

Rodríguez, F., D. Escoto, T. Mejía-Ordóñez, L. Ferrufino-Acosta, S. Y. Cruz, J. E. Duchamp, and J. L. Larkin. 2019. Influence of microhabitat on Honduran Emerald (*Amazilia luciae*) abundance in tropical dry forest remnants. *Avian Conservation and Ecology* 14(1):3. <https://doi.org/10.5751/ACE-01321-140103>

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Research Paper

## Influence of microhabitat on Honduran Emerald (*Amazilia luciae*) abundance in tropical dry forest remnants

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**ABSTRACT.** Understanding the ecology of at-risk species is the foundation for developing strategies to counteract continued population declines. The Honduran Emerald (*Amazilia luciae*) is an endemic hummingbird that inhabits tropical dry forest in Honduras. Remaining populations of this endangered species are restricted to habitat fragments located in landscapes dominated by agricultural activities. The conservation of this species is dependent on efforts to protect existing dry forest remnants and to restore additional areas. However, limited information exists regarding Honduran Emerald habitat use on which to base management decisions. We conducted a study to identify point-level habitat features that are important to Honduran Emerald abundance. In 2014–2015, we conducted avian and vegetation surveys at 174 points located within dry forest remnants. We constructed hierarchical multinomial mixture models using time-removal based point count data collected in three sampling periods. Honduran Emerald detection was influenced negatively by Julian date. Local abundance was positively correlated with shrub-sapling density and cacti structural diversity. Mean local abundance per point was  $(0.39 \pm 0.2 \text{ SD})$  and the number of individuals estimated to have used the combined area of the survey points (48.7 ha) was 68 (CI 95% 45–110). The shrub-sapling density and cacti structural diversity levels identified from our abundance models are characteristic to dry forest communities in this region. As such, the need for efforts to protect remaining dry forest remnants cannot be overstated. Future research should evaluate how the microhabitat features we found to be important to Honduran Emerald abundance influence fitness parameters such as survival and reproduction. Studies that examine how reciprocal effects of pollinator species declines and plant species diversity influences the long-term stability of tropical dry forest ecosystems are also warranted.

## Influence du micro-habitat sur l'abondance de l'Ariane de Lucy (*Amazilia luciae*) dans les vestiges de forêts tropicales sèches

**RÉSUMÉ.** Comprendre l'écologie des espèces en péril est la base de l'élaboration de stratégies visant à contrer le déclin continu des populations. L'Ariane de Lucy (*Amazilia luciae*) est un colibri endémique qui vit dans la forêt tropicale sèche du Honduras. Les populations restantes de cette espèce en danger sont limitées à des fragments d'habitat situés dans des paysages dominés par des activités agricoles. La conservation de cette espèce dépend des efforts déployés pour protéger les vestiges de forêt sèche existants et pour restaurer d'autres zones. Cependant, peu d'informations sont disponibles quant à l'utilisation de l'habitat de l'Ariane de Lucy sur lesquelles fonder les décisions de gestion. Nous avons mené une étude pour identifier les caractéristiques de l'habitat au niveau ponctuel qui sont importantes pour l'abondance de l'Ariane de Lucy. En 2014–2015, nous avons effectué des relevés d'oiseaux et de végétation sur 174 points situés dans des vestiges de forêts sèches. Nous avons construit des modèles de mélanges multinomiaux hiérarchiques à l'aide des données des dénombrements ponctuels, basées sur l'élimination du temps, collectées au cours de trois périodes d'échantillonnage. La détection de l'Ariane de Lucy était négativement corrélée au jour Julien. L'abondance locale était positivement corrélée à la densité d'arbustes et à la diversité structurelle des cactus. L'abondance locale moyenne par point était de  $0,39 \pm 0,2 \text{ DS}$  et le nombre d'individus ayant utilisé la superficie totale des points d'étude (48,7 ha) était de 68 (IC 95% 45–110). La densité d'arbustes et les niveaux de diversité structurelle des cactus identifiés à partir de nos modèles d'abondance sont caractéristiques des communautés de forêts sèches de cette région. En conséquence, on ne saurait trop insister sur la nécessité de déployer des efforts pour protéger les vestiges restants des forêts sèches. Des recherches futures devront évaluer dans quelle mesure les caractéristiques du micro-habitat que nous avons trouvées importantes pour l'abondance de l'Ariane de Lucy ont une incidence sur les paramètres de condition physique tels que la survie et la reproduction. Des études qui examineraient comment les effets réciproques du déclin des espèces pollinisatrices et de la diversité des espèces végétales influencent la stabilité à long terme des écosystèmes des forêts tropicales sèches sont également justifiées.

Key Words: *Agalta Valley; habitat use; hierarchical models; hummingbird*

## INTRODUCTION

Effective conservation of biodiversity in landscapes impacted by human activities is aided by the degree to which biodiversity is monitored and studied in the face of habitat degradation and loss (Collen et al. 2013). Ecologists have often considered species abundance as one of the fundamental population metrics to evaluate anthropogenic influences on wildlife (Apps et al. 2004, Heikkinen et al. 2004, Marsh and Trenham 2008). For example, abundance has been used in population-specific studies to inform management and conservation issues of rare or endangered species (Nichols and Mackenzie 2004, Kéry and Royle 2016). When species abundance can be evaluated in the context of habitat structure and composition, studies can offer insight to those habitat conditions that are important for population recovery. Moreover, results from such studies have the potential to inform habitat management and other conservation efforts (Iwata et al. 2003, Heikkinen et al. 2004, Segura and Arturi 2012).

Tropical dry forests are considered a globally threatened ecosystem, with an estimated 60% of their original extent lost and the rest highly threatened by fragmentation (Sánchez-Azofeifa et al. 2013, Blackie et al. 2014). These forests may not match tropical rainforests in their high level of plant diversity, but they hold a significant amount of plant endemism and are characterized by their high floristic turnover across their distribution (Gentry 1995, Banda et al. 2016). Areas that support tropical dry forests have been historically selected by humans for settlement (Gómez-Pompa et al. 1987, Bush et al. 1992), and today, many landscapes that support tropical dry forests remain important for human communities (Blackie et al. 2014). The area of tropical dry forest in the Agalta Valley, Honduras, has been drastically reduced over the past several decades as the valley continues to be transformed into a working landscape driven by dairy production (Banco Interamericano de Desarrollo 2009). Continued encroachment of human land uses on dry forest remnants may jeopardize the persistence of many species that specialize on this plant community.

Among the many species that have been affected by tropical dry forest loss is the Honduran Emerald, *Amazilia luciae* (Fig. 1), an endangered hummingbird that is endemic to tropical dry forests of Honduras (Anderson et al. 2013, BirdLife International 2016). The species is now restricted to only five locations, i.e., departments, throughout Honduras that support varying amounts of dry forest habitat (Fig. 2A; eBird 2017). The status of the Honduran Emerald in the Agalta Valley is especially tenuous because the species is predicted to become locally extinct within the next decade unless considerable conservation measures are employed (Anderson et al. 2013).

