

ASSOCIATIONS BETWEEN MANAKIN LEK BREEDING SYSTEMS AND  
FRUITING PLANT DISTRIBUTIONS IN NORTHWESTERN ECUADOR

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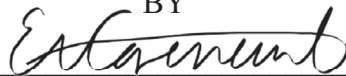
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FOR THE DEGREE OF

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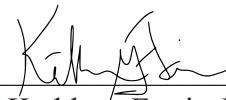
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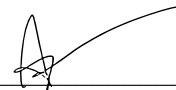
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Eleanor Casement. Associations Between Manakin Lek Breeding Systems and Fruiting Plant Distributions in Northwestern Ecuador.

(Professor Jordan Karubian, Ecology and Evolutionary Biology)

The distributions of tropical plant and animal communities are intrinsically linked through the reciprocal and dynamic processes of food acquisition and seed dispersal. Lekking species often exhibit sex-specific patterns of distribution and habitat use related to differential commitments to display activities. Display courts may be associated with distinct vegetative communities as a result of both resource-based establishment and directed dispersal by resident males. We sampled the mature, fruiting plant communities in *Manacus manacus* display courts and control sites to determine if display courts represent areas of high fruit biomass and diversity in relation to surrounding forest. We also compared this data to surveys from non-court lek areas to explore potential scale-dependent differences in plant communities. Our results show that display courts had more fruiting resources (fruit biomass, number of fruiting plants, and fruit biomass per individual plant) compared to control plots; leks showed a near-significant trend of more fruiting resources compared to control plots. Moreover, display courts contained a greater total abundance of Melastomataceae plants compared to control plots. Finally, display courts had greater diversity of fruiting species compared to control plots. We conclude that a clear association exists between *M. manacus* display territories and fruit abundance and diversity in the Ecuadorian Chocó. These non-random spatial associations may reflect both past preferences for court establishment near fruiting resources and current mechanisms of seed dispersal that maintain distinct plant communities within courts.

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## INTRODUCTION

The composition and distribution of terrestrial plant and animal communities are structured by a myriad of biotic and abiotic factors. Different mechanisms of seed dispersal can have important implications for how plants are organized in space and achieve reproductive success (Cortes & Uriarte, 2013). Animals function as seed dispersers in many ecosystems, and these interspecific interactions influence plant community composition in every region of the world (Howe & Smallwood, 1982). Animal vectors are especially common in tropical forests, where >85% of native trees produce fruits that are regularly consumed and dispersed by animals (Terborgh, 1990). Therefore, dispersers play a key role in the movement, survival, and eventual recruitment of seeds, thereby structuring the genetic and ecological distributions of tropical plant communities (Garcia et al., 2009). Reciprocally, food abundance is a strong determinant of the overall spatial distribution, habitat selection, and movement patterns of many animals (White, 2008; Crampton et al., 2011). In the case of frugivorous species, ranges may center around fruiting resources (Kissling et al., 2007). It remains difficult to disentangle how the spatial distributions of plant and animal populations are structured, and in turn structure one other in tropical systems.

Mechanisms of seed movement diverge across animal species, with dispersers offering a diverse suite of services that vary in the quantity, distribution, and distances of seeds dispersed (Dennis & Westcott, 2006; Muscarella et al., 2007; Karubian et al., 2012). Animal behavior plays a significant role in dictating inter- and intraspecific differences in dispersal patterns (Westcott, 1997; Karubian et al., 2012). Species with complex mating systems and strong sexual selection offer interesting opportunities to investigate differences in sex-based dispersal characteristics and effectiveness (Théry &

Larpon, 1993; Krijger et al., 1997). Neotropical birds demonstrate a wide range of social breeding schemes, many of which include sex-specific display behaviors. Therefore, they are compelling systems to investigate intraspecific variation in dispersal services (Diamond, 1986; Schlinger et al., 2008; Manica et al., 2014).

Lekking, a system of male-dominance polygyny, is a reproductive strategy in which males aggregate to attract mates through elaborate displays (Ryder & Sillett, 2015). The lek-breeding system has broad taxonomic and geographic distributions and is observed in approximately 100 avian species across 15 families in both tropical and temperate regions (Höglund & Alatalo, 2014). Nearly all tropical lek-breeding birds are frugivorous, and therefore play important roles in structuring the vegetation of tropical forests (Höglund & Alatalo, 2014). The seed dispersal services offered by frugivorous lekking birds may demonstrate a large degree of intraspecific variation on the basis of sex and age, due to differential commitments of male, female, and juvenile individuals to lekking activities (Cestari & Pizo, 2013).

A lek is a spatial conglomeration of display territories held by mature males and used to attract female mates (Graves et al., 1983). During breeding season, males usually remain within or near their display courts to maximize mating opportunities, and only leave the lek for short foraging bouts (Cestari & Pizo, 2012). Females and juveniles move between display territories and spend extended time away from the lek (Cestari & Pizo, 2012). Males often retain their display courts for repeated breeding seasons, and leks have been observed to persist in the same area for several decades (Durães et al., 2008). The daily and seasonal permanence of males in lek areas result in a high density of

deposited seeds, which in turn may influence the vegetative characteristics of the lek (Karubian et al., 2012; Théry & Larpin, 1993).

Numerous studies have investigated the relationships between lek placement, resource availability, and seed dispersal (Théry & Larpin, 1993, Krijger et al., 1997; Ryder et al., 2006; Cestari & Pizo, 2013). Various theories have emerged to explain the evolution of lek layout and placement within forests, especially in relation to plant communities (Westcott, 1994; Ryder et al., 2006; Endler & Théry, 1996; Wagner & Danchin, 2003). The environmental hot-spot hypothesis is a resource-based theory that suggests female movement and behavior drive the development of lek sites in areas of high female density (Ryder et al., 2006). Female activity is theorized to center around necessary resources, the most important of which is food (Balmford et al., 1993). In accordance with the hot-spot theory, males of frugivorous species will establish territories in areas with high fruit biomass to intercept female movement patterns (Emlen & Oring, 1977; Bradbury & Gibson, 1983).

Contrastingly, leks may become areas of high fruit density over time through continual deposition of seeds by resident males. Field studies of aggregation behavior in primates and birds report increased seed rain at communal roosting and display sites (Théry & Larpin, 1993; Krijger et al., 1997; Wenny & Levey, 1998; Cestari & Pizo, 2013); this dispersal pattern can increase survival if seeds are dispersed into sites with favorable abiotic conditions, or decrease survival due to density-dependent predation and pathogens (Wenny & Levey, 1998; Russo & Augspurger, 2004). Leks may also contain diverse plant communities in relation to surrounding areas because males will deposit seeds from a variety of off-lek sources (Cestari & Pizo, 2013; Karubian et al. 2010). High

diversity may permit greater plant abundance among heterospecific individuals due to microhabitat specializations (Cestari & Pizo, 2013; Karubian et al., 2016). It remains unclear whether the plant composition of leks results from lek construction among beneficial resources or behavior-directed dispersal of seeds into lek sites. Additionally, lek vegetative composition varies widely between and within species; this relationship has been studied using a variety of metrics, including seed rain, fruit biomass, and dispersal models (Ryder et al., 2006; Cestari & Pizo, 2013; Karubian et al., 2012). These methods explore related, but distinct characteristics of lek-plant associations, and therefore also report distinct conclusions. The first step in detangling these complex and highly variable relationships is to determine species-specific patterns of association between manakin habitats and plant communities on a local scale.

