

LEK HABITAT SELECTION BY FOUR SYMPATRIC MANAKINS IN NORTHWESTERN
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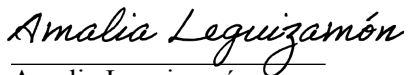
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ABSTRACT

Habitat selection plays a fundamental role in determining community structure and species coexistence and may especially contribute to the mating success of co-occurring, lek-breeding species. The ecological characteristics of selected lek sites were compared for four species of sympatric manakins in the Chocó Rainforest of northwestern Ecuador. Manakins are ecologically similar, both in terms of resource use and their dependence on elaborate visual signaling for mate choice. For such ecologically similar species, we expected the placement of lek sites to either overlap in areas of high resource availability, given their shared diets, or segregate along environmental characteristics associated with visual signaling, as each manakin has distinct coloration and thus, requires distinct forest microenvironments for optimal visual signaling. We found that the leks of different species were associated with distinct environmental characteristics, suggesting that these sympatric manakins may select display sites based on factors related to visual signaling. We observed considerable overlap in the lek habitat characteristics of two species (*Ceratopipra mentalis* and *Lepidothrix coronata*), although they significantly differed in display perch height. *Manacus manacus* exhibited the broadest lek habitat space, which aligns with their generalist tendencies. In contrast, the leks of *Masius chrysopterus* were entirely distinct in habitat space from the other three, suggesting the lek habitat of this species may be comparatively constrained and the potential for conservation risk. Further study is needed to evaluate whether forest light environments differ between the four species, and whether or not those differences contribute to lek site selection.

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CHAPTER 1: INTRODUCTION

Habitat selection is an important ecological and evolutionary phenomenon that influences population dynamics and community structure (Morris, 2003). Organisms are generally thought to select habitats that maximize their fitness (McLoughlin et al., 2006), and when species overlap in physical or niche space, competitive interactions or habitat partitioning may occur (Morris, 2003). Habitat selection can also have downstream consequences for mating success (Hingrat et al., 2006). As such, recognizing factors that influence habitat selection is crucial to understanding species' behavioral ecology and coexistence.

The role of habitat selection in mating success may be especially pronounced in lek-mating species, wherein males aggregate in fixed locations (“leks”) to perform elaborate courtship displays. Females visit these sites to select partners for copulation (Mackenzie et al., 1995), and only a small number of males typically succeeds in obtaining mating opportunities (Lill, 1974; Payne & Payne, 2010). Lekking males are often characterized by colorful, extravagant plumage to attract females for copulation (Oakes, 1992), and the attributes of a male's display habitat can influence the transmission and perception of these visual mating signals (Menezes & Santos, 2019). For example, males depend on light environments conducive to successful mating displays and may therefore select lek sites based on their light environments (Heindl & Winkler, 2003). Alternatively, males may select their display habitats to minimize predation risk, favoring lek locations where the surrounding topography either maximizes predator visibility to males at the lek or minimizes visibility of lekking males to predators (Alonso et al., 2012). Lastly, males may choose display sites that increase proximity to resources, as proposed by the hotspot hypothesis, which suggests that males aggregate in areas where they are more likely to encounter females (Bradbury et al., 1986). However, the ecological factors that influence lek placement and spatial positioning are understudied, particularly as it relates to

habitat partitioning of closely related species with similar ecological and behavioral niches (Loiselle et al., 2007).

Manakins (Pipridae) are a family of Neotropical passerine birds that exhibit lek-mating systems, known for elaborate male plumage and mating displays (Prum, 1994). Manakins are polygynous lek-breeding birds, wherein females have independent home ranges and visit male territorial leks to mate (Durães et al., 2007). They are abundant in the American tropics, with 16 named species of manakins in Ecuador alone, many co-occurring locally (Loiselle et al. 2007). When similar species occur in sympatry and exploit the same resources, they often adopt distinct patterns of resource or microhabitat use (Bazzaz & Catovsky, 2001). Yet, how these co-occurring, closely related species select their lek sites is an open question with important implications for basic ecology and the evolution of sexual signals. A previous study demonstrated that six sympatric species in eastern Ecuador select distinct microhabitats for lek sites, with leks of different manakin species being generally segregated by elevation and incline slope (Loiselle et al., 2007). However, it remains unknown whether these dynamics occur more broadly, and what other factors that influence lek site selection when lekking species occur in sympatry.

