. conceived the study; N.B., A.M.R. and G.C. designed the study. A.M.R. led the data collection, N.B. CG and A.M.R designed and carried out the analyses. A.M.R led the manuscript writing, and all authors contributed to text editing and approved the final version.

Figures

Figure 1. Location of the study area at A) the scale of Colombia and the municipality of Villavicencia and B) Google Earth images of the two study sites: Unillanos (Barcelona campus Universidad de los Llanos) and Agrosavia (Libertad-Agrosavia Research Center), showing land use types and the area in which resightings were carried out (white outline) and the survey routes.

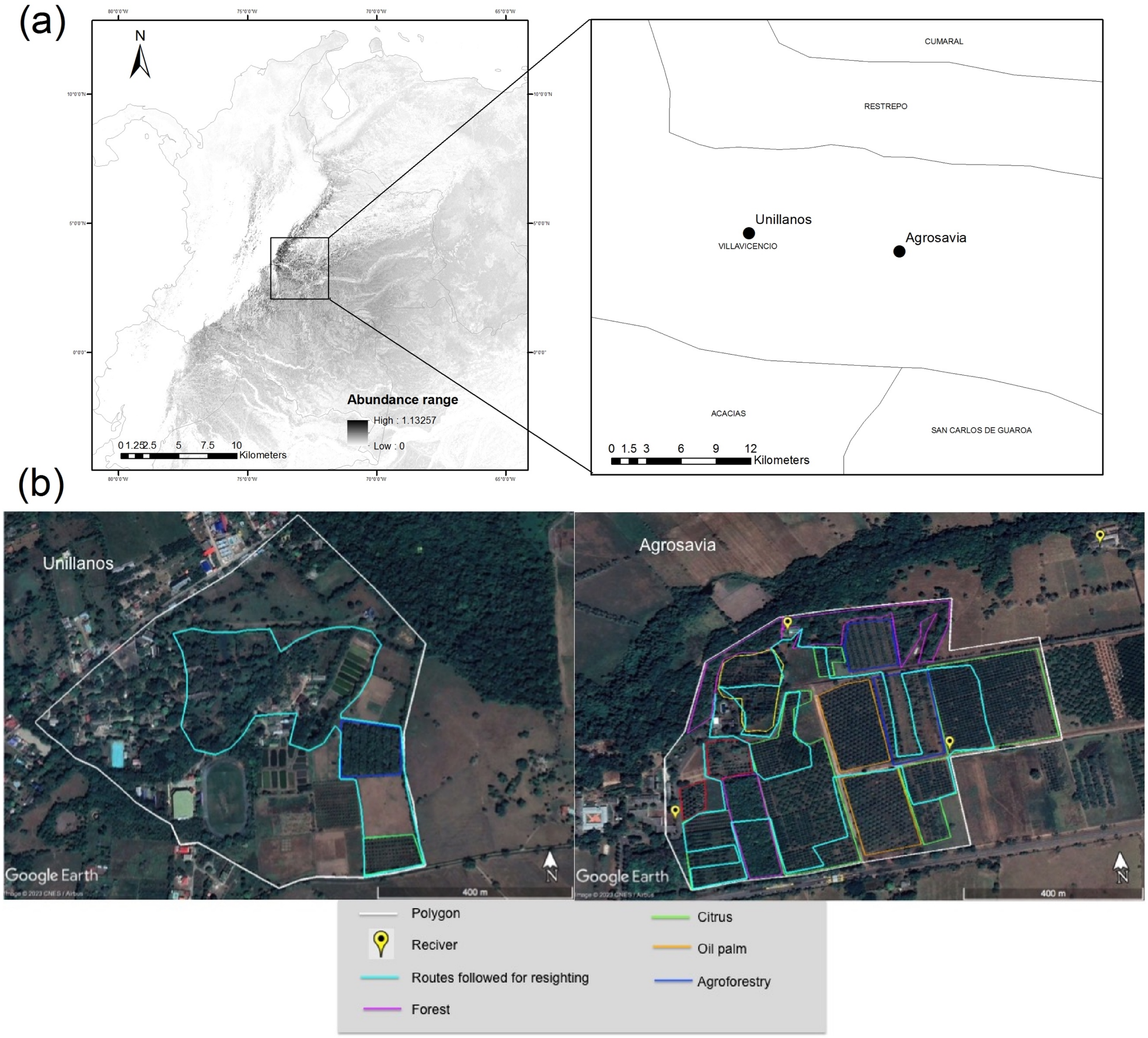


Figure 2. Apparent annual survival probability of Blackpoll Warbler in Colombia between 2017-2022, with 95% CI, model Φ(~time)p(~time)