Manakins (Pipridae) are neotropical frugivores that exhibit classical lekking behaviors (Fair et al., 2013). Several studies have investigated the densities of deposited seeds in manakin leks in comparison to non-lek sites. Krijger et al. (1997) reported a greater density of seeds in the seed bank of *Corapipo gutturalis* leks compared to control sites, but no such trend was observed for *Manacus manacus* leks. A study focused on seed rain in *Manacus manacus* leks found no difference in seed abundance and species richness between lek and non-lek regions, but that increased seed deposition by male *M. manacus* individuals occurred at the scale of the display court (Cestari & Pizo, 2013). While these studies provide insight on the dispersal services of manakins and their potential to structure future plant recruitment, they do not address the existing vegetative composition within leks. One study by Ryder et al. (2006) investigated mature plant communities in manakin leks and reported higher fruit biomass and abundance of fruiting

plants in the leks of three species of *Pipra* manakins in comparison to control sites.

However, literature on fruiting resources within lek sites remains sparse. Due to variation in lek characteristics and behaviors found across manakin species, local populations, and geographic space, additional studies are needed to investigate the relationships between mature plant communities on both lek and display court scales before drawing broad conclusions about associated distributions.

We investigated the abundance, fruit biomass, and diversity of mature plant communities in display territories of *M. manacus* in northwestern Ecuador to ask the following questions: (1) Do display courts represent areas of high fruit biomass in comparison to surrounding secondary forest? (2) Do display courts represent higher fruit potential, measured as total abundance of mature Rubiaceae and Melastomataceae, in comparison to surrounding secondary forest? (3) Do display courts have higher species diversity of fruiting plants than surrounding secondary forest? We also compared the fruit biomass of display courts and control plots to non-court areas within the lek to explore potential scale-dependent differences in plant communities. We hypothesized that display courts would represent areas of high fruit abundance and diversity in comparison to surrounding forest, demonstrating a relationship between manakin habitat use and local vegetative communities.

## **METHODS**

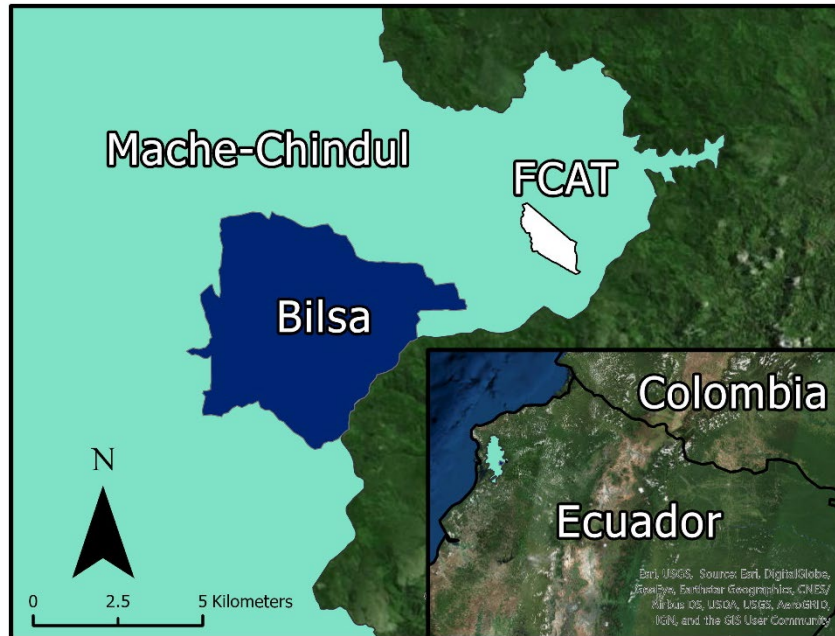
### *Study species*

*Manacus manacus* is a small, frugivorous bird that is widely distributed throughout continuous and fragmented lowland forests in the Neotropics (Snow et al.,

2004). The males have conspicuous, black and white plumage, while females and juveniles are a dull green color. Males exhibit lekking behavior year-round, however the rates of display increase during a primary breeding period, which usually coincides with the rainy season (Cestari & Pizo, 2013). During the breeding period, males spend the majority of daylight hours in the lek, and only leave for short foraging bouts (Cestari & Pizo, 2012; Snow, 1962). Leks are comprised of smaller, individual display courts (Snow, 1962; Ryder & Sillett, 2015). Display courts are cleaned of leaf litter and usually contain at least two small saplings, which are used for courtship dances and copulation (Cestari & Pizo, 2013). Females will visit multiple leks to observe male displays and choose mates, and juvenile males may also visit leks to practice courtship routines (Lill, 1974). Therefore, the ranges of *M. manacus* females and juveniles are generally 5-10x larger than those of males (Lill, 1974; Théry, 1992).

#### *Study site*

This study was conducted in the Fundación para la Conservación de los Andes Tropicales (FCAT) Reserve, which spans approximately 1,500 acres of the Esmeraldas Province in northwestern Ecuador (Karubian, 2022) (Figure 1). The reserve encompasses secondary and primary Chocó rainforests classified as tropical humid (300-600 m) and pre-montane (600-750 m) ecosystems (Ortega-Andrade et al., 2010). Average precipitation is between 1500-2000 mm per year, with a dry season spanning from July to December and wet season from January to June (Ortega-Andrade et al., 2010). The surrounding region is characterized by wide-spread deforestation and fragmentation due to small-scale agriculture (Sierra, 1999).



**FIGURE 1.** Location of Fundación para la Conservación de los Andes Tropicales (FCAT) Reserve within the Mache-Chindul Ecological Reserve and adjacent to the Bilsa Biological Reserve, in northwestern Ecuador.

Common plant families within the reserve include Orchidaceae, Araceae, Rubiaceae, Fabaceae, Gesneriaceae, Melastomataceae, Piperaceae, Moraceae, Bromeliaceae, Asteraceae, and Solanaceae (Clark et al., 2006). Of these families, manakins have been observed feeding on a wide variety of fruits of Rubiaceae, Melastomataceae, Solanaceae, and Asteraceae families (Steele, 2008; H. L. Anderson, personal communication, June, 2021). Four species of manakin coexist in the region, with *M. manacus* being the most common (Freile & Restall, 2018).

#### *Defining a lek*

Exhaustive searches and mapping of *M. manacus* display courts were conducted throughout the months of July – September 2020 and covered approximately 70% of the FCAT reserve (Sheehy, 2021). Searches took place during the daylight hours of 8 am - 5 pm when display behavior is most common (Cestari & Pizo, 2013). Individual territories

were located through observations of mating calls and auditory displays, followed by visual identification of the displaying male. The male was visually observed until his central display court and copulatory saplings were identified, which then served as the center of the male's territory. GPS points were taken from this center point. Display territories were defined as all area within a 10-meter radius to encompass the largest recorded territory sizes for *M. manacus* (Olson & McDowell, 1983), whilst minimizing overlap with adjacent plots.

Leks were delineated by acoustic separation; display courts were designated in the same lek if they were within auditory range of one another (Ryder & Sillett, 2016). Once display courts were grouped, ArcGIS was used to construct minimum convex polygons (MCP) from court centers. These polygons served as lek boundaries. Using these methods, we determined 23 display territories within four leks in the secondary forest surrounding the FCAT station and marked boundaries based on GPS coordinates.

