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SEED DISPERSAL BY NEOTROPICAL BIRDS: EMERGING PATTERNS AND UNDERLYING PROCESSES

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Resumen. – Se considera que la dispersión de semillas por las aves impacta considerablemente los patrones de diversidad ecológica y genética de numerosas especies de plantas. Por lo tanto, una comprensión más refinada de la dinámica de la dispersión de semillas en el Neotrópico es un tema de gran interés para los ecólogos y los biólogos evolutivos y de la conservación. Ofrecemos una visión general de temas de investigación y enfoques emergentes en el campo de la dispersión de semillas por aves neotropicales, seguido por cinco estudios detallados de trabajos actuales. El tema común que une nuestras investigaciones es la integración de los patrones espaciales y temporales de deposición de semillas con los procesos mecanísticos subyacentes y sus consecuencias ecológicas. Utilizamos métodos modernos de análisis molecular, rastreo de animales basado en GPS y señales de radio, observación y experimentación en el campo y teoría de redes, para abordar el tema común de como la dispersión de semillas por las aves afecta las especies y comunidades de plantas. La conclusión más contundente de este simposio es que la composición de las especies y la ecología de forrajeo de las aves neotropicales tienen importantes consecuencias (ej. transporte de semillas por grandes distancias y / o a “micrositios” favorables para el establecimiento de plántulas, la igualación de la abundancia de semillas comunes y raras en la lluvia de semillas, el aumento de la heterogeneidad genética de las poblaciones de plántulas), que a su vez es probable que moldean la plantilla inicial de la estructura genética de las plántulas, las densidades locales de las plantas adultas, los rasgos funcionales de las especies de plantas, e incluso los patrones de ensamblaje de las comunidades.

Palabras clave: *Cephalopterus penduliger*, *Euterpe edulis*, frugivoría, mutualismo, teoría de redes, *Oenocarpus bataua*, Pipridae, *Steatornis caripensis, Tyrannus dominicencis*

Abstract.—Seed dispersal by birds is thought to profoundly impact patterns of ecological and genetic diversity in many plant species. As such, a more refined understanding of avian seed dispersal dynamics in the Neotropics is a subject of intense interest for ecologists, evolutionary biologists, and conservation biologists. We provide an overview of emerging research themes and approaches in the field of seed dispersal by beotropical birds, followed by five detailed case studies of current work. The common theme uniting our research is the integration of spatial and temporal seed deposition patterns with underlying mechanistic processes and ecological consequences. We use contemporary methods in molecular analyses, GPS-based and radio-based animal tracking, field-based observation and experimentation, and network theory to address the common theme of how avian seed dispersal impacts plant species and communities. The over-arching conclusion of this symposium is that species composition and foraging ecology of neotropical birds have important consequences (e.g., moving seeds long distances and/or to favorable microsites seedling establishment, equalizing the abundance of common and rare seeds in seed rain, increasing genetic heterogeneity of seedling populations), which in turn are likely to shape the initial template of genetic structure among seedlings, local densities of adult plants, functional traits of plant species, and even patterns of community assembly.

Keywords: *Cephalopterus penduliger*, *Euterpe edulis*, frugivory, mutualism, network theory, *Oenocarpus bataua*, Pipridae, *Steatornis caripensis, Tyrannus dominicencis*

INTRODUCTION

Dispersal of seeds away from the parental plant impacts seed survival and patterns of genetic and ecological diversity within and between plant populations (Levey *et al.* 2002, Sork & Smouse 2006, Dennis *et al.* 2007). Most woody tropical plant species produce fleshy fruits adapted for animal consumption, and frugivorous vertebrates are the dominant vectors for seed dispersal in these habitats (Terborgh *et al.* 1990). In the Neotropics, species richness of both plants and frugivorous bird species reach their global maximum (Kier *et al.* 2005, Kissling *et al.* 2009). These conditions reflect the existence of a deep co-evolutionary relationship between neotropical birds and plants that continues to shape contemporary ecological and micro-evolutionary processes in both groups. As such, a more refined understanding of avian seed dispersal dynamics in the Neotropics is a subject of intense interest for ecologists, evolutionary biologists, and conservation biologists.

Research on seed dispersal by neotropical birds spans several decades (e.g., Snow 1961, 1981, 1982; Howe & Smallwood 1982). The field has continued to grow in the past decade (Fig. 1) and has recently benefitted from a number of exciting analytical, technological, and conceptual advances that promise continuing progress well into the future. We provide an overview of emerging research themes and approaches, followed by five detailed case studies of current work related to understanding pattern and process in neotropical avian seed dispersal. Here, '*pattern*' is broadly defined to include spatially explicit patterns of seed deposition, seedling establishment, and genetic structure and well as non-spatial representations of species interactions and community level relationships (e.g., network theory). '*Process*', in contrast, refers to the underlying mechanisms, such as frugivore foraging ecology or the spatial and temporal distribution of resources, which likely drive seed movement and observed ecological and genetic patterns.