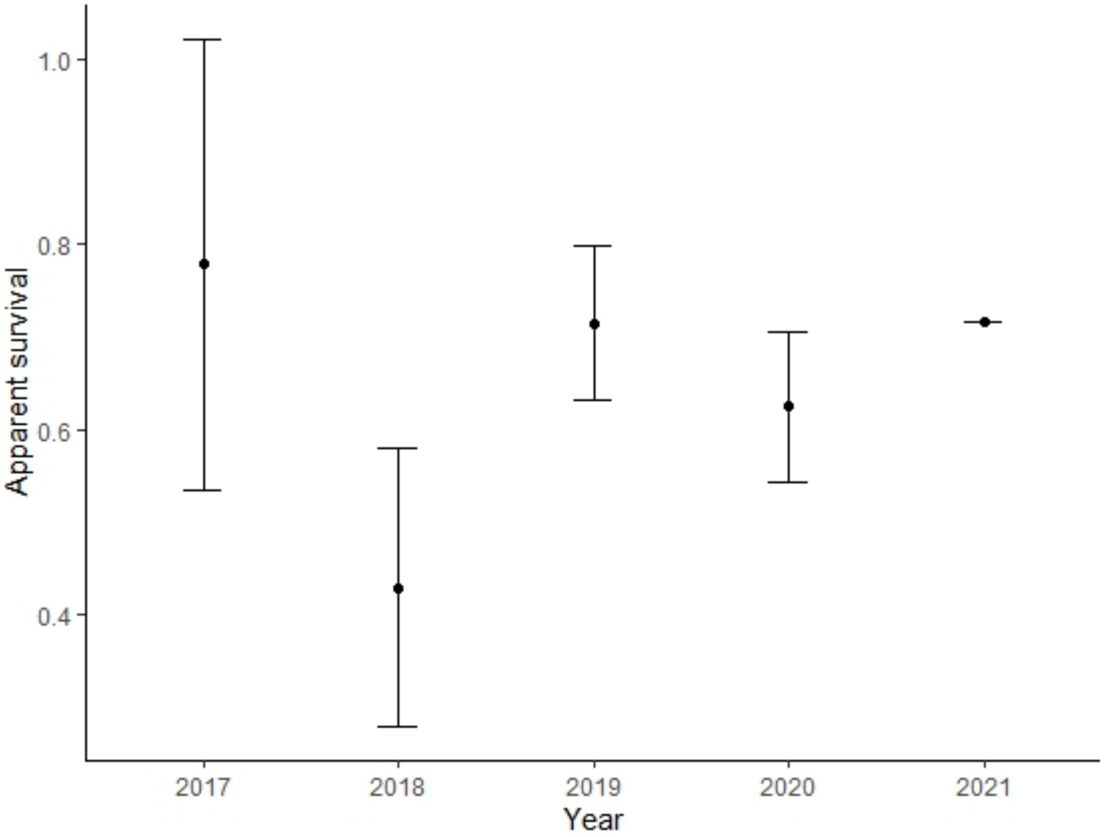


Figure 3. Apparent annual survival probability of Blackpoll Warbler in Colombia between 2017-2022, with 95% CI, model Φ(~Site)p(~time)

