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Research Paper

Factors influencing density of the Northern Mealy Amazon in three forest types of a modified rainforest landscape in Mesoamerica

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ABSTRACT. The high rate of conversion of tropical moist forest to secondary forest makes it imperative to evaluate forest metric relationships of species dependent on primary, old-growth forest. The threatened Northern Mealy Amazon (*Amazona guatemalae*) is the largest mainland parrot, and occurs in tropical moist forests of Mesoamerica that are increasingly being converted to secondary forest. However, the consequences of forest conversion for this recently taxonomically separated parrot species are poorly understood. We measured forest metrics of primary evergreen, riparian, and secondary tropical moist forest in Los Chimalapas, Mexico. We also used point counts to estimate density of Northern Mealy Amazons in each forest type during the nonbreeding (Sept 2013) and breeding (March 2014) seasons. We then examined how parrot density was influenced by forest structure and composition, and how parrots used forest types within tropical moist forest. Overall, parrot density was high in the breeding season, with few parrots present during the nonbreeding season. During the breeding season, primary forest had significantly greater density of 18.9 parrots/km² in evergreen forest and 35.9 parrots/km² in riparian forest, compared with only 3.4 parrots/km² in secondary forest. Secondary forest had significantly lower tree species richness, density, diameter, total height, and major branch ramification height, as well as distinct tree species composition compared with both types of primary forest. The number of parrots recorded at point counts was related to density of large, tall trees, characteristic of primary forest, and parrots used riparian forest more than expected by availability. Hence, the increased conversion of tropical moist forest to secondary forest is likely to lead to reduced densities of forest-dependent species such as the Northern Mealy Amazon. Furthermore, the species' requirement for primary tropical moist forest highlights the need to reevaluate conservation status of the Northern Mealy Amazon, and implement strategies to reduce forest conversion.

Facteurs influant sur la densité de l'Amazone guatémaltèque dans trois types forestiers d'un paysage altéré en forêt pluviale de Méso-Amérique

RÉSUMÉ. Le taux élevé de conversion des forêts tropicales humides en forêts secondaires rend impératif l'évaluation des relations entre les paramètres forestiers et les espèces dépendantes des vieilles forêts primaires. L'Amazone guatémaltèque (*Amazona guatemalae*), espèce menacée, est le plus gros perroquet continental; cette amazone s'observe dans les forêts tropicales humides mésoaméricaines, qui subissent de plus en plus de conversion en forêts secondaires. Cependant, les conséquences de la conversion forestière sur cette espèce, qu'on vient de séparer taxinomiquement, sont mal connues. Nous avons mesuré les paramètres dans des peuplements primaires de forêt tropicale humide d'arbres à feuillage persistant et riparienne, ainsi que dans des peuplements secondaires de forêt tropicale humide dans la région de Los Chimalapas, au Mexique. Nous avons aussi fait des dénombrements par point d'écoute pour estimer la densité d'Amazones guatémaltèques dans chaque type forestier, hors saison de nidification (septembre 2013) et en saison de nidification (mars 2014). Nous avons ensuite examiné de quelle façon la structure et la composition forestière influençaient la densité de ce perroquet, et comment les perroquets utilisaient les divers types forestiers de la forêt tropicale humide. Globalement, la densité de perroquets était élevée durant la saison de nidification et peu de perroquets étaient présents en dehors de cette saison. Durant la nidification, la forêt primaire accueillait des densités significativement plus élevées, tant dans les peuplements d'arbres à feuillage persistant (18,9 perroquets/km²) que les peuplements ripariens (35,9 perroquets/km²), comparativement à 3,4 perroquets/km² seulement dans les peuplements secondaires. En comparaison aux deux types de peuplements primaires, les paramètres suivants des peuplements secondaires étaient significativement plus faibles : la richesse spécifique d'arbres, la densité d'arbres, le diamètre, la hauteur totale, la hauteur de ramification des branches principales et la composition en certaines essences d'arbres. Le nombre de perroquets notés aux points d'écoute était relié à la densité de grands et gros arbres, caractéristiques des peuplements primaires, et les perroquets ont utilisé les peuplements ripariens au-delà de leur disponibilité. En somme, la conversion accélérée de la forêt tropicale humide en forêt secondaire va vraisemblablement mener à la réduction de la densité des espèces dépendantes des forêts telles que l'Amazone guatémaltèque. De plus, les besoins en matière de forêt tropicale humide primaire de l'Amazone guatémaltèque soulignent la nécessité de réévaluer son statut de conservation et d'élaborer des stratégies afin de diminuer la conversion forestière.

Key Words: *Amazona guatemalae; conservation ecology; forest conversion; forest structure and composition; General Additive Models; habitat use and availability; Psittacidae; tropical moist forest*

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INTRODUCTION

Land transformation due to anthropogenic activities affects almost half the Earth's surface, and is the primary driving force in the loss of biodiversity (Vitousek et al. 1997). Tropical moist broadleaf forest has one of the highest rates of deforestation, and is increasingly being reduced to forest remnants within a mosaic of agricultural land (Skole and Tucker 1993, de Jong et al. 2010). Tropical moist forest also has the highest rate of secondary forest succession (de Jong et al. 2010), where woody vegetation regrows after forest clearance, but these secondary forests tend to have low basal area, low variation in stem diameters, an even canopy height, and few large trees, compared to the original old-growth forests (Guariguata and Ostertag 2001). Species richness of birds declines with increasing forest disturbance (Lawton et al. 1998), and bird species that mainly inhabit forests are particularly prone to extinction risk (Şekercioğlu et al. 2004). This makes it imperative to evaluate avian habitat relationships of tropical species dependent on primary, old-growth forest that may be vulnerable to increased forest loss and conversion to secondary forest (Brook et al. 2006, Wright and Muller-Landau 2006*a,b*).

Almost a third of Psittaciformes (parrots) are currently threatened (BirdLife International 2016*a*), the majority of which occur in the Neotropics (Olah et al. 2016). Among these, the genus *Amazona* has the greatest species richness, two-thirds of which are internationally considered threatened (Snyder et al. 2000). The main cause of decline for the majority of threatened Psittaciformes is through anthropogenic impacts of agriculture, capture for trade, and logging, with large-bodied, forest-dependent parrot species more likely to be threatened (Olah et al. 2016). Large-bodied parrot species exhibit low population densities, and tend to be associated with primary forests (Marsden 1999, Marsden and Pilgrim 2003, Symes and Marsden 2007, Lee and Marsden 2012). In particular, forest structural characteristics of tree diameter, height, and canopy cover influence psittacine density (Marsden 1992, Evans et al. 2005, Marsden and Symes 2006). Nevertheless, the majority of studies have been conducted on Psittaciformes of Papua New Guinea and the Indonesian islands (Marsden and Royle 2015), and we have very limited information on the response to forest loss of threatened parrot species in tropical moist forests of continental America.