We examined the ecological factors associated with lek site selection in four species of sympatric manakins. To do so, we compared the habitat characteristics at lek sites of blue-crowned (*Lepidothrix coronata*), white-bearded (*Manacus manacus*), golden-winged (*Masius chrysopterus*), and red-capped (*Ceratopipra mentalis*) manakins. These species co-occur in the Chocó Rainforest of northwestern Ecuador, are characterized by strong sexual dichromatism and elaborate male courtship displays, and feed generally on the same fruit species, making them a useful system for investigating patterns of habitat selection and niche partitioning (Loiselle & Blake, 1999). Lek habitat variables such as canopy height, and forest openness may vary among species, reflecting differential preference for physical properties of leks that increase mating success. Also, use of the habitat, for example perch height, may also vary between species. If manakins are selecting their lek sites based on resource availability, we would expect to see all

four species select lek sites that overlap in environmental space, as these manakins share the same diet and largely have the same ecological needs. Alternatively, if manakins are selecting their lek sites based on habitat characteristics influencing visual signals, we would expect distinct segregation of lek sites in environmental space, as species-specific plumage coloration may necessitate distinct forest microenvironments for optimal visual signaling. Resolving the ways in which lek sites of different species segregate on the basis of environmental correlates allows for stronger understanding of lek-system ecology, habitat selection, and manakin population coexistence.

CHAPTER 2: METHODS

We conducted this study in the Mache Chindul Ecological Reserve, located in the Chocó Rainforest of northwestern Ecuador. The Chocó Rainforest is listed as a top biodiversity hotspot globally, as measured by high rates of diversity, endemism, and habitat loss (Myers et al., 2000). Despite being of high conservation priority, this ecosystem is greatly understudied. Research was focused at two sites—the Fundación para la Conservación de los Andes Tropicales Reserve (FCAT, 0°22.387' N, 79°39.919' W; 550 ha) and Bilsa Biological Station (BBS, 0°20.816' N, 79°42.659' W; 3500 ha). We exhaustively sampled approximately 50% of BBS and 70% of the FCAT reserve for manakin leks and opportunistically sampled surrounding forest fragments. We had previously determined the location of several lek sites in the area over nearly two decades of previous work in the area. However, we surveyed for new leks, confirmed activity for previously identified leks, and gathered relevant data for the current study by systematically searching, listening to, and observing manakins from July - September 2020, a period known to overlap with high lek activity.

For the purposes of this study, we only used a specific location (i.e., tree branch or display court) where an adult male was observed displaying and singing on at least two separate occasions (separated by at least one week) during the three-month sampling period. We considered these locations to be male display territories within a lek. To avoid pseudoreplication, we sampled a single male display territory per lek for habitat variables (below) and perch height. We ensured that there was a minimum distance of at least 200 m between each male display territory we measured and the nearest conspecific male display territory, to ensure that each display site corresponded to a unique and distinctive lek. To quantify the environmental characteristics of each lek site, we measured six key habitat variables: elevation, canopy cover, number of trees with diameters at breast height (DBH) between 10 and 50cm (DBH>10) within a 10m radius, trees with DBH greater than 50cm (DBH>50) within a 20m radius, and the

abundance of the pioneer tree species *Cecropia* spp. within a 10m radius. *Cecropia* species serve as indicators of disturbance (Zalamea et al., 2012), while trees with DBH > 50cm indicate relatively undisturbed and more intact forests. A spherical densiometer was used to quantify the amount of light entering the canopy, with measurements taken in the four cardinal directions and averaged. To evaluate habitat use differences between the species, we also measured perch height.

