Factors Affecting Habitat Quality for Wintering Wood Thrushes in a Coffee Growing Region in Honduras

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Factors Affecting Habitat Quality for Wintering Wood Thrushes in a Coffee Growing Region in Honduras

A Thesis Presented

by

Brett A. Bailey

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

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Environmental Conservation

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David I. King, Chair

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Environmental Conservation

DEDICATION

To my grandmother
who always kept a garden
full of love and birds

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I want to express my sincere gratitude to my advisor Dr. David King. This project, conducting applied research in the Neotropics, was precisely the type of work I was looking for when I began applying to graduate schools. I am eternally grateful to Dave for giving me the opportunity to take on this project and the freedom to make it my own. Furthermore, his support through both difficulties and victories has been unwavering. Lastly his thoughtful input on this thesis has been invaluable. I am looking forward to continuing our work together on this and other projects.

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ABSTRACT

FACTORS AFFECTING HABITAT QUALITY FOR WINTERING WOOD THRUSHES IN A COFFEE GROWING REGION IN HONDURAS

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Amongst the diversity of taxa that occur in the Neotropics, 200 migratory bird species that breed in temperate North America can be found. Many of these populations have seen significant declines since the 1960s. The Wood Thrush, *Hylocichla mustelina*, is one such species. Shade coffee and other agroforestry practices show potential for benefiting migratory species, but the quality of coffee habitat and optimal habitat characteristics for Wood Thrushes remain unknown.

I surveyed a spatially complex, agricultural landscape in Honduras outside the recognized winter range of the Wood Thrush and radio-tagged 46 individuals within rustic coffee farms during the winters of 2012 and 2013. I used telemetry data to calculate metrics of habitat quality based on survival and persistence while also collecting detailed vegetation measurements across the landscape and within each home-range. Mixed-effects models were used to explore the relationship of survival, transience, movement, and home-range size to habitat class and microhabitat variables.

Estimates for all four habitat quality metrics fell within the range of previous studies and were significantly related to habitat attributes. Structure, edge habitat, and shade coffee played a key role determining habitat quality.

The variables associated with higher habitat quality in this study suggest that rustic coffee farms have potential to support wintering wood thrush populations. However, estimates of survival may be overly optimistic in the presence of transients, transforming highly fragmented landscapes into winter sinks. This study highlights several gaps in current scientific knowledge about some of the most essential questions of Wood Thrush winter ecology.

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CHAPTER 1

FACTORS AFFECTING HABITAT QUALITY FOR WINTERING WOOD THRUSHES IN A COFFEE GOWING REGION IN HONDURAS

1.1 Introduction

The Neotropics hosts a tremendous diversity of animal taxa, including approximately 200 species of migratory birds that breed in temperate North America. Historically migrants were considered generalists on the wintering grounds that used ephemeral resources and thus were relatively unaffected by tropical deforestation(Herrera 1978, Tramer and Kemp 1980). Within only the past few decades, however, studies have begun to recognize that North American migrants are specialists on their wintering grounds, seeking specific habitat characteristics and food resources to which they are adapted (Schwartz 1980, Faaborg et al. 2010). In addition migrant populations may be disproportionately vulnerable to habitat modification on their wintering grounds in the Neotropics, where bird densities are as much as eight times higher than on the breeding grounds(Terborgh 1980).

Globally, Central America has cleared a greater percentage of forests than in any other region, mainly for agricultural production(Carr et al. 2006). Agroforestry, which refers to tree-dominated agricultural systems, has been highlighted as a promising approach to slowing biodiversity losses and may prove beneficial for Wood Thrush(Fahrig et al. 2011, Perfecto and Vandermeer 2015). Shade-grown coffee, an example of an agroforestry system, has gained considerable attention as a conservation tool for Neotropical, migratory birds based on a high abundance and diversity of species present (Petit and Petit 2003). With at least 19% of agricultural land in Central America dedicated to coffee production, finding ways to maintain elements of natural habitat within coffee landscapes may contribute to the conservation of some migratory species. However, questions remain surrounding best agroforestry practices and whether with many studies highlighting potentially detrimental effects of agroforestry expansion for species that require habitat features that are only available in forests. (Rappole et al. 2003, Chandler and King 2011). These same arguments have helped fuel the land-sharing versus land-sparing debate which respectively supports either low-intensity agriculture that includes natural habitat features or instead setting aside blocks of native habitat (Fischer et al. 2008).

Despite many studies highlighting the considerable diversity and abundance of Neotropical migrants found in shade coffee plantations (Perfecto et al. 1996, Greenberg et al. 1997, Moguel and Toledo 1999), since animals regularly occupy marginal habitats due to despotic interactions abundance does not necessarily reflect habitat quality(Van Horne 1983, Sherry and Holmes 1996, Johnson 2007). Habitat quality, dependent on the individual fitness advantage associated with the selection of a habitat patch, is difficult to quantify yet critical to informing conservation strategies (Johnson 2007). Survival is the most powerful indicator of habitat quality, but obtaining reliable estimates requires considerable field effort. For this reason site persistence, home-range size, or condition may be useful indicators of habitat quality (Winker et al. 1995, Johnson 2007).

Local vegetation characteristics, configuration of the landscape, proximity to protected areas, and farming methods have all been shown to influence patterns of bird presence and abundance within agroforestry landscapes (Bakermans et al. 2011, Luck and Daily 2003, Chandler and King 2011, Gilroy et al. 2014). This suggests that adjusting the configuration of these elements can influence habitat quality. Thus, there is an urgent need for research that quantifies the conservation value of existing landscapes and identifies features required to increase value for vulnerable species.

In response to this need for more informed conservation planning, I undertook this study to identify suitable habitat present across a landscape of traditional shade and rustic coffee farms and to identify characteristics that influence habit quality for the Wood Thrush. The Wood Thrush is a Neotropical migratory species of high conservation concern that has experienced a yearly population decline of 1.9% since 1966 (Sauer et al. 2012). The Wood Thrush is most commonly associated with lowland, primary forest from southern Mexico to northern Panama where they forage for soil arthropods(Holmes and Robinson 1988, Whitacre et al. 1992, Howell and Webb 1995). Survival and persistence of this species is known to differ between primary forest and disturbed habitats (Rappole et al. 1989, Winker et al. 1990), and a recent full life-cycle modeling exercise suggested this species may be primarily limited by the availability of suitable non-breeding habitat in Central America, making conservation of winter habitats an urgent priority (Taylor and Stutchbury 2015). The specific objectives were to calculate survival and persistence-based metrics of habitat quality, to test the relationship between my metrics and individual condition, and finally to model the effect of habitat characteristics on habitat quality. The outputs generated by this study will inform future conservation planning.

1.2 Methods

1.2.1 Study Area

The study area is located in the northern interior of Honduras, entirely within the Department of Yoro and to the south of the city of Subirana. The study area straddles the boundary between lowland and highland biogeographical regions and spans a significant moisture gradient. As elevation increases from 850 m to 1300 m conditions become cooler and wetter, pine and oak give way to humid broadleaf forest. The mountainous landscape produces numerous streams that also form riparian forest at lower elevations. From November to April, average temperatures steadily rise (Lows: 16-20 C, Highs: 27-33) and rainfall drops dramatically from 176 mm in October to approximately 20mm per month from February, through April. Coffee is a major source of income for the region, especially for land holders at higher elevations. Corn, beans, livestock, and lumber are produced at lower elevations. Despite common observances of Wood Thrushes across the study area, the area does not lie within the published winter range of the species(NatureServe 2012). However, recent abundance maps have identified isolated pockets of local habitat as potentially suitable(The State of North America's Birds 2016. 2016).

Bird banding sites were placed within local coffee farms and adjacent forest habitat to evaluate factors that influence habitat quality for Wood Thrushes. Banding sites were selected from a pool of point count locations identified in 2011 which included shade coffee farms, humid broadleaf forest and pine-oak forest distributed across a gradient of elevations. Both point counts with playback and passive mist netting were used to determine that Wood Thrush were absent from drier habitat classes common below 1200 m such as pine-oak forest, providing the motivation to focus efforts primarily on the diversity of coffee sites within the landscape. Accessibility during wet weather and previous detection of Wood Thrushes were requirements for candidate sites. An attempt was also made to distribute sites across a range of elevations, in addition to including sites with and without suitable adjacent forest. Twelve banding sites were located within a 7,300 hectare area (Table 1.1). Nine sites were classified as either rustic traditional or polyculture shaded coffee systems. A traditional polyculture maintains part of the original forest canopy to maintain shade but selectively removes trees and other vegetation to make room for coffee (Moguel and Toledo 1999). Vegetation structure and composition within coffee sites varied widely with different densities of coffee and trees and a range of pruning and weeding regimes. A small stream was present within the boundaries of every coffee site and small patches of secondary forest or early successional vegetation up to 0.5 ha were also common. Banding was also conducted in three areas of humid forest 500 m from but contiguous with existing coffee sites consisting of a lowland riparian forest regenerated from coffee, a highland broadleaf forest relatively free of disturbance, and a selectively logged highland broadleaf forest. All sites were embedded within a landscape of pasture, other coffee farms and remnant pine oak, broadleaf and mixed forest. Adjacent coffee and forest sites were combined as single sites for telemetry-based analyses since many individuals used both areas of habitat, resulting in a total of nine sites.

1.2.2 Capture

Wood Thrushes were captured using fixed grids of 10 to 15 mist nets during two winter seasons, January 6th to March 4th, 2012 and January 10th to February 22nd, 2013. Nets were operated at least 2 consecutive days per site each season. Effort was increased if fewer than two individuals were captured at a site during the first two days. All captured Wood Thrushes were banded with a USGS numbered aluminum band and a unique color combination of three plastic bands. When possible, birds were aged using the shape of rectrices and primaries and the color of wing coverts (Pyle 1997). Age was assigned one of two values, “after first year” for individuals that fledged the previous summer, and “after second year” for older individuals. Subcutaneous fat scores (0-5), tail length, wing length and weight were also measured for each individual (Salewski et al. 2009). The regressed residuals of mass divided by tail were used as a supplemental condition index (Conway et al. 1994). A 1.5-g radio transmitter with a 16-cm antenna of thin, flexible wire was attached to the lower back of each Wood Thrush. The transmitter was secured with leg loops made of a thin elastic string that extended around the bird's upper leg (Naef-Daenzer 2007). After banding and radio transmitter attachment, birds were released and observed for an additional 15 minutes to verify that the harness did not restrict movement.