The near-threatened Northern Mealy Amazon (*Amazona guatemalae*) is one of the largest Amazon parrot species in continental America, and occurs in Mesoamerica from southern Mexico to western Panama (Forshaw 1989, Birdlife International 2016*b*). Given that the Northern Mealy Amazon has only recently been taxonomically separated from the more widely distributed Southern Mealy Amazon (*Amazona farinosa*) in South America (Wenner et al. 2012, del Hoyo and Collar 2014), it is essential to determine the status and ecological requirements of the Northern Mealy Amazon in Mesoamerica. However, only one study has been conducted on the Northern Mealy Amazon, which determined that the species undertakes long-distance seasonal movements from the Petén in Guatemala to tropical moist forest in southern Mexico (Bjork 2004).

Forest loss is one of the main factors affecting wild populations of the Northern Mealy Amazon, and in Mesoamerica area of forest cover has declined at an annual rate of 0.5%, with a forest area loss of 4186 km² per year from 1990–2015 (FAO 2015). Mexico contains three quarters of Mesoamerican forests, but has experienced the greatest annual decline in forest area (FAO 2015). Notably, in Mexico, the Northern Mealy Amazon has now been extirpated from a large part of its historic range, suffering a 45% to 46.8% reduction from its original distribution (Ríos-Muñoz and Navarro-Sigüenza 2009, Monterrubio-Rico et al. 2016).

In the present study, we aimed to evaluate forest metrics associated with density of Northern Mealy Amazons, and determine whether parrots used forest types according to availability in the modified landscape of Los Chimalapas, Mexico. We hypothesized that the large-bodied Northern Mealy Amazon would occur at low density, and be associated with primary tropical moist forest, that is characterized by a high density of large, tall trees. Therefore, specific objectives of our study were the following: (1) to determine density of Northern Mealy Amazons in three forest types of primary evergreen tropical moist forest (evergreen hereafter), primary riparian tropical moist forest (riparian hereafter), and tropical moist forest at various stages of secondary succession (secondary hereafter); (2) to identify differences among forest types in metrics of forest structure and tree species richness; (3) to evaluate relationships of metrics of forest structure and tree species composition with occurrence and number of parrots at point counts; and (4) to determine whether use of forest types by Northern Mealy Amazons differed from availability of forest types in the landscape. In this way, we aimed to identify forest types with high parrot density that are used disproportionately by Northern Mealy Amazons, and forest metrics that influence parrot density, so as to guide management and conservation for this large, threatened parrot species.

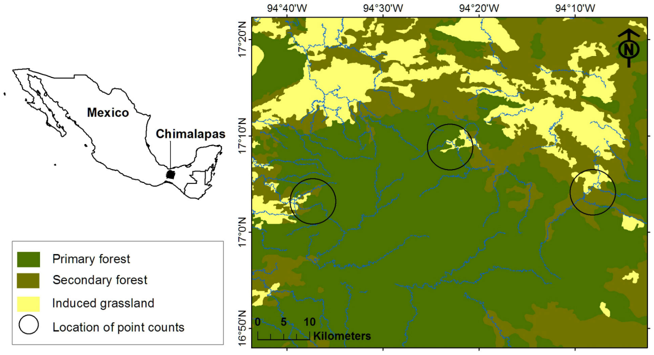
METHODS

Study area

We conducted the study in the highland region of Los Chimalapas (17°08' - 17°02' N, 94°38' - 94°08' W; Fig. 1) in northeastern Oaxaca, Mexico. The 6000 km² region of Los Chimalapas is owned and managed by the Zoque indigenous group, and is one of the most biologically diverse areas in Mesoamerica that is largely unstudied (Peterson et al. 2003, Navarro-Sigüenza et al. 2008). Annual rainfall is 2000 – 4500 mm, with average temperatures 22 – 26°C, and a short dry season from March to June (Trejo 2004). The region has an elevation range of 70 – 1800 m asl, where tropical moist forest covers 64% of the landscape (Martínez-Pacheco 2012).

Los Chimalapas comprises predominantly primary evergreen forest covering 1866.3 km², with common tree species of *Dialium guianense*, *Terminalia amazonia*, and *Cojoba arborea* (Torres Colín 2004). Primary riparian forest occurs along permanent rivers, mainly below 500 m asl, and comprised 491.9 km² of land cover. Common tree species of riparian forest are *Ficus* sp., *Garcinia macrophylla*, *Vochysia guatemalensis*, and *Inga vera* (Torres Colín 2004). Clearance of primary forest followed by later abandonment of cleared plots has resulted in the regrowth of secondary forests that comprised 120.5 km² of land cover in Los Chimalapas by 2003 (Martínez-Pacheco 2012). The Northern Mealy Amazon occurs in northern Chimalapas, in the Municipality of Santa Maria Chimalapa, which is located within the tropical moist broadleaf forest biome (Olson et al. 2001). Therefore, we surveyed parrots and measured forest metrics at point counts in three forest types of evergreen, riparian, and secondary forest below 600 m asl, across a 60 km section of the Municipality of Santa Maria Chimalapa.

Fig. 1. The study area in northern Chimalapas, Mexico, showing the modified tropical moist forest landscape, main rivers (dark lines), and the general location of point counts.



Parrot surveys

To determine the density of Northern Mealy Amazons in the landscape matrix of Los Chimalapas, we established 120 variable radius point counts, stratified as 60 in primary forest, and 60 in secondary forest. Within the primary forest, we located 33 point counts in tropical evergreen forest and 27 point counts in riparian forest. Point counts were separated by 250 m to increase independence of counts (Marsden 1999). Reproductive activity of the Northern Mealy Amazon commences in January with nest-site selection and copulation by breeding pairs (Bjork 2004). Nests are initiated in late February with the start of egg-laying, and nesting continues through to early July when the last chicks fledge (Bjork 2004). Therefore, we conducted surveys of parrots in the breeding season of March 2014 and the nonbreeding season of September 2013.

All surveys were conducted by the same observer (MADLH), and each point count was surveyed only once in both the breeding and nonbreeding season. We conducted a 10 min count at each point to increase the likelihood that birds close to the observer were detected (Marsden 1999). We recorded all parrots seen or heard, and noted the number of parrots, form of detection (observation, vocal), whether the parrot was perched, and compass direction of the detection. We also measured distance from the observer to the bird with a Bushnell Yardage Pro 450 range-finder. Surveys were conducted after sunrise and until 10:30 h, which is the period of greatest parrot activity (Marsden 1999).