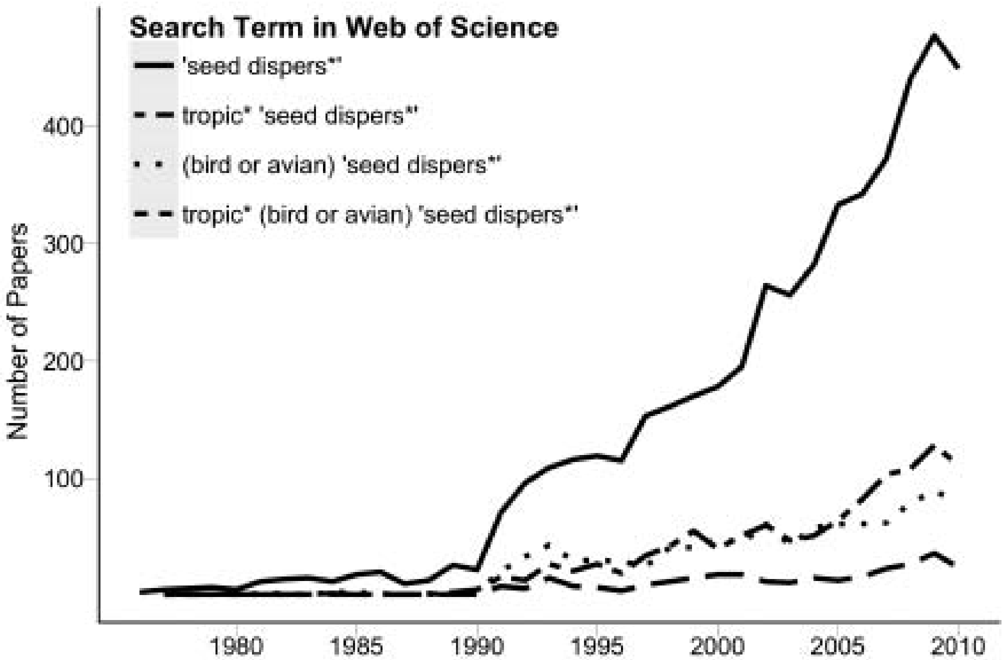

FIG.1. The number of published papers by year in the ISI Web of Science database (searched Oct. 2011) with the search terms 'seed dispers*', tropic* 'seed dispers*', (bird or avian) 'seed dispers*', tropic* (bird or avian) 'seed dispers*'.

A unifying theme of the research summarized in this article is to identify and understand relationships between mechanistic processes and observed seed dispersal patterns. Differences in patterns of seed deposition, seed survival, the genotypic diversity of seed pools, and the nature of seed dispersal networks are all likely to be impacted by the movement and foraging ecology of dispersal agents (Schupp *et al.* 2002) and by the distribution of resources in time and space that may drive disperser movements (Castro *et al.* in press). However, challenges associated with tracking both seeds and the vertebrates that disperse them have slowed efforts to understand these relationships. As such, a current focus of the field is to strengthen our understanding of the linkages that may exist between various species of dispersal agent (and/or specific behaviors) and the dispersal outcomes they generate. A related goal is to scale up this information to the level of the community. Establishing this mechanistic understanding of the processes underlying observed patterns is a key step toward predicting dispersal services of frugivore species and, by extension, dispersal dynamics in communities. This knowledge can also assist in predicting what the consequences of species loss, habitat alteration, and other forms of anthropogenic disturbance may be for seed dispersal mutualisms. Below, we briefly summarize contemporary research themes in the pattern and process of seed deposition before turning to our case studies.

Pattern. The consequences of seed dispersal has received extensive attention since Darwin, but it was Janzen (1970) and Connell (1971) who proposed that movement of seeds away from the parent plant shapes the distribution of seedlings through avoidance of density-dependent sources of mortality and localized pathogens, amelioration of intense competition between siblings, and enhanced probability of arriving at a favorable establishment site (Howe & Smallwood 1982). As Janzen and Connell observed, the vast majority of seeds are typically dispersed not at all or very short distances, with probability of deposition steeply declining as distance from the source plant increases but extending out in a 'tail' representing low frequency, longer-distance dispersal events. Within this broad pattern, however, there appears to be significant variation in deposition patterns produced by different vertebrates, including the distances they transport seeds, the microsite where seeds are deposited, the density and genotypic characteristics of the seed rain they generate across the landscape (Schupp *et al.* 2010). Our ability to characterize and analyze these spatial patterns of seed dispersal has improved dramatically in the past decade thanks to advances in molecular and associated analytical analyses, and isotope-marking methods for tracking seed dispersal and seedling establishment.