1.2.3 Telemetry

Wood Thrushes were tracked on foot using handheld VHF receivers and three-element Yagi antennas. Each individual was typically located once or twice each week for the life of the transmitter, at least 6 weeks. Locations were determined using a combination of homing and triangulation (White and Garrott 2012). Since bird movements are often influenced by the approach of observers and visual confirmation of individuals is not always possible in dense vegetation, GPS points and bearings were collected during pursuit to triangulate locations. At least three points and bearings were recorded on approach towards a target Wood Thrush. Special effort was made to record GPS points and signal bearings from a variety of angles to minimize error in the resulting triangulation location. One or more GPS points collected for triangulation calculations were typically within at least 20 m of the target individual. For individuals that could not be located, a search was conducted from nearby peaks. Program Location of a Signal ((LOAS) 2010) was used to calculated triangulated locations from GPS waypoints and associated bearings to the target Wood Thrush. Within the LOAS software Andrews maximum likelihood estimation was used to calculate triangulated locations since it automatically removes aberrant combinations of bearings from the calculation (White and Garrott 2012). If triangulated locations and visually verified, homing locations were both available for a single tracking attempt, the triangulated location was dropped. Standard maximum likelihood or biangulation were occasionally used to triangulate locations if the Andrews method failed to converge. Triangulated points were screened for outliers and locations were removed if field notes, and GPS tracks did not provide support for the estimated location.

1.2.4 Landscape

Landscape-level analysis was conducted using an existing land cover GIS layer for Honduras derived from high resolution satellite imagery captured primarily in 2013(Duarte n.d.). The data did not specify areas of coffee cultivation within the study area. Coffee farms used by radio tagged Wood Thrushes were manually digitized using ArcMap 10.3 (ESRI 2011). The total land class composition of the study landscape and the assignment of land classes to individual Wood Thrush Locations were also completed using ArcMap. Edge habitat located with 20 meters of habitat class boundaries was also identified within each Wood Thrush home-range.

1.2.5 Vegetation

Vegetation structure and composition were quantified using a modified protocol developed by James and Shugart(1970). For each tagged Wood Thrush, plots were located at three telemetry locations and three paired, random locations positioned 50 m away at a random compass bearing. Since paired, random points were intended to identify microhabitat features selected by Wood Thrush; an alternate bearing was selected if the point was located in non-habitat, such as a river, open field or road. Vegetation was also measured at capture locations.

The vegetation surveys were conducted within a 5 m radius circular plot. All trees within the survey circle were assigned to a size class using a Biltmore stick and identified by local name when possible. A vertical, 3m pole was used to count touches of vegetation along five height classes (A: 0-0.25 m, B: 0.25-0.5 m, C: 0.5-1m, D: 1-2, E: 2-3 m) while also identifying the dominant type of understory (0-1 m) and subcanopy (1-3 m) vegetation at 20 random points along four, 5 m transects. Dominant vegetation classes included coffee, woody vegetation, ferns, forbs, grass, vines, and heliconia-like vegetation. Leaf litter depth was measured at four points, 1 m from the center of each survey site. Two dbh size classes of woody stems (<2.5 cm & 2.5-8 cm) were also counted within the survey radius. See appendix A for a complete list of variables generated from the vegetation protocol.

In order to supplement the Wood Thrush data collected during telemetry 408 vegetation points collected as part of the study were used to more thoroughly to characterize Wood Thrush habitat use at the home-range scale. Vegetation was measured at random locations, and a subset of Wood Thrush telemetry and mist net locations. A spatially explicit script written in Program R was used to associate individual Wood Thrush locations to nearby vegetation points within 20 meters, which we assumed represented the habitat the bird was occupying. The script continued through visual and then triangulated locations until 5 vegetation points were assigned to each Wood Thrush. For Wood Thrushes with fewer points available, the search radius was expanded to include the entire 70% kernel home-range. Variables were averaged over all points for each individual for inclusion in final models.

During the 2011 exploratory season vegetation measurements were also taken at 50 sites distributed across the landscape (25 coffee and 25 forest (uncultivated habitat with canopy cover)). Compared to the five-meter protocol described above, the exploratory measurement protocol included several differences. The circular measurement radius was 11.2 m or 0.04 ha. The presence or absence of vertical structure was noted in each height class, A-E, instead of an actual count of vegetation touches. Tree diversity was also noted as part of these surveys.

1.2.6 Home-range

Home-ranges were estimated to establish areas occupied by Wood Trushes for the purposes of characterizing habitat(above), as well as to provide a supplemental indicator of habitat quality since bird movements yield larger home ranges in poorer habitats (Winker et al. 1995). Both capture locations and telemetry locations were used to estimate home-range. All locations were separated by at least two hours, but 95% of points were recorded at least one day apart (Range:0-38 days, Mean:4 days). All tagged individuals with at least five locations were included in home-range analysis. The locations of depredated individuals were not included since they may have been relocated by a predator.

Five home-range estimators commonly employed in the literature were considered in the analysis of Wood Thrush location data(Signer et al. 2015). Maximum Convex Polygon(MCP), was used in our final analysis and selected to allow for comparison with previous studies. Three kernel bandwidth selectors were also calculated because MCP methods fail to reflect unused habitat within home range areas, particularly when birds use several discrete activity centers(Downs and Horner 2008). These kernel estimators were reference bandwidth (REF), least-squares cross-validation (LSCV), and plug-in, each producing different smoothing parameters based on the distribution of datapoints. MCP, REF, and LSCV home-ranges were calculated using the adehabitatHR package in R(version 0.4.13; Calenge 2006). Bandwidths for plug-in analysis were generated using the ks package in R(version 1.9.4, Duong 2007). LSCV was selected as the most suitable kernel bandwidth estimator based on its ability to generate comparable results across all individuals, mainly by accommodating multiple centers of activity for many of the non-territorial individuals.

Two different contours from the resulting LSCV utilization distributions (UDs) were used in analysis. To identify the core home-range contour, total area was graphed for each Wood Thrush across contour values of 5% to 95% to identify a common inflection point (Harris et al. 1990). A 70% contour captured the core home-range for all individuals and a visual review of the home-ranges showed that this value also maintained separation between disjoint centers of activity. Disjoint centers of activity are common for non-sedentary individuals, underscoring the need for an estimator and contour capable of identifying them. The 95% contour, commonly used to assess habitat availability, was used to compare maximum home-range size.

1.2.7 Movement

Two movement patterns are most commonly associated with Wood Thrushes on the wintering grounds, sedentary or wanderer (Rappole et al. 1989). Mean squared distance from the center of activity (MSD) and a linearity index (LI) are two movement metrics that have been used to quantify these patterns (Spencer et al. 1990). The R package rhr (version 1.2.906, (Signer and Balkenhol 2015)) was used to calculate MSD and LI for each Wood Thrush. The metrics were then compared to 1000 MSD and LI values generated from random, bootstrapped samples of movement distances and angles for each individual. If the actual MSD and LI values appeared within the lower 10% of bootstrapped values, indicating restricted movement around a center of activity, the individual was considered Sedentary. Observed values above the 10% threshold were assigned a wanderer pattern, consistent with more linear movements away from a single center of activity.

The adehabitatLT package(version 0.3.19, Calenge 2006) was used to calculate maximum linear distance from capture location for comparison with previous studies. This metric, set at one of several arbitrary thresholds, has been used in multiple Wood Thrush studies to differentiate between sedentary and wandering individuals (Rappole et al. 1989, Roberts 2007).

1.2.8 Survival & Transience

Survival rates were calculated using the R package SURVIVAL (version 2.39-2, Therneau 2013). Kaplan-Meier survival curves for the entire study were calculated using the survfit function. Kaplan-Meier estimates allow for integration of right-censored data, such as individuals that disappear from the study site (Kaplan and Meier 1958, Krebs 1989).

Wood Thrushes that could not be re-located within the minimum expected lifetime of the transmitters were believed to be transients that permanently emmigrated from the study site. Transients were typically observed making long, directional movements prior to loss of signal. Since the data for transients posed the same challenges as right-censored survival data, transience rates were calculated using the same process as survival.

1.2.9 Statistical Analysis

1.2.9.1 Variable Screening and Preparation

Prior to using habitat variables for analysis, some variables were combined to reduce the total number of variables and minimize the number of zeros present in several measures (Appendix A). Tree diameter classes were combined into three groups, small (2.5-9 cm dbh), medium (9-27 cm dbh), and large (27-50+ cm dbh). Basal area was estimated for each original size class based on the midpoint of each class. Habitat structure counts were combined into two classes, understory (0-1 m) and subcanopy (1-3 m).

1.2.9.2 Habitat & Microhabitat Selection

A use versus availability approach was used to identify habitat classes selected by Wood Thrushes. Analysis was conducted using individual classes as defined by the GIS layer and a second round of analysis was performed using combined classes. Habitat availability was calculated for each Wood Thrush using the 95% contour of the LSCV home-range and use was determined from all point locations. Compositional analysis and Manly selection ratios were calculated to evaluate habitat selection amongst land classes using R package adehabitat HS (version 0.3.12, (Calenge 2011)). Compositional analysis generates a ranked list of selected habitat and identifies significant levels of selectivity between any two habitat classes using the individual Wood Thrush as the sampling unit. The Manly approach produces ratios of used versus available habitat taking into account the number of locations for each individual in determining confidence intervals. A manly ratio of 1 indicates no selectivity(Alldredge and Griswold 2006).

A one-way MANOVA was used to test for Wood Thrush selection of microhabitat variables between random vegetation points and vegetation points measured at Wood Thrush locations. One-way ANOVA was used for univariate comparisons, to identify individual microhabitat variables selected by Wood Thrushes(Clark et al. 1983).

1.2.9.3 Variable Selection and Model Building

Survival, transience, wanderer status, and home-range area were selected as response variables, referred to as habitat quality performance metrics since we're interested in how different habitat classes and microhabitat variables perform for wood thrushes. By definition high survival should be associated with higher habitat quality. Smaller home-ranges should also be associated with higher habitat quality, sense presumably these individuals are able to acquired sufficient resources in a smaller area. Following the same logic, since more movement incurs a time and energy cost in addition to increasing exposure to predators, transience and wandering may also be associated with lower quality habitat. However, a dearth of data on these behaviors, especially transience, prevents us from suggesting a supported relationship between habitat quality and movement, the benefits of which may be dependent on larger scale features of the geography or landscape (Winker et al. 1995, Johnson 2007).