Forest structure and composition

At each point count we marked out a 25-m radius circular plot to survey forest structure, and composition in an area of 1963.5 m^2 around the point. Within this survey plot we determined the number of trees with diameter at breast height (dbh) ≥10 cm. We considered 10 cm dbh as the lower limit for trees recorded in our surveys because this is frequently used in forest surveys (Bullock and Solis-Magallanes 1990, Chapman et al. 1994), and large trees are more likely to be used by the Northern Mealy Amazon, which is a large-bodied canopy species (Greenberg 1981, Loiselle 1988, Bjork 2004). For each tree, we measured dbh at 1.3 m height using a 10 m diameter tape, and determined total tree height, and ramification height to the first major branch, using a tree-measuring pole extendable to 15 m for trees < 15 m height, and a Criterion RD 1000 digital dendrometer for trees > 15 m height. Trees that ramify at over half their total height are indicative of having grown in shady closed-canopy conditions of primary forest, whereas trees that ramify at less than half their total height are indicative of having grown in more open conditions of disturbed or secondary forests (Torquebiau 1986). These variables of forest structure could therefore provide an indication of the condition of forests around each point count.

We also identified tree species within each 25-m radius circular plot using reference guides of Pennington and Sarukhán (1998), and Vázquez Torres et al. (2010). Where tree species could not be identified in the field, we collected samples for identification in the Herbario Nacional of the Instituto de Biología, Universidad Nacional Autónoma de México in Mexico City. In particular, we recorded the abundance of tree species used as resources by mealy parrots (*A. guatemalae*, and *A. farinosa*) because abundance of tree species used as food or nest-site resources has been found to influence occurrence and density of other parrot species (Kinnaird et al. 2003, Berkunsky et al. 2015). Tree species occurring in Santa Maria Chimalapa that have been reported in the diet or used as nest-sites by mealy parrots (Bjork 2004, Lee et al. 2014) include *Terminalia amazonia*, *Dialium guianense*, *Ficus* sp., *Spondias mombin*, *Ochroma pyramidale*, and *Sloanea meianthera* (Table A1.1).

Statistical analyses

To ensure that parrots were using the particular forest type, rather than just flying over, we used only records of perched individuals to estimate parrot density per forest type (Marsden 1999). We modeled Northern Mealy Amazon density using the program Distance 6.0 (Thomas et al. 2010), but could only model density estimates for the breeding season because we did not have sufficient records of perched birds to model parrot density in the nonbreeding season. We used the Multiple Covariates Distance Sampling engine of Distance 6.0, both to increase the reliability of density estimates where there may be few observations in a subset of data by forest type, and to enable inferences regarding covariates of forest structure (Marques et al. 2007). We included the forest structure covariates of tree density, mean tree dbh, and mean tree height recorded at each point count. However, we excluded mean tree ramification height to the first major branch because this was strongly correlated with total tree height ($r = 0.81$, $P < 0.5$), and highly correlated variables may lead to bias in density estimates (Marques et al. 2007). Data were not truncated so as to include the greatest number of detections of perched birds. We used a stratification approach to analyze survey data by forest type, which together with the incorporation of covariates, minimizes heterogeneity in detection probabilities (Buckland et al. 2001, Marques and Buckland 2003). We generated Distance models using the half-normal and hazard functions, with cosine and simple polynomial series adjustments, and all combinations of covariates (Table A1.2).

We used Akaike Information Criteria (AIC) to evaluate model fit and complexity (Buckland et al. 2001). We then calculated the difference in AIC of each model with the lowest AIC model

(ΔAIC), and their Akaike weights (*wi*), to identify parsimonious candidate models that had ΔAIC ≤ 2 (Burnham and Anderson 2002, Wagenmakers and Farrell 2004). We selected the most appropriate density model based on their AIC *wi* ratios that may be interpreted as the conditional probability of being the model with best fit to the data (Wagenmakers and Farrell 2004). Finally, we evaluated the importance of each covariate by calculating the sum of AIC *wi* of all models containing the covariate (Symonds and Moussalli 2011).

We then used the Distance model that had best fit to the data to obtain Northern Mealy Amazon density estimates, and their 84% confidence intervals, for each forest type. Density estimates were considered to differ significantly among forest types where upper and lower 84% confidence intervals did not overlap because this robustly mimics the 0.05 probability obtained from statistical tests (Payton et al. 2003, MacGregor-Fors and Payton 2013).

To determine whether forest types differed in species richness and forest structure around point counts, we compared metrics of tree species richness, tree density, mean tree dbh, mean tree height, and mean ramification height among evergreen, riparian, and secondary forests. Data did not present a normal distribution, therefore we applied Kruskal-Wallis ANOVA to compare metrics among forest types. Where significant differences were detected, we applied Dunn posthoc analysis to determine which forest type contributed the significant difference (Zar 1999). We also calculated the Morisita index of similarity to compare the abundance of each tree species among the three forest types (Krebs 1999).

To evaluate relationships of the complete set of forest structure and tree species composition metrics with occurrence and number of parrots recorded at point counts, we first used principal component analysis (PCA) to convert 11 forest metrics to a reduced set of composite axes. These included four forest structure variables of tree density, mean dbh, mean tree height, and mean ramification height, as well as seven floristic composition variables of tree species richness, and the abundance of each of the six common tree species used as resources by mealy parrots (*T. amazonia*, *D. guianense*, *Ficus* sp., *S. mombin*, *O. pyramidale*, and *S. meianthera*). We retained only the principal components with eigenvalues > 1, which were incorporated as predictor variables in generalized additive models (GAMs) to evaluate their relationships with number of parrots and presence/absence of parrots at point counts. We used GAMs because these are less restrictive, generating nonlinear response curves that are modeled as a series of additive smoothing functions dictated by the data (Hastie and Tibshirani 1986). This is more suited to deal with nonlinear complex relationships that may occur in nature. We fitted penalized cubic regression splines to the data to control complexity of the curve (degrees of freedom) and avoid overfitting (Wood 2006). We used the mgcv package in R (Wood 2011, R Core Team 2016) to run Poisson GAMs to model the relationship with number of parrots recorded at point counts, and binomial GAMs to model the presence/absence of parrots perched within a 50-m radius of the point count. We identified the model with lowest AIC as having the best fit to the data (Buckland et al. 2001), and calculated ΔAIC and AIC *wi* to identify competing models (Burnham and Anderson 2002), and their conditional probability of being the best-fitting model (Wagenmakers and Farrell 2004).