To effectively address conservation needs of the Honduran Emerald it is important to quantify population parameters, i.e., population size (Anderson et al. 2010), and to link such parameters with empirically accessed habitat conditions. Despite first being described by Lawrence (1867), little is known about Honduran Emerald ecology (Anderson et al. 2010). Most of what is known about the species is the result of anecdotal observations, descriptive accounts, contemporary expeditions, and environmental impact assessment reports (Howell and Webb 1989, Thorn et al. 2000, Anderson and Hyman 2007, Anderson et al. 2010, Espinal and Mora 2012, INGTELSIG 2013). To date, no studies have quantified the influence of point-level vegetation on Honduran

Emerald abundance. Several studies in avian ecology have previously demonstrated the utility of habitat-species abundance relationships to highlight the role of vegetation structure and composition for species conservation (Pardini et al. 2005, Gómez-Montes and Bayly 2010) and to assess the population status of species in a given locality (Sillett et al. 2012, Rivera-Milán et al. 2015). Therefore, blueprints exist to study how Honduran Emerald local abundance is driven by vegetation characteristics in tropical dry forest remnants. Furthermore, floristic communities that shape tropical dry forests across the Americas are considered irreplaceable with areas in need of conservation throughout the continent (Banda et al. 2016). As such, understanding the interrelationships of the species within this ecosystem will increase our knowledge of Honduran Emerald ecology and of the impact that anthropogenic threats will have on these species (Sánchez-Azofeifa et al. 2013).

**Fig. 1.** Honduran Emerald hummingbird (*Amazilia luciae*) is a species endemic to Honduras. (A) An area of dry forest dominated by shrub. (B) Honduran Emerald feeding from *Aechmea bracteata* in Santa Bárbara department, the western range of the species (Photo by: Mayron Mejía, 2018). (C) A Honduran Emerald hovering in its habitat in the department of Cortés (Photo by: Alex Martínez Matute, 2018).



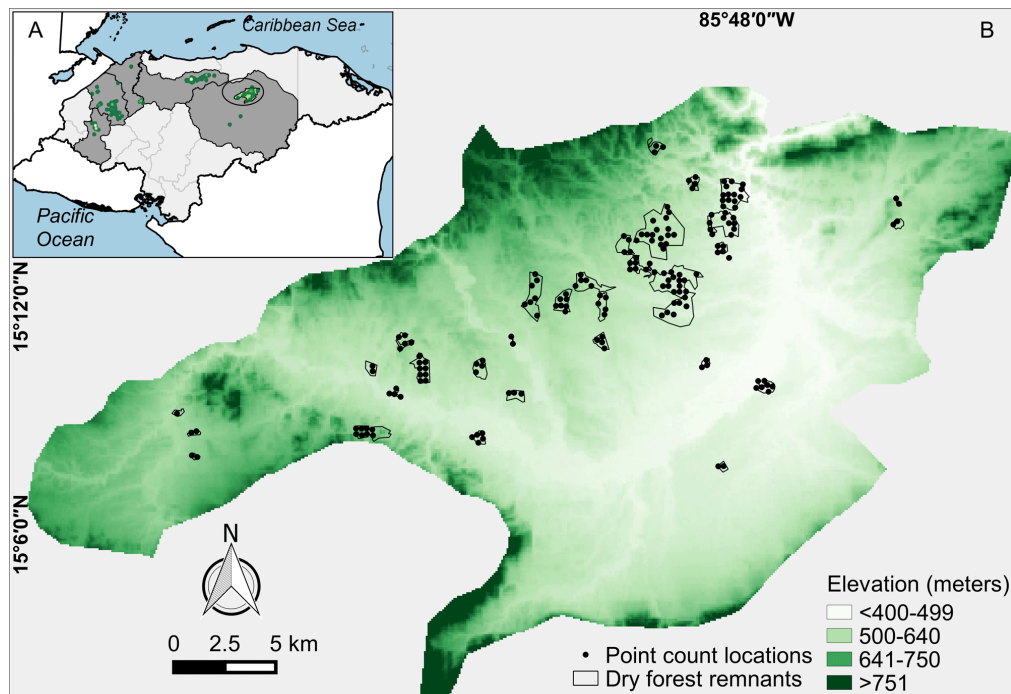
Our aim was to evaluate the relationship between Honduran Emerald abundance and microhabitat features of tropical dry forest remnants in the Agalta Valley. Our use of the term “microhabitat” is similar in context to Cahill and Matthysen (2007) or Renfrew and Ribic (2008) and refers to vegetation structure and species composition features that are quantified at the survey point level. Study objectives were to (i) determine mean detection probability and local abundance of Honduran Emerald, (ii) identify how microhabitat features influence local abundance of Honduran Emerald, and (iii) summarize the microhabitat features of dry forest remnants in which we detected Honduran Emeralds.

## METHODS

### Study area

During August 2014 to July 2015, we conducted surveys in 35 dry forest remnants (0.5–380 ha) within the Agalta Valley (Fig. 2B). The geographic extent of the Agalta Valley is approximately

**Fig. 2.** (A) Honduran Emerald (*Amazilia luciae*) locations within its range in Honduras (eBird 2017). (B) Study area in the Agalta Valley with tropical dry forest remnants (NASA LP DAAC 2011; Asociación de Investigación para el Desarrollo Ecológico y Socioeconómico [ASIDE] 2014, shapefile) where Honduran Emerald surveys and vegetation sampling were conducted during 2014–2015.



70,000 ha in which tropical dry forest communities exist as patchily distributed remnants of varying successional stages, within a landscape dominated by pasture and croplands (~77%; Espinal and Mora 2012, Rodríguez et al. 2015). The 35 dry forest remnants we studied were selected based on accessibility and permission from landowners. Remnants were composed of a mosaic of dry forest vegetation and open to semiopen areas associated with cattle farming activities (Fig. 1A, 1C). Tropical dry forest of the Agalta Valley comprises open thorn or semideciduous forests, semideciduous dry forests, or shrub dominated areas, with a mean canopy height of  $5.95 \pm 0.02$  SE m, of which the majority may be considered low standing trees. In these communities, dominant plant species include *Acacia picachensis* (Fabaceae), *Eugenia hondurensis* (Myrtaceae), *Casearia nitida* (Salicaceae), and *Erythroxylum areolatum* (Erythroxylaceae). The understory strata ranges from sparse to dense and may comprise saplings and shrub species such as *Solanum dasyanthum* (Solanaceae), *Schoepfia schreberi* (Schoepfiaceae), *Bernardia nicaraguensis* (Euphorbiaceae), and *Mimosa tenuiflora* (Fabaceae). Additionally, the understory strata may include nonwoody species such as *Hechtia guatemalensis* (Bromeliaceae), *Aechmea bracteata* (Bromeliaceae), and *Opuntia hondurensis* (Cactaceae; Ferrufino-Acosta, Cruz, Mejía-Ordóñez, et al., unpublished manuscript).

### Avian surveys

We used QGIS to randomly select point count survey locations within each of the 35 tropical dry forest remnants (Quantum GIS Development Team, <https://qgis.org/en/site/>). This resulted in the

selection of 179 points that were spaced at least 300 m apart (Fig. 2B). Of these we only analyzed data from 174 points because of loss of habitat or access to the points within the study period. We conducted point count surveys between 0600 and 1000 hrs on days with appropriate weather conditions, e.g., no rain (Lynch 1995). We surveyed each point during three periods throughout the year-long study (30 September–9 December; 4 March–28 April; 21 June–27 July). At the beginning of each point count survey, we allowed a 1-minute “settle period” to elapse before starting the survey (Bibby et al. 1992). Each point count consisted of a 10-minute passive listening phase in which all Honduran Emeralds seen or heard were recorded. Listening phases were organized into five 2-minute time-removal intervals (Farnsworth et al. 2002).