Statistical Analyses

We used discriminant function analysis to investigate whether different species of manakin leks overlapped in environmental space (following Loiselle et al. 2007). Discriminant function analysis is a form of dimensionality reduction that optimizes the distance between means to maximize the separability of *a priori* groups (Tharwat et al., 2017). In this case, the *a priori* groups were the four manakin species. All analyses were conducted in version 1.2.1335 of R (R Core Team, 2013) and discriminant function analysis was used to determine the composite axis loadings for the lek habitat variables. The datapoints collected for each lek were centered and scaled prior to use in analyses. We used an ANOVA followed by Bonferroni-corrected t-tests to compare perch heights between the four manakins to further evaluate differential habitat use.

CHAPTER 3: RESULTS

Environmental Correlates of Leks

We collected habitat measures at total of 44 lek sites, including 16 *Ceratopipra mentalis* leks, 16 *Manacus manacus* leks, 6 *Lepidothrix coronata* leks, and 6 *Masius chrysopterus* leks (Figure 1). Discriminant function analysis identified elevation, number of surrounding *Cecropia* spp., canopy height, number of surrounding trees with DBH>10 or DBH>50, and canopy cover as the most useful variables for differentiating leks of different species. The first discriminant function explains 53.75 percent of the between-group variation and separates leks by elevation, canopy height, and number of surrounding *Cecropia* spp. (Figure 2; Table 1). The second discriminant function explains 30.83 percent of the between-group variation and separates leks based on canopy height, elevation, and number of large trees (i.e., DBH > 50cm) (Figure 2; Table 1). Finally, the third discriminant function (not shown) explains 15.41 percent of the between-group variability and separates leks according to the proportion of large trees (i.e., DBH >50cm vs. DBH>10), number of *Cecropia*, and canopy height (Table 1).

Manakin leks separate along axes of elevation and canopy height. *Ceratopipra mentalis* and *Lepidothrix coronata* lek sites overlap almost entirely in environmental space and overlap with *Manacus manacus* lek sites particularly along the first discriminant function (Figure 2). *Manacus manacus* was found to have the broadest niche, which was expected as *Manacus manacus* are more generalists than the other three species. *Masius chrysopterus* leks achieve near-complete separation from the leks of other species along the first discriminant function, likely due to their exclusive occurrence at the higher-elevation site to have the least overlap in lek habitat space with other species (Figure 2).

Using the jackknife (i.e., "leave-one-out") prediction method, 61.36% of the 44 leks were correctly classified to species based on environmental correlates. *Ceratopipra mentalis* leks were classified with 81.25% accuracy, *Manacus manacus* with 56.25% accuracy, *Masius chrysopterus* with 50% accuracy, and *Lepidothrix coronata* with 33.33% accuracy (Table 2).

Use of perches

Ceratopipra mentalis were observed to generally use thin branches at heights between 3 to 8 meters as lek sites, wherein males use these perches to perform fast dances as well as rest for long periods of time. *Masius chrysopterus* males were seen to perform their displays on roots that grow lying on the ground. The dances are performed for short periods before the males return to their perches at heights between 2 to 6 meters. *Manacus manacus* move among shrub branches from the ground up to 4 meters, though they perform at leks that are close to the ground by jumping from the ground to branches less than a meter high. *Lepidothrix coronata* males were observed to perform displays on perches very close to the ground (30 centimeters) up to branches of the forest canopy. This species has a large range of movement in the forest, both horizontally and vertically.

Display perch height also varied across the four species (ANOVA: $df_{3,40}$; $F = 16.51$; $p < 0.0001$). Based on pairwise Bonferroni-corrected t-tests, the display perches of *Ceratopipra mentalis* (mean = 7.56 ± 0.88 m) were significantly higher than the other three species (*C. mentalis* vs. *L. coronata*, $p = 0.00013$; *C. mentalis* vs. *M. manacus*, $p < 0.0001$; *C. mentalis* vs. *M. chrysopterus*, $p = 0.00073$), whereas there was no significant difference in perch height among *L. coronata* (mean = 1.87 ± 0.45 m), *M. manacus* (mean = 2.06 ± 0.42 m), or *M. chrysopterus* (mean = 2.52 ± 0.61 m) ($p > 0.05$; Table 3).