Finally, to determine whether use of forest types by Northern Mealy Amazons differed from that expected by availability, we applied *G*-test to compare the number of parrots recorded in each forest type with the number of parrots expected based on availability of forest types. For observed use in each forest type, we considered only parrots perched within a 50-m radius around each point count. We determined proportional availability of each forest type using estimates of land-cover area determined for Los Chimalapas by Martínez-Pacheco (2012) based on 28.5-m resolution Landsat ETM satellite images from 2000–2003. We calculated riparian forest cover considering a 50-m band-width at each side of permanent rivers in the region, which were overlaid from a hydrogeological map of 1:250,000 (INEGI 2012) using the QGIS 2.12 Geographic Information System (QGIS Development Team 2015). To obtain the expected number of parrots in each forest type, we multiplied the total number of parrots recorded over all forest types by the proportional land cover of each forest type. This gave the number of parrots that would be expected in each forest type based on the proportional availability of that forest type in the landscape, which was compared with the observed number of parrots recorded in each forest type.

To determine whether a particular forest type was used by parrots significantly more than expected, we generated simultaneous Bonferroni confidence intervals for the proportional use observed for each forest type, applying an alpha adjusted to $P < 0.017$ for the set of three forest types (Nue et al. 1974, Byers et al. 1984). Utilization differs significantly when the expected proportion of use based on availability falls outside the adjusted alpha confidence interval of actual use (Byers et al. 1984), with the resource category being used either more or less than expected by availability. All statistical analyzes were carried out using R version 3.3.0 (R Core Team 2016). Descriptive statistics are presented as mean with standard deviation, except where stated, and we considered $P < 0.05$ as significantly different in statistical analysis.

RESULTS

Parrot density

We obtained 133 detections of Northern Mealy Amazons in Los Chimalapas, although the majority of these were obtained during the breeding season with a total of 128 detections in March 2014, compared to only 5 detections during the nonbreeding season of September 2013. During the breeding season, detections were made at a mean distance of 47.7 ± 28.9 m (range = 17 – 120 m, n = 29) in evergreen forest, 37.8 ± 22.2 m (range = 4 – 90 m, n = 46) in riparian forest, and 85.8 ± 57.9 m (range = 5 – 254 m, n = 53) in secondary forest. We recorded a mean 3.1 ± 3.6 parrots per 10 min point count in the breeding season, with a mean group size of 2.8 ± 2.3 parrots (range = 1 – 12 parrots). By comparison, parrots were largely absent from the study site during the nonbreeding season, recording an average of only 0.15 ± 1.0 parrots per 10 min point count in September 2013, with a mean group size of 4.6±2.9 parrots (range = 2 – 9 parrots).

We obtained three candidate Distance models that had ΔAIC ≤ 2 for density of Northern Mealy Amazons during the breeding season (Table A1.2). Of these, the model with lowest AIC and coefficient of variation (25.6%) included the two covariates of tree density and mean tree height, and was generated using the

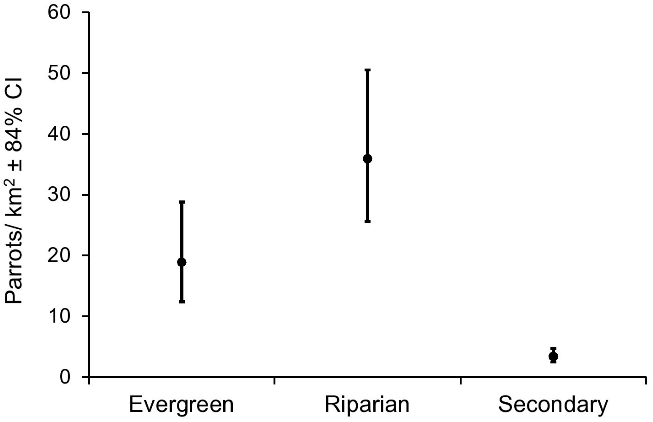
Table 1. Multiple-covariates Distance Sampling model parameters for density estimates to 84% confidence intervals of Northern Mealy Amazons (*Amazona guatemalae*) during the breeding season (March 2014) in Los Chimalapas, Mexico.

Stratum	Number of point counts	Mean density (ind/km² ± SE)	Mean cluster size (ind ± SE)	Mean density of cluster (ind/km² ± SE)	Effective detection radius (m) ± SE
Global	120	19.5 ± 6.2	2.8 ± 0.2	6.3 ± 2.9	61.7 ± 4.7
Evergreen forest	33	18.9 ± 5.7	4 ± 0.5	4.7 ± 1.2	57.8 ± 5.5
Riparian forest	27	35.9 ± 8.7	2.8 ± 0.3	12.6 ± 2.6	55.5 ± 4.3
Secondary forest	60	3.4 ± 0.8	2.1 ± 0.2	1.5 ± 0.3	73.5 ± 5.3

half-normal probability function with cosine adjustment (Table A1.2). This model was 2.0 and 2.4 times more likely to be the best explanation for parrot density compared with the second and third models, respectively. Furthermore, this best-fitting model incorporated the two covariates with greatest weight over all models, where the most important covariate was mean tree height (sum AIC *wi* = 0.87), followed by mean tree density (sum AIC *wi* = 0.65). By comparison, mean tree dbh was not included in the best-fitting model, and had lower importance in the models (sum AIC *wi* = 0.41).

The best-fitting Distance model estimated an overall mean density of 19.5 ± 6.2 Northern Mealy Amazons/km² (84% CI: 13.5 – 28.1) during the breeding season (Table 1). Density estimates of parrots were significantly higher in both types of primary forest, with 18.9 ± 5.7 parrots/km² (84% CI: 12.5 – 28.9) in evergreen forest, and 35.9 ± 8.7 parrots/km² (84% CI: 25.6 – 50.5) in riparian forest, compared to only 3.4 ± 0.8 parrots/km² (84% CI: 2.5 – 4.8) in secondary forest (Fig. 2).