Surveys throughout the study period were conducted by two observers (FR and DE). These observers trained together during two days in August 2014, in one of the largest dry forest fragments and conducted trial point counts to learn the point count protocols. Subsequently, the observers conducted the first period of sampling (September–December) together to standardize their ability to record data: detections of Honduran Emeralds and recording of Honduran Emeralds in the adequate intervals. In the subsequent sampling periods (March–April and June–July), each observer worked separately to maximize the points visited per survey. For this reason in these two sampling periods, we considered observer as a potential variable in our models to account for possible differences between them in our ability to detect Honduran Emeralds.

## Vegetation surveys

We conducted vegetation surveys at each point where we had conducted avian point counts. In each plot we collected vegetation structure and plant species composition data within nested plots based on Nudds (1977), Bibby et al. (1992), Martin et al. (1997), Nassar et al. (2008), and García-Villacorta (2009). Within a 5-m radius plot we recorded (1) average shrub-sapling height (m) estimated by observers, and (2) shrub-sapling stem count including woody species in the shrub strata < 2 m. Within a 12.6 m radius plot we recorded the following: (1) diameter at breast height (DBH) for woody plants  $\geq 3$  cm DBH; (2) tree height (m) for each woody plant  $\geq 3$  cm DBH estimated by observers; (3) tree species; (4) count of trees or cacti with presence of epiphytic bromeliads; (5) number of cacti; (6) cacti height (m) for each individual estimated by observer; (7) count of woody stems < 3 cm DBH; and (8) average horizontal vegetation density measured using a 2-m tall density board consisting of a cloth scroll comprising twenty 20X20 cm grid cells. To quantify this measurement an observer stood at plot center while another observer held the density board 10 m away in each of the four cardinal directions. The observer at plot center recorded the number of grid cells covered  $\geq 50\%$  by vegetation. To minimize errors in estimation, all vegetation measurements were collected by the same observers during all surveys. Once vegetation measurements were completed, we collected representative plant samples throughout each plot, preferably from individuals with fruit or flowers. Plants were pressed, transported to the Universidad Nacional Autónoma de Honduras (UNAH), to be identified to species and deposited at the Herbarium Cyril Hardy Nelson Sutherland (TEFH) in UNAH. We deposited a duplicate of the samples at the A. G. Shields Herbarium in Indiana University of Pennsylvania.

## Statistical analysis

First, we summarized the vegetation metrics to generate 15 variables (Table 1). These variables reflect the structure and taxonomic composition of microhabitat features of each survey location (Table 1). Prior to analysis, we standardized all microhabitat features to have a mean zero and standard deviation of one. Additionally, we evaluated for correlations using the Pearson coefficient ( $r \geq 0.75$  or  $\leq -0.75$ ). Only two covariates, woody species richness and Shannon Diversity, were highly correlated (Pearson coefficient = 0.85), and we chose to exclude the latter from our analyses. Ultimately, we included 14 variables (Table 1) in the hierarchical models to relate Honduran Emerald abundance to microhabitat features.

We analyzed data from our three Honduran Emerald survey periods separately to limit our inferences to time periods when the population was sampled consistently. We assume that within each survey period, populations are likely to be closed. However, because of the mobility of our study species we interpreted our abundance values as the number of individuals that potentially use the sampling points at a given time, as opposed to absolute number of individuals (Chandler et al. 2011). We screened the raw counts of Honduran Emeralds and included detections that were  $\leq 30$  meters from the observer. Observations beyond this distance were sparse and may not have captured the microhabitat features that we measured. Honduran Emerald counts within

each sampling period were tested for spatial autocorrelation using Moran's I test within the "ape" package in R (Paradis and Schliep 2018).

We analyzed the local abundance patterns with the "unmarked" package in program R for model building (Fiske and Chandler 2011, R Core Team 2017). We followed the multinomial N-mixture modeling framework using the Poisson mixture, incorporating a time-removal specification with the information from the count time-intervals (Farnsworth et al. 2002, Royle 2004a). We fit models in a two phase process. First, we fitted models that only considered the detection probability covariates of Julian date, observer, and vegetation density and kept abundance constant. We used the highest-ranking model from this phase for posterior modeling of abundance. Then, we fit models with the top detection covariate of the previous phase and the vegetation variables that may influence Honduran Emerald abundance (Table 1). To avoid overparameterization in the models, because of low number of detections, we fit single variable models and single variable with quadratic terms for each of the 14 variables. We ranked the models based on the Akaike Information Criteria corrected for small sample sizes (AICc) using the package "AICc modavg" (Hurvich and Tsai 1989, Mazerolle 2017). The top model was selected for the estimation of mean abundance per point and local abundance. We evaluated the confidence intervals at the 85% level because we consider them appropriate for exploring the informative value of our proposed variables (Arnold 2010). Additionally, we conducted a goodness of fit test with three fit statistics (Chi-square, FreeTukey, and sums of squares) and 10,000 repetitions following Kéry and Royle (2016). Models up to  $\Delta AICc = 7$  were evaluated to identify variables that could be considered in future studies, albeit these are less likely to influence abundance based on our data (Burnham and Anderson 2002). We present the results of the models fit in phase two and the null model in a table.

Finally, we summarize the vegetation variables of used and unused point count locations. For all vegetation variables, we conducted a two-sample t-test and applied a Holm's correction factor to account for multiple testing (Holm 1979). We present test results for both corrected and uncorrected comparisons. The corrected comparisons were used to consider the effect of the differences between used and unused points, whereas the uncorrected comparisons were used to identify microhabitat features that warrant inclusion in future Honduran Emerald studies.

## RESULTS

We detected Honduran Emeralds at 86 of 174 point count locations in tropical dry forest remnants during all three survey periods combined. In period one (September–December), we recorded 46 Honduran Emeralds at 41 of 174 (24%) survey points. During period two (March–April), we recorded 67 Honduran Emeralds at 57 of 174 (33%) survey points, and during period three (June–July), 30 Honduran Emeralds at 28 of 174 (16%) survey points. A total of five detections > 30 m were not included in the analyses (four and one for the first and second sampling periods, respectively). We did not find evidence for spatial autocorrelation for Honduran Emerald counts for all sampling periods (Appendix 1).

**Table 1.** Structure and composition microhabitat features of the Agalta Valley’s tropical dry forest remnants used in the analysis of Honduran Emerald (*Amazilia luciae*) local abundance.