CHAPTER 4: DISCUSSION

In general, we found that each of the four focal manakin species preferentially select lek sites with certain, distinctive environmental characteristics, either in terms of habitat structure, when structural components of structure overlapped, or in terms of height off the forest floor. The environmental correlates that most strongly segregated lek placements by species were elevation, canopy height, and number of *Cecropia* spp. These are variables that may reflect degree of forest disturbance (e.g., *Cecropia* and canopy height) and that may affect ambient light preferences, competition for display sites, or niche partitioning. While *C. mentalis* and *L. coronata* overlapped greatly in lek space, the lek placements of *Masius chrysopterus* were entirely distinct from the other three, which could potentially imply restricted habitat suitability and heightened ecological limitations on lek placement for *Masius chrysopterus*. Such limitations may contribute to the relatively small abundance of *Masius chrysopterus* leks observed. *Manacus manacus* had the broadest range of lek placements, many alongside forest edges with open canopy, which may relate to optimal light environment preferences for mating signals.

The four manakins share similar plumage features, having mainly black bodies with different, vivid, pigmentation on each manakin's respective crown, except for *Manacus manacus* which has a black body with a white belly, throat, and nape. Such color patches, and the manakin's reliance on visual displays, makes these manakins ideal species to study differential forest light environments and their impact on sexual signaling. Previous studies suggest that ambient light plays a significant role in the mating success of lek-breeding birds. Perception of color, in this case, plumage, is dependent on the interaction between the light environment and the reflectance color of the animal and can thereby affect the distinction of visual signaling for mates (Endler & Théry, 1996). Previous studies have indicated four distinct forest light environments for visual signaling, all of which reflect different wavelengths of light. Thus, manakin color patches and their interactions with forest spectral conditions could influence patterns of lek placement. There are some indications from our study that manakins may select lek sites with preferential light

environments for mating. First, there is relatively strong separation among most species pairs in environmental space in the LDA analysis, consistent with each species seeking different light environments. Moreover, among the only two species with high overlap in the LDA analysis, closer analysis showed that *Ceratopipra mentalis* constructed lek sites at higher perch heights than the other three species, perhaps allowing for coexistence with the otherwise closely sympatric *Lepidothrix coronata*.

However, there are also reasons to be skeptical of the visual signal hypothesis. Discriminant function analysis showed that across all three axes, canopy cover *per se* was not a prominent selective environmental correlate. Canopy cover was found to load more moderately along discriminant function 2, suggesting that *Ceratopipra mentalis* and *Lepidothrix coronata* lek sites have slightly more canopy cover than either *Manacus manacus* or *Masius chrysopterus*, however, canopy cover was not as strong a differentiator as several other variables on discriminant function 2 (Table 1). However, canopy height and other structural attributes of habitat did vary and there are many other fine-scale features of forest light environments that we did not explore in this study, such as reflectance spectra measurements, vegetation geometry, sun angle, and weather (Théry, 2001). Future studies could comprehensively measure the spectral composition of each manakins' plumage and corresponding lek light environment to analyze potential differences in ambient light environments, thus giving us a better understanding of what light environments are used during lek displays and how selection influences lek placement. Thorough ambient light measurements may further explain lek segregation patterns in relation to light environments.