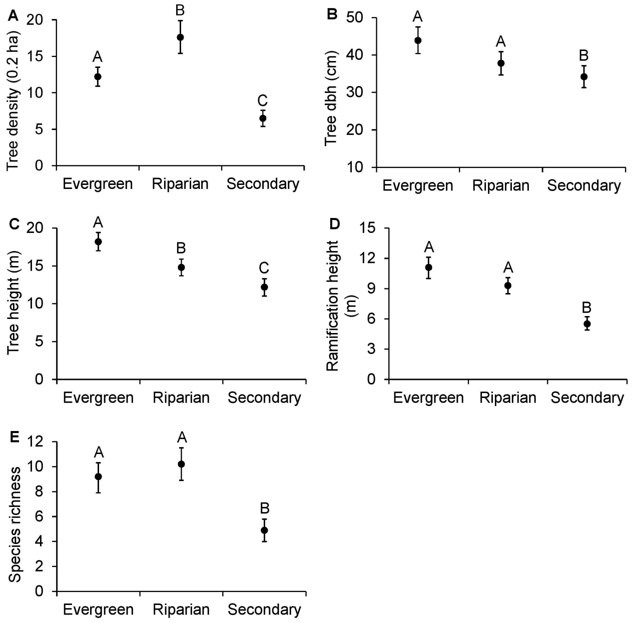
Fig. 2. Northern Mealy Amazon (*Amazona guatemalae*) density estimates with 84% confidence intervals in evergreen, riparian, and secondary tropical moist forest in Los Chimalapas, Mexico, during the breeding season of March 2014.



Forest structure and composition

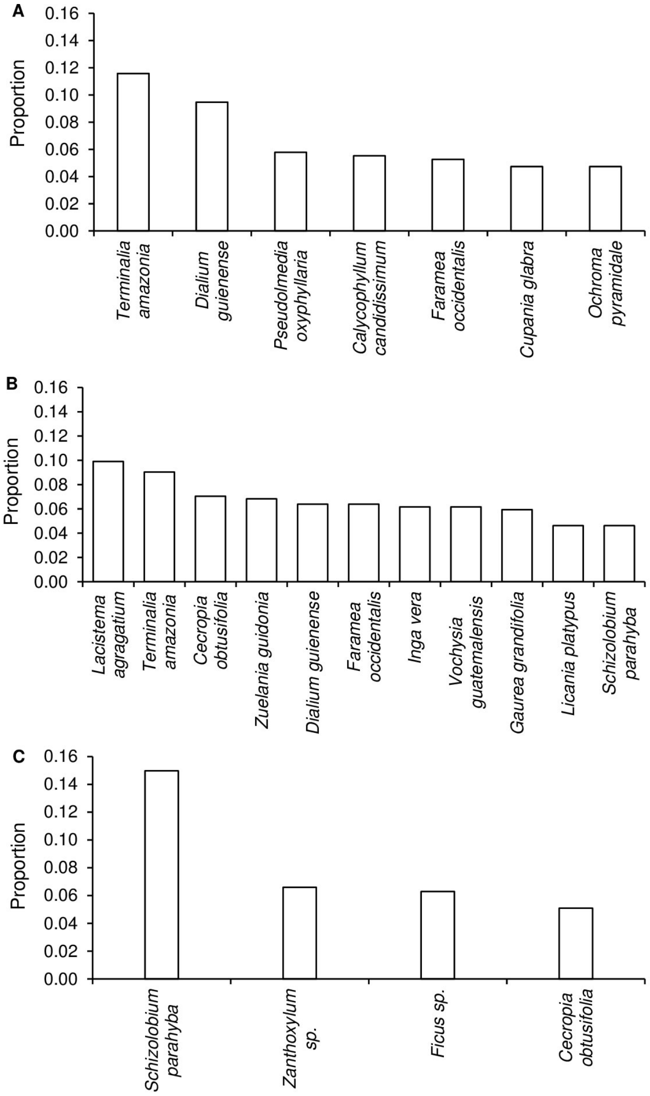
Forest structure within a 25-m radius of point counts differed significantly among forest types (Fig. 3). Secondary forest had significantly fewer trees ($H_2 = 62.7$, $P < 0.001$; Fig. 3A) than evergreen ($q = 5.0$, $P < 0.001$) and riparian ($q = 7.4$, $P < 0.001$) forests, where tree density was 47% and 63% lower in secondary forest compared to evergreen and riparian forest, respectively (Fig. 3A). Tree density also differed significantly between the two primary forest types ($q = 2.5$, $P < 0.05$), being 31% higher in riparian compared to evergreen forest (Fig. 3A). Moreover, forest types differed in mean tree dbh ($H_2 = 18.8$, $P < 0.001$; Fig. 3B), total height ($H_2 = 40.8$, $P < 0.001$; Fig. 3C), and ramification height ($H_2 = 54.3$, $P < 0.001$; Fig. 3D). In all cases, secondary forest differed from the two primary forest types (Fig. 3), having trees with 22% and 10% smaller dbh, respectively (Evergreen: $q = 4.3$, $P < 0.001$, Riparian: $q = 2.0$, $P < 0.05$), of 32% and 16% lower total height (Evergreen: $q = 6.4$, $P < 0.001$, Riparian: $q = 2.8$, $P < 0.01$), and 51% and 41% lower ramification height (Evergreen: $q = 6.9$, $P < 0.001$, Riparian: $q = 4.8$, $P < 0.001$). Furthermore, within primary forest, trees in evergreen forest had significantly greater total height ($q = 2.9$, $P < 0.01$), being 19% taller than trees in riparian forest (Fig. 3C).

Fig. 3. Variation among forest types in metrics of trees (≥ 10 cm dbh) within a 25-m radius of point counts for (A) tree density in 0.2 ha, (B) tree diameter at breast height (cm), (C) total tree height (m), (D) ramification height to the first major branch (m), and (E) tree species richness, in tropical moist forest of Los Chimalapas, Mexico. Mean values per point count with 95% confidence intervals are shown. Letters indicate significantly different Dunn posthoc pairwise comparisons among forest types.



Species richness of trees was also significantly lower in secondary forest ($H_2 = 42.6$, $P < 0.001$), with 47% fewer species than evergreen forest ($q = 5.6$, $P < 0.001$), and 52% fewer species than riparian ($q = 4.9$, $P < 0.001$) forest (Fig. 3E). Tree species composition was similar between evergreen and riparian forest (Morisita = 0.66), whereas secondary forest differed in species composition compared to evergreen (Morisita = 0.42) and riparian (Morisita = 0.46) forest. The most abundant tree species in evergreen forest were *Terminalia amazonia* and *Dialium guianense* (Fig. 4A), and these were also among the most abundant tree species in riparian forest (Fig. 4B). By comparison, the most common tree species in secondary forest was the fast-growing *Schizolobium parahyba* (Fig. 4C).

Fig. 4. Proportional abundance of tree species within a 25-m radius of point counts in (A) evergreen, (B) riparian, and (C) secondary tropical moist forest in Los Chimalapas, Mexico. Only tree species contributing > 5% of tree abundance in each forest type are shown.