Microhabitat feature	Description	Rationale
Holdridge Complexity Index (HCI)	Incorporates height, stand basal area, density of stems $\geq$ 3 DBH (each tree stem contributing individually), wood plant species richness (Holdridge et al. 1971).	Quantifies the structural physiognomy and complexity of Agalta’s dry forest remnants and its value represents succession gradients (Espirito-Santo et al. 2014).
Density of woody stems < 3 cm DBH	Density per ha of tree and sapling stems under 3 cm DBH.	May reflect cover for Honduran Emerald against predators.
Standardized Pretzsch index (Cacti structural diversity)	This index combines height and presence of species to reflect the contribution of cacti species richness in each of three levels of a vertical distribution (Pretzsch 2009). Three levels were determined based on the raw individual height distribution for cacti: 0–7.5 m (level III or lower stratum), 7.5–12 m (level II or medium stratum), and 12–15 m (level III or high stratum).	This standardized species profile index (Arel) was adapted to cacti. Three levels were selected based on applications in other vegetation ecology studies (Jiménez et al. 2001, Mora-Donjuán et al. 2014). Cacti are one of the characteristic families of tropical dry forest floristic composition (Gentry 1995).
Proportion of <i>Opuntia hondurensis</i> cacti	Proportion of individuals of <i>Opuntia hondurensis</i> relative to all cacti individuals present in the plot.	Indicates the availability of one of the Honduran Emerald common food sources in the height stratum where most individuals of this cactus species were concentrated (0–7.5 m).
Proportion of <i>Pilosocereus leucocephalus</i> cacti	Proportion of individuals of <i>Pilosocereus leucocephalus</i> relative to all cacti individuals present in the plot.	Indicates the availability of one of the Honduran Emerald common food sources in the height stratum where most individuals of this cactus species were concentrated (0–7.5 m).
Shrub-sapling density (no. stems/ha)	Shrub density is represented by all woody plants under two meters that have solely a shrub growth habit or may have both shrub and tree growth habit.	Shrub strata encompasses plant species that are Honduran Emerald feeding source or nesting substrate.
Vegetation density (%)	Percentage of horizontal cover present within two m of height.	A complementary value to complexity of a stand that represents the cover wildlife uses (Nudds 1977). It may indicate the potential cover that may serve the Honduran Emerald for several purposes such as predation protection or nesting attributes.
Importance Value (IVI) <i>Acacia picachensis</i>	Quantified at the plot level with the two available parameters of height and basal area (Mostacedo and Fredericksen 2000) for <i>Acacia picachensis</i> one of the highest IVI values overall for Agalta as composition microhabitat features.	To incorporate the composition of Agalta’s plant community.
Importance Value (IVI) <i>Eugenia hondurensis</i>	Quantified at the plot level with the two available parameters of height and basal area (Mostacedo and Fredericksen 2000) for <i>Eugenia hondurensis</i> one of the highest IVI values overall for Agalta as composition microhabitat features.	To incorporate the composition of Agalta’s plant community.
Importance Value (IVI) <i>Erythroxylum areolatum</i>	Quantified at the plot level with the two available parameters of height and basal area (Mostacedo and Fredericksen 2000) for <i>Erythroxylum areolatum</i> one of the highest IVI values overall for Agalta as composition microhabitat features.	To incorporate the composition of Agalta’s plant community.
Importance Value (IVI) <i>Casearia nitida</i>	Quantified at the plot level with the two available parameters of height and basal area (Mostacedo and Fredericksen 2000) for <i>Casearia nitida</i> one of the highest IVI values overall for Agalta as composition microhabitat features.	To incorporate the composition of Agalta’s plant community.
Epiphyte tree count	Count per plot of the individual woody plants greater than three cm DBH with presence of at least one epiphytic bromeliad.	Indicates the availability of plant species that may be used by Honduran Emeralds as a food resource.
Patch size	Area in ha of the polygon representing the study site that contains the point count location.	Indicates the extent of the property that holds the mosaic of tropical dry forest habitat and cattle farm use areas.
Shannon Diversity Index	Shannon Diversity Index presented in effective species units. Effective species units (D) is calculated by taking the base of the natural logarithm of the Shannon Diversity Index. $D = e^H$ .	Indicates plant species diversity.
Woody plant species richness	Species richness of all individuals $\geq$ three cm DBH.	Indicates plant species richness.

**Table 2.** Honduran Emerald (*Amazilia luciae*) top detection probability and abundance models, and abundance estimates for two sampling periods in the Agalta Valley, during 2014–2015 at 174 sampled point locations (48.7 ha). Mean values with SD for detection and abundance per point also shown. A complete AICc table of all fitted models of detection and abundance can be found in Appendices 2 and 3.

Sampling period	$p^\dagger$	$\beta(\text{SE})$	$\lambda^\ddagger$	Mean detection per point (SD)	Mean abundance per point (SD)	Local abundance	95 % Confidence intervals
September–December $p(\text{Julian date}^\S)\lambda(\text{Shrub-sapling density}^\S)$	-0.80(0.27)	0.77(0.24)		0.23(0.12)	0.39(0.20)	68	46-110
March–April $p(\text{Julian date}^\S)\lambda(\text{Cacti structural diversity})$	-0.44(0.26)	0.38(0.13)		0.15(0.19)	0.96(0.38)	167	107-242

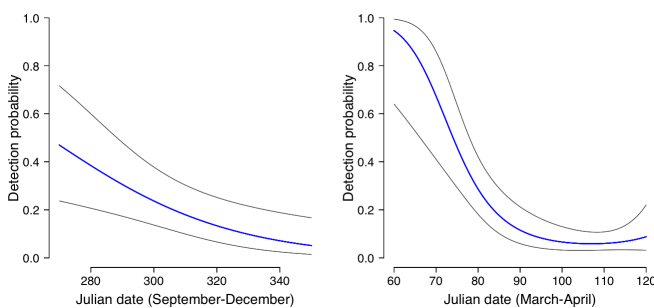
<sup>†</sup> Detection probability

<sup>‡</sup> Abundance

<sup>§</sup> Variable with quadratic term

The probability of detecting a Honduran Emerald declined over time (Julian date) during the first two sampling periods (Fig. 3). During the second sampling period this decline was best characterized by a polynomial model with a quadratic term. Mean detection probability was the highest in the first sampling period (Table 2). Models constructed using data collected during our third sampling period were unable to estimate detection probability and abundance. We expect this is due to the lower number of detections. As such, we did not attempt further modeling using data collected during the third survey period.

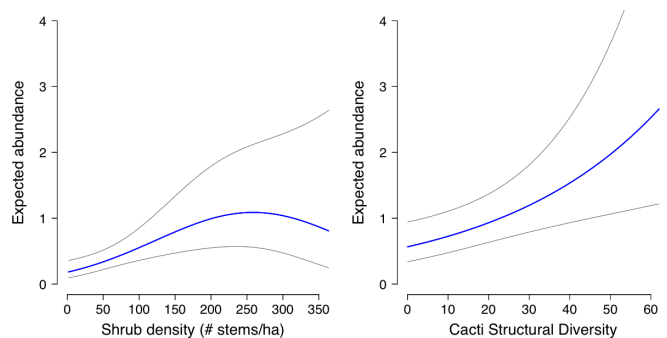
**Fig. 3.** Honduran Emerald (*Amazilia luciae*) detection probability varied with Julian date, with a higher mean detection probability during September–December 2014 (left) than March–April 2015 (right). Graphs represent the top-ranked models for each survey period, and gray lines represent 95% confidence intervals.



During our first sampling period, Honduran Emeralds were most abundant at locations with greater shrub-sapling density. This relationship was described best with a polynomial model including a quadratic term. This positive relationship (Table 2; Fig. 4) appeared to peak around 200 stems/ha, beyond which our model was not able to characterize a relationship. During our second sampling period, Honduran Emeralds were most abundant at locations with greater cacti structural diversity (Table 2; Fig. 4). Cacti structural diversity suggested that cacti at the lower strata between zero and seven meters were more prevalent with mean  $22.62 \pm 15.17\%$  SD for all points used during sampling period two (N = 57 points). These values of cacti structural

diversity represent the used points with mean cacti height of  $2.47 \pm 1.66$  m (range = 1–8.2 m), total cacti density of all species of  $235.44 \pm 89.84$  individuals/ha (range = 40–400), and cacti species richness of  $2.09 \pm 1.1$  (range = 0–4 species) where *Opuntia hondurensis* and *Pilosocereus leucocephalus* were the most frequent cacti species in the points. The highest local abundance was estimated during the second sampling period, albeit this period had the lowest detection probability (Table 2). Models from both sampling periods were not overdispersed ( $c\text{-hat} = 1.01$  sampling period one, and 0.99 for sampling period two) and had good fit according to the sums of squares, Chi-square, and Freeman Tukey statistics ( $p > 0.05$ ).