Molecular analyses have improved our ability to characterize patterns of seed movement within and between populations, yielding important insights to complement ecological observations of dispersal. In the past decade, more informative and less expensive molecular markers such as allozymes, microsatellites and Amplified Fragment Length Polymorphisms (AFLP) have allowed workers to characterize patterns of genetic structure of dispersed seeds and seedlings within populations (e.g., Loiselle *et al.* 1995). For example, Sezen *et al.* (2005) used AFLP analysis to show that genetic diversity among seedlings of *Iriartea deltoidea*, a bird dispersed palm tree, was reduced in secondary forest because only the seeds from a small sub-set of adults in nearby primary forest were dispersed and germinated in this habitat type. Godoy & Jordano (2000) introduced a finer-grained molecular approach that exploits the fact that seed pericarp tissue is purely maternal tissue (i.e., not a mixture of maternal and paternal genotypes), making it possible to link each seed back to a maternal source tree by genotype matching. This methodological approach permits direct quantification of the number of maternal genotypes contributing to a given pool of dispersed seeds, and associated analytical approaches such as the Probability of Maternal Identity (PMI; Grivet *et al.* 2005) allow estimation of the effective number of maternal trees contributing to a seed pool. These tools provide new perspectives into genotypic consequences of dispersal at small spatial scales. At the landscape level, molecular approaches can be used to document levels of gene flow via seed dispersal between patches or populations (Sork & Smouse 2006), though examples from neotropical avian dispersal systems are rare. While molecular approaches have proved extremely powerful at illuminating patterns of seed movement, they often have little to say about the mechanistic processes which result in observed patterns because dispersed seeds are collected in the field with little knowledge of how they came to arrive in a given location (but see below).

More recently, ^{15}N stable-isotope marking methods have been developed as an alternative to molecular genetic markers in the study of dispersal from specific plant sources (Carlo *et al.* 2009) and are currently being used by a number of in-progress studies to examine long-distance dispersal in fragmented landscapes (Daniel García and collaborators in Oviedo, Spain), the movement of plants with different natural history traits (Joshua Tewksbury and collaborators in the Savanna River Site corridor project in South Carolina, USA), the effects of population density on seed dispersal kernels (Morales *et al.* in press), and others. The advantage of stable isotope marking is that it allows for the mass-processing of seeds when used in combination with mixing models, which increases chances of detecting rare events with less laboratory work—solving the "needle in the haystack" problem faced by most studies of dispersal at longer distances (Carlo *et al.* 2009). However, stable isotope-marking is not appropriate for population-wide studies of dispersal because seeds from only a small number of individual plants can be tagged in a given population, and thus, it does not replace molecular genetics for many important questions in the field.

Network theory is another powerful tool for ecologists attempting to visualize and understand patterns of plant-animal interactions (Ings et al. 2009). In contrast to molecular and isotopic approaches, network theory is typically not spatially explicit. Rather, network theory allows visual representation of species interactions and analysis of community structure and dynamics. This may facilitate understanding of mutualistic networks by simplifying complex relationships to reveal higher levels of organization and properties not apparent when focusing on pairs of interacting species. For example, network theory has demonstrated that plant-seed disperser networks have a skewed distribution of links (i.e., dispersal interactions) per species, with a few super-generalists and many specialists (Jordano *et al.* 2003). Plant-seed disperser networks are also highly nested, in that interactions between specialists form a subset of generalist species interactions, which is thought to maintain potential biodiversity (Bascompte *et al.* 2003, Bastolla *et al.* 2009). Plant-seed disperser network structure can also be described in terms of modules or closely connected subgroups of species within the network that interact more frequently within their module than with other subgroups. This pattern of modularity, or compartmentalization, is well studied in pollination networks where it has been suggested that modules represent coevolutionary units (Olesen *et al.* 2007), but has only recently been investigated in plant-seed dispersal networks (Donatti *et al.* 2011, Mello *et al.* 2011). Network theory has only recently been applied to the specific question of plant-animal mutualisms, and it holds great promise to further our understanding of these systems. However, additional advances in network theory (e.g., synthesizing multiple networks, incorporating spatial and temporal contextual information) are required to adequately address many long-standing questions about seed dispersal.