#### *Lek surveys*

Plant surveys took place in July 2021. The fruiting plant resources (total number of ripe fruits on an individual plant and total number of fruiting plants) of four leks were exhaustively sampled using parallel, continuous belt transects (1 m on either side) to cover the entire demarked region (Ryder et al., 2006). Manakins are generalist frugivores (Snow, 1962; Worthington, 1982), and therefore we surveyed all plants bearing small, fleshy fruit (e.g. Melastomataceae, Rubiaceae, Solanaceae, and Araceae) (Ryder et al., 2006). For each fruiting plant, we took GPS points and counted the number of ripe fruits. In cases when the number of fruits was too great to directly count (i.e. >500), we counted fruits from individual branches or infructescences and estimated total plant biomass from

these counts (Worthington, 1982). All fruiting plants were marked to ensure they were not double counted. Pictures were taken of each unique fruit and compared to reference photos and descriptions of plant species manakins have been observed feeding on (Steele, 2008; H. L. Anderson, personal communication, June, 2021). When species could not be determined, collected specimens (including fruits, leaves, stem and flowers) were used to define morphospecies. We also collected fruit samples (5-10 fruits per species) to determine the average biomass per fruit for each morphospecies and calculate total fruit biomass per surveyed individual (Ryder et al., 2006). Average individual biomass per fruiting plant was calculated by summing total court biomass and dividing by the number of sampled individuals within each court. Additionally, every mature (>1 m) plant (fruiting and non-fruiting) in the Melastomataceae and Rubiaceae families were counted (G. Rivas-Torres, personal communication, June, 2021), as these families have been found to contribute most heavily to *M. manacus* diets (Snow, 1962; Worthington, 1982; Cestari & Pizo, 2013).

Lek-wide surveys were used to determine average total biomass for non-court lek area. Using ArcGIS, we calculated the total area of each lek MCP excluding display court radii. Total biomass was calculated by summing the individual biomasses of all plants located outside of display courts. The total area of the lek was divided by the area of each control or court plot (314 m<sup>2</sup>), and the fruiting data outside of courts was divided between the number of 314 m<sup>2</sup> plots fitting into the non-court lek, therefore providing average total biomass for non-court lek areas. These lek-wide averages were calculated for all four of the sampled leks.

#### *Display Court Surveys*

We sampled 14 display territories for total Melastomataceae and Rubiaceae abundance and fruiting plant resources using the methodology described above. All 14 of these display territories served as corners for lek MCPs.

In addition to sampling edge display courts, data for courts located within the lek MCP (internal display courts) were determined using the lek wide sampling. The center of each internal court was marked with a GPS point, and a 10 m radius was constructed using ArcGIS. These plots were overlaid with GPS data of lek-wide fruiting plants surveys, and the number, morphospecies, and biomass of fruiting plants located within each display court were recorded. One lek contained six internal display courts with considerable overlap of space and fruiting resources. Of the six internal courts, only three were used at one time for analysis to minimize overlap. Several groupings of three were tested to determine if results changed based on which three display courts were used; all combinations gave the same results (p-values changed by  $< 0.01$  between versions). No plants were attributed to two different plots; there was only one grouping in which two plants fell into an overlap zone between two display courts. In this case, one plant was a counted in each display court. Analyses were run on two versions of this grouping, in which the plants were alternatively attributed to each court; both versions gave the same results (p-values changed by  $< 0.0001$ ). As all tested combinations of three display courts gave the same results in terms of significance, the analyses reported in this paper used the three courts with the least amount of spatial overlap and no plant overlap.

Data from both internal and edge display territories were used in analyses of biomass and diversity, for a total of 20 courts. No GPS points were taken of non-fruiting

plants; therefore, internal courts were excluded from abundance analyses of Rubiaceae and Melastomataceae.

### *Control Plot Surveys*

Non-lek control sites were generated using ArcGIS. All four lek sites were established in secondary forest, and therefore non-lek plots were also constrained to secondary forest to decrease extraneous variables. Secondary forest was defined as forest within 50 meters of the road shoulder, based on personal observations of forest composition within the reserve. GPS points were taken along the road center. Using ArcGIS, these points were connected to form a center line and buffered by 12.5 meters on each side, thus creating a polygon of the road itself and proximate forest that is highly impacted by traffic. A 50-meter buffer was calculated on either side of the road polygon, and these 50 meters were used to constrain non-lek controls to secondary forest. The road itself and any intersecting lek polygons were excluded from the secondary forest polygon, and within this polygon, 15 randomly placed, 10-meter radius circular plots were generated. Observations took place in these localities to ensure no male display behaviors were heard or witnessed. The GPS coordinates of these plots were used to mark plot boundaries in the forest, and each plot was exhaustively sampled for Rubiaceae, Melastomataceae, and fruiting resources using the methods described above.

### *Data analysis*

All statistical tests were conducted in Microsoft Excel and RStudio (version 1.2.5033). Maps were generated using ArcGIS.

All data were checked for normality using the Shapiro-Wilks test (Rohlf & Sokal, 1981). In cases when data were not normal, we attempted transformations to correct for

non-normal distributions. Parametric tests were used when normal distributions were achieved; non-parametric tests were used when data did not assume normal distributions.

Raw data for total fruit biomass per display court and control plot were log transformed and compared using a Welch two sample t-test. Untransformed data for total biomass were also compared between display courts, control plots, and non-court lek averages using a Kruskal-Wallis one-way analysis of variance to account for non-normal distributions and large variation in sample sizes.

Fruiting plant abundance was compared between display courts and control plots using a Wilcoxon rank sum test with continuity correction. Raw data for average fruit biomass per plant were log transformed and compared with a Welch two sample t-test.

Total Rubiaceae abundance (fruiting and non-fruiting) was compared between display courts and control plots using a Welch two sample t-test. Total Melastomataceae abundance in display courts and control plots was log transformed and compared with a Welch two sample t-test.

Fruiting plant diversity was compared between display courts and control plots using both Shannon's Diversity Index and species richness; sampled courts and controls that contained 0 fruiting individuals were excluded from diversity analyses. Shannon's Diversity (H) was calculated from the number of each morphospecies in each display court and control plot, and H values were compared using a Welch two sample t-test. Species richness was calculated as the number of species in each display court and control plot and compared using a Wilcoxon rank sum test with continuity correction.