**Fig. 4.** Expected abundance of Honduran Emerald (*Amazilia luciae*) in the Agalta Valley was most influenced by shrub-sapling density during September–December 2014 (left) and most influenced by cacti structural diversity during March–April 2015 (right). Gray lines indicate 95% confidence intervals.



Our t-test results indicated that the proportion of the cactus *Pilosocereus leucocephalus*, relative to other cacti at a given plot, was higher at used points (Mean = 0.2; SD = 0.27; Table 3) compared with unused points (Mean = 0.08; SD = 0.18; Table 3). We propose the following variables to be included in future studies: cacti structural diversity, dominance (IVI) of *Casearia nitida*, *Eugenia hondurensis*, species richness of woody plants, epiphyte tree count, Holdridge Complexity Index, stems under 3 cm DBH, and patch size. These variables approached the threshold of significance in our t-tests that evaluated sites with

**Table 3.** Comparison of vegetation variables between point count locations that were used and unused by Honduran Emeralds (*Amazilia luciae*) in the Agalta Valley during 2014–2015.

Vegetation variable	Used point count locations (N = 86)			Unused point count locations (N = 88)			t-test statistics			
	Mean	SD	Range	Mean	SD	Range	t	df	p-value uncorrected	p-value corrected
Proportion of <i>Opuntia hondurensis</i> cacti	0.49	0.33	0-1	0.5	0.39	0-1	0.21	168.58	0.84	1
Holdridge Complexity Index	117.4	130.5	0.03-825.78	122.27	155.75	0-758.51	0.22	168.1	0.82	1
Density of woody stems < 3 cm DBH	2092.1	1514.27	0-7340	1934.32	1611.31	0-10280	-0.67	171.74	0.51	1
IVI <i>Eugenia hondurensis</i>	13.46	28.56	0-142.37	10.24	23.39	0-88.3	-0.81	164.08	0.42	1
Vegetation density (%)	59.14	29.06	0-100	55.51	27.84	0-100	-0.84	171.26	0.4	1
Epiphyte presence	6.35	8.3	0-47	4.69	6.57	0-27	-1.4571	161.73	0.147	1
Shrub-sapling density (no. stems/ha)	76.16	83.78	7.2-587.6	58.96	64.47	1.8-456.4	-1.52	159.61	0.13	1
Shannon Diversity Index	2.45	0.89	0-3.6	2.2	1.09	0-5.24	-1.68	166.74	0.09	1.0
IVI <i>Acacia picachensis</i>	42.62	54.46	0-200	59.09	66.44	0-200	1.79	166.96	0.08	1.0
IVI <i>Erythroxylum areolatum</i>	16.12	29.89	0-143.03	8.9	19.42	0-87	-1.89	145.45	0.06	0.86
Woody plant species richness	11.83	4.55	1-20	10.32	5.07	1-20	-2.07	170.77	0.04*	0.56
IVI <i>Casearia nitida</i>	8.83	14.65	0-56.98	5.03	9.71	0-53.52	-2.11	153.25	0.04*	0.5
Cacti structural diversity	21.29	14.65	0-48.11	14.96	15.41	0-61.36	-2.78	171.87	0.006*	0.09
Proportion of <i>Pilosocereus leucocephalus</i> cacti	0.2	0.27	0-1	0.08	0.18	0-0.86	-3.54	149.09	0.0005*	0.007*

\* p = 0.05

and without presence of Honduran Emeralds (Table 3) and were within  $\Delta AICc=4-7$  (Table 4).

## DISCUSSION

Our study revealed that shrub-sapling density and cacti structural diversity explained Honduran Emerald local abundance in tropical dry forest remnants of the Agalta Valley. In other parts of the species range, shrubs and cacti species have been highlighted as components of the tropical dry forest used by this species (Thorn et al. 2000, House 2004). In fact, it is well documented that shrub and cacti are ecologically important to many species of tropical hummingbirds for feeding, or perching close to feeding areas (Skutch 1958, Wolf 1964, Wolf and Stiles 1970, Feinsinger 1976, Hainsworth 1977, Snow and Snow 1986, Fraga 1989). In addition, small trees or saplings are considered to have suitable floral resources that are suitable for hummingbirds (Snow and Snow 1986). Honduran Emeralds' use of shrubs and cacti as a floral resource has been reported elsewhere (Anderson et al. 2010). The use of the shrub-sapling strata by Honduran Emeralds as a source of floral resources was observed previously in the Agalta Valley (Mora et al. 2016). Moreover, field observations during our study revealed that the species used floral resources of four shrub and two cacti species: *Aphelandra scabra* (Acanthaceae), *Combretum fruticosum* (Combretaceae), *Pedilanthus tithymaloides* (Euphorbiaceae), *Cnidocolus aconitifolius* (Euphorbiaceae), and *Opuntia hondurensis* (Cactaceae) and *Pilosocereus leucocephalus*

(Cactaceae), respectively. Honduran Emeralds also used shrub-sapling and cacti strata as nesting substrate (Rodríguez et al. 2016).

In addition to shrub-sapling density, cacti structural diversity most explained variation in Honduran Emerald abundance across our survey locations. This finding reinforces the previous observations and highlights the importance of cacti species as nesting and feeding sites (Anderson et al. 2010, Rodríguez et al. 2016). Furthermore, when all sampling periods were pooled, the percent cover of the cactus, *Pilosocereus leucocephalus*, was the only vegetation feature we measured that differed between used and unused points whereby used points had higher values. Our results regarding the influence of shrub-sapling density and cacti structural diversity on Honduran Emerald abundance should be considered in future studies that attempt to evaluate the influence of habitat conditions on the species fitness parameters (Johnson 2007). For example, most Honduran Emerald nests found in dry forest remnants in the Agalta Valley were placed in the shrub-sapling strata (Rodríguez et al. 2016). But it remains unknown how shrub-sapling density or vegetation composition affects nest success. Our results in combination with those from studies that evaluate reproductive success and other fitness parameters can guide habitat management recommendations for the species.

We also found that the probability of detecting Honduran Emerald varied within sampling periods and that it was best explained by Julian date. Although we are uncertain why Julian

**Table 4.** Honduran Emerald (*Amazilia luciae*) models of abundance in the Agalta Valley during 2014–2015 for the first (September–December) and second (March–April) sampling periods. We present models up to  $\Delta AICc = 7$ , which illustrate microhabitat features that may influence Honduran Emerald abundance. Coefficients ( $\beta$ ) with SE in parenthesis and 85% confidence intervals (CI) shown.