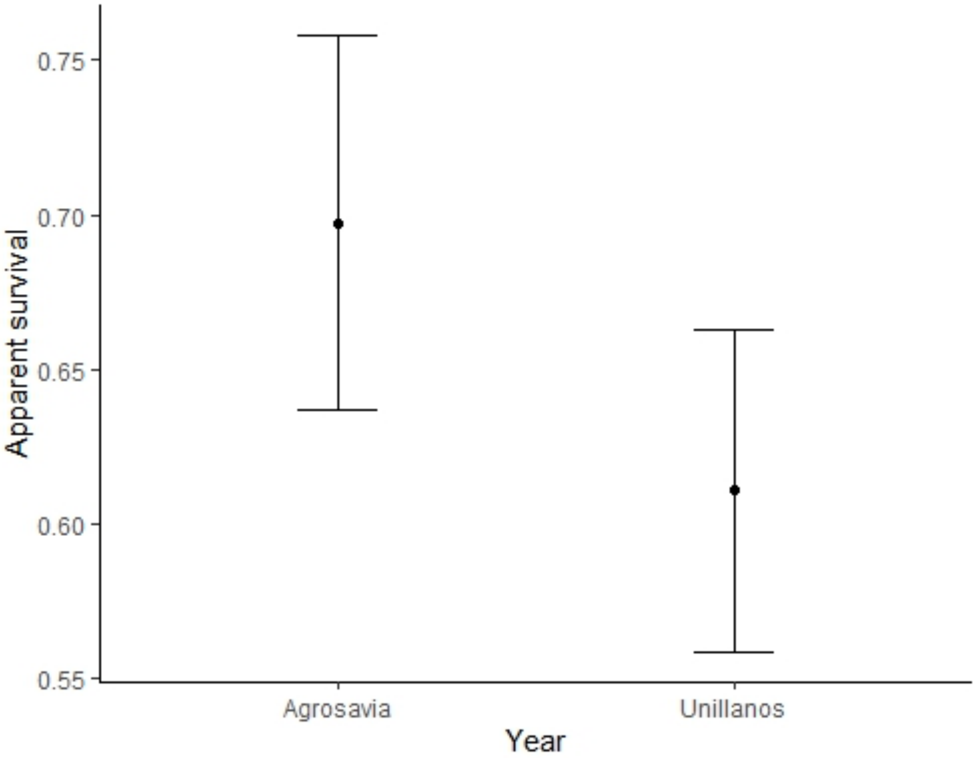


Figure 4. Apparent annual survival probability of Blackpoll Warbler in Colombia between 2017-2022, with 95% CI, model Φ(~Age)p(~time)