## RESULTS

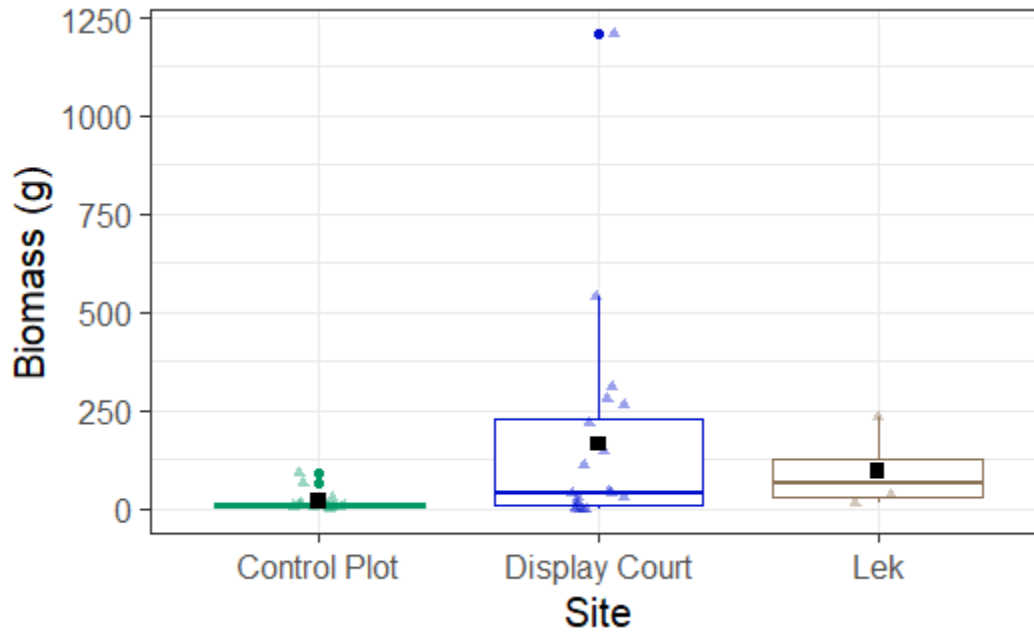
### *Fruit Biomass*

Display courts had significantly more ripe fruit than control plots ( $t = -2.14$ ,  $df = 30.14$ ,  $P < 0.05$ ), more plants with ripe fruit ( $W = 87$ ,  $P < 0.05$ ), and a greater biomass of ripe fruit per plant ( $t = -2.87$ ,  $df = 27.24$ ,  $P < 0.01$ ) (Table 1). Biomass also differed between control plots, display courts, and non-display lek areas ( $H = 6.48$ ,  $df = 2$ ,  $P < 0.05$ ). Post-hoc comparisons using Dunn's Multiple Comparison Test indicated significantly higher biomass in display courts compared to control plots ( $P < 0.05$ ), a near significant trend of higher biomass in non-display lek areas compared to control plots ( $P = 0.056$ ), and no difference in biomass between display courts and non-display lek areas ( $P > 0.05$ ) (Figure 3).

**TABLE 1.** Fruit biomass, number of fruiting plants, biomass per plant, mean diversity (Shannon's Index and species richness), and abundance of Rubiaceae and Melastomataceae at *M. manacus* display courts and control plot sites in northwestern Ecuador.

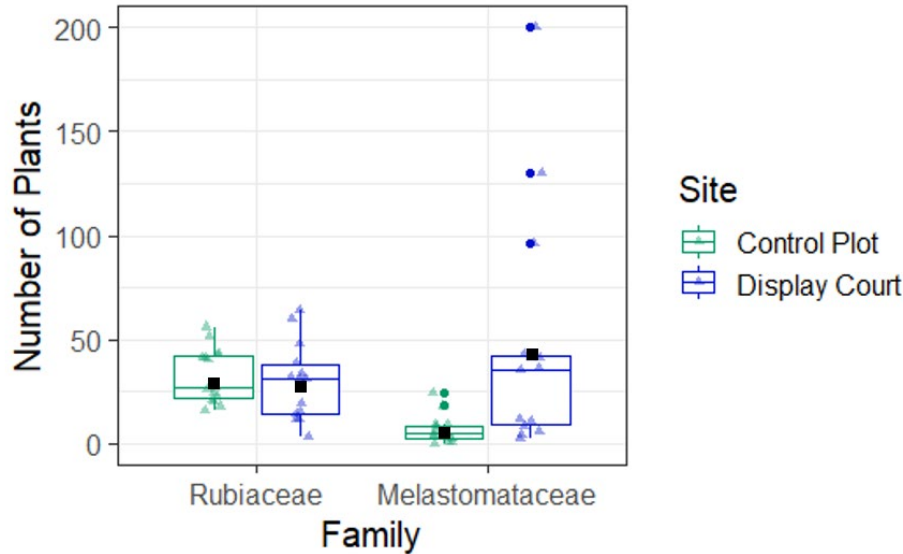
	Display Court (mean $\pm$ SD)	Control Plot (mean $\pm$ SD)	<i>W</i>	<i>t</i>	<i>P</i> <sup>a</sup>
Ripe fruit biomass (g)	165 $\pm$ 285	17.8 $\pm$ 25.6	-	-2.14	<b>0.040</b>
Average biomass per plant (g)	6.68 $\pm$ 5.81	2.78 $\pm$ 2.03	-	-2.87	<b>0.008</b>
Number of fruiting plants	31.5 $\pm$ 43.9	5.73 $\pm$ 7.40	87	-	<b>0.036</b>
Species richness	4.3 $\pm$ 1.25	2.2 $\pm$ 0.94	20	-	<b>&lt;0.001</b>
Shannon's Diversity (H)	0.96 $\pm$ 0.41	0.63 $\pm$ 0.46	-	-2.13	<b>0.042</b>
Number of Rubiaceae	29.6 $\pm$ 18.5	32.7 $\pm$ 12.9	-	0.52	0.609
Number of Melastomataceae	47.5 $\pm$ 57.3	6.8 $\pm$ 6.54	-	-3.67	<b>0.001</b>

<sup>a</sup> Significant values shown in bold.



**FIGURE 2.** Fruit biomass (g) in control plots, display courts, and non-court lek areas. Black squares indicate mean abundance by site. Transparent triangles represent each individual plot and solid circles represent outliers.

Display courts and control plots showed no difference in total Rubiaceae abundance. However, display courts contained significantly more Melastomataceae plants than control plots ( $t = -3.67, df = 22.76, P < 0.01$ ) (Figure 4).



**FIGURE 3.** Abundances of fruiting and non-fruiting Rubiaceae and Melastomataceae plants in display courts and control plots. Black squares indicate mean abundance by site. Transparent triangles represent each individual plot and solid circles represent outliers.

### Diversity

We recorded a total of 991 individual fruiting plants in surveys of corner display courts, lek MCPs, and control plots. These plants represented 22 morphospecies across five families: Rubiaceae (11), Melastomataceae (6), Solanaceae (3), Asteraceae (1), and Myricaceae (1). We recorded one individual of an unidentified family, for a total of 23 different morphospecies. Three families accounted for >99% of fruiting plants: Melastomataceae (87.4%), Rubiaceae (8%), and Solanaceae (3.7%). The other families (Asteraceae, Myricaceae, one unidentified family) combined accounted for <1% of sampled individuals. Melastomataceae were dominated by species in the genera *Miconia* and *Leandra*.

Display courts had significant higher Shannon's Diversity (H) of fruiting plants than control plots ( $t = -2.13$ ,  $df = 28.11$ ,  $P < 0.05$ ). Display courts also had higher species richness than control plots ( $W = 20$ ,  $P < 0.001$ ).

## DISCUSSION

This study refines our understanding of the complex biotic factors that structure interdependent avian and plant distributions in tropical forests. In the case of *M. manacus*, there is a clear association between male display territories and fruit abundance and diversity in the Ecuadorian Chocó. As hypothesized, display courts represent areas of high fruit abundance and diversity in comparison to surrounding secondary forest. These non-random spatial associations likely reflect both past preferences for court establishment in close proximity to fruiting resources, as well as current mechanisms of seed dispersal and micro-habitat conditions that maintain, and potentially amplify the abundance and diversity of such resources.

### *Court establishment and patch ecology*

Fruiting patch quality and abundance influence animal foraging ecology, but also show wide temporal and spatial variation (Sallabanks, 1993). Among neotropical birds, many of which exhibit strong sexual selection, foraging must be balanced with time-intensive and energetically-costly reproductive activities (McDonald, 1989; Ryder & Sillet, 2016). In these systems, foraging efficiency and intake rate is closely linked to fitness; the amount of time and energy allocated towards display activities is contingent upon the availability and quality of patches in the surrounding forest (Charnov, 1976; Fiske et al., 1998).

