Destination-based seed dispersal homogenizes genetic structure of a tropical palm

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Abstract

As the dominant seed dispersal agents in many ecosystems, frugivorous animals profoundly impact gene movement and fine-scale genetic structure of plants. Most frugivores engage in some form of destination-based dispersal, in that they move seeds towards specific destinations, resulting in clumped distributions of seeds away from the source tree. Molecular analyses of dispersed seeds and seedlings suggest that destination-based dispersal may often yield clusters of maternal genotypes and lead to pronounced local genetic structure. The long-wattled umbrellabird *Cephalopterus penduliger* is a frugivorous bird whose lek mating system creates a species-specific pattern of seed dispersal that can potentially be distinguished from background dispersal processes. We used this system to test how destination-based dispersal by umbrellabirds into the lek affects gene movement and genetic structure of one of their preferred food sources *Oenocarpus bataua*, a canopy palm tree. Relative to background dispersal processes, umbrellabird mating behaviour yielded more diverse seed pools in leks that included on average five times more seed sources and a higher incidence of long-distance dispersal events. This resulted in markedly lower fine-scale spatial genetic structure among established seedlings in leks than background areas. These species-specific impacts of destination-based dispersal illustrate how detailed knowledge of disperser behaviour can elucidate the mechanistic link driving observed patterns of seed movement and genetic structure.

Keywords: animal behaviour, chocó rain forest, gene flow, lek mating system, maternity analysis, seed movement

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Introduction

Seed dispersal by vertebrates has a major impact on seedling establishment, gene flow and genetic structure in plants (Howe & Smallwood 1982; Levey *et al.* 2002; Wang & Smith 2002). This impact is especially intense in tropical rainforests, where vertebrates disperse up to 85% of all tree species (Terborgh 1990). Most vertebrate dispersal agents engage in some form of 'destination-

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based' dispersal by centering their movement around certain spots where they are likely to deposit a significant proportion of seeds they ingest (Howe & Smallwood 1982; Wenny 2001). Behaviours driving destination-based dispersal include displaying, resting, nesting, roosting, food processing or territoriality (Schupp *et al.* 2002). Destination-based dispersal is notable because it yields clumped distributions of seeds away from the source tree, potentially resulting in different patterns of seedling establishment than expected under the classic, leptokurtic kernels for seed source based dispersal (*sensu* Janzen 1970). Resolving how destination-based dispersal processes impact the genetic heterogeneity of dispersed seeds is therefore an important step towards

understanding plant population dynamics and the forces responsible for patterns of local genetic structure observed in adult plant populations.

The use of genotypes from maternally – inherited tissue in seed or fruit (Godoy & Jordano 2001) provides a powerful tool to assess the genetic consequences of destination-based dispersal. One way to document those consequences is the seed pool structure approach (Grivet *et al.* 2005), which estimates the probability of maternal identity (PMI) using maternal genotypes determined from dispersed seeds. This approach estimates the number of seed sources per seed pool, which can tell us whether clumped distributions represent genetic bottlenecks or areas of unusually high genetic mixing. This approach can also utilize the degree of genetic overlap in seed sources between different seed pools to gain insight into the dispersal kernel. An advantage of this method is that one can test the genetic consequences of seed dispersal without locating and mapping the genotypes of all adults. At the same time, if one has a site where all adult trees are mapped and genotyped, traditional maternity analysis can be used to document exact dispersal distances (e.g. Garcia *et al.* 2007, 2009) as well as the frequency of immigrant seeds, which do not match any maternal genotype in the study area and are therefore likely to represent long-distance dispersal events (e.g. Jordano *et al.* 2007).

Applying these tools to natural systems, researchers have found that destination-based seed dispersal often appears to result in a nonrandom and highly structured distribution of maternal genotypes (i.e. seeds) away from the maternal seed source. In temperate woodlands of Spain, for example, dispersal of *Prunus mahaleb* by the frugivorous bird community yielded strong patterns of genetic differentiation among seed pools despite relatively frequent long distance dispersal events (Garcia *et al.* 2009). In California, acorn dispersal of the oak *Quercus lobata* by acorn woodpeckers *Melanerpes formicivorous* also resulted in pronounced structuring of seed pools in granaries where the acorns are stored (Grivet *et al.* 2005). In a separate study of dispersed *Q. lobata* seedlings (Grivet *et al.* 2009), vertebrate dispersal agents also produced pronounced structuring of seedling populations. In tropical rain forests, dispersal by birds and bats across fragmented landscapes yielded genetic bottlenecks among recruiting seedlings (Aldrich & Hamrick 1998; Sezen *et al.* 2005). A model based on data from the bird-dispersed shrub *Ilex leucodia* also suggests that frugivore seed dispersal contributes to kin-structured seedling populations (Torimaru *et al.* 2007).