Model	Sampling period	$\beta$ (SE)	CI 85%	$K^\dagger$	AICc	$\Delta AICc$	AICc $W_i^\ddagger$	Cumulative $W_i^\ddagger$	LL $^\S$	
		$\lambda$	$\lambda$							
<i>September–December</i>										
1	$\lambda$ (Shrub strata density)	0.77(0.24)	0.42;1.12	5	348.70	0.00	0.64	0.64	-169.17	
	$\lambda$ (Shrub strata density) <sup>l</sup>	-0.15(0.08)	-0.26;-0.04							
2	$\lambda$ (Shrub strata density)	0.21(0.09)	0.08;0.35	4	353.36	4.67	0.06	0.70	-172.56	
3	$\lambda$ (Stems under 3 cm)	-0.17(0.21)	-0.47;0.13	5	354.81	6.11	0.03	0.73	-172.23	
	$\lambda$ (Stems under 3 cm) <sup>l</sup>	-0.32(0.24)	-0.66;0.02							
4	$\lambda$ (Stems under 3 cm)	-0.25(0.17)	-0.50;0.01	4	355.22	6.52	0.02	0.75	-173.49	
5	$\lambda$ (.)	-0.9(0.2)	-1.19;-0.61	3	355.33	6.63	0.02	0.77	-174.59	
6	$\lambda$ ( <i>Eugenia hondurensis</i> )	-0.28(0.30)	-0.70;0.15	5	355.41	6.72	0.02	0.80	-172.53	
	$\lambda$ ( <i>Eugenia hondurensis</i> ) <sup>l</sup>	0.12(0.08)	0.02;0.23							
7	$\lambda$ ( <i>Pilosocereus leucocephalus</i> )	0.17(0.12)	0.001;0.35	4	355.48	6.78	0.02	0.82	-173.62	
<i>March–April</i>										
1	$\lambda$ (Cacti structural diversity)	0.38(0.13)	0.20;0.57	5	452.75	0.00	0.47	0.47	-221.20	
2	$\lambda$ (Cacti structural diversity)	0.37(0.14)	0.18;0.57	6	454.87	2.11	0.16	0.63	-221.18	
	$\lambda$ (Cacti structural diversity) <sup>l</sup>	0.02(0.12)	-0.15;0.19							
3	$\lambda$ ( <i>Pilosocereus leucocephalus</i> )	0.61(0.23)	0.27;0.94	6	456.87	4.12	0.06	0.69	-222.18	
	$\lambda$ ( <i>Pilosocereus leucocephalus</i> ) <sup>l</sup>	-0.32(0.14)	-0.52;-0.12							
4	$\lambda$ (Epiphyte tree count)	0.58(0.24)	0.24;0.92	6	457.02	4.27	0.06	0.74	-222.26	
	$\lambda$ (Epiphyte tree count) <sup>l</sup>	-0.22(0.13)	-0.41;-0.04							
5	$\lambda$ (Patch size)	0.53(0.21)	0.22;0.84	6	457.66	4.91	0.04	0.78	-222.58	
	$\lambda$ (Patch size) <sup>l</sup>	-0.26(0.13)	-0.44;-0.08							
6	$\lambda$ ( <i>Opuntia hondurensis</i> )	0.03(0.14)	-0.17;0.23	6	458.01	5.26	0.03	0.82	-222.75	
	$\lambda$ ( <i>Opuntia hondurensis</i> ) <sup>l</sup>	-0.40(0.17)	-0.64;-0.16							
7	$\lambda$ (HCI)	0.25(0.21)	-0.05;0.55	6	458.32	5.56	0.03	0.85	-222.91	
	$\lambda$ (HCI) <sup>l</sup>	-0.34(0.19)	-0.62;-0.06							
8	$\lambda$ (Epiphyte tree count)	0.17(0.10)	0.02;0.32	5	459.50	6.75	0.02	0.86	-224.57	
9	$\lambda$ (.)	-0.11(0.19)	-0.39;0.17	4	459.72	6.97	0.01	0.88	-225.74	

<sup>†</sup> Number of parameters

<sup>‡</sup> Weight

<sup>§</sup> log-likelihood

<sup>l</sup> Variable with a quadratic term

date had a negative influence on Honduran Emerald detection, we consider that detectability was influenced negatively by variability in the detection history for any survey location, e.g., one individual detected in one point versus three in a different point (Royle 2004b, Dénes et al. 2015). In turn, we propose that the variability in detection history within each sampling period may reflect the patterns of hummingbird movement within the heavily fragmented study area that are driven by seasonal variability and availability of resources. That is, the need for individuals to periodically shift activity centers throughout the year in response to shifting floral resources, may translate to variability in detection history for any given survey location. Past studies have indicated how hummingbird detections vary per month, most likely because of flower availability driven by vegetation phenology in these environments (Arizmendi and Ornelas 1990, Murphy and Lugo 1995, Rodríguez-Flores and Wethington 2017). Furthermore, if floral resources are patchily distributed, hummingbird movements could be influenced by the landscape configuration making their availability and detection more variable (Hadley and Betts 2009, Volpe et al. 2014). Future studies that examine Honduran Emerald ecology at the territory or home range scales throughout the entire annual cycle will likely provide insight needed to understand mechanisms that explain the influence of Julian date on detection probability.

Our local abundance estimates extrapolated to the extent of dry forest remnants (2840 Honduran Emerald individuals, CI 95% 1880–4720) are comparable to population estimates for the Agalta Valley presented in the Endangered Species Act ruling for the species (United States Fish and Wildlife Service 2015). However, we suggest a caveat to this observation, which is the observed variability of abundance across our survey points that was influenced by microhabitat features described above. This influence reflects the variation of habitat conditions throughout the study area, thus making the assumption of a uniform distribution of Honduran Emeralds in the dry forest remnants difficult to meet (Kéry and Schmidt 2008). Nevertheless, our population estimate is valuable for understanding the current conservation status of this species in the Agalta Valley. The rate at which dry forest is being converted to cattle farms in the Agalta Valley will result in continued habitat loss that will negatively influence Honduran Emerald local abundance and ultimately its population dynamics. Between 2016 and 2017, two years after our study was conducted, at least 30 ha of dry forest were lost within our study sites based on a global forest cover change database (Hansen et al. 2013). As such, our abundance estimate supports the assertion by others that conservation of existing habitat is needed to prevent further population decline (Anderson et al.



2010, Mora et al. 2016). Such conservation actions should begin immediately and be implemented at biologically meaningful scales.

Our study is the first to account for imperfect detection in abundance estimates for the endangered Honduran Emerald. We provided additional insight on the species abundance patterns by estimating detection probability with a hierarchical modeling approach. In doing so, we avoided the assumption that detection probability is always perfect, and we correct by estimating the variability in detection to obtain an abundance estimate (Kéry and Schmidt 2008). We stress that future studies or monitoring aimed at estimating Honduran Emerald local abundance or population size use a framework that accounts for imperfect detection (Kéry and Schmidt 2008). Indeed, future Honduran Emerald surveys could be conducted when detection probability is expected to be high, i.e., September–December  $p = 0.23 \pm 0.12$ ). However, to relate abundance with reproductive success and assess habitat quality, surveys should be conducted within the breeding season (January–April; Rodríguez et al. 2016) and should include quantification of cacti structural diversity and shrub-sapling strata density. Equally important to future monitoring will be to conduct multiple visits to each survey point within these months, e.g., two-three visits, to counter the factors that contribute to imperfect detection (Royle 2004b). Parallel to the considerations in survey design to model Honduran Emerald abundance, our characterization of the vegetation at points used by Honduran Emeralds can be informative for future studies and conservation actions (Table 4). The microhabitat values we quantified may serve as a guideline for habitat restoration activities (Janzen 1988). Subsequently, different habitat managed treatments could be evaluated to assess their effectiveness for restoring and maintaining Honduran Emerald habitat.