The relatively strong separation among species in the LDA analysis is not consistent with resource partitioning. Because available diet data shows that both species largely consume the same plant species (Loiselle, Blake, Durães, Ryder, & Tori, 2007) we would also expect their lek site selection to overlap if proximity to fruiting resources were driving habitat selection. However, as with visual signals, we were unable to directly measure the distribution of fruiting resources and this hypothesis also requires additional work. In addition to overlapping diet, these

species of manakins could overlap in visual and auditory space. As song and dance are key components to successful manakin mating displays, coinciding displays may muddle sexual signals and prevent female choice. *Ceratopipra mentalis* and *Lepidothrix coronata* lek sites overlap in ecological space, however, *Ceratopipra mentalis* constructed lek sites at higher perch heights than the other three species. *Ceratopipra mentalis* and *Lepidothrix coronata* may further mitigate competition by selecting display perches at different heights, which may also enable each species to take advantage of different light wavelengths higher in the canopy vs. the forest floor. Thus, separation in vertical space may serve two functions: (1) mitigating interspecific competition and (2) enhancing species-specific color patches during displays.

Manacus manacus had the largest range of lek sites, aligning with their generalist tendencies (Ridgely & Greenfield, 2006). *Manacus manacus* lek sites frequently occur at the edges of secondary and gallery forests, and due to their preference for edges, seem to adapt well to anthropogenically disturbed environments. *Manacus manacus* lek sites are found in more open canopy, as expected for secondary forest, which may be associated with optimal light environments for *Manacus manacus* visual signaling. Previous studies have indicated four distinct forest light environments for visual signaling, all of which reflect different wavelengths of light (Endler & Thery, 1996). One light environment, large gap light, is associated with very open canopy and is rich in almost all wavelengths, letting in essentially white light. Such a light environment could enhance the white plumage of males during displays, which may explain the tendency of *Manacus manacus* to choose lek sites in open canopy areas.

The relatively low abundance of *Masius chrysopterus* sites may reflect limited environmental space for their leks. *Masius chrysopterus* lek sites were entirely distinct from the other three, having constructed leks at higher elevations with higher canopy heights, fewer surrounding large trees (i.e., DBH >50cm), and relatively few surrounding *Cecropia* spp. *Masius chrysopterus* only occur in these high elevation sites, and thus we are unable to disentangle whether *Masius chrysopterus* is restricted to high elevations for reproductive reasons (e.g., particular lek habitat

requirements), or whether other aspects of its ecology (e.g., diet) or physiology constrain its occurrence to these high elevation sites, unrelated to lek placement. Based on these findings, we suggest *Masius chrysopterus* may prefer to construct lek sites in minimally disturbed forest environments at the upper limit of elevation gradients, alluding to conservation implications for *Masius chrysopterus*, which may not adapt to anthropogenically disturbed conditions and climate change as well as the other three manakins. In relation to lek elevation selection, *Masius chrysopterus* may have a narrower thermal tolerance response to temperature than the other three manakins. This could further culminate in reduced acclimatization, limited dispersal capabilities, and increased vulnerability to climate change and disturbance.

More research is necessary to evaluate lek selection on the basis of environmental features, specifically regarding differential light environments as a component of visual signaling. The discriminant function analysis was able to classify some leks more accurately than others, perhaps due to evident overlap in environmental space (Table 2). High overlap in the environmental space defined by discriminant function analysis, particularly with *Ceratopipra mentalis* and *Lepidothrix coronata* lek sites, may contribute to lek misclassification. The relatively low sampling of *Masius chrysopterus* may reflect habitat limitations, and thus, a skewed representation of lek site selection within the area sampled. Further exploration of ambient forest light environments and distribution of fruiting resources may elucidate manakin lek habitat selection.

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Fig. 1. Location of manakin leks on two study plots, BBS and FCAT, within the Mache Chindul Ecological Reserve.