Process. Animal tracking, modeling, and the ability to link individual dispersed seeds to the individual or species of frugivore that dispersed them are three useful tools for improving our understanding of processes underlying seed dispersal outcomes. Neotropical birds are relatively well represented in studies seeking to characterize animal movement via radio telemetry (e.g., Murray 1988, Westcott & Graham 2000). These movement data, when combined with gut retention times for commonly consumed fruit species, allow estimates of the seed deposition patterns generated by individual bird species (see below). Recent technological developments in the production of lightweight satellite (PTT) transmitters and GPS tags allow us document movement patterns over increasingly large spatial areas. PTT and GPS units allow us to quantify the frequency and extent of landscape level dispersal events by large frugivores, providing new information on connectivity between habitat patches and the scale of long-distance dispersal. These devices also provide detailed data on movement and activity patterns, providing more resolution in dispersal dynamics at relatively fine spatial scales (Holland *et al.* 2009, Lenz *et al.* 2011). PTT and GPS units are currently only available for relatively large birds because of weight considerations, but the number of species that can be tracked using these tools increases each year as battery size decreases (Wikelski *et al.* 2007). Relatively few studies have been conducted in neotropical birds using these methods, but we expect more studies using this technology as prices and weight of units continue to drop.

Mechanistic models integrate information on disperser movement, fruit availability, and/

or habitat characteristics to illuminate the processes that drive variation in dispersal and deposition patterns. Mechanistically modeling seed dispersal has been especially amenable for wind-dispersed species (Nathan *et al.* 2001, Tackenberg 2003), but the complex nature of animal movements makes this a much more elusive goal in zoochorous systems. Empirical data on frugivore movement and gut retention times have been used to predict animal-generated seed dispersal distributions (Murray 1988, Westcott & Graham 2000, Westcott *et al.* 2005), and, more rarely, to apply these in a spatially-explicit context (Holbrook & Loiselle 2007). More recently, the use of stochastic, individual-based models has allowed for more refined spatial predictions (Russo *et al.* 2006, Will & Tackenberg 2008), as well for investigation of the influence of landscape, plant or animal variables upon seed dispersal patterns (Morales & Carlo 2006, Carlo & Morales 2008). As increasingly refined data on movement and genetic and demographic consequences of dispersal become available, models are expected to become increasingly informative and realistic.

In circumstances where the dispersal agent responsible for the deposition of a seed or a pool of dispersed seeds can be identified with a fair degree of certainty, we can study characteristics of these dispersed seeds to gain a more detailed understanding of how that particular agent contributes to ecological and genetic patterns of dispersal. Examples of conditions where this might apply to neotropical birds include dispersed seeds encountered beneath regularly used display, nesting, or roosting sites. At the ecological level, these conditions have been exploited to demonstrate, for example, that directed dispersal by displaying Three-wattled Bellbirds (*Procnias tricarunculata*)to favorable microsites for seedling establishment increases probability of seedling establishment (Wenny & Levey 1998). Similarly, we can use molecular analyses to assess the genetic consequences of dispersal by a given dispersal agent. The seed pool structure (PMI) approach of Grivet *et al.* (2005), for example, can translate clumped distributions of seeds into inference on genetic bottlenecks and/or genetic mixing produced by a given dispersal agent (Scofield *et al.* 2010, 2011; see also Garcia *et al.* 2009). If one has a site where all adult trees are mapped and genotyped, this method can be combined with traditional maternity analysis to identify the seed source and thus directly measure dispersal distance (e.g., Jordano *et al.* 2007). Thus, when the dispersal agent responsible for the deposition of a pool of dispersed seeds can be identified, we can conduct unambiguous tests of how a given dispersal agent or behavior impacts the initial template of plant genetic structure or seed survival, and by extension what the consequences of losing this vector might be.

These and several other studies have provided a strong empirical and theoretical foundation for new approaches to long-standing questions about seed dispersal by neotropical birds. How far do birds move seeds? Where do they deposit them? What drives variation within and between bird species in seed movement and deposition? How do birds affect relative abundance of seeds arriving at suitable deposition sites? What are the genetic and demographic consequences of variation in these parameters for plant populations? In the following sections, we provide more detailed summaries of five active research projects that employ combinations of these approaches to address these and related questions about seed dispersal by neotropical birds.

NIGHTLY AND SEASONAL MOVEMENTS OF A SPECIALIZED FRUGIVORE, THE OILBIRD (STEATORNIS CARIPENSISI), IN VENEZUELA

Birds capable of transporting seeds long distances (e.g., Holbrook *et al.* 2002, Powell & Bjork 2004, Holland *et al.* 2009) are of particular interest to seed dispersal researchers because of their potential to provide connectivity between forest fragments and their importance for conservation (Kremen 2005). We describe here how Oilbirds (*Steatornis caripensis*) perform nightly foraging trips of tens of kilometers on a regular basis, and we examine their use of protected areas in northeastern Venezuela.