Our research revealed how microhabitat features influence the local abundance of the endangered Honduran Emerald and how the use of modeling techniques for avian counts can be fine-tuned to inform the species status in the Agalta Valley. Similar work should be conducted in the other valleys where the Honduran Emerald is known to occur to obtain insight to the species status across its entire distributional range. Our study framework could be useful in other dry forests in the valleys of Aguán and Telica, which share similar composition and structure to the Agalta Valley (Anderson et al. 2010). Furthermore, because of past detections of the species in ecotones between dry forest and pine-oak in the Agalta Valley, a study that compares Honduran Emerald abundance between these two cover types should be conducted (Mora et al. 2016). Until more insight on Honduran Emerald ecology is gained from additional research and monitoring, conservation activities for this species should target dry forest protection and restoration, as well as promote dense shrub-sapling strata and structurally diverse cacti components. Periodic monitoring of Honduran Emerald response to conservation activities is warranted, but in a geography with limited conservation resources we urge that the immediate priority should be to focus available funding on working with landowners to protect existing dry forest and to restore additional areas.

Although our study focused on the relationship between microhabitat features and the abundance of a single species, our findings provide a broad reminder of the implications species

declines can potentially have on the intricate codependencies that exist between plant communities and their associated pollinators. For instance, Honduran Emerald local abundance was positively influenced by cacti structural diversity that included *Opuntia hondurensis*, suggesting that this imperiled hummingbird is likely a key pollinator of this dry forest endemic plant, as seen in other *Opuntia* sp. pollinated by hummingbirds (Díaz and Cocucci 2003). Researchers have previously highlighted the importance of hummingbirds as “generators of biodiversity” due to their pollination services (Arizmendi 2017). We are unaware of the magnitude of the role the Honduran Emerald plays as a pollinator of *Opuntia hondurensis* and other dry forest species, but it is well known that reductions in pollinator species diversity can have negative impacts on plant communities (Potts et al. 2010). For example, increasing the functional diversity of both pollinators and plants led to the persistence of more diverse plant communities (Fontaine et al. 2006). Moreover, reductions in pollinator functional diversity has the potential to initiate plant population declines or extinctions (Kearns et al. 1998). With tropical dry forests being floristically distinct across the Americas (Banda et al. 2016), understanding how hummingbirds and dry forest plant communities interact will need to go hand-in-hand to guarantee effective conservation of these tropical dry forests and the species they support. Indeed, studies that examine how reciprocal effects of pollinator species declines and plant species diversity influences the long-term stability of tropical dry forest ecosystems are warranted. Conservation efforts such as the one ongoing in the Agalta Valley, that acknowledge the needs of both human and natural communities, should increase awareness for the importance of plant-animal interactions and the need to work at both microhabitat and landscape scales to most effectively conserve those interspecific relationships.

*Responses to this article can be read online at:*  
<http://www.ace-eco.org/issues/responses.php/1321>

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#### Acknowledgments:

*We are grateful for the support of the community and producers of the tropical dry forest in San Esteban and Gualaco, department of Olancho in Honduras. We thank the valuable effort, field research, and herbarium work of Rosa Ramirez, Denis Padilla, as well as the team of the TEFH herbarium of the Universidad Nacional Autónoma de Honduras. We thank Elvin Urbina for his field research support. Special thanks to the team of the Asociación de Investigación para el Desarrollo Ecológico y Socioeconómico (ASIDE) and to American Bird Conservancy for their interest and support to conservation of the Honduran Emerald in Agalta Valley. Camila Gómez and John Herbert offered helpful comments and advice to improve this manuscript. Funding for this study was provided and managed by Inversión Estratégica de Honduras (INVESTH-MCA) and the Interamerican Development Bank (IDB).*

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**Appendix 1.** Spatial autocorrelation test for Honduran Emerald counts during three sampling periods within 2014-2015 in Agalta Valley.

Variable	Moran's I observed	Expected Moran's I	SD Moran's I	<i>p</i> uncorrected	<i>p</i> corrected
Counts sampling period 1	0.0091	-0.00578	0.01489	0.3174	1
Counts sampling period 2	-0.00595	-0.00578	0.01489	0.99	1
Counts sampling period 3	-0.01733	-0.00578	0.01461	0.4292	1

**Appendix 2.** Complete AICc results for Honduran Emerald detection models for all sampling periods in Agalta Valley during 2014-2015. In sampling period one, both observers conducted the count together for calibration purposes.

Sampling Period	K <sup>†</sup>	AICc	Δ AICc	AICc Wt <sup>‡</sup>	Cumulative Wt <sup>‡</sup>	LL <sup>§</sup>
<i>September-December</i>						
<i>p</i> (Julian date)	3	355.33	0.00	0.69	0.69	-174.59
<i>p</i> (Julian date <sup>⌋</sup> )	4	357.27	1.94	0.26	0.95	-174.52
<i>p</i> (Vegetation density <sup>⌋</sup> )	4	362.34	7.01	0.02	0.97	-177.05
<i>p</i> (.)	2	362.59	7.26	0.02	0.99	-179.26
<i>p</i> (Vegetation density)	3	364.48	9.15	0.01	1.00	-179.17
<i>March-April</i>						
<i>p</i> (Julian date <sup>⌋</sup> )	4	459.72	0.00	0.85	0.85	-225.74
<i>p</i> (Julian date)	3	463.14	3.42	0.15	1.00	-228.50
<i>p</i> (.)	2	476.50	16.77	0.00	1.00	-236.21
<i>p</i> (Observer)	3	477.55	17.83	0.00	1.00	-235.71
<i>p</i> (Vegetation density)	3	478.38	18.65	0.00	1.00	-236.12
<i>p</i> (Vegetation density <sup>⌋</sup> )	4	480.21	20.49	0.00	1.00	-235.99
<i>June-July</i>						
<i>p</i> (Julian date)	3	264.25	0.00	0.29	0.29	-129.05
<i>p</i> (Vegetation density <sup>⌋</sup> )	4	264.61	0.36	0.24	0.54	-128.19
<i>p</i> (.)	2	265.29	1.04	0.17	0.71	-130.61
<i>p</i> (Vegetation density)	3	265.98	1.74	0.12	0.83	-129.92
<i>p</i> (Julian date <sup>⌋</sup> )	4	266.29	2.04	0.11	0.94	-129.03
<i>p</i> (Observer)	3	267.36	3.11	0.06	1.00	-130.61

<sup>†</sup> Number of parameters

<sup>‡</sup> Weight

<sup>§</sup> log-likelihood

<sup>⌋</sup> Variable with quadratic term

**Appendix 3.** Complete AICc results for Honduran Emerald abundance models for two sampling periods in Agalta Valley during 2014-2015.

Sampling period	K <sup>†</sup>	AICc	Δ AICc	AICc Wt <sup>‡</sup>	Cumulative Wt <sup>‡</sup>	LL <sup>§</sup>
<i>September-December</i>						
<i>p</i> (Julian date) λ(Shrub strata density <sup>l</sup> )	5	348.70	0.00	0.64	0.64	-169.17
<i>p</i> (Julian date) λ(Shrub strata density)	4	353.36	4.67	0.06	0.70	-172.56
<i>p</i> (Julian date) λ(Stems under 3 cm <sup>l</sup> )	5	354.81	6.11	0.03	0.73	-172.23
<i>p</i> (Julian date) λ(Stems under 3 cm)	4	355.22	6.52	0.02	0.75	-173.49
<i>p</i> (Julian date) λ(.)	3	355.33	6.63	0.02	0.77	-174.59
<i>p</i> (Julian date) λ( <i>Eugenia hondurensis</i> <sup>l</sup> )	5	355.41	6.72	0.02	0.80	-172.53
<i>p</i> (Julian date) λ( <i>Pilosocereus leucocephalus</i> )	4	355.48	6.78	0.02	0.82	-173.62
<i>p</i> (Julian date) λ( <i>Eugenia hondurensis</i> )	4	356.01	7.32	0.02	0.83	-173.89
<i>p</i> (Julian date) λ(Cacti structural diversity)	4	356.51	7.81	0.01	0.85	-174.14
<i>p</i> (Julian date) λ( <i>Erythroxylum areolatum</i> )	4	356.60	7.91	0.01	0.86	-174.18
<i>p</i> (Julian date) λ( <i>Casearia nitida</i> )	4	356.64	7.94	0.01	0.87	-174.20
<i>p</i> (Julian date) λ(Epiphyte tree count)	4	356.79	8.09	0.01	0.88	-174.28
<i>p</i> (Julian date) λ(Patch size)	4	357.00	8.31	0.01	0.89	-174.38
<i>p</i> (Julian date) λ( <i>Opuntia hondurensis</i> )	4	357.06	8.36	0.01	0.90	-174.41