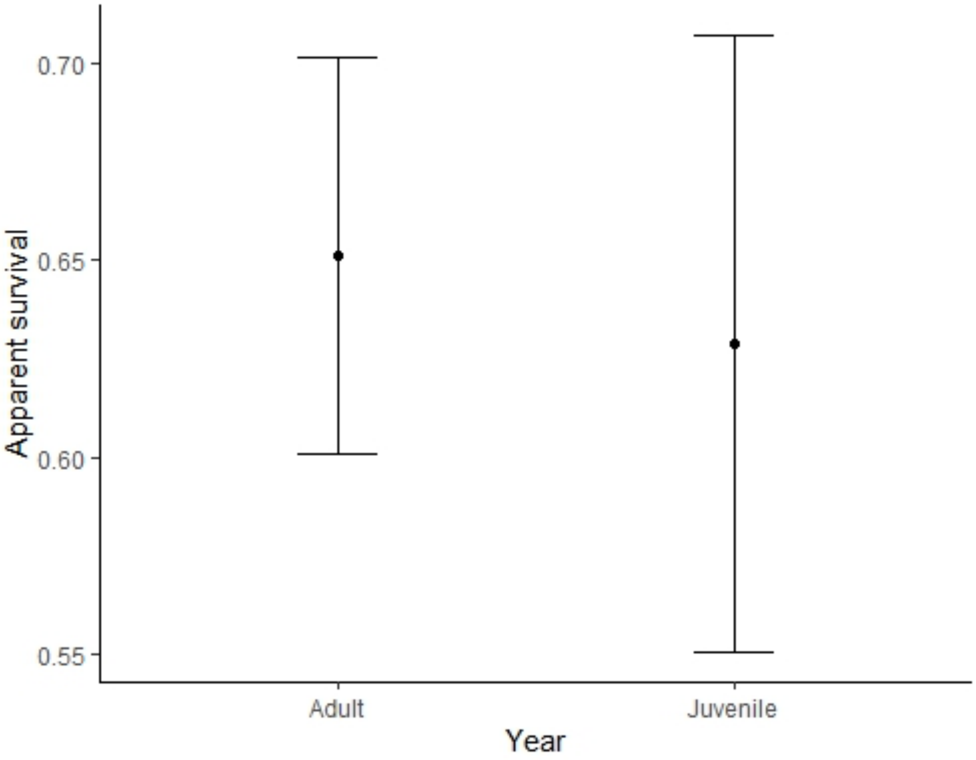


Figure 5. Apparent annual survival probability of Blackpoll Warbler in Colombia between 2017-2022, with 95% CI, model Φ(~Sex)p(~time)

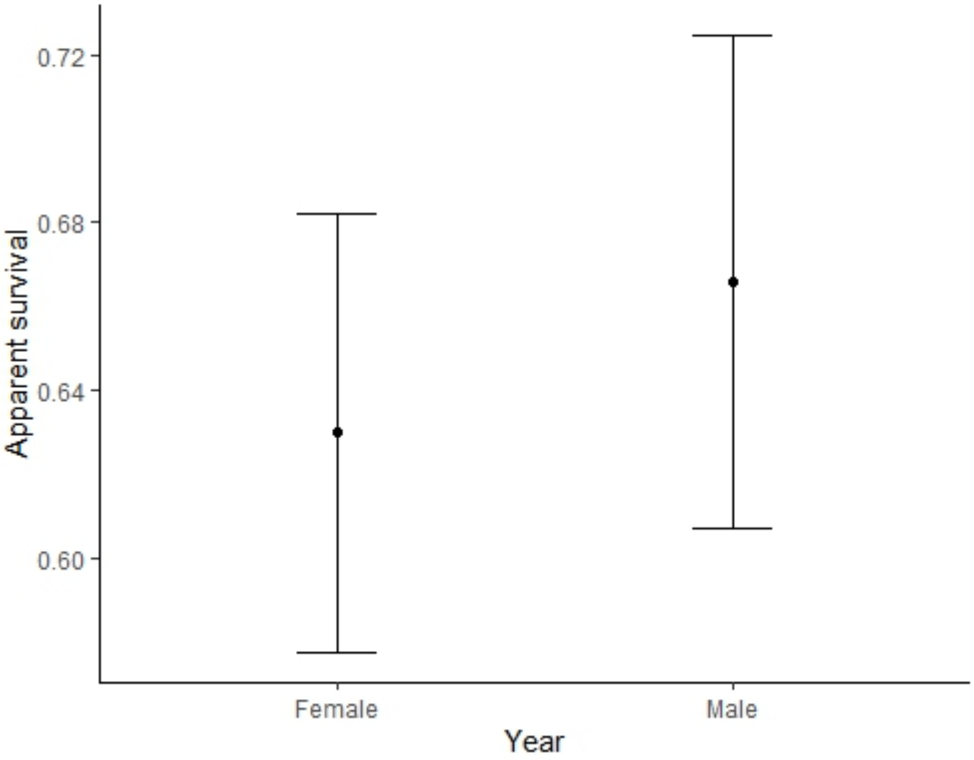


Figure 6. Apparent annual survival probability of Blackpoll Warbler in Colombia, with 95% CI, model Φ(~Between.Site)p(~time)