Habitat quality performance metrics were analyzed relative to habitat class, microhabitat variables, demographics, and condition characteristics using mixed-effects models with site as a random-effect to account for non-independence of multiple birds within sites (Appendix A). Candidate habitat class variables included: the percent of Wood Thrush locations within coffee-vegetation edge zone, percent of locations within each major habitat class, elevation, and all interactions between habitat class and elevation. Elevation was included as an interaction because the same habitat classes were observed to vary noticeably along the gradient of elevations present within the study site. Candidate microhabitat variables included leaf litter depth, vertical structure counts within the ground cover and subcanopy strata, percent cover coffee, and basal area for small, medium, and large size classes. Survival, persistence, movement and home range area were also analyzed relative to fat scores, the residual weight condition index, and age class. A forward, stepwise model selection process using Akaike's Information Criterion (AIC) was conducted to identify models that best explained variation in each of the four habitat quality metrics. Models with AIC values within 2 of the best model were considered to be strongly supported (Burnham and Anderson 2002).

1.2.9.3.1 Survival & Transience

Survival model selection for each group of explanatory variables was conducted using R package COXME (version 2.2-5, Therneau 2012). The coxme function was selected to identify factors important to Wood Thrush survival using hazard ratios, exp(B) (Murray 2006). COXME was also used to model the relationship between explanatory variables and transience. In both survival and transient models, a positive parameter estimate indicates an increase in risk of mortality or of leaving the study site.

1.2.9.3.2 Home-range and Movement

The relationships between home-range area, wanderer status, and explanatory variables were modeled using Generalized Linear Mixed Models in R package ‘lme4’ (R Development Core Team 2015). A gamma distributed GLMM with logit link was selected to model 100% MCP home-range area, based on diagnostic quantile-quantile plots. Wanderer status was modeled using a binomial GLMM. Sedentary individuals were assigned a response variable value of zero while individuals displaying a wanderer pattern were assigned a one. Positive parameter estimates for the wanderer model indicate a positive correlation with a wanderer movement pattern.

1.3 Results

1.3.1 Capture and Condition

Eighty-two Wood Thrushes were captured during two seasons of banding across all banding sites and 46 individuals were radio-tagged (Table 1.4). Between 2 and 9 individuals were tagged at each site across years. 51% of captures were SYs, 44% were ASYs and 5% were not clearly classifiable. The proportion of SYs vs ASYs was similar for radio-marked individuals (50% and 44%, respectively). Fat scores ranged from 0 to 5 (avg=2) and from 0 to 4 for the radio tagged population. Condition indices ranged from -9.7 to 13.9, similar for the radio-tagged population (Table 1.5).

1.3.2 Telemetry Data

A total of 432 locations were recorded for tagged Wood Thrushes (Table 1.6). One-hundred-seventy locations were visual, 199 were obtained through triangulation, and the remainder were capture locations. We were unable to track all Wood Thrushes for the entire 6-

week tracking period (range: 1-70 days, mean=33 days). Between 2 and 17 points were recorded for each individual (avg=9.4 points). Individuals with fewer than 5 points either died (n=1) or left the study site (n=7) within the first few weeks of tracking.

1.3.3 Home-ranges

Home-range Estimated home-range areas for radio-tagged Wood Thrushes varied widely. 9.67 ha (mean = 1.24 ha) and 100% MCP values ranged from 0.02 ha to 20.7 ha (mean = 1.44 ha) (Table 1.6, Table 1.7). For further comparison with previous studies, the range of home-range values for sedentary individuals was LSCV (0.07 ha to 1.74 ha, mean = 0.61 ha), MCP (0.02 ha to 1.25 ha, mean = 0.37 ha) and the range of values for wandering individuals was LSCV (0.28 ha to 3.39 ha, mean = 1.7 ha), MCP (0.09 ha to 7.32 ha, mean = 1.84 ha). The 70% contour of the LSCV home-ranges produced two or more distinct centers of activity for 20 of the 38 ranges calculated.

1.3.4 Movement

Mean squared distance (MSD) values for tagged Wood Thrushes ranged from 131 to 38,519 (mean = 4,764). The maximum distance moved from the site of capture by each of 46 individuals ranged from 20 m to 1,215 m (Mean=181.7, Median=113.0, SD=223.02). Compared to bootstrapped permutations of movement distances and angles for each individual, 21 Wood Thrushes had MSD values below the 0.1 threshold of significance, indicating a sedentary movement patterns. Ten of the 21 sedentary individuals also demonstrated a significant Linear Index value. After transient individuals were removed from the pool, a total of 15 individuals showed wanderer movement patterns.

1.3.5 Habitat

1.3.5.1 Landscape Habitat Class Distribution

The landscape from which all exploratory and banding site locations as defined by a rectangular bounding box covered 36,744 ha. The primary habitat classes covering at least 5% of the total area are (in decreasing order of area) Pasture and Crops, Humid Secondary Vegetation, Sparse Pine, Humid Broadleaf Forest, Dense Pine, and Mixed Forest. Each class represents a range of habitat conditions on the ground, especially Pasture and Crops and Humid Secondary Vegetation classes. Pasture and Crop habitat can be devoid of trees and have only limited ground cover or can include scattered trees with sparse crop cover. Humid secondary vegetation can range from early secondary growth to habitat resembling a forest, especially one composed of deciduous oak species. Due to the canopy covering many coffee farms and the similarity of coffee plants to many humid broadleaf tree species, for the purposes of GIS classification, coffee farms were indistinguishable from other types of habitat in this region of Honduras. Sixty-eight hectares of coffee were manually digitized in areas where tagged Wood Thrushes were present. The distribution of habitat classes within these digitized area was 27.7% Humid Secondary Vegetation (Shade Coffee), 63.4% Humid Broadleaf Forest (Heavily Shaded Coffee), 3.6% Mixed Forest (Shade Coffee), and 5% Pasture, Crops, and Dispersed Trees (Open Coffee). The distribution of habitat classes was also associated with elevation. Humid Broadleaf forest was exclusively associated with higher elevation sites while its coffee counterpart, heavily shaded coffee, was mostly associated with lower elevations. Open habitats such as sparse pine and pasture were more likely to be found at lower elevations while humid secondary vegetation was scattered across the landscape (Figure 1.3).

1.3.5.2 Landscape Class Vegetation Composition

Exploratory vegetation measurements were made at 25 coffee sites, and 25 forest sites which can be used to characterize the vegetation associated with the major habitat classes present in the landscape. All surveyed coffee sites had at least partial canopy cover and forest was defined as any uncultivated area of at least 0.5 hectares with canopy cover. Humid broadleaf forest had the highest basal area of trees across all class, especially within the large tree size class. Tree species diversity was also twice that of any other class. The corresponding coffee class, heavily shaded coffee, also had the highest basal area values, twice that of other coffee classes. Coffee and forest classes universally different in vertical structure attributes, with forest having twice the density of touches at the ground cover level but coffee having two to three times more structure at the subcanopy level (Table 1.1).

1.3.5.3 Wood Thrush Vegetation Composition

We used a five-meter radius vegetation protocol to characterize the vegetation associated with mist nets (183), telemetry locations (119), and paired random locations (106), for a total of 408 points (Table A.5). The vegetation composition of habitat classes based on exploratory measures largely corresponded to the five-meter results, especially for the 106 random locations. Basal area remained highest for humid forest and heavily shaded coffee. Coffee sites had lower ground cover structure but higher or similar subcanopy vertical structure. Additional variables collected as part of the five-meter protocol found that small stem densities were three to four times higher forest sites, and leaf litter was deepest in secondary vegetation and corresponding shade-coffee sites.

1.3.5.4 Habitat Selection

Compositional analysis found a significant level of habitat selection among habitat classes located within the 95% contour of all Wood Thrush home-ranges (Lambda = 0.5, p=0.01). Wood Thrushes showed a significant level of preference for all coffee classes compared to their corresponding forest type. Manly selectivity ratios generated a more conservative picture of habitat selection. Coffee habitats were again preferred but all confidence intervals overlapped with zero with the exception of uncultivated, open habitat types. (Figure 1.3)

A comparison between vegetation characteristics measured at paired Wood Thrush and random location revealed a significant difference between the two groups (MANOVA Wilks Lambda = 0.86, F=1.64, p=0.04). Wood Thrushes selected habitat with higher levels of subcanopy structure (difference = 12.19, p = 0.001) and higher percent coffee cover (difference = 11, p = 0.02). They were also positively associated with large tree basal area (difference = 1.06, p = 0.19) (Table 1.2).

1.3.6 Modeling

1.3.6.1 Survival

The overall daily survival rate for all Wood Thrushes for all years was 0.995 (SE=0.001), which corresponds to a 0.471 probability of a Wood Thrush surviving the 150 day winter season. A total of 6 individuals died during the tracking period: 1 in 2012 and 5 in 2013. Predation was the likely cause of death for all individuals. Feathers were the only remains found at the sites of recovered transmitters, with the addition of cleanly severed legs at one location. Raptors appeared to be the most common predator based on the location and composition of remains at several sites. Four transmitters were recovered from forested or secondary vegetation with

20 meters of a coffee plot. One was located near a culvert just outside a coffee plot and one was located in a grassy area between humid forest and a stream.

Two habitat classes were associated with an increase in mortality risk in the best model: secondary vegetation (pct4, B = 66.53) and heavily shaded coffee (pct113, B = 18.7). Use of coffee-forest edge also increased risk (pctCFE, B = 54.46). Risk was reduced with increasing elevation (avgelev, B = -15.36), but a significant interaction reversed that association for heavily shaded coffee habitat (pct113*avgelev, B = 19.16).

The best microhabitat model as determined by AIC contained two fixed effects covariates: Ground Cover Structure (GCabc, B = 0.07), and basal area of medium trees (bAreaMP, B = 1.23). The estimates for all fixed effects were positive, indicating an increase in risk of mortality with increasing values. Decreased survival was associated with dense structure from the ground up to one meter in addition to medium sized trees with dbh between 9 and 27 cm.

Univariate mixed models for Age and condition did not improve the Null model (Tables 1.9 & 1.13).