Oilbirds (c.415 g), the only nocturnal fruit-eating bird in the world, inhabit evergreen lowland and montane forests locally, from northern South America along the Andes, to Perú and Bolivia. They forage for fruit at night and roost in caves during the day, where up to thousands of individuals may breed (Snow 1961). Oilbirds feed almost exclusively on the single-seeded fruits of lipid-rich Lauraceae, Arecaceae (palms), and Burseraceae (Bosque *et al.* 1995). They swallow fruits whole and regurgitate the seeds intact after stripping the pulp. Fruits are also fed whole to nestlings; hence, seeds are regurgitated in large numbers in the breeding caves. Given the strong connection to the breeding caves, the role of Oilbirds as effective seed dispersers has been disputed (Moermond & Denslow 1985, Bosque *et al.* 1995). The purpose of this study was thus to examine their nightly and seasonal movements and roosting activity of Oilbirds outside caves to gain insight into their role as seed dispersers of forest trees. In addition, we assessed the importance of national parks and other legally protected areas in relation to habitat use by Oilbirds.

We studied Oilbirds at "Cueva del Guácharo" in northeastern Venezuela by deploying a total of 40 GPS/acceleration loggers with remote UHF download readout in November 2007 (see Holland *et al.* 2009) and August 2008, towards the end of the birds' chick-rearing period. We downloaded 35 of the loggers at the cave before battery life expired. Twelve of the loggers (in 2007) were programmed with 600–900 s intervals between GPS fixes, allowing for the recording of activity for three to four nights. The rest of the loggers (in 2008) were programmed to obtain GPS fixes at hourly intervals once a week, allowing for scrutiny of seasonal activity.

In total, we recorded over 3500 GPS locations, providing novel insights into the movement ecology of Oilbirds. Birds foraged over tens of kilometers nightly; among the eight birds whose loggers we downloaded in 2007, the average distance from the Guacharo Cave to the farthest foraging site was 44.4 ± 10.7 (mean ± SE) km, with a maximum distance of 73.5 km (Holland *et al.* 2009). In 2008, average nightly distance from roost to foraging sites was over 30 km. During 2008, when the programming of the GPS tags allowed for recording from late August 2008 to January 2009, maximum distance varied by season. Distances traveled were lowest during the late chick-rearing period in August and highest from October to December, when fruit availability is lowest in the study area (Bosque *et al.* 1995). The maximum distance that we recorded Oilbirds foraging from the Guácharo Cave in 2008 was over 300 km. Contrary to common belief, we found that Oilbirds did not always return to caves each night but sometimes made extended foraging trips over a number of nights, even during the chick rearing period (Holland *et al.* 2009). Preliminary analyses of the 2008 data indicate that approximately 50% of all foraging and roosting locations fell within the boundaries of the national parks designed to protect Oilbirds and the surrounding forests.

Our results show that Oilbirds regularly make long- distance foraging trips while potentially dispersing the seeds of Lauraceae and palms over considerable distances and between forest patches. The high lipid content of fruit pulp that they consume requires a lengthy processing in the digestive tract (Bosque & Parra 1992), which in combination with the observed extensive nightly movements indicate that Oilbirds effectively transport seeds tens of kilometers away from parent plants. Our findings confirm that Oilbirds are important seed dispersers and likely contribute significantly to forest diversity and regeneration.

THE IMPACT OF FRUGIVORY NETWORKS ON PLANT RELATIVE ABUNDANCES

Network models of frugivory and seed dispersal predict that structural properties of community-wide interactions are linked to the stability of mutualistic communities and to the maintenance of diversity. Still, we lack empirical validation for most network model predictions. How exactly might frugivory networks maintain diversity? How do processes translate into observed pattern? Here we study patterns of avian seed dispersal from forest fragments into tropical pastures and examine some of their effects on successional communities.

Every month for a year we quantified the production of seeds by fleshy fruited plants in forest fragments in Puerto Rico and compared it to the arrival of seeds and recruitment of seedlings at ten experimental forest regeneration plots in pastures. We also quantified the abundance, seed dispersal, and foraging activity of avian frugivores in forest fragments and experimental pasture plots and correlated these with the arrival and recruitment of plant seeds in pastures.