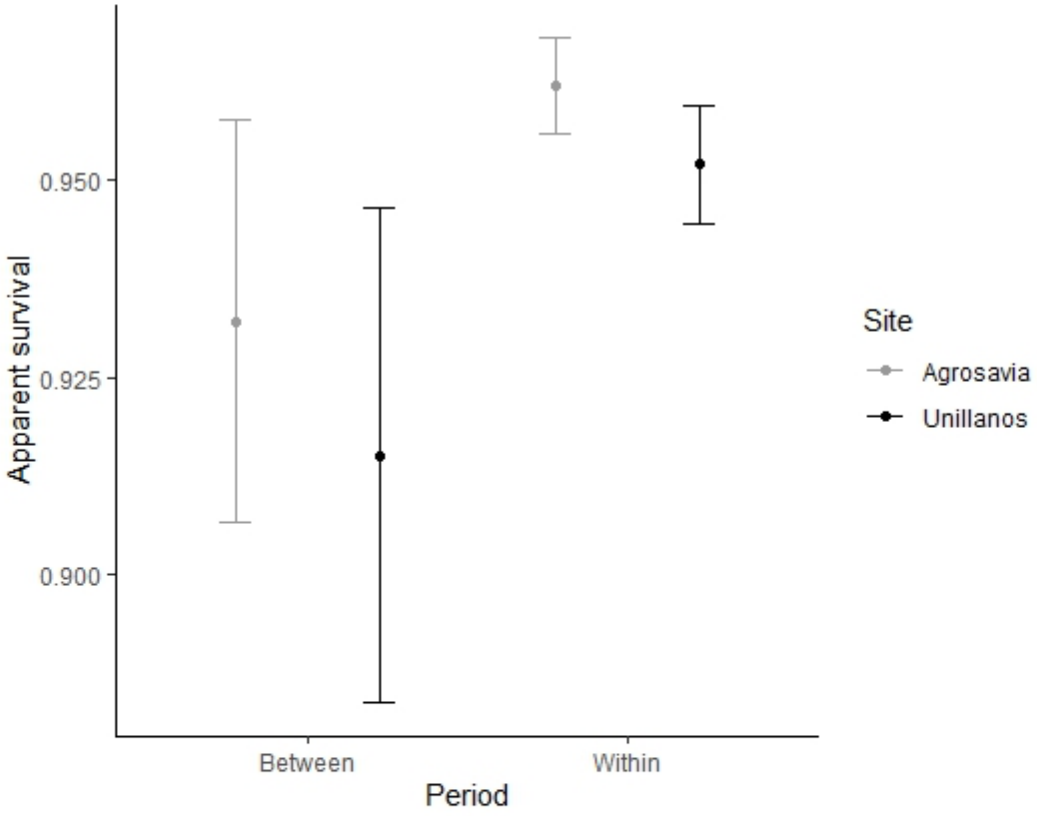


Figure 7. Apparent annual survival probability of Blackpoll Warbler in Colombia, with 95% CI, model Φ(~Between.Sex)p(~time)