Three characteristics of patch quality measured here (fruit biomass/area, number of fruiting plants, and fruit biomass/individual plant) suggest that display courts function as high quality patches, thus reducing the amount of time and energy resident males spend foraging away from the lek. Previous studies found weight loss was positively

correlated with amount of courtship display in *Chiroxiphia* manakins (McDonald, 1989a). Additionally, *M. manacus* males have been reported to spend between 82-90% of daylight hours in the lek during breeding season, reducing time allocated to foraging (Cestari & Pizo, 2012; Snow, 1962). Reliable food resources, especially in close proximity to display courts, allow males to achieve sufficient food intake while spending maximal time at their courts. Therefore, the co-occurrence of courts and patches likely impacts the overall health and fitness of *M. manacus* males. However, the complex process of individual court establishment and maintenance is contingent on many dynamic factors in addition to fruit availability; further experimental and behavioral studies are necessary to determine causal relationships between fruit availability and *M. manacus* body condition and reproductive success.

In addition to increasing the foraging efficiency of male *M. manacus* individuals, the co-occurrence of fruit patches and display courts provides support for the environmental hot spot theory that males settle in areas of high female traffic (Parker, 1978). The movement and ranges of female manakins are centered around fruiting resources, and males may establish courts in close proximity to fruit patches to increase encounters with prospective mates (Lill, 1976; Emlen & Oring, 1977; Bradbury & Gibson, 1983). This dependency of male dispersion as a function of female distribution is fundamental to many evolutionary theories for avian mating systems (Emlen & Oring, 1977; Vehrencamp & Bradbury, 1984; Davies, 1991). The environmental hot spot hypothesis posited here suggests a direct connection between resource availability, female movement, and male dispersion and aggregation. Therefore, plant distributions

may structure the placement, layout, and size of leks in tropical forests and affect the reproductive opportunities of resident males (Höglund & Alatalo, 1995).

Fruit availability shows a large degree of temporal variability based on the phenology of different plant species (Levey, 1988; Loiselle & Blake, 1991). We addressed potential fruiting resources through surveys of all mature Melastomataceae and Rubiaceae individuals, and found greater Melastomataceae abundance in display courts relative to controls. The most common species of Melastomataceae we encountered were bushes and trees in the genus *Miconia*. These species often produce thousands of berries during a several-month-long fruiting season (Pessoa et al., 2012). Therefore, while high Melastomataceae abundance may indicate high fruit biomass in display courts, actual fruit availability is likely to vary seasonally. However, the higher diversity observed in display territories may reduce seasonal disparities in fruit abundance in courts compared to off-lek controls due to variable fruiting seasons of different species. Additionally, long-term site fidelity of male manakins to territories suggests that display courts are inherently high-quality resource bases (Ryder et al., 2006).

While this data provides a first look at the current and potential fruiting communities of *M. manacus* display courts, it represents resources at single moment in time and should be further developed through long-term studies of fruit phenology and manakin movement. Repeated surveying and radio telemetry would provide insight on temporal and spatial changes in plant and avian distributions, which could eventually be linked to manakin fitness and plant recruitment over several years.

*Seed dispersal and recruitment*

Processes of habitat selection and use have important implications for the geographical distributions, biotic interactions, and evolutionary trajectories of dispersed species (Loiselle & Blake, 1993). Seed dispersal and recruitment are alternative explanations that may contribute to observed patterns of high fruit biomass in display courts (Karubian et al., 2012; Krijger et al., 1997; Théry & Larpin, 1993). Seed survival has been found to be a function of distance and density in relation to conspecific plants (Janzen, 1970; Connell, 1971), and this movement is often directed by animal dispersal agents. We investigated dispersal through the lens of mature plants to provide insight on past recruitment.

The higher abundance of both fruiting plants and Melastomataceae in display territories relative to control plots is likely a product of extensive and repeated time spent by resident males in these areas. Non-court lek area also showed a marginally non-significant trend of high biomass in comparison to control plots. This potentially contrasts the findings of Cestari and Pizo (2013), who reported an increase in seed abundance and diversity within *M. manacus* display courts in Brazil, but not entire lek sites. Krijger et al. (1997) also found no increase in seed abundance in *M. manacus* lek sites in French Guiana, although this study was constrained by a small sample size (two leks sampled). Discrepancies between previous studies and results reported here could potentially stem from variable movement and dispersal patterns of different *M. manacus* populations, it is more likely that these differences reflect sampling seed rain vs mature plants. While seed rain can be directly linked to recent movement and dispersal by local *M. manacus* individuals (Cestari & Pizo, 2013), the community composition of mature plants reflects past variation in dispersal and selective pressures that influence survival

and ultimately recruitment (Loiselle & Blake, 1993). Leks are temporally and spatially dynamic landscapes; while site traditionality and court replacement has been reported in several manakin species (Berres, 2002), court abandonment has been previously observed in our study region (H. L. Anderson, personal communication, June, 2021). It is also possible that not all display courts have been identified in our studied leks. Therefore, while measuring mature vegetative communities can provide insight on the long-term patterns of dispersal and recruitment, these studies are complicated by the lack of knowledge of past lek conditions and layout. Further studies should investigate mature plant communities on a longer temporal scale to determine how dynamic processes of court establishment and seed dispersal structure plant communities over many years.

The increased average biomass of individual fruiting plants in courts may reflect indirect, foraging-based selection for the consumption and dispersal of high-biomass species and individuals. Foraging efficiency is maximized when feeding on plants with a high fruit biomass by reducing the energy and time spent searching for new foraging targets. Foraging efficiency is especially important for *M. manacus* males for whom feeding trips are a tradeoff with potential reproductive encounters (Ryder & Sillet, 2016). Therefore, male manakins may seek out or feed intensely on high-biomass individuals, whose seeds are then dispersed back into the court at high rates. Additionally, plants with greater fruit production may be easier to locate, either as a repeated food source or through copy-cat foraging and information sharing among conspecific males (cf. information-center hypothesis; Ward & Zahavi, 1973; Orians, 1979; Schoener, 1979). Therefore, the high average biomass of individual plants in display sites relative to controls may stem from an indirect selection to feed on high biomass plants, whose

genotypes are expected to be over-represented in the seed bank, and eventual plant community of the court. However, further studies are needed to compare fruit biomasses of same-species individuals to verify the evolutionary implications of manakin foraging on plant phenotypes.

High species diversity at display territories may offer a solution to density-dependent sources of mortality among dispersed seeds. Courts represent ecological traps if disproportionate death of seedlings occurs from density-driven hazards, and species over-representation may be limited by conspecific competition and species-specific pathogens (Janzen, 1970; Connell, 1971; Cestari & Pizo, 2013). Selection may operate at the court level by promoting the survival and coexistence of a diverse vegetative community through differential habitat use, and discouraging dominance of single species. In this case, *M. manacus* driven dispersal may influence the structure of plant communities in courts as found in other avian species. Théry and Larpin (1993) reported that cock-of-the-rock (*Rupicola rupicola*) leks were comprised of a mosaic of plant species, demonstrating that long-term seed dispersal promoted a diverse vegetative community. Similarly, the seed pool of long-wattled umbrella bird (*Cephalopterus penduliger*) leks has been shown to contain five times more source trees in comparison to control regions, emphasizing the role that lekking birds play in increasing the genetic diversity of proximate plant communities (Karubian et al., 2010). Therefore, it is likely that *M. manacus* dispersal services structure both the physical and genetic layout of local vegetation. In addition to the biotic processes of competition and pathogen specialization, micro-habitat characteristics of court sites also include a myriad of abiotic factors (Loiselle & Blake, 1993; Murray, 1998). While this study provides insight on the

potential biotic drivers of high fruiting plant abundance and diversity, further studies are needed to investigate the environmental qualities of display courts that may compound these processes.