$p(\text{Julian date}) \lambda(\text{Vegetation density})$	4	357.21	8.51	0.01	0.91	-174.49
$p(\text{Julian date}) \lambda(\text{Species richness})$	4	357.25	8.55	0.01	0.92	-174.51
$p(\text{Julian date}) \lambda(\text{Cacti structural diversity})$	5	357.33	8.63	0.01	0.93	-173.48
$p(\text{Julian date}) \lambda(\textit{Acacia picachensis})$	4	357.35	8.65	0.01	0.94	-174.55
$p(\text{Julian date}) \lambda(\text{HCI})$	4	357.37	8.67	0.01	0.95	-174.56
$p(\text{Julian date}) \lambda(\textit{Opuntia hondurensis}^{\dagger})$	5	357.42	8.72	0.01	0.95	-173.53
$p(\text{Julian date}) \lambda(\textit{Pilosocereus leucocephalus}^{\dagger})$	5	357.45	8.75	0.01	0.96	-173.55
$p(\text{Julian date}) \lambda(\text{HCI}^{\dagger})$	5	357.90	9.21	0.01	0.97	-173.77
$p(\text{Julian date}) \lambda(\text{Epiphyte tree count}^{\dagger})$	5	358.10	9.40	0.01	0.97	-173.87
$p(\text{Julian date}) \lambda(\textit{Casearia nitida}^{\dagger})$	5	358.25	9.55	0.01	0.98	-173.95
$p(\text{Julian date}) \lambda(\text{Patch size}^{\dagger})$	5	358.31	9.61	0.01	0.98	-173.98
$p(\text{Julian date}) \lambda(\text{Vegetation density}^{\dagger})$	5	358.40	9.70	0.00	0.99	-174.02
$p(\text{Julian date}) \lambda(\textit{Erythroxylum areolatum}^{\dagger})$	5	358.57	9.88	0.00	0.99	-174.11
$p(\text{Julian date}) \lambda(\text{Species richness}^{\dagger})$	5	359.36	10.67	0.00	1.00	-174.50
$p(\text{Julian date}) \lambda(\textit{Acacia picachensis}^{\dagger})$	5	359.45	10.76	0.00	1.00	-174.55
$p(.) \lambda(.)$	2	362.59	13.90	0.00	1.00	-179.26
<i>March-April</i>						
$p(\text{Julian date}) \lambda(\text{Cacti structural diversity})$	5	452.75	0.00	0.47	0.47	-221.20
$p(\text{Julian date}) \lambda(\text{Cacti structural diversity}^{\dagger})$	6	454.87	2.11	0.16	0.63	-221.18

$p(\text{Julian date}) \lambda(\text{Pilosocereus leucocephalus}^{\dagger})$	6	456.87	4.12	0.06	0.69	-222.18
$p(\text{Julian date}) \lambda(\text{Epiphyte tree count}^{\dagger})$	6	457.02	4.27	0.06	0.74	-222.26
$p(\text{Julian date}) \lambda(\text{Patch size}^{\dagger})$	6	457.66	4.91	0.04	0.78	-222.58
$p(\text{Julian date}) \lambda(\text{Opuntia hondurensis}^{\dagger})$	6	458.01	5.26	0.03	0.82	-222.75
$p(\text{Julian date}) \lambda(\text{HCI})$	6	458.32	5.56	0.03	0.85	-222.91
$p(\text{Julian date}) \lambda(\text{Epiphyte tree count})$	5	459.50	6.75	0.02	0.86	-224.57
$p(\text{Julian date}) \lambda(.)$	4	459.72	6.97	0.01	0.88	-225.74
$p(\text{Julian date}) \lambda(\text{Patch size})$	5	460.00	7.25	0.01	0.89	-224.82
$p(\text{Julian date}) \lambda(\text{Casearia nitida})$	5	460.48	7.73	0.01	0.90	-225.06
$p(\text{Julian date}) \lambda(\text{Stems under 3 cm})$	5	460.55	7.79	0.01	0.91	-225.09
$p(\text{Julian date}) \lambda(\text{Species richness})$	5	460.79	8.04	0.01	0.92	-225.22
$p(\text{Julian date}) \lambda(\text{Species richness}^{\dagger})$	5	460.88	8.13	0.01	0.93	-224.19
$p(\text{Julian date}) \lambda(\text{Vegetation density})$	5	460.90	8.14	0.01	0.93	-225.27
$p(\text{Julian date}) \lambda(\text{Erythroxylum areolatum})$	5	461.33	8.57	0.01	0.94	-225.48
$p(\text{Julian date}) \lambda(\text{Pilosocereus leucocephalus})$	5	461.39	8.64	0.01	0.95	-225.52
$p(\text{Julian date}) \lambda(\text{Shrub strata density})$	5	461.52	8.77	0.01	0.95	-225.58
$p(\text{Julian date}) \lambda(\text{HCI})$	5	461.52	8.77	0.01	0.96	-225.58
$p(\text{Julian date}) \lambda(\text{Eugenia hondurensis})$	5	461.52	8.78	0.01	0.96	-225.58
$p(\text{Julian date}) \lambda(\text{Shrub strata density}^{\dagger})$	6	461.57	8.82	0.01	0.97	-224.53

$p(\text{Julian date}) \lambda(\textit{Opuntia hondurensis})$	5	461.74	8.98	0.01	0.97	-225.69
$p(\text{Julian date}) \lambda(\textit{Acacia picachensis})$	5	461.83	9.08	0.00	0.98	-225.74
$p(\text{Julian date}) \lambda(\textit{Acacia picachensis}^{\dagger})$	6	461.91	9.16	0.00	0.98	-224.70
$p(\text{Julian date}) \lambda(\text{Stems under 3 cm}^{\dagger})$	6	461.94	9.19	0.00	0.99	-224.72
$p(\text{Julian date}) \lambda(\textit{Casearia nitida}^{\dagger})$	6	462.50	9.75	0.00	0.99	-225.00
$p(\text{Julian date}) \lambda(\text{Vegetation density}^{\dagger})$	6	463.03	10.27	0.00	1.00	-225.26
$p(\text{Julian date}) \lambda(\textit{Erythroxylum areolatum}^{\dagger})$	6	463.04	10.29	0.00	1.00	-225.27
$p(\text{Julian date}) \lambda(\textit{Eugenia hondurensis}^{\dagger})$	6	463.61	10.86	0.00	1.00	-225.55
$p(\cdot) \lambda(\cdot)$	2	476.50	23.75	0.00	1.00	-236.21

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† Number of parameters

‡ Weight

§ log-likelihood

† Variable with quadratic term