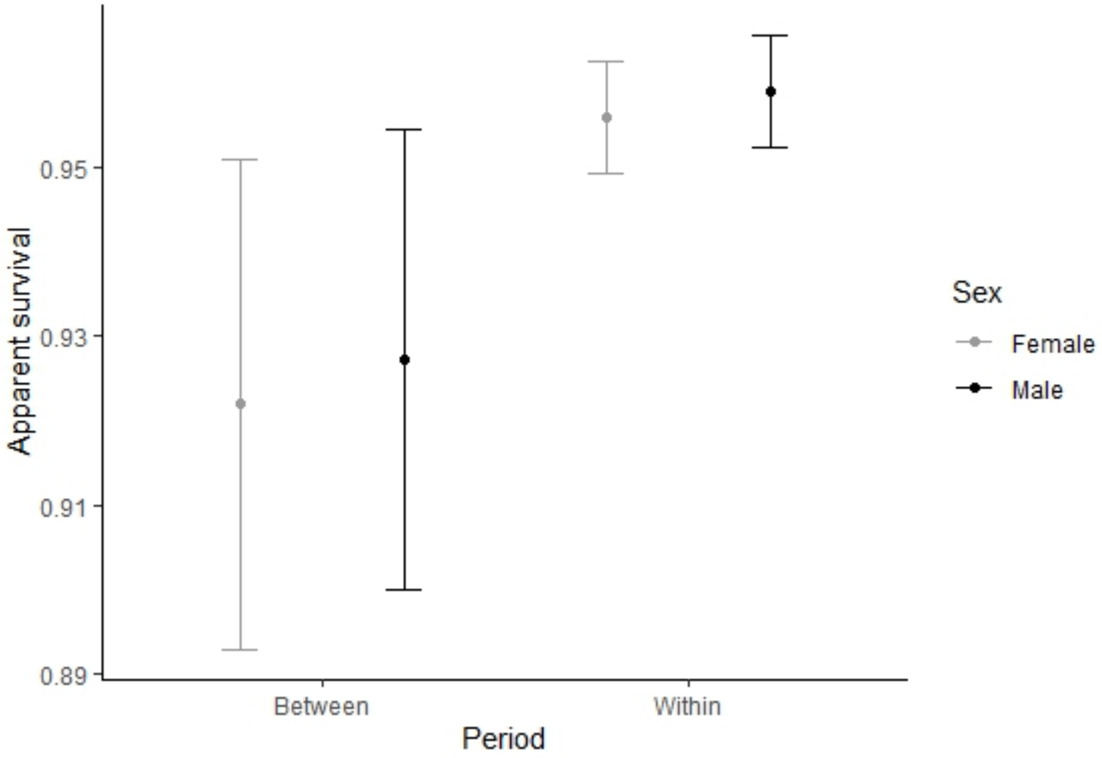
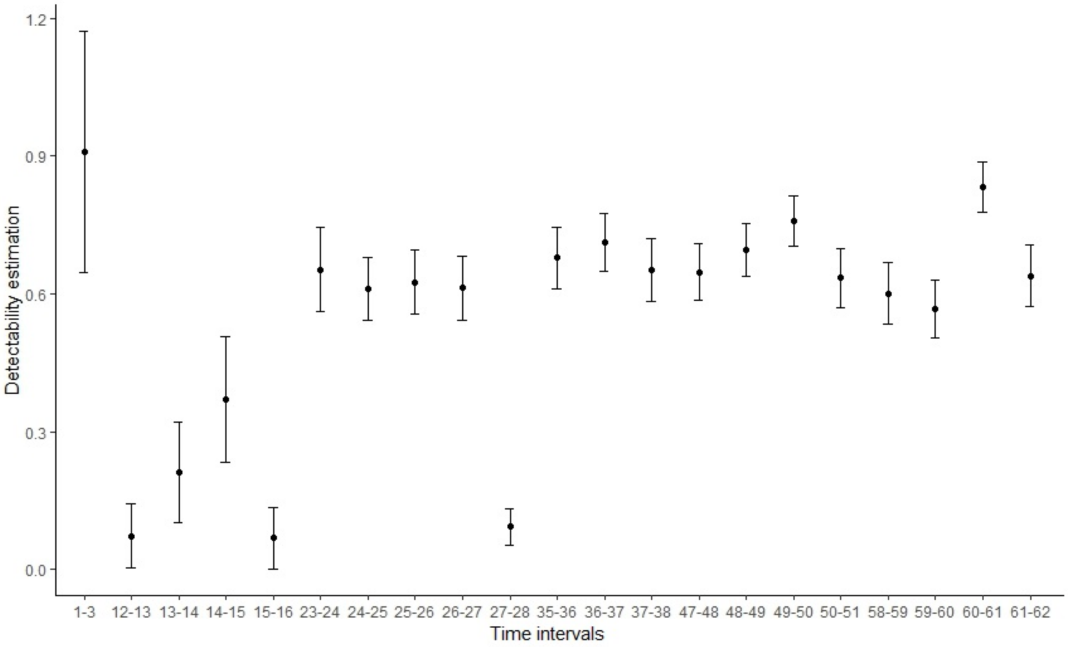


Figure 8. Dectability estimation of Blackpoll Warbler in Colombia, with 95% CI, model Φ(~Between)p(~time) , 27 capture events , there are 26 intervals, and all time intervals are in months.



Tables

Table 1. Summary of model Φ time p time examining variation in apparent survival of Blackpoll Warblers based on resightings of color-banded birds in Colombia between 2017 to 2022. se: standart error; LCL: lower confidence limit; UCL: upper confidence limit.