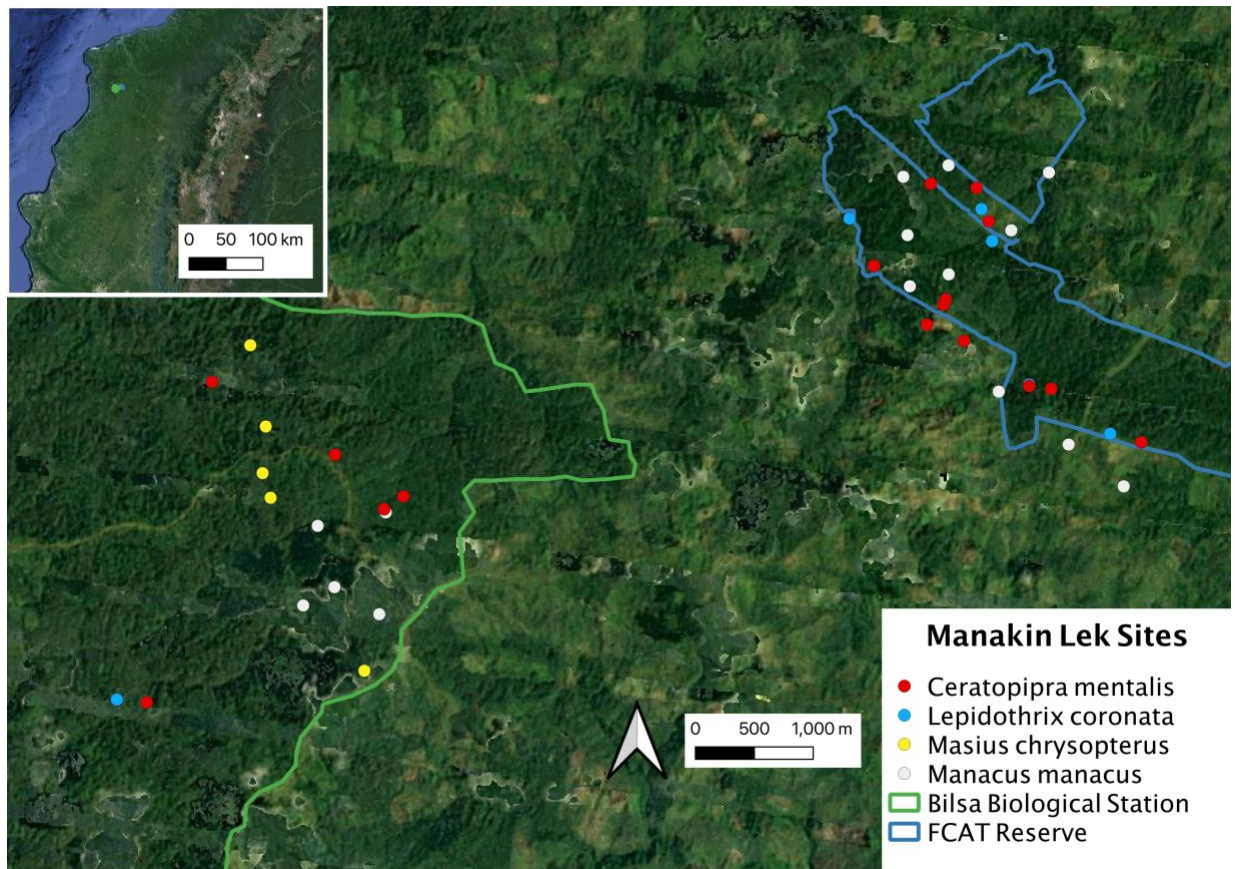


Fig. 2. Location of leks of four sympatric manakin species in northwest Ecuador (n = 44) in environmental space based on the results of discriminant function analysis.