Relationship of forest metrics with parrot occurrence

The 11 forest structure and composition variables were reduced to three principal components that explained 94.7% of the variation (Table 2). Principal Component 1 explained 63.3% of the variance, and the variable with greatest weight was mean tree dbh ($r = 0.93$; Table 2). Principal Component 2 explained 25.2% of the variance, and was influenced by tree density ($r = 0.81$; Table 2). Finally, Principal Component 3 explained only 6.2% of variance, and was mainly influenced by mean tree height ($r = 0.71$; Table 2).

Table 2. Principal components analysis of forest structure and floristic composition variables within a 25-m radius of point counts in tropical moist forest of Los Chimalapas, Mexico ($r > 0.7$ marked in bold font).

	Component 1	Component 2	Component 3
Eigenvalue	3.7	1.9	1.2
% Explained	63.3	25.2	6.2
Correlations with individual variables			
Mean tree diameter at breast height	**0.93**	0.23	0.27
Tree density	0.12	**0.81**	0.16
Mean tree height	0.28	0.14	**0.71**
Mean ramification height	0.19	0.25	0.49
Species richness	0.07	0.44	0.36
Terminalia amazonia	0.04	0.06	-0.05
Dialium guianense	0.04	0.08	-0.05
Ficus sp.	(-)	(-)	0.06
Spondias mombin	(+)	-0.01	0.02
Ochroma pyramidale	(-)	(+)	-0.08
Sloanea meianthera	(-)	-0.03	0.02

Poisson GAMs for number of parrots recorded at point counts revealed a single candidate model, which incorporated all three principal components, and this model explained 73.8% of the deviance (Table A1.3a). Therefore, abundance of Northern Mealy Amazons at point counts during the breeding season was most likely influenced by forest structure of a high density of large, tall trees.

Binomial GAMs for presence/absence of parrots perched within a 50-m radius of the point count revealed two candidate models (Table A1.3b). The first model included all three principal components and explained 34.9% of deviance (Table A1.3b), with a 53% likelihood of being the best model. A competing model comprised principal Components 1 and 2 and explained 29.5% of deviance (Table A1.3b), and had an almost equal 45% likelihood of being the best model. However, the first model including all three principal components was 1.2 times more likely to provide the best fit for parrot occurrence compared with the second model containing only the first two principal components. Therefore, parrots may be more likely to perch within 50 m of a point count in forest with a high density of large trees.

Finally, use of forest types by Northern Mealy Amazons differed significantly from that expected by availability of forest types in the landscape ($G_2 = 39$, $P < 0.001$). Almost all records of Northern Mealy Amazons perched within 50 m of point counts occurred in primary forest (94% of perched birds), with very few parrots (6%) recorded within 50 m of point counts in secondary forest (Table 3). In particular, parrots were most frequently recorded in primary riparian forest (54% of perched birds), and used this forest type more than expected by availability (Table 3).

Table 3. Proportional availability and use of three forest types by Northern Mealy Amazons, with Bonferroni confidence intervals, in tropical moist forest of Los Chimalapas, Mexico, during the breeding season of March 2014. * = $P < 0.05$

Forest type	Proportion available	Proportion used	Bonferroni confidence intervals
Evergreen forest	0.75	0.40	$0.26 \le obs \le 0.55$*
Riparian forest	0.20	0.54	$0.39 \le obs \le 0.68$*
Secondary forest	0.05	0.06	$0.00 \le obs \le 0.13$

DISCUSSION

Parrot density

During the breeding season we recorded an overall density of 19.5 ± 6.2 Northern Mealy Amazons/km² in the tropical moist forest of Los Chimalapas, Mexico, with greatest density in primary forest. This is relatively high compared to other large-bodied parrots that have density estimates of less than 14 individuals/km² (Symes and Marsden 2007, Lee and Marsden 2012), and is higher than the density estimate of 13.6 parrots/km² for the Southern Mealy Amazon in tropical moist forest of South America (Lee and Marsden 2012). By comparison, high densities of 22.5 – 29 parrots/km² are usually recorded for smaller parrot species (Marsden and Symes 2006). The unexpectedly high density of Northern Mealy Amazons in tropical moist forest of Los Chimalapas during the breeding season highlights the importance of the region for this threatened species. Therefore, large tracts of tropical moist forest such as Los Chimalapas may be biologically important not only for their high biodiversity (Peterson et al. 2003), but also because they support high densities of threatened species.

Notably, Northern Mealy Amazons were almost absent from Los Chimalapas during the nonbreeding season, with such low encounter rates that it was not possible to model density estimates. Various studies have reported seasonal variation in abundance of psittacines (Renton 2002, Karubian et al. 2005, Lee and Marsden 2012), suggesting that parrots make seasonal movements among areas. Bjork (2004) also recorded a decline in relative abundance of the Northern Mealy Amazon during the nonbreeding season in the Petén of Guatemala, and showed that Northern Mealy Amazons undertake migrations of 138 ± 61.9 km from the Petén in Guatemala to Campeche and Chiapas in Mexico. Therefore, it is highly likely that Northern Mealy Amazons in Los Chimalapas are undertaking similar long-distance migrations during the nonbreeding season to potential alternative sites of El Ocote (80 km) or La Sepultura Biosphere Reserve (135 km) in Chiapas. Future research could apply radio-telemetry techniques (Bjork 2004) to identify alternate migration sites used by Northern Mealy Amazons in Mexico.

We also determined spatial variation in Northern Mealy Amazon density with a low density of parrots in secondary forest. Other studies have demonstrated lower parrot densities in human modified forests. Marsden and Pilgrim (2003) found lower densities of the Blue-eyed Cockatoo (*Cacatua ophthalmica*) in disturbed forests on Papua New Guinea, and Kinnaird et al. (2003) determined higher densities of the Salmon-crested Cockatoo (*Cacatua moluccensis*) in primary forests with high basal area and canopy closure. Similarly, Karubian et al. (2005) found that relative abundance of large macaws declined with increasing levels of human activity and landscape modification. These studies all relate to large parrot species, and along with the results obtained for the Northern Mealy Amazon, suggest that large threatened parrot species in particular may be more closely associated with primary forests.

Factors influencing use of forest types by parrots

Northern Mealy Amazons in Los Chimalapas were more frequently recorded within 50-m of point counts in primary evergreen and riparian forests during the breeding season, and used riparian forests significantly more than expected by availability, whereas parrots were rarely encountered in secondary forest. This corresponds with the findings of Bjork (2004) for the Northern Mealy Amazon in the Petén of Guatemala, who determined greater relative abundance of Northern Mealy Amazons in primary forest, whereas parrots were rarely observed perched in secondary forest. These results provide further support that the Northern Mealy Amazon is a primary forest specialist throughout its range in Mesoamerica.