Fleshy-fruited plant species varied greatly in their cumulative yearly production of seeds. For example, we estimated that only three species in the community (5.1%) produced more than 100 seeds per m^2 in the study area, 41 (69.5%) of species had less than one seed per m^2, 21 (35.6%) species had less than 0.01 seeds per m^2, and 14 (23.7%) produced less than 0.001 seeds per m^2. Overall, there were differences of up to eight orders of magnitude between the abundances of the seeds of the most common (>300 seeds per m^2) and the rarer plant species (< 0.00001 seeds per m^2). For example, seeds of common plant species like *Bursera simaruba, Citharexylon fruticosum, Eugenia monticola*, and *Guapira fragrans* were produced at densities between 16 to 309 seeds per m^2, and seeds of uncommon or rare plant species like *Gyminda latifolia, Guettarda scabra, Cayaponia amaricana, Trema micrantha*, and *Ardisia obovata* were produced at densities between 0.18 and less than 0.0001 seeds per m^2. However, when looking at densities in the seed rain of experimental plots in the open pastures, the differences between the most common and the rarer plant species amounted up to only three orders of magnitude. In such frugivore-generated seed rain, many rare or uncommon species were as dense or even more dense than the most common plant species in the environment. With few exceptions, the recruitment and establishment patterns of bird-dispersed plants observed in experimental plots closely mirrored the seed rain. These results show that the frugivore community "transformed" the relative abundances of seeds from what's available in the environment to their presence in the seed rain, effectively reducing the magnitude of the interspecific differences in abundance—similar to the way in that a statistician log-transforms a skewed data set to make the distribution more even and representative.

In terms of the species of birds conducting seed dispersal into pastures, we found that despite there being seven frugivores species present and abundant in the forest fragments, just two—*Tyrannus dominicencis* and *Mimus polyglottus*—accounted for 82.5% of all seed dispersal and foraging activity on the forest regeneration plots and statistically sufficed to explain the absolute number and species richness of seeds arriving in plots through time.

Results show that community-wide frugivory networks can transform the net quantities of seeds produced in plant communities and have an "equalizing" effect that benefits the dispersal and recruitment of rare plant species early on during processes of forest regeneration and serve to create resilience to the loss of many tropical plant species in fragmented and altered habitats. Results also confirm the important of role of a few generalist species in providing dispersal services for a wide variety of plant species in degraded habitats. Equalizing transformations of seed abundances in the seed rain generated by networks of frugivory and seed dispersal can thus serve as a mechanism to explain the stability and puzzling persistence of rare plant populations in tropical forests and to maintain and generate diversity patterns.

AVIAN SEED DISPERSAL NETWORK OF THE PALMITO EUTERPE EDULIS POPULATIONS IN A DEFAUNATION LANDSCAPE

The analysis of complex networks in plant-animal interactions can be used to interpret possible effects of species extinctions in mutualistic interactions (Rezende *et al.* 2006). The palm *Euterpe edulis*, popularly known as "palmito", is a keystone fruit species for several frugivorous bird species in the Brazilian Atlantic forest. Only 12% of this forest remains (Ribeiro *et al.* 2009), and many fragments now lack large frugivorous birds, such as toucans, guans, and cotingas to disperse seeds. Here, we describe qualitatively and quantitatively the networks between bird species and *E. edulis* populations across a defaunation gradient.

We studied nine palmito populations through at least 1180 hours of focal observations (at least 60 hours per fragment), during which we obtained data on consumption of palmito fruit. We compared our observed matrix with a hypothetical network of 52 populations of *E. edulis*, based only on data from the presence and absence of those frugivorous species in these selected areas of palm populations, to make more robust the analyses of network modularity.

The interactions network showed a high degree of nestedness: the species richness of frugivorous bird species in defaunated areas represents only a subset of the species diversity in pristine areas. This finding demonstrates that there was no "substitution" effect in which other species would replace locally extirpated species. Further, the observed extinctions were not random. Large avian frugivores, particularly toucans and trogons, had a strong effect on the network structure of palmito-bird interaction in pristine forests. Small fragments have few frugivores that eat palmito fruits, and most interactions in these fragments involve thrushes (*Turdus* spp.).

The interaction network was divided in three modules by the analysis of modularity, defining three different groups of seed dispersers and types of fragments that differ by the rate of consumption of fruits. One was composed of defaunated areas and small frugivorous, such thrushes and flycatchers, and represents a low rate of fruit consumption, while in the other two modules the rate of consumption was higher, coinciding with the presence of large dispersers, such as toucans, aracaris and cotingas. The hypothetical network showed the same pattern found in the observed network. It also showed a high degree of nestedness and was also divided by the analysis of modularity in three modules, one composed almost entirely of small size species, high degree of generalization, and in very degraded areas, and two other modules that were mostly composed of large species, with high degree of frugivory in most preserved areas. Overall, these data suggest a loss of important seed dispersers, and consequently a loss of interaction strength in defaunated areas. The next steps are to understand the effects of bird extinction on plant recruitment in distinct fragments, and how changes in bird assembly affects gene flow of palmitos.

PATTERN AND PROCESS IN A NEOTROPICAL SEED DISPERSAL MUTUALISM

Three current priorities in the field of seed dispersal are: (1) to better characterize seed movement and deposition patterns generated by specific avian dispersal agents; (2) to document the demographic and genetic consequences of those deposition patterns; and, (2) to elucidate the causes and consequences of these dispersal patterns. We addressed these questions by focusing on a mutualistic relationship between an endangered Cotingid, the Long-wattled Umbrellabird (*Cephalopterus penduliger)*, and a canopy palm species (*Oenocarpus bataua*) in Ecuador's Chocó rainforest.