Name	estimate	se	lcl	Ucl
Φ 2017	0.78	0.24	0.18	0.98
Φ 2018	0.43	0.15	0.19	0.71
Φ 2019	0.71	0.08	0.53	0.85
Φ 2020	0.62	0.08	0.46	0.77
Φ 2021	0.71	0.00	0.71	0.71
p 2017	0.57	0.21	0.20	0.88
p 2018	0.39	0.17	0.14	0.72
p 2019	0.74	0.09	0.54	0.88
p 2020	0.80	0.09	0.59	0.92
p 2021	0.70	0.00	0.70	0.70

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3.8 Supplementary information

Table S1A. Multiple models for apparent survival estimate and resighting probability for Blackpoll Warbler

Model	**npar**	**AICc**	**DeltaAICc**	**weight**	**Deviance**
Phi(~1)p(~time)	6	376.50	0.00	0.37	105.44
Phi(~Site)p(~time)	7	377.21	0.71	0.26	104.01
Phi(~Sex)p(~time)	7	378.38	1.88	0.14	105.18
Phi(~age)p(~time)	7	378.59	2.08	0.13	105.38
Phi(~Site+Age+Sex+Site*Age+Site*Sex)p(~time)	11	380.32	3.82	0.05	98.34
Phi(~time + age)p(~time)	11	382.41	5.91	0.02	100.43
Phi(~time)p(~time)	10	383.12	6.62	0.01	103.37
Phi(~time + Site)p(~time)	11	384.36	7.86	0.01	102.36
Phi(~time + Sex)p(~time)	11	384.62	8.12	0.01	102.63

Table S1B. Model Φ(~Between) p(~time). Apparent survival estimate and resighting probablity for Blackpoll Warbler. SE: standard error; LCL: low control limit; UCL: upper control limit.

Name	**estimate**	**se**	**lcl**	**ucl**
Within	0.96	0.005	0.95	0.97
Betweeen	0.92	0.027	0.85	0.96
t3	0.91	0.263	0.02	1.00
t12	0.42	0.151	0.18	0.71
t13	0.07	0.070	0.01	0.38
t14	0.21	0.110	0.07	0.49
t15	0.37	0.136	0.16	0.65
t16	0.07	0.067	0.01	0.36
t23	0.10	0.095	0.01	0.47
t24	0.65	0.092	0.46	0.81
t25	0.61	0.069	0.47	0.74
t26	0.63	0.070	0.48	0.75
t27	0.61	0.070	0.47	0.74
t28	0.09	0.040	0.04	0.21
t35	0.46	0.080	0.32	0.62
t36	0.68	0.067	0.54	0.79
t37	0.71	0.063	0.58	0.82
t38	0.65	0.069	0.51	0.77
t47	0.50	0.080	0.34	0.65
t48	0.65	0.061	0.52	0.76
t49	0.70	0.058	0.57	0.80
t50	0.76	0.055	0.64	0.85
t51	0.64	0.064	0.50	0.75
t58	0.26	0.069	0.15	0.42
t59	0.60	0.066	0.47	0.72
t60	0.57	0.063	0.44	0.69
t61	0.83	0.055	0.70	0.91
t62	0.64	0.068	0.50	0.76

Conclusions and recommendations

Conclusions

Nearctic-Neotropical migrants spend at least half of their life cycle in Neotropical ecosystems. Studies on the non-breeding grounds are important to understand which factors influence their distribution, habitat use and demographic parameters that, ultimately, influence breeding success and population viability. The results of this thesis provide new insights into understanding the ecological niche, winter habitat use and demographic parameters of Blackpoll Warblers in the Orinoco and Amazon bioregions, where the species is predicted to be most abundant.

The main conclusions corresponding to the three chapters developed are presented below:

Chapter 1 Occupancy rates in Blackpoll Warblers: a multiscale analysis in Eastern Colombia reveals climate, landscape and vegetation as key variables