Furthermore, the occurrence and number of parrots perched within a 50-m radius of point counts was predicted by the density of large, tall trees around the point count. This is similar to studies in lowland Atlantic forest of Brazil where use of selectively logged forests by two Amazon parrot species was associated with large trees (Marsden et al. 2000). Legault et al. (2011) also found that presence of three parrot species in New Caledonia is related to canopy cover, where parrots selected areas with 80–100% canopy cover, avoiding areas with less than 20% canopy cover. Density of large trees was the main environmental variable influencing the abundance of avian species associated with primary tropical wet forest in Malaysia (Peh et al. 2005). Our results therefore indicate that during the breeding season Northern Mealy Amazons are strongly associated with primary forests where there is a greater density of canopy trees.

Comparison with Southern Mealy Amazon

The high seasonal fluctuation in abundance of Northern Mealy Amazons in Los Chimalapas, Mexico, corresponds with a similar seasonal fluctuation in abundance of Northern Mealy Amazons in the Petén of Guatemala (Bjork 2004). By comparison, Lee and Marsden (2012) recorded only slight seasonal variation in density of the Southern Mealy Amazon in floodplain forest of Southeast Peru. Therefore, it may be that the Northern Mealy Amazon in Mesoamerica exhibits greater seasonality in use of forest areas compared to the Southern Mealy Amazon in the Amazonian forests of South America.

Humid forests in Mesoamerica demonstrate marked seasonality in fruiting phenology, generally with peak fruit production during the dry season and in the transition from dry to wet season, while in South America the variation in fruiting phenology is less marked (Morellato et al. 2013). Given the high seasonality in fruit production of Central American forests, animal species that depend on these resources need to track fluctuations in resource abundance (Leighton and Leighton 1983, Fleming 1992). This could potentially lead to seasonal movements by the Northern Mealy Amazon in Central America, and Bjork (2004) determined that the seasonal decrease in abundance of Northern Mealy Amazons in Guatemala was associated with a corresponding decline in fruit production, suggesting that parrots make movements in search of food resources.

The Northern Mealy Amazon may also be facing greater pressures of forest loss resulting from anthropogenic activities compared to the Southern Mealy Amazon. In Mesoamerica, tropical moist forest is becoming increasingly fragmented (Holzman 2008). Added to which, the Northern Mealy Amazon has large area requirements making seasonal movements over an area of 10,000 km² (Bjork 2004). The dependence of Northern Mealy Amazons on primary tropical moist forest, and their high seasonality in abundance and use of areas, emphasizes the need to conserve tracts of continuous primary tropical moist forest for the Northern Mealy Amazon in both breeding and migration areas.

Implications of tropical moist forest conversion

The results of our study demonstrate the importance of primary tropical moist forest, and in particular riparian forest, for the large-bodied Northern Mealy Amazon during the breeding season. Within the modified landscape of Los Chimalapas, secondary forest had distinct structural and floristic characteristics to primary forest, with a low density of smaller trees of lower tree and ramification height, indicative of trees of disturbed or regenerating forests (Torquebiau 1986). Secondary forests also had lower tree species richness and distinct species composition to that of primary evergreen and riparian forests. Hence, conversion of primary forest to secondary forest may have a negative effect on the status of Northern Mealy Amazon populations in the wild, as determined for the Carnaby's Cockatoo (*Zanda latirostris*) in the wheatbelt of Western Australia, which was unable to exploit dispersed food resources in fragmented landscapes resulting in eventual extirpation of the species (Saunders 1990). Tropical moist forests have the greatest rate of biomass loss of all forest types in Mexico and present the highest increment in secondary forests (de Jong et al. 2010). This may be detrimental to Northern Mealy Amazon populations in the long-term because secondary forest had significantly lower densities of Northern Mealy Amazons. It should be noted however, that forest metrics associated with population density are not necessarily indicative of high fecundity (van Horne 1983), therefore we also require information on the reproductive output of Northern Mealy Amazons to evaluate the respective quality of each forest type for parrots.

Anthropogenic activities of clearing for agriculture or cattle grazing have been the main cause of primary forest loss in Los Chimalapas (Martínez-Pacheco 2012). Over the period of 2000 – 2003, there was an overall loss of 22 km² of tropical moist forest in the region, whereas the area dedicated to pasture lands increased by 29 km² (Martínez-Pacheco 2012). As for the majority of Mexico's forests, tropical moist forest in Los Chimalapas is owned by the local community with rights to exploit and sell timber and forest products (Bray et al. 2005). No legally protected areas exist within Los Chimalapas, and a recent proposal for the area to be considered a community ecological reserve was rejected by the Mexican government (Anaya and Álvarez 1994). This makes it imperative to establish community-based forest conservation and management strategies to maintain tropical forest resources and biodiversity in Los Chimalapas.

CONCLUSIONS

Understanding the requirements of large threatened parrot species such as the Northern Mealy Amazon is essential to develop appropriate strategies for forest management and conservation, and to assess the potential impact of anthropogenic activities on parrot populations in modified landscapes. Large-bodied, frugivorous, canopy species are among the avian species unlikely to persist in modified forests (Peh et al. 2005), however, almost nothing is known of the ecological requirements of the Northern Mealy Amazon in Mesoamerica. The results of our study in Mexico, and that of Bjork (2004) in Guatemala, both suggest that the Northern Mealy Amazon is a primary forest specialist that exhibits marked seasonality in use of forest areas. Therefore, the Northern Mealy Amazon in Central America may present important differences in ecological requirements from that of the Southern Mealy Amazon in South America. Northern Mealy Amazons are also under increased pressure from forest loss and capture for the pet trade, making their populations especially vulnerable, and in need of immediate evaluation, and possible status reclassification.

Los Chimalapas in Mexico, and Petén in Guatemala, represent some of the largest tracts of primary tropical moist forest in Mesoamerica. However, both regions are suffering high rates of forest loss (Martínez-Pacheco 2012, Hodgdon et al. 2015), further reducing the availability of primary tropical moist forest for the Northern Mealy Amazon. As determined in our study, the increased conversion of primary tropical moist forest to secondary forest (de Jong et al. 2010) is likely to lead to reduced densities of large, threatened species such as the Northern Mealy Amazon. Brook et al. (2006) argue that afforestation via secondary forest succession may be a poor substitute for primary forest, particularly for the fraction of species that depend on primary old-growth forest, and do not persist in disturbed tropical forest (Peh et al. 2005). This makes it essential to implement strategies and incentives to conserve primary tropical moist forest in relatively undisturbed regions such as Los Chimalapas (Peterson and Navarro Sigüenza 2016), and reduce the rate of conversion to secondary forest, if we are to maintain populations of large forest-dependent species in the long term.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/957

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Appendix 1. Supplementary tables of model parameters used in Distance and GAM analyses.