## CONCLUSION

Plant and animal interactions are complex and dynamic processes that rarely operate unilaterally. The data presented here provides support for the role of environmental hot spots in influencing the physical, ecological, and behavioral aspects of avian aggregations and seed dispersal. While fruit availability is not the only factor driving habitat use by manakins, it is an important aspect structuring the movement and fitness of lek breeding species. Reciprocally, the lek breeding system has significant consequences for seed dispersal and recruitment in tropical forests. Lekking behavior may establish, maintain or improve patches, which in turn reinforce site fidelity of *M. manacus* males. While it remains difficult to attribute the physical characteristics of display courts to habitat selection vs. seed dispersal, this work emphasizes the importance of resources to the establishment and continuity of leks. Moreover, we suggest that distribution associations between *M. manacus* and fruiting plant resources are strongest at individual court level, demonstrating the predicament of approaching lek areas as units of collective space and not simply conglomerations of individual territories. The patterns of avian and plant distributions described here illustrate the complexities of studying tropical communities and the interspecific interactions shaping these dynamic systems.

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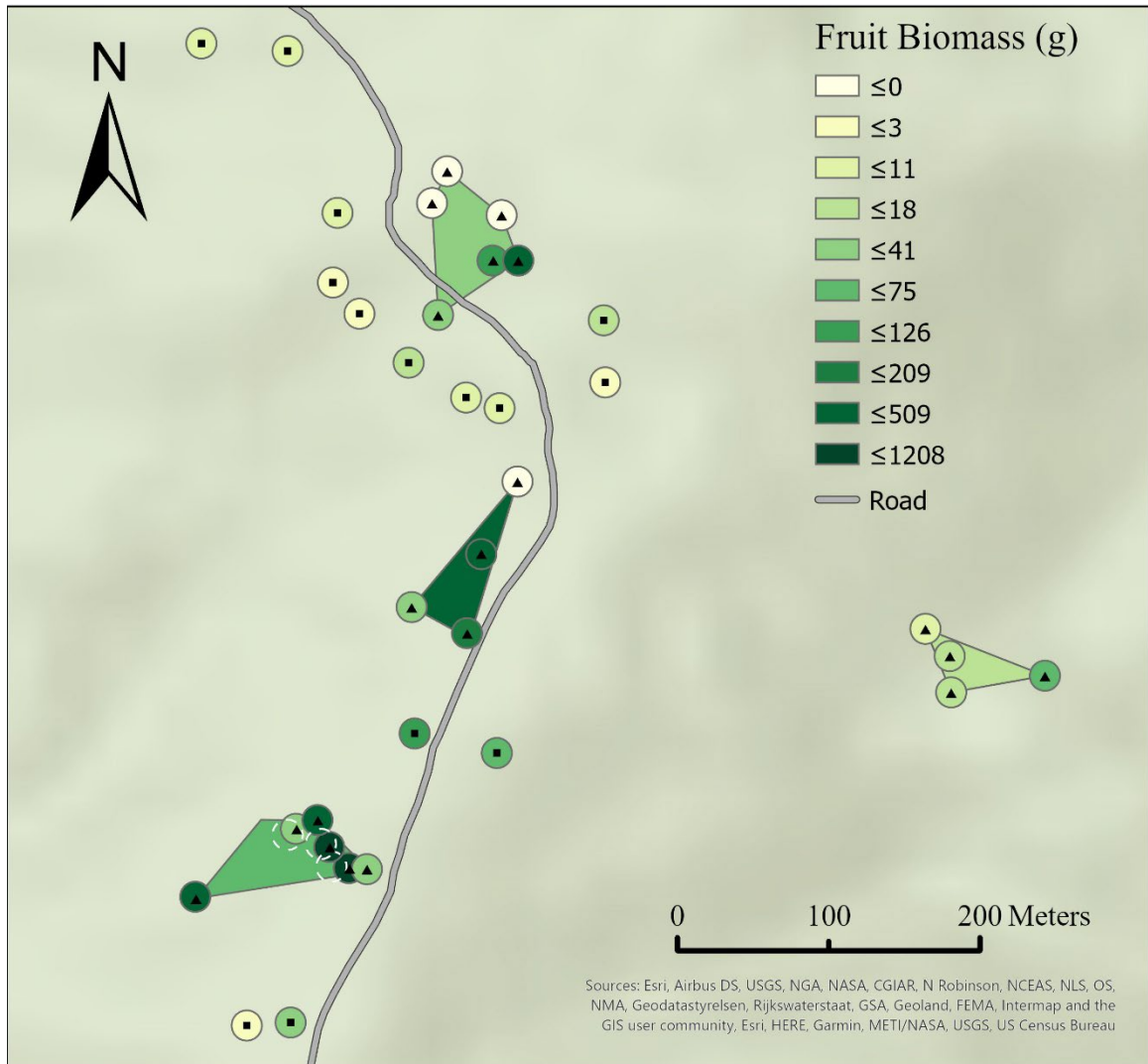
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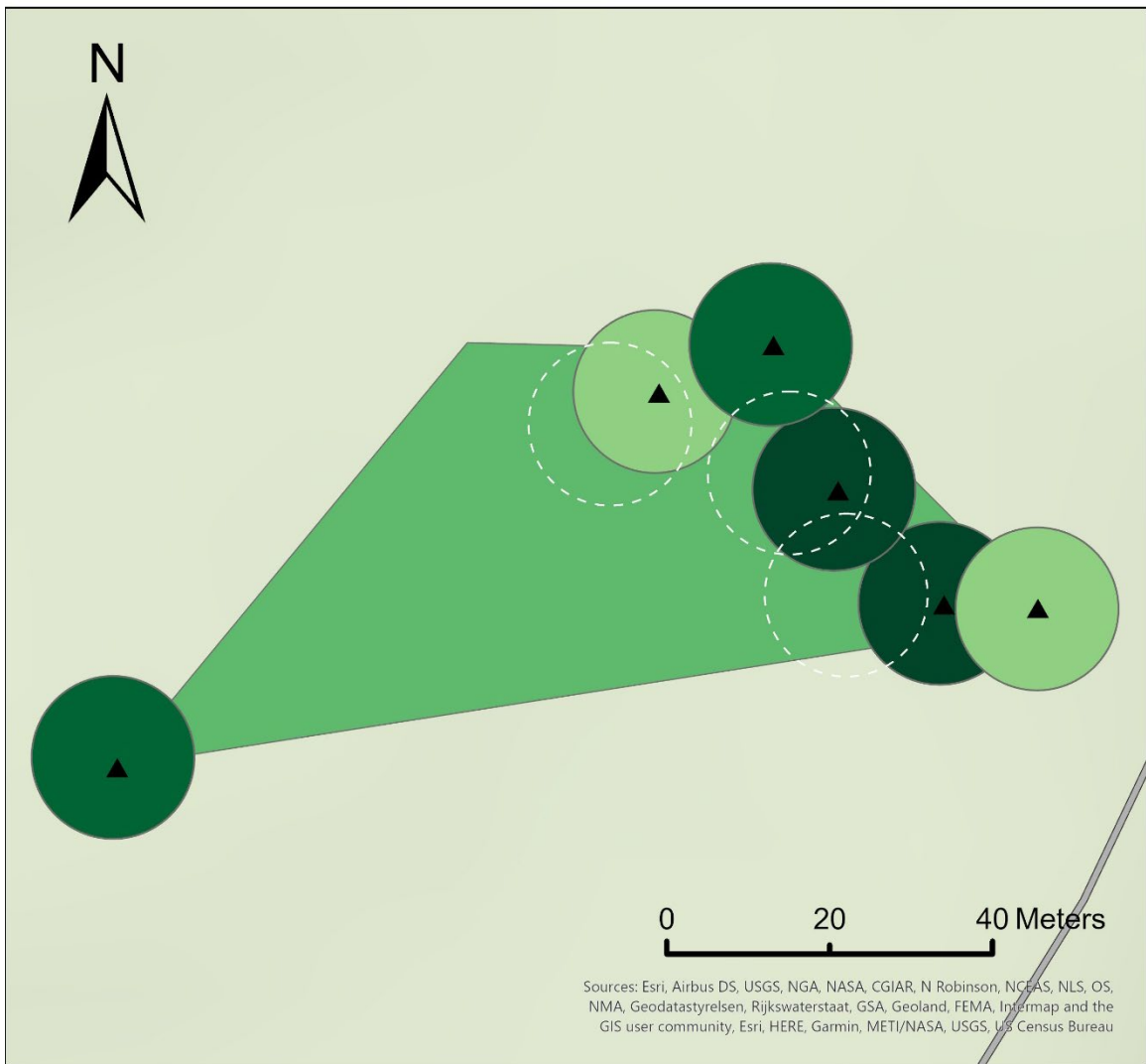
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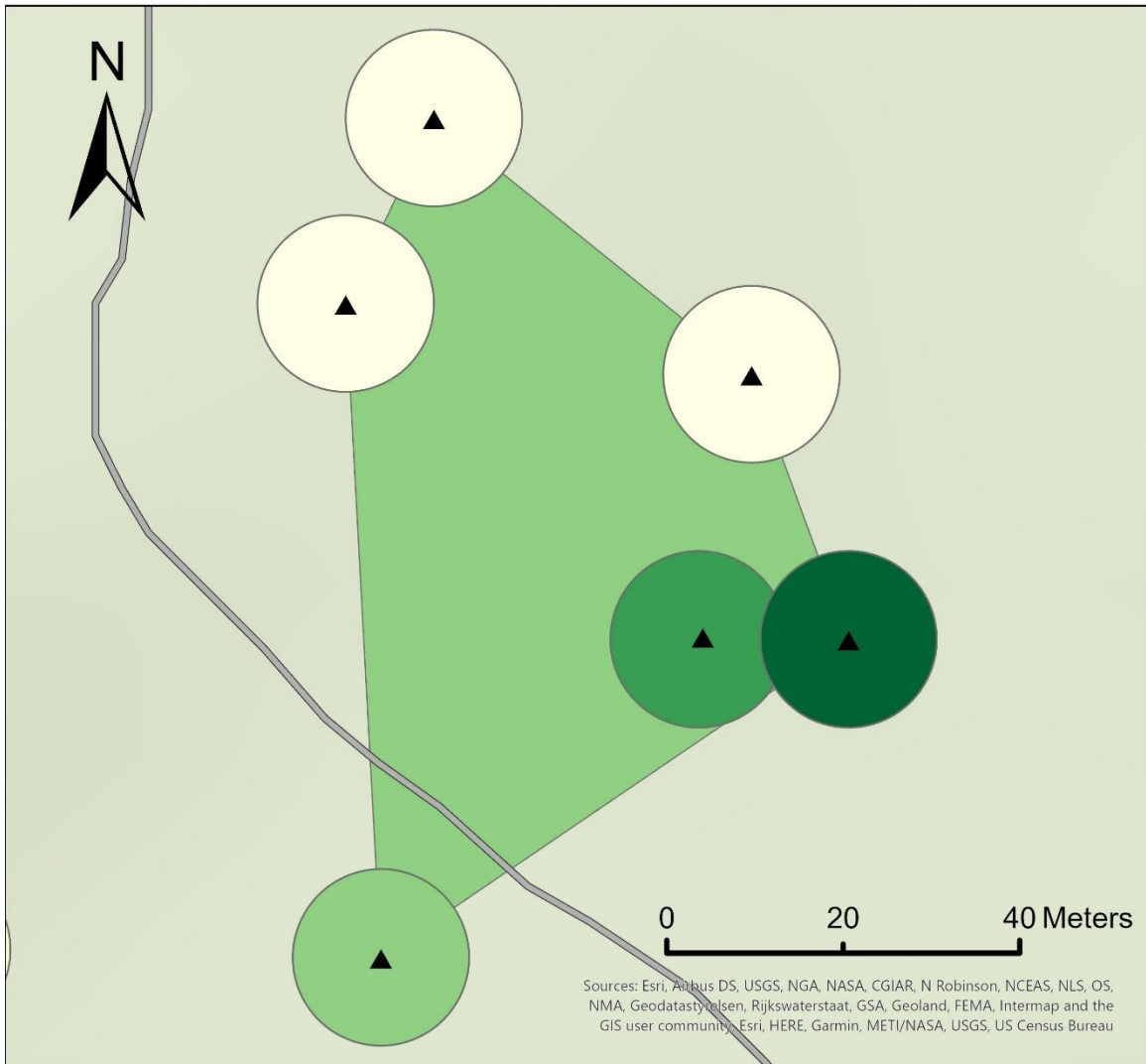
## APPENDIX