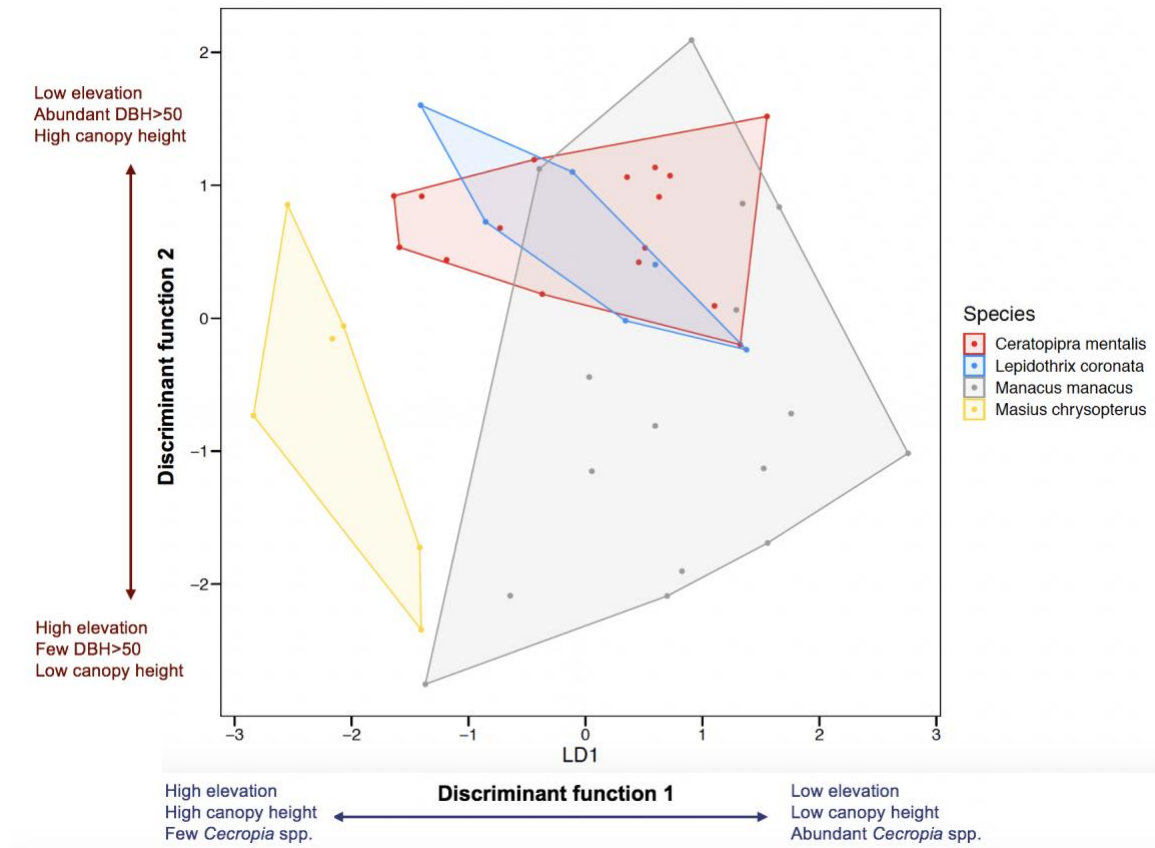


Table 1. Discriminant function loadings, most strongly represented by elevation, canopy height, and *Cecropia* spp. Proportion of between-group separation achieved by each discriminant function is indicated by the proportion of trace.

	DF1	DF2	DF3
Elevation	-1.2548	-0.4203	-0.0783
<i>Cecropia</i>	0.6465	0.1238	-0.4630
DBH.10	-0.0204	0.2258	-0.5600
DBH.50	-0.2812	0.4011	0.8935
Canopy Height	-0.5460	0.8268	-0.8058
Avg. Densiometer	-0.0944	0.1580	0.1521
Proportion of trace	0.5375	0.3083	0.1541

Table 2. Accuracy of the jackknife leave-one-out classification tests for manakin leks based on lek environmental data.

	Percentage Correctly Classified
<i>Ceratopipra mentalis</i>	0.8125
<i>Lepidothrix coronata</i>	0.3333
<i>Manacus manacus</i>	0.5625
<i>Masius chrysopterus</i>	0.5000
Total percent correct	0.6136

Table 3. Pairwise comparisons of manakin display perch heights using Bonferroni-corrected t-tests with pooled standard deviation. *Ceratopipra mentalis* exhibited significantly different perch heights compared with the other three manakins.

	<i>Ceratopipra mentalis</i>	<i>Lepidothrix coronata</i>	<i>Manacus manacus</i>
<i>Lepidothrix coronata</i>	p = 0.00013	-	-
<i>Manacus manacus</i>	p < 0.0001	1.00000	-
<i>Masius chrysopterus</i>	p = 0.00073	1.00000	1.00000