1.3.6.2 Transience

The overall daily transience rate for all Wood Thrushes for all years was 0.996 (SE=0.001). The daily rate corresponds to a 0.548 probability of a Wood Thrush remaining within the site for an entire 150 day winter season, under the assumption that individuals are equally likely to make long-distance movements throughout the season. Eight individuals left the study area, four in each year. In many cases individuals began making pronounced directional movements prior to loss of signal, and in no case did an individual maintain a stable home-range and then suddenly disappear.

The final habitat class model for transience included three habitat classes: open pasture and crop land (pct7, B = 21.5), heavily shaded coffee (pct113, B = 9.78), and secondary vegetation (pct4, B = 5.75). All three classes were associated with an increased chance of transient behavior. Coffee-forest edge was also associated with increased risk (pctCFE, B = 6.79).

The best microhabitat model for transience included 3 variables: litter depth (litterAvgP, B = -1.07), small tree basal area (bAreaSP, B = -37.28), medium tree basal area (bAreaMP, B = -6.86), large tree basal area (bAreaLP, B = -1.74), ground cover coffee (gcCP, B = -12.48), and subcanopy coffee (scCP, B = -26.47). All parameters were negative, indicating that higher values that increase cover, structure, and foraging substrate decrease that chance of transience.

Wood Thrushes captured with high fat scores were significantly more likely to leave the site, while birds with higher condition scores were more likely to stay. Age was unrelated to transience (Table 1.10).

1.3.6.3 Movement

The null model was best for both habitat class and microhabitat models. Only the condition index improved the model out of all our explanatory variables groups (condition2, B = -0.3). Individuals with a higher condition index were more likely to be sedentary (Table 1.11).

1.3.6.4 Home-Range

The top habitat class model included three classes: humid forest (pct13, B = 2.03), shade coffee (pct104, B = -51.09), and open coffee (pct107, B = 3.72). Elevation (avgelev, B = 0.71) was also included in the final model. While higher elevation was associated with increased home-range area, two strong negative interactions highlighted an inverse relationship with shade coffee (pct104*avgelev, B = -103.02) and open coffee (pct107, B = -6.18). A positive interaction was observed between humid forest and elevation (pct13*avgelev, B = 0.88). Heavily shaded coffee appeared in a competitive model (pct113, B = -2.22; pct113*avgelev, B = 2.95).

The best microhabitat model explaining variation in home-range included two fixed effects: percent cover coffee (gcscCP, B = -2.28), and large trees (bAreaLP, B = -0.06). These two negatively associated variables are associated with smaller home-range areas.

High condition values were associated with smaller home-range areas (Table 1.12).

1.4 Discussion

1.4.3 Landscape in Context

Our study site is somewhat unusual both as a coffee growing region and as a site for the study of Wood Thrushes. Coffee is typically not grown below 900 m and on the wintering grounds Wood Thrushes are typically associated with lower elevation rainforest. Below approximately 1200 m virtually all the remaining natural habitat types such as pine and pine-oak forest are unsuitable for Wood Thrushes, based on two years of point count results. Individuals were only detected at lower elevation within shade coffee farms. Although it is possible that riparian corridors in the same area may have once provided suitable Wood Thrush habitat, today that habitat type has been entirely replaced by coffee or other forms of agriculture within our study site. This observation suggests that at low elevation shade coffee provides habitat that would otherwise be unsuitable for Wood Thrushes.

At higher elevations, more commonly associated with the production of high quality coffee, the context of coffee in the landscape changes considerably. At these elevations much of the remaining area of uncultivated habitat is suitable for Wood Thrushes. We are especially interested in the identification of habitat characteristics associated with higher habitat quality at higher elevation since the expansion of coffee production threatens to remove remaining fragments.

Regardless of elevation, high numbers of Wood Thrushes were detected and captured at both low and high elevation sites. Coupled with the distance of our study site from the published winter range for the Wood Thrush, our results suggest that the remaining winter habitats within that range may be over-saturated. While, our over-saturation hypothesis cannot be tested with our existing study structure, we can identify what features are most favorable for the Wood Thrush in this landscape and how similar habitat may be influencing the general population.

1.4.2 Demographics Comparisons

Despite the fact that this study took place in a highly disturbed agricultural region of Honduras, the survival rates we observed were similar to those reported for Wood Thrush telemetry studies within primary forest in Mexico and Costa Rica by Rappole et al. (1989) and Roberts(2007) (0.996 and 0.994, respectively). Our survival rates are far higher than those derived by Conway et al. (1995) based on capture-recapture data from standardized mist-netting for either mature or disturbed habitat. However, since home-range size and movements appear to differ in relation to habitat disturbance, comparisons of estimates based on capture-recapture models are likely to be confounded with habitat-specific movement patterns(Rappole et al. 1989, Ruiz-Gutierrez et al. 2016). The fact that survival rates in the mixed habitat of our study are similar to survival rates reported elsewhere in forest may be partially attributed to the archaic coffee cultivation methods employed, as well as a long legacy of coffee cultivation at our study sites. Coffee farms in this area are best classified as “rustic coffee”, a system in which native trees are retained and allowed to grow, and which are characterized by diverse forest structure, characteristics that have become more developed over time. Notably, these attributes are more similar to native forest than the commercial polyculture, in which coffee is planted under non-native shade species, which is currently expanding and threatening forests in the region (Jha et al. 2014).

Although winter survival is the most informative metric for assessing habitat quality it is difficult to estimate; overwinter persistence (sustained occupancy of a site) may also reflect habitat quality in this sense because individuals that survive should be less inclined to abandon a high quality site (Holmes and Sherry 1992). In support of this notion, Rappole et al.(1989) reported that wandering individuals that typically occupied secondary habitats were more likely to disappear from the study site than sedentary individuals in primary habitat. Similarly, Roberts(2007) reported a higher incidence of disappearance of individuals from fragments compared to continuous forest. Our study is the third telemetry study to observe the disappearance of individuals from the study site, individuals that I label transients. As transients were associated with more disturbed habitats in previous studies, their prevalence in this study may point to an unusually fragmented and unsuitable landscape.

Similar to transient individuals, wanderers also avoided sustained occupancy of a well-defined home-range during the tracking period. However, compared to long-distance movements, wanders make more gradual, local movements often stopping for days or weeks before moving again. This behavior is well documented and has been associated with positive trade-offs compared to the investments associated with defending a territory(Brown and Long 2007). Forty-four percent of tagged Wood Thrush were identified as wanderers (movements of > 150m from capture) by Rappole et al(1989). By the same criteria, 50% of individuals tracked in this study would have been considered wanderers.

As with overwinter persistence within a relatively large area, maintenance of well-defined home-ranges may carry similar information about the quality of the habitat within which they are situated. Rappole et al. (1989) found that sedentary individuals, those moving less than 150 m from capture location, were found almost exclusively in humid forest while wandering individuals also used secondary and riparian vegetation. Rappole et al. documented that sedentary individuals actively defended territories against conspecifics. Roberts (2007) reported different rates of persistence for primary forest (95%), large fragments (100%), and small fragments (60%). We found that 47.7% of Wood Thrushes were sedentary, limiting their movements to a relatively small area, typically around a single center of activity. The territorial interactions described by Rappole et al. (1989) including chases, vocalizations and posturing, were also commonly observed at our study site (pers. obs.).

Since our home-range estimates include both sedentary and wandering Wood Thrushes, this metric should capture a similar range of habitat use behaviors as the studies by Rappole et al (1989) and Roberts (2007) who also worked in a range of habitats. A comparison of our results with those of the two previous studies required re-calculation of home-range using only sedentary individuals and a modified estimator. The home-range areas observed in this study were similar: 0.02 ha to 0.66 ha versus Rappole et al. 0.12 ha and 1.03 ha; 0.09 ha to 2.00 ha versus Roberts .2 ha to 2.8 ha.

Although high fat loads have also been interpreted as indicators of habitat quality in wintering migrants, our findings as well as those of other researchers suggest caution in the application of this metric in this context. In our study, high subcutaneous fat scores were commonly associated with transient individuals. Though the relationship was not significant in the final model, smaller home-ranges were also associated with moderate fat scores (Fat=2). Winker et al. (1990) documented significantly higher fat levels in wandering Wood Thrushes in

Veracruz compared to sedentary ones, and reasoned that high fat scores reflect the need to maintain energy reserves under condition of uncertain food availability. Additional fat storage is potentially maladaptive in tropical habitats due to increased exposure to predators while foraging for extra calories and reduced capacity to escape predators (Kullberg et al. 1996, Katti and Price 1999). Extended periods of rain and brief periods of cold can reduce foraging opportunities even during tropical winters, resulting in some fat deposition in even sedentary individuals. Our condition index was negatively correlated with transience, home-range area, and wanderer status, suggesting that it succeeds at improving upon simple fat scores as an index of condition(Labocha and Hayes 2011).

1.4.3 Habitat Selection & Performance Metrics

The results of our habitat class and microhabitat selection analysis found that Wood Thrushes preferred shade coffee habitat, avoided more open habitats, and selected areas with high levels of subcanopy structure. Given the large areas of unsuitable habitat present within the study landscape, the preference for coffee habitat classes is not surprising, especially at lower elevation where shade coffee farms are islands of suitable habitat. At higher elevation a preference for shade coffee over humid broadleaf forest was surprising. The observed preference may be related to a clear structural difference between coffee and other habitat types with humid forest and secondary vegetation having much higher levels of ground cover structure and lower levels of subcanopy than their coffee counterparts. Overlap between the selected microhabitat variables (coffee and subcanopy structure) and selected habitat classes reinforce the assertion that vegetation structure is a critical component of Wood Thrush habitat selection.

As ground-based foragers, Wood Thrush need an open understory, preferably with a layer of humid leaf litter(Petit et al. 1992). An open understory may provide the reduced structure required for foraging while a developed subcanopy may provide protection from aerial predators, supplement the leaf litter layer, and provide shade to reduce the growth of understory vegetation and maintain moisture levels. These proposed effects of structure are supported by our performance models. Higher mortality was associated with increased understory structure and with edge habitat. Since the majority of our mortalities were attributed to raptors and all remains were located within the edge zone, ground cover and more open edge areas may increase Wood Thrush availability to predators. Increased leaf litter, a key foraging substrate, was associated with reduced levels of transience.