Using seed traps and standardized census plots, we found that the density of seeds and seedlings in Umbrellabird leks is roughly double that found in control sites located outside leks. By differentiating between seeds and seedlings located under conspecific crowns and those that had been dispersed, we found that this difference is almost entirely due to a higher rate of dispersed seeds in the lek (Karubian *et al.*, in press). We conclude that lekking behavior by Umbrellabirds causes males to deposit large proportions of seeds they consume beneath their display perches on the lek.

There is widespread empirical evidence for density-dependent mortality among clumps of undispersed seeds at the base of maternal (source) plants, but the degree to which these density –dependent mechanisms play out at clumps of dispersed seeds away from source trees is less well understood. Despite higher seed density in leks versus outside the lek, we found no evidence for differential establishment rates for seeds arriving into the lek versus outside the lek. This suggests that there may be important survival benefits associated with dispersal into lek sites that outweigh density-dependent mortality processes at these sites. A manipulative experiment involving planting of 560 young seedlings in 7 leks and respective control sites indicates that, after three years time, survival is indeed higher in lek sites relative to control sites among seedlings. These findings indicate that Umbrellabirds are engaging in 'directed dispersal' to lek sites and increasing recruitment probability as a result. We are currently investigating the relative contribution of genotypic diversity of dispersed seeds, microhabitat attributes, and seed predator densities in shaping this pattern.

Turning to the genetic consequences of Umbrellabird dispersal, we note that many ecological and genetic studies suggest that vertebrate dispersal often yields 'genetic bottlenecks' consisting of highly related seeds at dispersal sites such those found at Umbrellabird leks. For example, acorn woodpecker granaries (Grivet *et al.* 2005) and resting/roosting sites for temperate zone birds (García *et al.* 2009) have low levels of genotypic diversity. Taking advantage of the fact that we can confidently link seeds located under Umbrellabird display perches to dispersal by Umbrellabird males, we have found that seed pools in Umbrellabird leks have on average five times more genotypic diversity than control seed pools located outside the lek (Karubian *et al.* 2010). This serves to homogenize local genetic structure among seedling populations of this species, though the degree to which these impacts on seedling genetic structure translate through to established adults is unknown.

To better understand the mechanistic causes that may be responsible for the dispersal patterns generated by lekking Umbrellabirds, we have used radio tracking and gut retention trials to gain insights into how movement and foraging ecology impacts dispersal outcomes. Seed dispersal distributions generated by integrating distributions of distances moved and seed retention times, we found that males are expected to bring > 50% of the seeds they ingest while foraging away from the lek back to their display territories on the lek (Karubian *et al.* in press). Females, in contrast, retain fixed home ranges and disperse seeds evenly across these areas. These findings highlight the importance of social behavior and foraging ecology in shaping vertebrate seed dispersal outcomes.

SEED DISPERSAL BY SYMPATRIC MANAKIN SPECIES IN THE ECUADORIAN AMAZON

Mutualistic interaction between plants and animals is a well-known feature of many ecosystems, but considerable controversy remains regarding the degree to which animals shape plant distribution patterns and act as selective forces on plant traits. In biodiversity-rich communities, untangling the web of interactions and determining the relative strength of pair-wise interactions over temporal and spatial scales is a particular challenge. Tropical lowland wet forests of western Amazonia are one of the most species-rich locations on the planet. Compared to tropical wet forests of Costa Rica, where one to two manakin species (Aves: Pipridae) are regularly found in forests year round, one can commonly encounter no less than six forest manakin species in the understory and sub-canopy of forests in eastern Ecuador. Manakins are highly frugivorous and often are numerically the most important seed dispersers in understories of neotropical forests. Thus, species-rich forests of western Amazonia provide an opportunity to investigate the relative ecological roles of manakins as seed dispersers for tropical plants. Specifically, one can ask the degree to which species are ecologically redundant in the dispersal services they provide, and, if not, whether any species play a particularly strong role in predicting spatial distribution of a target plant at early life history stages.