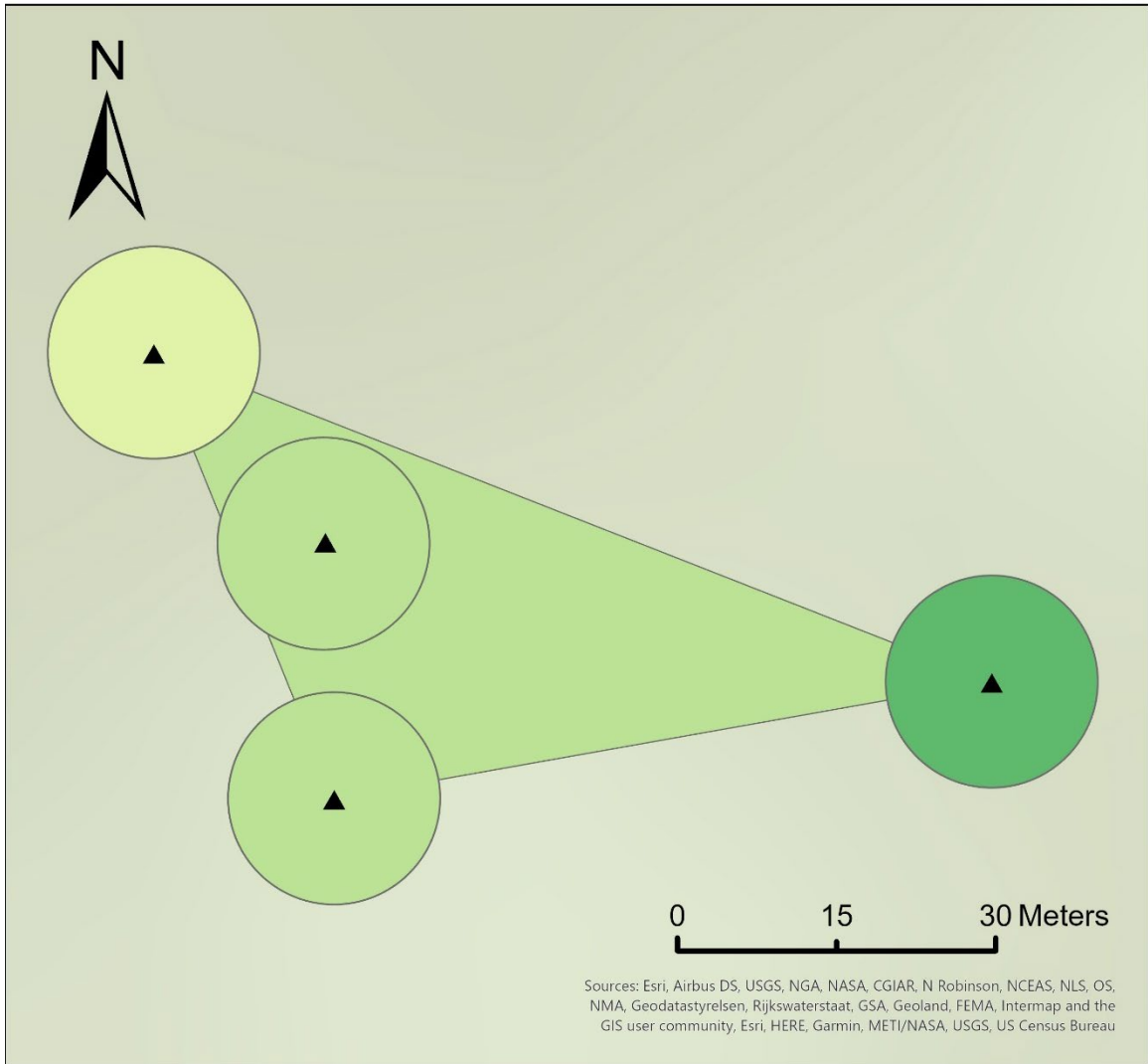
**FIGURE 4.** Location of sampled leks, display courts, and control plots. Triangles represent the centers of display courts, squares represent the centers of control plots. Radii color indicates the ripe fruit biomass of each display court and control plot. Minimum convex polygon color represents the average ripe fruit biomass of the non-court lek area. Radii marked by white dashed lines show the location of three additional display courts that were excluded from analyses due to extensive overlap of space and fruiting resources.