Trees were another important component in several performance models. Across the landscape humid forest had the highest basal area of trees and the highest diversity of species. Secondary vegetation and heavily shaded coffee also had higher tree basal areas. In our models trees played a competing role with higher basal areas being associated with less transience and smaller home-ranges, but also being associated with increased mortality. Trees provide shade to help maintain moisture levels and generate leaf litter and they can also provide fruit, an alternative food source for Wood Thrushes exploited during the driest part of the winter (pers. obs., Blake et al. 2008). The survival model suggests that trees may also increase the presence of aerial predators.

Elevation was another important contributor to our final models. While complex, the spatial distribution of habitat classes is largely determined by use, moisture, and soil, each interacting with elevation. Moisture is perhaps the most important of these, driving understory anthropod abundance (Şekercioğlu et al. 2002) and promoting a healthy humid broadleaf canopy. Based on the distribution of humid habitat classes, elevation following an increasing moisture gradient within our study landscape. In addition to increasingly dry conditions at lower elevations, conditions also become increasingly dry during the course of the winter season throughout much of northern central America. Lower mortality was associated with higher elevation and the strongest habitat class relationships correlated with smaller home-ranges were associated with higher elevations.

Coffee, both shaded and heavily shaded coffee classes and percent coffee cover appeared frequently in our models, but the overall relationship was complex. Heavily shaded coffee was associated with higher mortality, the effect was strengthened with higher elevation. This interaction suggests that the benefits of shade coffee may vary depending on the surrounding landscape which changes dramatically in our study system with elevation. At higher elevations a variety of suitable habitats lead Wood Thrushes to frequently move between coffee and forested habitats, resulting in more edge use. Home-range models reveled strong connections with coffee across both habitat class and microhabitat. Overall, where Wood Thrushes used more coffee, home-range areas were lower, but depended on elevation.

With sedentary individuals maintaining small territories and many of our habitat quality metrics falling within the range of similar studies executed in primary forest, our results suggest that some high quality habitats are present within our study area. Specific vegetation characteristics such as subcanopy structure and elevation quantify tangible differences between low and high quality habitat, but how do those translate into greater patterns of coffee cultivation? Perfecto et al. (1996) found that understory species were less common in farms with increased pruning and a less diverse vegetation. Greenberg et al.(1997) found that understory species like the Wood Thrush were nearly absent from all commercial shade or sun coffee plantations, though some were detected in in farms dominated by Inga trees. Many other studies highlight the structural and compositional habitat characteristics that improve species richness and include understory insectivores (Perfecto et al. 2003, Mas and Dietsch 2004, Leyequién et al. 2010). Farms with extensive or regularly pruned trees and coffee plants, as well as commercial farms lacking diverse canopies and natural vegetation, represent low quality or incompatible habitat for Wood Thrushes. These cultivation practices are known to reduce habitat suitability for understory insectivores, and based on the results of this study they would reduce the developed subcanopy and open understory attributes identified by this study as promoting high quality habitat.

A final point of discussion relates to the importance of wanderers and transients both in this study and the study of Wood Thrush winter ecology. With the exception of a significant relationship found between condition and wanderer status, all candidate variables failed to improve upon the null model. Perhaps the most reasonable explanation for this finding, is that an ecologically relevant criterion for determining wandering status was not employed by this study. Despite frequent mention of wanderers in the literature, no effective metric for identifying them has been agreed upon. Until the wandering behavior of this species is better understood we cannot pursue it as a meaningful metric of habitat quality. Transients, however, are easily identified yet difficult to study with VHF telemetry due to sudden long-distance movements that take them out of receiver range. While long assumed to be a minority of the wintering population, recent archival GPS results suggest that in some habitats the majority of individuals are transients and more sedentary individuals reside in disturbed habitats (pers. comm. Calandra Stanley). This tentative finding would run contrary to our characterization of Wood Thrushes as a primarily sedentary species on the wintering grounds and to previously published work suggesting that sedentary individuals are associated with less disturbed habitats. High numbers of transients would have important conservation implications especially in light of the overlap between our survival and transient models. Those models reveal that transients are using the habitats associated with significantly higher levels of mortality risk in addition to open habitat avoided by most individuals. Since these individuals cannot be tracked using telemetry general estimates of survival may be overly optimistic, transforming highly fragmented landscapes like ours into winter sinks. In addition, high densities of transients complicate our ability to estimate abundance. Abundance and survival are statistics vital to effective full annual cycle modeling required for conservation planning.

1.5 Conclusion

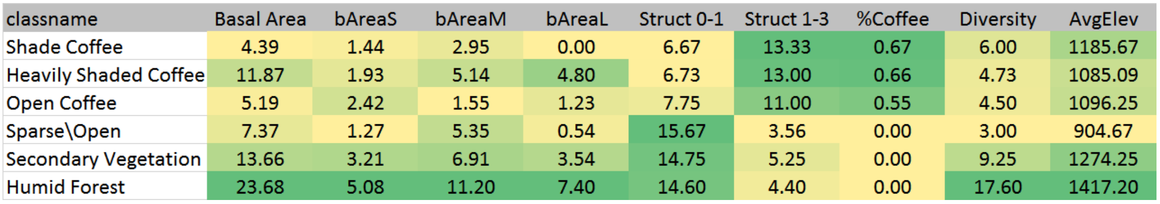
In the preceding results and discussion, I have developed three major outcomes useful for future research and conservation planning. First, I have quantified key demographic parameters (i.e. survival, home-range size, transience, and wanderer-status) across a highly disturbed coffee-growing landscape, and I compared these findings with the range of values indicated by previous studies. Second, I have evaluated habitat quality across this system by modelling relationships between condition and persistence metrics by quantifying the physical condition of a sample of 46 radio-tagged Wood Thrushes, values known to vary with habitat quality in both Wood Thrush and other migratory species. Finally, I have identified other ecologically relevant habitat variables that also vary with the same metrics of habitat quality.

Several indicators suggest poor quality habitat across the study landscape: The distribution of Wood Thrushes; the baseline metrics of survival; the absence of individuals from many habitat classes; and higher mortality risk associated with common habitat types, particularly edge and secondary vegetation. The apparent preference for coffee over non-coffee vegetation, even at higher elevations, may relate to a generally disturbed landscape, with more edge and more understory structure in all but rustic coffee farms. While coffee appears to provide islands of suitable habitat at lower elevation, high capture rates in those areas coupled with the distance from the published winter range suggest that winter habitat is oversaturated. If additional high quality habitat is lost in the future, more individuals may be forced into lower quality habitat. Lastly, increased mortality associated with heavily shaded coffee within the more suitable high elevation landscape suggests that highly fragmented landscapes may reduce the local-level quality of shade-coffee habitat, especially for non-sedentary individuals.

These results have important implications, particularly as coffee cultivation expands into more remote areas and traditional farms are replaced by large scale operations. My study sites included small-scale, traditional shade coffee farms across a wide gradient of elevations and habitat types. Along the spectrum of all coffee cultivation methods these study sites have a comparatively high wildlife conservation value. Due to the high level of structural and compositional variation observed both within and amongst sites, no single habitat type or cultivation method can be identified as promoting the highest quality habitat for Wood Thrushes. However, each variable in my models can be used to evaluate the conservation value and likely consequences of future coffee cultivation practices. The variables in my models associated with higher habitat quality are found primarily within forest and traditionally cultivated coffee. As cultivation expands and intensifies, forest is lost and structural and compositional diversity disappear from the landscape. My results highlight the critical need to maintain these elements of structural diversity across large areas, yet market forces often support their reduction (Rappole et al. 2003). For example, market pressures resulting from increasing global demand for coffee alongside spreading diseases such as coffee rust promote the removal of traditional shade canopies and the destruction of remaining fragments of intact forest. Since broadleaf forest is known to be high quality habitat for Wood Thrushes and many other resident understory insectivores, in addition to the irreplaceable ecosystem services offered by forests, setting aside larger blocks forested habitat within coffee landscapes is essential to maintaining their conservation value (Chandler et al. 2013).

Another equally important implication of this study is that it highlights several gaps in current scientific knowledge about some of the most essential questions of Wood Thrush winter ecology. For example, where do Wood Thrushes winter? This study identifies suitable Wood Thrush habitat for large numbers of Wood Thrushes far outside the published range. How common are non-sedentary movement behaviors on the wintering grounds? Our failure to identify models that relate habitat quality to wandering status highlight the need for an ecologically relevant criterion for identifying wandering individuals. A complete lack of data on transient individuals requires urgent attention. What is the over-winter survival rate for the Wood Thrush? Our daily survival rate of 0.995 is already low for population maintenance. However, our results suggest that transients are at much higher risk of morality, making commonly accepted survival rates overly optimistic. Effective conservation planning requires a deeper understanding of Wood Thrush winter ecology and more accurate estimates of the vital statistics informing conservation models. With the emergence of new technologies such as miniaturized archival GPS tags and coded vhf nano-tags, those needs will hopefully be addressed before too much critical habitat is lost.

Table 1. 1. Landscape-level vegetation measurement summary. The yellow to green color gradient shows low to high values across habitat classes.



classname	Basal Area	bAreaS	bAreaM	bAreaL	Struct 0-1	Struct 1-3	%Coffee	Diversity	AvgElev
Shade Coffee	4.39	1.44	2.95	0.00	6.67	13.33	0.67	6.00	1185.67
Heavily Shaded Coffee	11.87	1.93	5.14	4.80	6.73	13.00	0.66	4.73	1085.09
Open Coffee	5.19	2.42	1.55	1.23	7.75	11.00	0.55	4.50	1096.25
Sparse\Open	7.37	1.27	5.35	0.54	15.67	3.56	0.00	3.00	904.67
Secondary Vegetation	13.66	3.21	6.91	3.54	14.75	5.25	0.00	9.25	1274.25
Humid Forest	23.68	5.08	11.20	7.40	14.60	4.40	0.00	17.60	1417.20

Table 1. 2. Microhabitat selection results generated by ANOVA. Columns from left to right: difference between Wood Thrush and random locations, lower confidence interval, upper confidence interval, p-value.

	W - R diff	lwr	upr	Padj
bAreaS	0.04	-0.15	0.22	0.88
bAreaM	0.18	-0.41	0.77	0.76
bAreaL	1.06	-0.37	2.49	0.19
sStemStd	9.08	-26.15	44.32	0.82
litterAvg	0.09	-1.88	2.05	0.99
GCabc	-3.43	-11.45	4.59	0.57
SCde	12.19	4.19	20.20	**0.00**
gcC	0.00	-0.02	0.02	0.97
scC	0.11	0.02	0.21	**0.02**

Table 1. 3. Description and capture statistics for all 12 banding sites. Type F sites are paired forest sites that were combined with their adjacent coffee sites for analysis.