Table A1.1. Tree species occurring in our study site that are reported in the diet or used as nest-sites by mealy parrots (*Amazona guatemalae* and *A. farinosa*)

Family/Plant species	Data sourced	Region	Country	Reference
Apocynaceae				
Aspidosperma megalocarpo	Diet	Central and South America	Guatemala, Peru	Bjork 2004, Lee et al. 2014
Anacardiaceae				
Astronium graveolens	Diet	South America	Peru	Lee et al. 2014
Spondias mombin	Nest-tree	Central America	Guatemala	Bjork 2004
Bombacaceae				
Ochroma pyramidale	Diet	South America	Peru	Lee et al. 2014
Clusiaceae				
Calophyllum brasiliense	Nest-tree and diet	Central America	Guatemala	Bjork 2004
Combretaceae				
Terminalia amazonica	Nest-tree and diet	Central America	Guatemala	Bjork 2004
Fabaceae				
Dialium guienense	Diet	South America	Peru	Lee et al. 2014
Enterolobium cyclocarpum	Nest-tree	Central America	Guatemala	Bjork 2004
Vatairea lundelii	Nest-tree and diet	Central America	Guatemala	Bjork 2004
Elaeocarpaceae				
Sloanea sp.	Diet	South America	Peru	Lee et al. 2014
Moraceae				
Brosimun alicastrum	Nest-tree and diet	Central and South America	Guatemala, Peru	Bjork 2004, Lee et al. 2014
Ficus sp.	Nest-tree and diet	Central and South America	Guatemala, Peru	Bjork 2004, Lee et al. 2014
Sapotaceae				
Manilkara zapota	Nest-tree	Central America	Guatemala	Bjork 2004
Pouteria sapota	Nest-tree	Central America	Guatemala	Bjork 2004

Table A1.2. Multiple-covariates distance sampling models with forest structure covariates for density of Northern Mealy Amazons during the breeding season (March 2014) in tropical moist forest of Los Chimalapas, Mexico. Models are ordered by the lowest Akaike's Information Criterion (AIC), with delta Akaike differences (ΔAIC), and Akaike weights (AIC*wi*) between models. K = number of parameters; % CV = Coefficient of Variation for each density model.

Model and adjustment terms	Covariates	% CV	K	AIC	ΔAIC	AIC*wi*
Half-normal cosine	Tree density + mean height	25.6	5	1220.0	0.0	0.26
Half-normal simple polynomial	Tree density + mean height	80.8	5	1221.3	1.3	0.14
Half-normal cosine	Tree density + mean height + mean dbh	25.9	6	1221.7	1.7	0.11
Half-normal cosine	mean height	25.7	4	1222.5	2.5	0.07
Half-normal cosine	mean dbh + mean height	25.9	5	1222.6	2.6	0.07
Half-normal simple polynomial	mean height	63.1	4	1223.3	3.3	0.05
Hazard simple polynomial	mean dbh + mean height	25.8	4	1223.3	3.3	0.05
Hazard cosine	mean dbh + mean height	25.8	4	1223.3	3.3	0.05
Half-normal simple polynomial	mean dbh + mean height	65.6	5	1223.8	3.8	0.04
Hazard simple polynomial	Tree density + mean dbh	31.2	5	1223.9	3.9	0.04
Half-normal cosine	Tree density + mean dbh	25.7	5	1224.5	4.5	0.03
Half-normal cosine	Tree density	25.7	4	1224.6	4.6	0.03
Hazard cosine	Tree density + mean dbh	25.4	4	1225.9	5.9	0.01
Hazard simple polynomial	mean height	90.3	5	1226.1	6.1	0.01
Half-normal simple polynomial	Tree density	79.9	4	1226.3	6.3	0.01
Hazard simple polynomial	Tree density + mean height	25.7	5	1226.6	6.6	0.01
Half-normal simple polynomial	Tree density + mean dbh	80.3	5	1226.7	6.7	0.01
Hazard cosine	Tree density + mean height	25.4	4	1228.1	8.1	0.00
Hazard simple polynomial	Tree density	25.8	4	1228.6	8.6	0.00

Hazard simple polynomial	Tree density + mean height + mean dbh	59	6	1228.7	8.7	0.00
Hazard cosine	Tree density + mean height + mean dbh	60.8	5	1229.3	9.3	0.00
Hazard cosine	Tree density	25.9	4	1230.6	10.6	0.00
Hazard simple polynomial	mean dbh	25.6	4	1231.3	11.3	0.00
Hazard cosine	mean dbh	25.4	3	1231.4	11.4	0.00
Hazard cosine	mean height	25.3	3	1231.4	11.4	0.00
Half-normal cosine	mean dbh	25.5	4	1234.8	14.8	0.00
Half-normal simple polynomial	mean dbh	57.8	4	1236.0	16.0	0.00

Table A1.3. Results of GAMs incorporating three principal components (PC) to predict: a) abundance, and b) presence of Northern Mealy Amazons during the breeding season (March 2014) in a modified landscape of tropical moist forest, Los Chimalapas, Mexico. Models are ordered by the lowest Akaike's Information Criterion (AIC), with delta Akaike differences (ΔAIC), and Akaike weights (AIC*wi*) between models. K = total number of parameters.

a) Number of Northern Mealy Amazons at point count

Models	Deviance explained (%)	K	AIC	Δ AIC	AIC*wi*
PC1 + PC2 + PC3	73.8	4	508.3	0.0	1.0
PC1 + PC2	57.3	3	543.9	35.6	0.0
PC2 + PC3	50.4	3	576.7	68.4	0.0
PC2	37.6	2	596.8	88.5	0.0
PC1+ PC3	37	3	636.1	127.8	0.0
PC1	26.1	2	674.9	166.6	0.0
PC3	11.6	2	718.9	210.6	0.0

b) Presence of Northern Mealy Amazons within 50 m of point count

Models	Deviance explained (%)	K	AIC	Δ AIC	AIC*wi*
PC1 + PC2 + PC3	34.9	4	94.1	0.0	0.53
PC1 + PC2	29.5	3	94.4	0.3	0.45
PC2 + PC3	28.1	3	101.6	7.5	0.01
PC2	20.7	2	103.4	9.3	0.01
PC1 + PC3	12.9	3	106.6	12.5	0.00
PC1	7.5	2	108.1	14	0.00
PC3	3.8	2	112.1	18	0.00