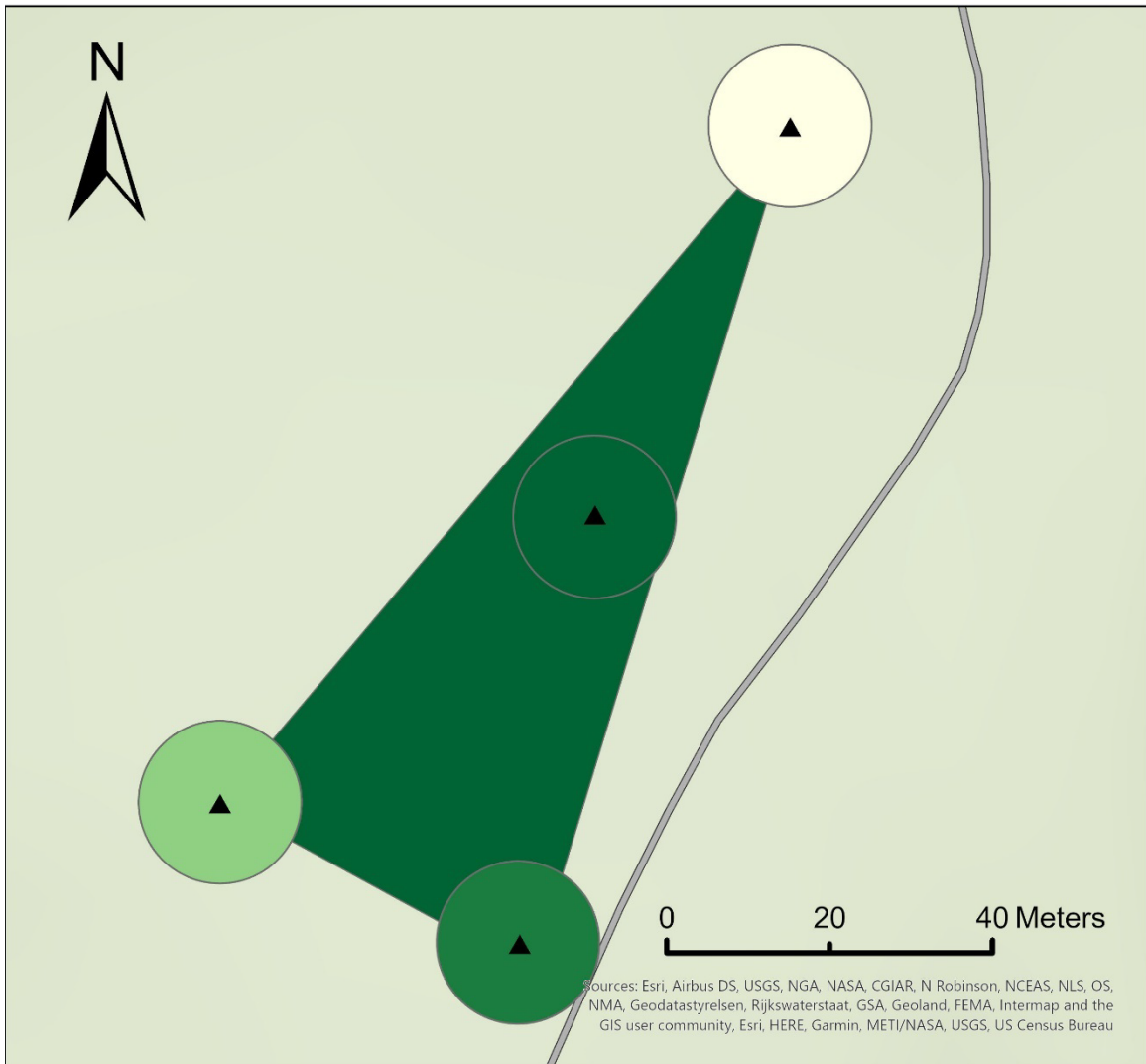
**FIGURE 5.** Close up map of Lek 6 and display courts. Triangles represent the centers of display courts. Radii color indicates the ripe fruit biomass of each display court. Minimum convex polygon color represents the average ripe fruit biomass of the non-court lek area. Radii marked by white dashed lines show the location of three additional display courts that were excluded from analyses due to extensive overlap of space and fruiting resources.



**FIGURE 6.** Close up map of Lek 8 and display courts. Triangles represent the centers of display courts. Radii color indicates the ripe fruit biomass of each display court. Minimum convex polygon color represents the average ripe fruit biomass of the non-court lek area.



**FIGURE 7.** Close up map of Lek 14 and display courts. Triangles represent the centers of display courts. Radii color indicates the ripe fruit biomass of each display court. Minimum convex polygon color represents the average ripe fruit biomass of the non-court lek area.



**FIGURE 8.** Close up map of Lek M and display courts. Triangles represent the centers of display courts. Radii color indicates the ripe fruit biomass of each display court. Minimum convex polygon color represents the average ripe fruit biomass of the non-court lek area.