ID	Type	Name	Forest	Elevation	2012 caps	2012 trans	2013 caps	2013 trans	Description
5	C	Elias	Dry	910	0	0	9	2	Coffee surrounded by a pine-oak matrix
12	C	Ovidio	None	1044	5	5	5	2	Rustic surrounded by Coffee and fields
24	C	Maria	None	1231	2	2	2	2	More open coffee with a few remaining slivers of forest
27	C	Vincente	Mixed	1154	5	2	10	2	Rustic Coffee with small to large patches of veg and forest
35	C	Quebrada Larga	Mixed	1017	2	2	3	2	Shade coffee with high canopy
47	C	Hincho	Dry	846	0	0	4	2	Coffee with limited dry forest nearby
15	C	Allan	Humid	1270	6	3	7	6	Rustic coffee surrounded by various stages of secondary growth & forest
30	F	Allan		1196	2	2	2	2	Humid secondary forest along stream
19	C	Mario	Humid	1141	1	1	3	2	Rustic Coffee bordered by fields and forest
43	F	Mario		1174	1	1	3	1	Fragment of humid forest
42	C	Melvin	Mixed	879	1	1	9	2	Rustic coffee, drier forest nearby with exception of reclaimed coffee
57	F	Melvin		898	0	0	2	2	Mostly coffee reclaimed by forest

Table 1. 4. Capture and condition statistics for 46 Wood Thrushes. Data were collected during the 2012 and 2013 banding seasons in the Department of Yoro, Honduras. Dashes indicated undetermined or missing data.

WOTHID	Site	Tag Date	Age	Fat	Weight	Tail	condition
W04	24	23-Jan-13	SY	1	50.31	72	0.79
W14-1	24	23-Jan-12	SY	3	-	64	-
W18	42	01-Feb-13	ASY	4	55.39	71	5.66
W18-1	15	06-Jan-12	SY	1	44.1	65	-4.37
W20	15	14-Jan-13	ASY	0	48.04	72	-2.09
W22	5	25-Jan-13	SY	3	57.01	69	5.63
W22-1	42	20-Jan-12	SY	1	49.58	73	-0.97
W23	24	17-Jan-13	ASY	2	57.37	73	5.16
W25	15	16-Jan-13	ASY	2	48.64	70	-0.25
W26	42	01-Feb-13	ASY	3	53.38	77	2.82
W26-1	24	17-Jan-12	ASY	2	57.37	73	5.16
W27	5	25-Jan-13	SY	4	55.38	70	5.24
W27-1	19	30-Jan-12	ASY	3	51.79	71	1.23
W28-1	15	28-Jan-12	ASY	4	54.67	68	4.53
W29	19	05-Feb-13	ASY	2	52.35	73	0.55
W50-1	27	09-Feb-12	-	0	46.94	64	-1.53
W51-1	12	05-Feb-12	SY	1	42.83	68	-7.3
W54-1	15	07-Jan-12	ASY	2	47.82	69	-1.9
W56-1	27	08-Feb-12	SY	1	40.13	68	-10
W58-1	35	04-Mar-12	ASY	4	51.4	73	-0.39
W60	47	08-Feb-13	SY	2	52.45	68	4.38
W61	15	10-Jan-13	-	3	53.05	70.3	0.84
W62	15	10-Jan-13	SY	2	59.9	66	12.66
W62-1	35	04-Mar-12	ASY	4	53.5	74	0.05
W63	42	28-Jan-13	SY	4	51.89	67	3.41
W63-1	15	16-Feb-12	SY	1	44.85	71	-5.7
W64	15	11-Jan-13	ASY	1	48.7	75	-2.67
W64-1	19	12-Feb-12	SY	3	47.2	71	-2.52
W65	15	11-Jan-13	ASY	1	47.25	71	-1.85
W65-1	15	19-Feb-12	SY	0	49.95	70	-1.01
W66	19	04-Feb-13	ASY	1	57.76	72	6.79
W66-1	12	05-Feb-12	SY	2	41.86	67	-5.79
W67-1	12	04-Feb-12	SY	2	50.36	72	-1.01
W68	42	28-Jan-13	ASY	3	53.79	76	2.82
W68-1	12	05-Feb-12	SY	3	53.26	76	-0.6
W69	19	05-Feb-13	SY	1	49.32	68	-0.4

W69-1	12	25-Jan-12	-	4	47.15	74	-3.81
W72	35	22-Feb-13	ASY	1	51.33	75	-1.7
W73	15	11-Jan-13	SY	1	44.81	65.5	-3.25
W75	35	21-Feb-13	SY	1	50.99	75	0.02
W77	27	14-Feb-13	ASY	0	47.37	77	-3.59
W93	27	14-Feb-13	SY	1	47.07	66	-2.65
WHI	47	08-Feb-13	ASY	4	51.44	70	1.3
WLO	15	11-Jan-13	SY	3	48.8	68	-0.09
WOV	12	11-Feb-13	SY	1	50	70	-0.96
WRG	12	11-Feb-13	ASY	1	47.51	76	-2.62

Table 1. 5. Summary statistics of condition variables for 46 radio-tagged Wood Thrushes.

Variable	**Min**	**Max**	**Mean**	**Median**	**SD**
Fat Score	0	4	2.02	2	1.27
Weight	40.13	59.9	50.31	50.15	8.68
Tail Length	64	77	70.73	71	3.49
Condition Index	-10	12.66	-0.10	-0.5	4.07

Table 1. 6. Distribution of locations obtained through mist net captures and radio telemetry for 46 individual Wood Thrushes. Individuals that left the study site or died during the study are indicated.

WOTHID	**Homing**	**Triangulation**	**Capture**	**Re-capture**	**Total**	**Outcome**
WLO	0	0	1	0	1	Lost
W66-1	1	1	1	0	3	Lost
W22	2	1	1	0	4	Lost
W27	1	1	1	1	4	Lost
W51-1	3	0	1	0	4	Lost
W64-1	2	1	1	0	4	Dead
W69-1	3	0	1	0	4	Lost
WHI	2	0	1	1	4	Lost
W69	0	3	1	1	5	Dead
W72	1	1	1	2	5	Dead
W14-1	1	4	1	0	6	
W77	2	3	1	0	6	
W93	3	2	1	0	6	
WRG	3	2	1	0	6	
W20	2	3	1	1	7	Dead
W58-1	3	3	1	0	7	
W60	4	2	1	0	7	

WOV	2	3	1	1	7	
W26	4	3	1	0	8	Dead
W28-1	4	4	0	0	8	Lost
W75	1	4	1	2	8	
W62-1	4	4	1	0	9	
W63	4	4	1	0	9	
W66	3	6	1	0	10	
W04	6	4	1	0	11	
W18	8	2	1	0	11	
W22-1	10	0	1	0	11	
W23	4	6	1	0	11	
W29	6	4	1	0	11	
W50-1	6	4	1	0	11	
W68	6	4	1	0	11	
W27-1	10	0	1	1	12	
W56-1	9	2	1	0	12	
W68-1	11	0	1	0	12	
W65	4	7	1	1	13	
W54-1	2	10	1	1	14	
W64	3	10	1	0	14	
W67-1	3	10	1	0	14	
W73	4	8	1	1	14	
W26-1	7	7	1	0	15	
W61	2	11	1	1	15	Dead
W62	3	10	1	1	15	
W63-1	3	10	1	1	15	
W65-1	1	13	1	0	15	
W25	4	11	1	0	16	
W18-1	3	11	1	2	17	
Totals	**170**	**199**	**45**	**18**	**432**	

Table 1. 7. Summary statistics of home-range areas estimated using 100% minimum convex polygon, 70% LSCV kernel, and 95% LSCV kernel estimators.

	Min	**Max**	**Mean**	**Median**	**SD**
MCP 100	0.02	20.72	1.44	0.4	3.514257
LSCV70	0.07	9.67	1.24	0.7	1.655295
LSCV95	0.19	23.99	2.92	1.63	4.016217

Table 1. 8. Estimated individual home-range areas in hectares in ascending order for each of three estimators.

WOTHID	MCP100	LSCV70	LSCV95
W64	0.05	0.08	0.19
W93	0.02	0.14	0.32
W72	0.05	0.17	0.42
W18-1	0.25	0.15	0.43
W68	0.31	0.24	0.65
W62-1	0.09	0.28	0.67
W62	0.44	0.26	0.67
W60	0.08	0.32	0.77
W61	0.37	0.37	0.82
W26	0.21	0.39	0.88
W25	0.34	0.41	1.09
W26-1	0.65	0.47	1.09
W23	0.37	0.48	1.10
W66	0.21	0.48	1.11
W20	0.19	0.54	1.19
W27-1	0.89	0.49	1.20
W04	0.27	0.44	1.26
W67-1	0.67	0.65	1.50
W18	0.36	0.73	1.59
WRG	0.29	0.68	1.68
W54-1	0.41	0.92	2.01
W29	0.40	0.92	2.25
W50-1	1.69	1.10	2.42
W68-1	1.57	0.90	2.48
W22-1	1.00	0.98	2.60
W69	0.23	1.22	2.77
W56-1	1.51	1.35	3.10
W75	0.33	1.36	3.20
W63-1	3.39	1.45	3.58
W63	0.45	1.58	3.68
W65-1	1.25	1.75	3.72
W65	7.33	1.68	4.20
W58-1	1.01	2.69	5.82
W14-1	0.56	2.50	6.15
W77	0.76	2.91	6.44
W73	4.98	2.98	6.86
WOV	1.04	3.39	7.21
W28-1	20.72	9.67	24.00

Table 1. 9. Output of Survival model. The best habitat model, additional variables added to created alternate models < 2 AICc greater, and the best condition model are included. The estimate listed is the coefficient for fixed effects and the standard deviation of variation amongst sites for the random effect.