We examined the seed dispersal function of six manakin species that consume and disseminate the seeds of *Miconia nervosa* (Melastomataceae), a relatively common understory shrub. To do this, we used data on captures of manakins and locations of male display areas (i.e., leks) that have been gathered over an 11 year period on a 100 ha plot at Tiputini Biodiversity Station. These data were simplified to provide presence information at georeferenced locations. Using ecological niche modeling techniques (i.e., MAXENT) and GIS databases of environmental conditions (e.g., elevation, slope, distance to stream, etc.), we developed a spatially-explicit model of seed dissemination by birds based on the probability of occurrence in 25 m x 25 m grid cells on the plot. Separate models were developed for males and females and, because males spend most of their day at display sites, occurrence of males was further restricted to the vicinity of leks; vicinity was based on known maximum recapture distances on the plot. A composite model for male and female manakins was also produced that weighted probability of occurrence by relative abundance of the manakin species. We also mapped the distribution of adults, juveniles, and seedlings of *M. nervosa* on 20 ha of the 100 ha plot and determined the number of seedlings within 25 m x 25 m grid cells. We used regression models and likelihood analyses to test hypotheses that biotic (bird activity), abiotic (environmental variables), or adult distribution (number of adults per 25 m x 25 m grid cell) to explain abundance or presence of seedlings.

We found that although manakin species feed on similar species of fruits (mean pairwise diet overlap = 0.87; Loiselle *et al.* 2007), their spatial use of the environment, as measured by MAXENT models, suggests that different species of manakins often deliver seeds to different locations. Males tended to overlap less in spatial use of the environment than did females (males: pairwise *r*-values ranged from -0.63 to 0.70; females: 0.32 to 0.80). Thus, manakins show some redundancy in spatial dissemination patterns but behave in a complementary fashion. Consequently, over all species, seeds should be delivered to more forest environments in this species-rich community than if species showed greater correlations in spatial patterns of occurrence. However, despite apparent differences in the spatial dissemination of seeds by manakins, little relationship was found between biotic variables and the distribution of seedlings. Within the 20 ha plot, 121 seedlings, 244 juveniles, and 267 adult individuals were mapped. Most seedlings and juveniles were found close to adult plants (i.e., within 5 m), although molecular genetic analyses are needed to determine if these nearest adults were actually maternal plants. We found that the best predictor of seedling distribution was the distribution of adult plants. Two environmental variables (sine and cosine of aspect) and probability of occurrence of *Pipra erythrocephala* females also helped explain seedling distribution, but they explained relatively little of the variation relative to the amount explained by adult plants.

In this system, dissemination of seeds appears to be distance-restricted as most seedlings and juveniles are found close to adult plants. Adult *M. nervosa* are aggregated in space and tend to be found near small forest streams. Although birds provide the spatial template of seeds in the environment through their movement behavior following seed ingestion, it appears that activity by birds does not provide a strong signal to predict seedling distribution. Further experimental work is needed to confirm the pattern of distance-restricted dispersal, as other factors, such as environmental conditions, may significantly alter the seed shadows left by birds through differential seed germination and seed and seedling survival.

CONCLUDING REMARKS

The five case studies presented here provide examples of contemporary approaches to long-standing ecological questions concerning seed dispersal dynamics. The over-arching conclusion of these studies, and this symposium, is that species composition and foraging ecology of neotropical birds have important consequences for spatial and temporal patterns of seed movement and survival, which in turn are likely to shape patterns of genetic structure, local densities of adult plants, functional traits of plant species, and even patterns of community assembly.

We consider it likely that the next decade will continue to bring significant advances in the field of seed dispersal. We believe that improved animal and seed tracking methods will continue to refine our understanding of how frugivore behaviors impact dispersal outcomes. This is expected to provide better understanding of disperser quality, continuing progress toward a potentially predictive paradigm for how different behavioral traits (e.g., territorial versus colonial, etc) affect vertebrate dispersed plant species. Advances on this front are expected to be increasingly important for conservation biology in addition to evolutionary ecology in proportion to the degree to which anthropogenic activities continue to perturb seed dispersal mutualisms.

We also expect that molecular and isotopic methods will improve our resolution of the seed dispersal kernel and patterns of gene flow and connectivity within and between populations. These same tools will also allow better integration of the relative importance of seed versus pollen movement to gene flow and genetic structure. Extending our understanding of how dispersal affects establishment and genetic structure of seeds or seedlings, we expect that future studies will connect dispersal consequences through to the adult stage through longer-term longitudinal studies. In particular, longitudinal studies which track seed fate through to reproductive adults are needed to inform the degree to which differing dispersal mechanisms impact community structure and genetic structure of plant populations (Schupp *et al.* 2010). Finally, we expect that more sophisticated modeling approaches and applications of network theory (e.g., incorporating spatially and temporally explicit contextual information, interaction strength, and phylogenetic information) will serve as a key tool for understanding how aspects of seed dispersal mutualisms described above structure communities and shape ecological, genetic, and phylogenetic diversity of plant populations. Studies of seed dispersal by neotropical birds have been central to our understanding of seed dispersal as a whole, and our expectation is that the tools and approaches outlined in this article will continue to bring exciting advances in this field.

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