In Chapter 1, our goal was to comprehend variation in Blackpoll Warbler occupancy rates at the regional, landscape, and local scales in the Orinoco and Amazon bioregions of Colombia. One way of describing the distribution of these birds in non-breeding areas is through metrics like presence/absence, occupancy probability, and relative abundance (Johnston et al., 2019). We used single-species, single-season hierarchical occupancy models and N-mixture models to describe occupancy and abundance patterns. Blackpoll Warbler is one of few Nearctic-Neotropical migrants that selects areas in the Andean foothills at the base of the eastern slope of the Eastern Andes and in northern Amazonia. We found at the regional scale, that the main environmental variable that positively influences the occupancy of Blackpoll Warbler was Net Primary Productivity, which is correlated with precipitation (+) and elevation (400-800 masl). Patterns of precipitation during the dry season (i.e., precipitation from December to April, and during the driest month) may represent a significant limiting factor for occupancy by Blackpoll Warbler populations in Colombia, and may have major effects on food availability during the non-breeding season. Additionally, Blackpoll Warblers had lower occupancy rates at lower elevations in our study area, with rates increasing between 400 to 800 m.

The primary landscape-scale variable influencing Blackpoll Warbler occupancy in the Orinoco region was habitat type and the landscape matrix. At the landscape scale, we observed that occupancy and abundance was higher in agroforestry systems (citrus plantations, shade-grown cocoa, and silvopastures) relative to forested habitats, and was negatively correlated with the amount of forest in the landsacpe. At the local scale, occupancy was negatively correlated with tree density. We identified variables influencing occupancy at multiple scales, and the importance of landscapes with different types of agroforestry systems as wintering habitats for the Blackpoll Warbler in Colombia.

Chapter 2 Home range size and space use by Blackpoll Warblers (*Setophaga striata*) on their non-breeding grounds in Colombia

In Chapter 2, our aim was to estimate and compare home range size, space use, and site fidelity across different landscapes and between two contrasting agroforestry systems in the Orinoco region of Colombia using complementary methods (i.e., resightings of color-banded birds, and manual telemetry). By estimating home-range sizes for exurban and rural landscapes using minimum convex polygons, we found that home range estimates were similar between landscapes (<0.90 ha) but were different across years, with home range size potentially being influenced by the ENSO cycle. Although home ranges, as determined by kernel density estimators, were variable in both agroforestry systems, we identified differences in home range size between shade-grown cocoa and citrus plantations. The estimate for shade-grown cocoa was smaller than citrus plantations, potentially implying higher habitat quality in cocoa. Small territories could be influenced by resource availability, and this attribute is considered a proxy of habitat quality.

Site fidelity was consistently observed across various scales, including landscapes and habitats, at all study sites. The Blackpoll Warblers' high level of site fidelity in their non-breeding grounds may render them more vulnerable to changes in landcover. Our findings lend support to the notion that landscapes featuring a combination of natural and agricultural matrices could play a pivotal role in mitigating population declines among Blackpoll Warblers in the eastern foothills of the Eastern Andes within the Meta department of Colombia

Chapter 3 Survival estimation and sex-age ratios of Blackpoll Warbler in non-breeding areas in Colombia

In Chapter 3, based on demographic factors such as the proportion of sexes and ages and apparent survival, we investigated whether two contrasting landscapes - rural and exurban - in the Orinoco region constituted habitat of higher quality for Blackpolls. We fitted a Cormack-Jolly-Seber (CJS) capture-recapture model to estimate monthly survival probabilities, apparent annual survival and resighting probability based on a 6-year live-encounter dataset. We found large variation in annual survival (0.4-0.7), with 2018 year as the lowest estimate, which may be attributed to climatic conditions influenced by El Niño-Southern Oscillation (ENSO) during the period spanning 2018 to 2019. We found high overwinter survival (>0.9) and slightly differences in annual survival between landscapes and sexes, demonstrating that matrices with a mosaic of habitats (e.g., agricultural and natural covers), may provide suitable winter habitat for migratory species like the Blackpoll Warbler. It seems that survival in non-breeding sites is not a limiting factor for the Blackpoll Warbler population.

Recommendations

It is important to consider that the Orinoquia region is projected to undergo significant transformations in natural cover. Therefore, preserving the remaining forest patches in the foothills and the agroforestry systems, which are limited in extent and are being replaced by monocultures without shade, is crucial.

Similarly, it is worthwhile to conduct sampling in open areas and grasslands to evaluate the issue of forest percentage.

Generating long-term data is essential to understand the effects of climate change and phenomena such as ENSO, as well as to observe variations in demographic parameters and home range.

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