Survival: Best Habitat Class Model

Parameter	Type	Estimate	exp(B)	SE	z	p
pctCFE	Fixed	54.46	4.50E+23	35.42	1.54	0.12
pct4	Fixed	66.53	7.84E+28	39.11	1.7	0.08
pct113	Fixed	18.7	1.34E+08	12.91	1.45	0.15
avgelev	Fixed	-15.36	2.11E-07	10.45	-1.47	0.14
pct113*avgelev	Fixed	19.16	2.10E+08	15.44	1.24	0.21
Site	Random	11.42				

Survival: Best Microhabitat Model

Parameter	Type	Estimate	exp(B)	SE	z	p
GCabc	Fixed	0.07	1.07	0.04	1.73	0.08
bAreaMP	Fixed	1.23	3.42	0.53	2.29	0.02
Site	Random	0.44				

Survival: Best Condition Model

Parameter	Estimate	exp(B)	SE	z	p
NULL					

Survival: Alternate Condition Model

Parameter	Estimate	exp(B)	SE	z	p
NULL					

Survival: Best Age Model

Parameter	Estimate	exp(B)	SE	z	p
NULL					

Table 1. 10. Output of Site Fidelity model. The best habitat model, additional variables added to created alternate models < 2 AICc greater, and the best condition model are included. The estimate listed is the coefficient for fixed effects and the standard deviation of variation amongst sites for the random effect.

Transience: Best Habitat Class Model

Parameter	**Type**	**Estimate**	**exp(B)**	**SE**	**z**	**p**
pctCFE	Fixed	6.79	8.96E+02	2.33	2.92	0.003
pct4	Fixed	5.75	3.17E+02	3.42	1.68	0.09
pct113	Fixed	9.78	1.77E+04	2.2	2.22	0.02
pct7	Fixed	21.5	2.17E+09	8.49	2.53	0.01
Site	Random	3.8				

Transience: Best Microhabitat Model

Parameter	**Type**	**Estimate**	**exp(B)**	**SE**	**z**	**p**
bAreaSP	Fixed	-37.28	6.39E-17	13.73	-2.72	0.006
bAreaMP	Fixed	-6.86	1.04E-03	2.81	-2.44	0.01
litterAvgP	Fixed	-1.07	3.40E-01	0.62	-1.71	0.08
Site	Random	11.28				

Transience: Best Condition Model

Parameter		**Estimate**	**exp(B)**	**SE**	**z**	**p**
condition2	Fixed	-0.206	0.81	0.13	-1.55	0.12
Fat 2:1	Fixed	-1.49	0.22	1.53	-0.97	0.33
Fat 2:3	Fixed	1	2.73	1.25	0.8	0.42
Fat 2:4	Fixed	2.35	10.57	1.2	1.96	0.05
Site	Random	0.8				

Transience: Best Age Model

Parameter	**Estimate**	**exp(B)**	**SE**	**z**	**p**
NULL					

Table 1. 11. Output of floater status model. The best model, additional variables added to created alternate models < 2 AICc greater, and the best condition model are included. The estimate listed is the coefficient for fixed effects and the standard deviation of variation amongst sites for the random effect.

Wanderer: Best Habitat Class Model

Parameter	Type	Estimate	SE	z	p
NULL					

Wanderer: Best Microhabitat Model

Parameter	Type	Estimate	SE	z	p
NULL					

Wanderer: Best Condition Model

Parameter		Estimate	SE	t	p
Condition2	Fixed	-0.3	0.03	-2.65	0.007
Site	Random	0			

Wanderer: Best Age Model

Parameter		Estimate	SE	z	p
NULL					

Table 1. 12. Output of Home-range model. The best model, additional variables added to created alternate models < 2 AICc greater, and the best condition model are included. The estimate listed is the coefficient for fixed effects and the standard deviation of variation amongst sites for the random effect.

Home-range: Best Habitat Class Model

Parameter	Type	Estimate	SE	z	p
pct13	Fixed	2.03	0.79	2.55	0.01
pct104	Fixed	-51.49	88.64	-0.58	0.56
pct107	Fixed	3.72	2.47	1.5	0.13
avgelev	Fixed	0.71	0.25	2.85	0.004
pct107*avgelev	Fixed	-6.18	3.69	-1.67	0.09
pct104*avgelev	Fixed	-103.02	90.97	-1.13	0.25
pct13*avgelev	Fixed	0.88	0.64	1.36	0.17
Site	Random	0.00E+00			

Home-range: Competative Habitat Class Model variables

Parameter	Type	Estimate	SE	z	p
pct113	Fixed	-2.22	1.24	-1.79	0.07

pct113*avgelev	Fixed	2.95	1.21	2.42	0.01
Site	Random	0.00E+00			

Home-Range: Best Microhabitat Model

Parameter	Type	Estimate	SE	z	p
gcscCP	Fixed	-2.28	0.73	-3.11	0.001
bAreaLP	Fixed	-0.06	0.03	-1.67	0.09
Site	Random	8.05E-10			

Home-Range: Best Condition Model

Parameter		Estimate	SE	z	p
condition2	Fixed	-0.11	0.04	-2.87	0.004
Site	Random	0.09			

Home-Range: Best Age Model

Parameter	Estimate	SE	z	p
NULL				

Table 1. 13. Matrix of significant variables from all models. Values in red indicate that increasing values of the predictor reduces metrics associated with habitat quality. Bolded values appeared in the bests models and non-bold variables appeared in secondary models.

	Survival	Transient	HR	Wander
%Edge	**54.46**	**6.79**		
%Secondary	**66.53**	**5.75**		
%Humid Forest			**2.03**	
%Shade Coffee			**-51.49**	
%Heavily Shaded	**18.7**	**9.78**	-2.22	
%Open Coffee			**3.72**	
%Pasture/Open		**21.5**		
Elevation	**-15.36**		**0.71**	
2ndary*elev			**-103.02**	
Humid*Elev	**19.16**		**0.88**	
Open*Elev			**-6.18**	
Heavilyshade*Elev			2.95	
NULL				**X**
	Survival	Transient	HR	Wander
GCabc	**0.07**			
SCde				

litterAvgP		**-1.07**		
gcscCP			**-2.28**	
bAreaSP		**-37.28**		
bAreaMP	**1.23**	**-6.86**		
bAreaLP			**-0.06**	
NULL				**X**
Condition	Survival	Transient	HR	Wander
condition2		**-0.206**	**-0.11**	**-0.3**
Fat 2:1		**-1.49**		
Fat 2:3		**1**		
Fat 2:4		**2.35**		
NULL	**X**			
Age	Survival	Transient	HR	Sed_Wan
Age SY:ASY				
NULL	**X**	**X**	**X**	**X**

Figure 1. 1. Maps of banding sites distributed across the survey area depicting the eastern boundary of Pico Pijol National Park, minor roads used to reach sites and a gradient of elevation.

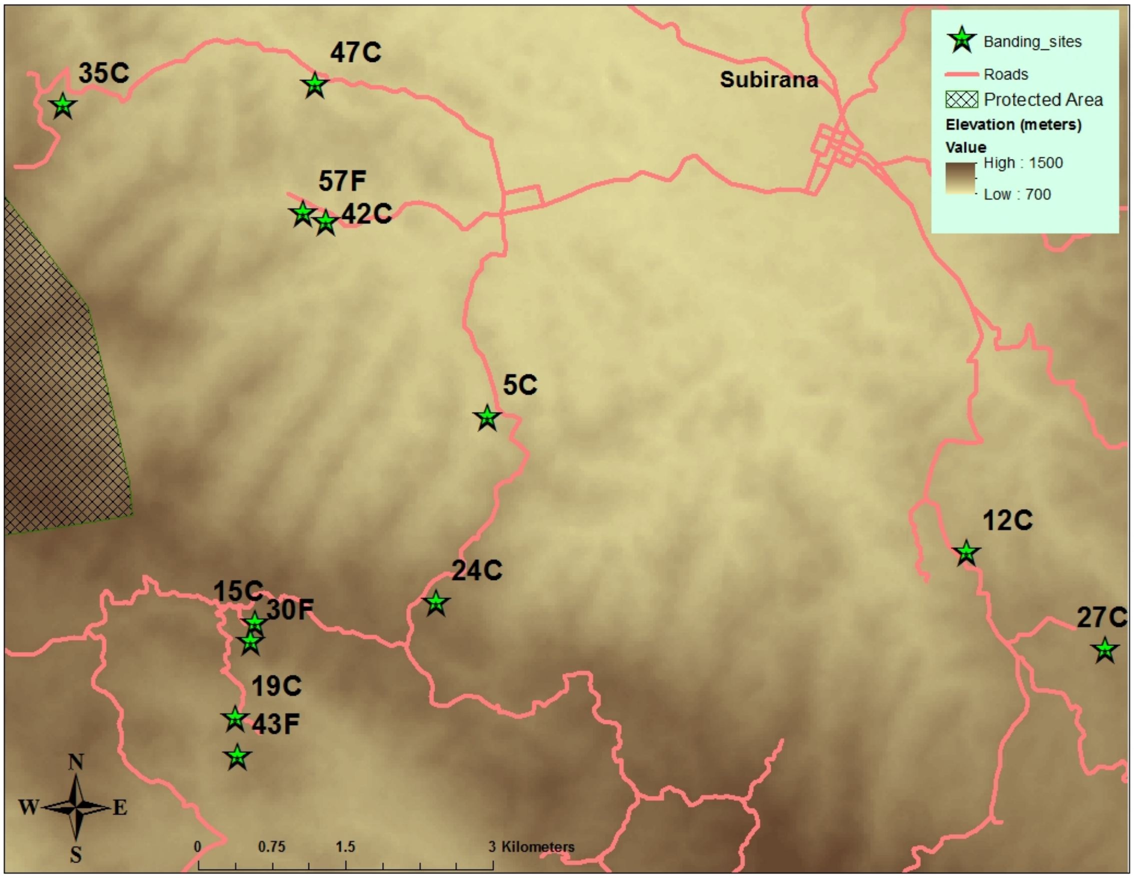


Figure 1. 2. Manly Selectivity Ratios, a value of 1 indicates no selection

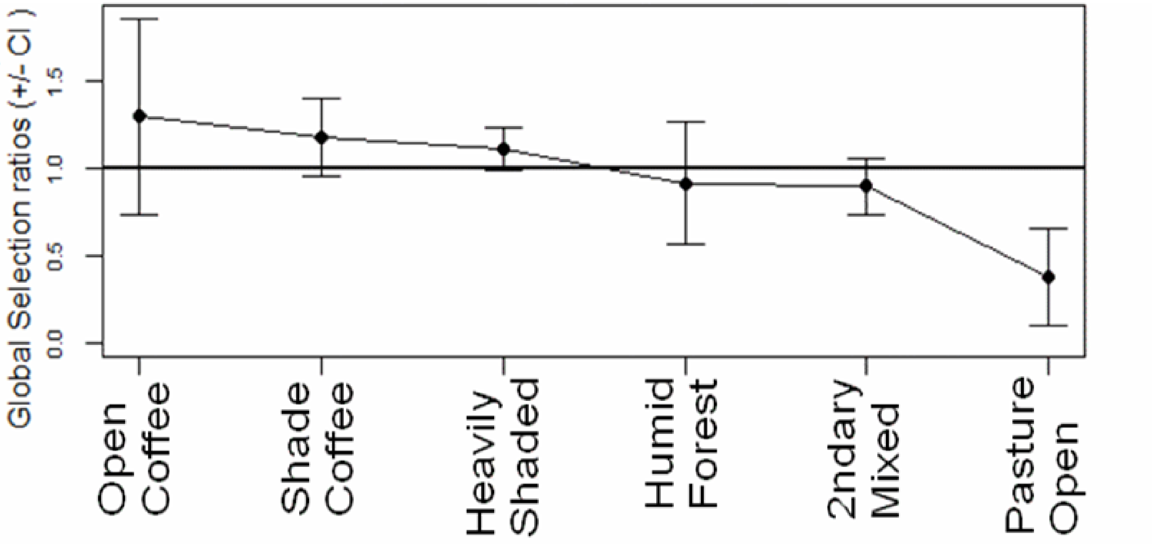
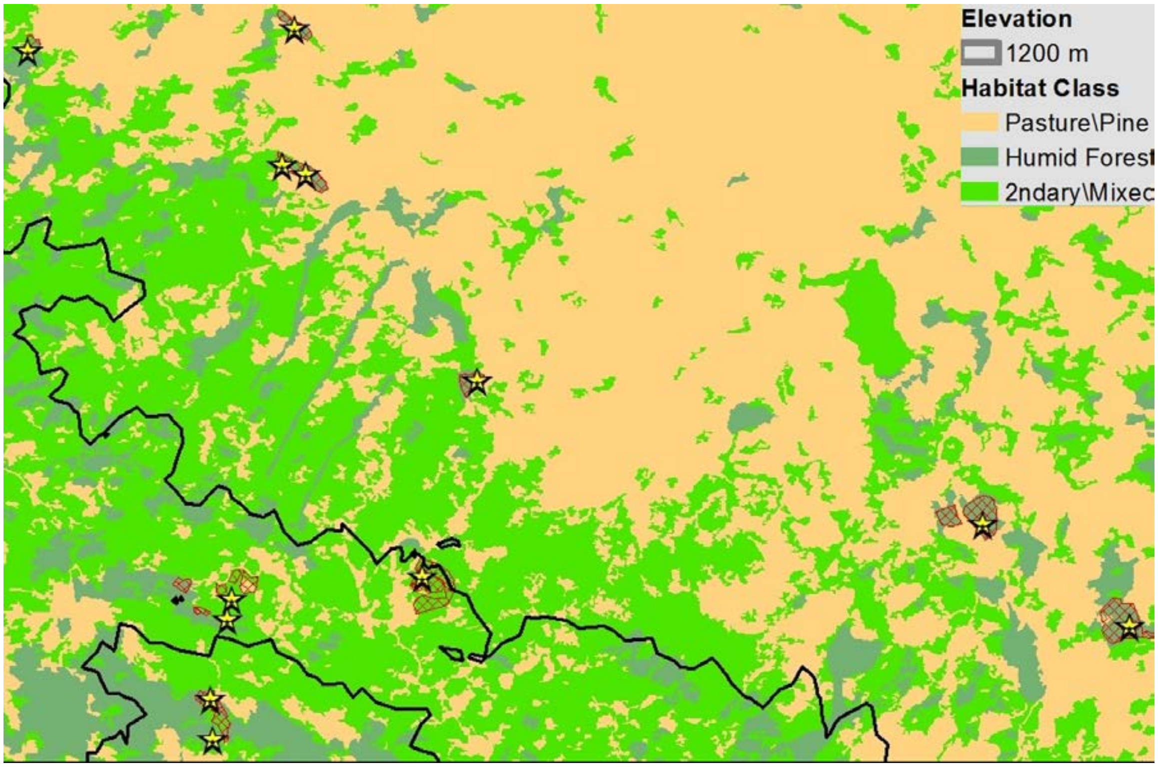


Figure 1. 3. Habitat classification map including manually digitized coffee and banding sites. The link line indicates the 1200 m elevation contour above which more humid vegetation types become more common.



APPENDIX

PREDICTOR VARIABLE TABLES

Table 1. 14. Measured Vegetation Variables, values in bold indicate use as a candidate variable and italicized variables did not appear in any final model.

Variable	Description
litterAvg	**Average of 4 litter depth measurements**
sStemStd	**Count of stems less than 2.5cm**
mStemStd	Count of stems 2.5-8cm
CanopyAvg	***Average of 4 spherical densiometer measurements***
gcC	Count of pts, 0-20, with ground cover (0-1 m) by coffee
scC	Count of pts, 0-20, with sub canopy (1-3 m) of coffee
GCa	Count of vegetation touches (0-.25 m)
GCb	Count of vegetation touches (.25-.5 m)
GCc	Count of vegetation touches (.5-1 m)
SCd	Count of vegetation touches (1-2 m)
SCe	Count of vegetation touches (2-3 m)
gcB	Count of pts, 0-20, with ground cover (0-1 m) bare
gcF	Count of pts, 0-20, with ground cover (0-1 m) by forbs
gcG	Count of pts, 0-20, with ground cover (0-1 m) by grass
gcL	Count of pts, 0-20, with ground cover (0-1 m) by leaf litter
gcM	Count of pts, 0-20, with ground cover (0-1 m) by heliconia-like vegetation
gcN	Count of pts, 0-20, with ground cover (0-1 m) by fern
gcV	Count of pts, 0-20, with ground cover (0-1 m) by vines
gcW	Count of pts, 0-20, with ground cover (0-1 m) by woody vegetation
gcO	Count of pts, 0-20, with ground cover (0-1 m) by other vegetation
scG	Count of pts, 0-20, with sub canopy (1-3 m) of grass
scM	Count of pts, 0-20, with sub canopy (1-3 m) of heliconia-like vegetation
scN	Count of pts, 0-20, with sub canopy (1-3 m) of fern
scV	Count of pts, 0-20, with sub canopy (1-3 m) of vines
scW	Count of pts, 0-20, with sub canopy (1-3 m) of woody vegetation
div	Count of tree species
A-H, Z	9 variables, count of trees falling with the respective size class

Table 1. 15. Combined and Calculated Variables, values in bold indicate use as a candidate variable and italicized variables did not appear in any final model.

Gcabc	**Sum of GCa,GCb and GCc**
Scde	**Sum of SCd and Sce**
gcscCP	**Percent Cover Coffee**
bAreaSP	**Basal Area of small trees (Z-B size classes)**
bAreaMP	**Basal Area medium trees (C-E size classes)**
bAreaLP	**Basal Area large trees (F-H size classes)**

Table 1. 16. GIS derived variables, values in bold indicate use as a candidate variable and italicized variables did not appear in any final model.

Variable	Description
Pct4	Percent of locations within secondary vegetation
Pct7	Percent of locations within open habitat types
Pct13	Percent of locations within humid broadleaf forest
Pct104	Percent of locations within shade coffee
Pct113	Percent of locations within heavily shaded
Pct107	Percent of locations within open coffee
PctCFE	Percent of locations 20m from coffee-vegetation boundary
PctCOE	Percent of locations 20m from coffee-open boundary
Avgelev	Average elevation of individual locations

Table 1. 17. Wood Thrush Condition Variables, values in bold indicate use as a candidate variable and italicized variables did not appear in any final model.

Variable	Description
Fat	Fat Score
Condition2	Mass/Tail residuals
Age	SY or ASY age classification

Table 1. 18. Summary statistics for averaged predictor variables

	Min	**Max**	**Mean**	**Median**	**SD**
litterAvgP	2.7	14.9	8.67	8.72	2.56
gcWP	0	7.63	1.05	0.67	1.35
GCaP	6.89	63	24.34	22.36	10.91
SCeP	6	57	21.59	19	10.06

bAreaP	0.4	14.35	5.09	4.32	3.7
ctP	1	36	12.43	10	8.93
sStemStdP	28.67	236.58	88.32	72.08	52.37
mStemStdP	6	44	15.19	12.32	8.1
CanopyAvgP	0	90.06	49.53	52.4	24.75
gcBP	0	3.1	0.71	0.54	0.71
gcCP	0	5.78	1.03	0.71	1.29
gcFP	0	13.5	4.26	4	2.99
gcGP	0	11	2.45	1.67	2.65
gcLP	1	16.5	9.37	9.24	3.54
gcMP	0	1.43	0.27	0	0.41
gcNP	0	4	0.29	0.2	0.59
gcVP	0	1.33	0.26	0.12	0.37
scCP	0	19.33	8.9	10.01	4.63
scGP	0	1.74	0.15	0	0.35
scMP	0	1	0.11	0	0.26
scNP	0	0.22	0.05	0	0.07
scVP	0	2.38	0.36	0.08	0.59
scWP	0	14	3.09	1.42	3.82
GCbP	0	23	10.03	10.43	3.79
GCcP	2	23	10.42	10.1	3.7
SCdP	5	65	17.66	14.61	12.78
divP	0.67	4	2.11	2.08	0.75
smTreesP	0	23	3.32	2.45	3.93
mTreesP	0	2.16	1.17	1.14	0.53
lTreesP	0	1.31	0.31	0.24	0.35
gcscCP	0	19.66	9.93	10.66	5.2
Comp.1P	-1.91	2.16	0.13	0.17	0.76
Comp.2P	-3.62	1.33	-0.08	0.01	1.01
Comp.3P	-1.91	2.16	-0.15	-0.01	0.69
Comp.4P	-2.22	1.01	-0.11	-0.06	0.68
Distance	1.03	9.99	3.84	2.48	3.04
avgelev	854	1272	1094.62	1134.79	144.78
Fat	1	5	3.02	3	1.27
Condition2	-10	12.66	0	-0.4	4.12

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