These studies consistently point to structured seed populations among vertebrate-dispersed plants, but it would be premature to conclude that destination-based dispersal universally results in genetic bottlenecks. This is because studies often lack a detailed knowledge of the frugivore species responsible for observed patterns of dispersal, meaning that genetic patterns observed among dispersed seeds could be because of a variety of dispersal agents exhibiting a potentially wide range of behaviours and activities. To effectively address the genetic consequences of destination-based dispersal, it would be useful to establish a direct linkage between a single dispersal agent or behaviour and subsequent dispersal outcomes. There has been a recent focus on this linkage (e.g. Grivet *et al.* 2005; Jordano *et al.* 2007; Garcia *et al.* 2009), but the putative dispersal agents in these studies exhibit similar forms of social organization consisting of social pairs or cooperative family groups that defend and forage within a territory. The genetic consequences arising from different forms of social organization and/or from specific behaviours remains an open question. Making the connection between disperser behaviour, seed movement and resulting genetic structure is therefore an important step to understanding how vertebrate dispersal affects both plant reproduction and local genetic structure of plant populations.

In this study, we explore the linkage between lek mating behaviour of the long-wattled umbrellabird *Cephalopterus penduliger* and dispersal of the canopy palm species *Oenocarpus bataua* (hereafter umbrellabirds and *Oenocarpus*). The strength of this system is that it allows us to test consequences of destination-based dispersal directly attributable to a single behaviour by a single dispersal agent. Males of frugivorous lek breeding species spend up to 80% of their time on display areas in leks (Snow 1962), providing the opportunity for pronounced destination-based dispersal into the lek. *Oenocarpus* is the favoured food source for male Umbrellabirds, which deposit over half the seeds they ingest in leks, leading to a higher density of seeds and seedlings in leks relative to control areas (J. Karubian, unpublished). This clear link between *Oenocarpus* seeds arriving in leks and male umbrellabird mating behaviour permits novel tests of the impact of destination-based dispersal (by umbrellabirds into the lek) relative to background dispersal (by other dispersal vectors outside the lek; see next) on gene movement, seed pool structure and local spatial genetic structure of established seedlings. Our specific objectives in the current study were to: (i) employ direct maternity assignment to assess how umbrellabird dispersal affects the incidence of long distance dispersal; (ii) use Grivet *et al.* (2005) PMI models combined with regression analyses to test consequences of lek mating for seed pool structure, gene movement and genetic heterogeneity over space; and (iii) use spatial autocorrelation to quantify consequences for spatial genetic structure of *Oenocarpus* seedlings.

Methods

Study species

The canopy palm *Oenocarpus bataua* is widely distributed throughout Neotropical rain forest on both sides of the Andes cordillera in South America (Henderson *et al.* 1995). It is a long-lived, slow-growing monoecious species that produces large-seeded, lipid-rich fruits in single infructesences of up to 2000 fruits (Goulding & Smith 2007). Ripe fruits, available for 4–8 weeks, are an important food source for large-bodied mammals and birds (Goulding & Smith 2007). The long-wattled umbrellabird *Cephalopterus penduliger* is a large (*c.* 550 g) frugivorous bird endemic to Chocó rain forests of Ecuador and Colombia (Snow 1982, 2004) and 'Vulnerable to Extinction' because of the habitat loss (BirdLife International 2000). Umbrellabirds swallow whole *Oenocarpus* fruits and regurgitate intact, viable seeds. On our study site, umbrellabirds are the most commonly observed species consuming *Oenocarpus* fruits and *Oenocarpus* are the most common seeds recovered from seed traps placed beneath male display perches in leks (J. Karubian, unpublished). *Oenocarpus* in our study area is also dispersed by vectors other than male umbrellabirds, including toucans (which are very rarely observed in lek sites), female umbrellabirds, rodents, gravity and water. We group these alternative dispersal modes as background dispersal, defined as the net effect of source-based dispersal processes by vectors other than lekking male umbrellabirds.

Study site and sampling design

Samples were collected from the Bilsa Biological Station (79°45′W, 0°22′N; 330–730 m elevation), a 3500-ha reserve of humid Chocó rain forest in northwest Ecuador. Since 2003, we have continuously monitored activity at a focal umbrellabird lek consisting of 8–12 males. Each male holds a fixed territory of ∼25 m², and the entire lek is ∼1.5 ha in area. We established a 30-ha study parcel (500 × 600 m) centred around the lek and mapped the location of and collected leaf tissue samples from every live adult *Oenocarpus* located therein (Fig. 1). Density of *Oenocarpus* adults was 3.4 trees/ha.

To sample seeds, we established 9 lek plots within the lek and 16 background plots randomly located throughout the rest of the study parcel. Each circular sampling plot had 10-m diameter and was located >15 m from the crown of a reproductive adult to ensure all seeds collected had been dispersed into the plot. Within each plot, we collected established seedlings with attached seeds. We only sampled seedlings that were aged 12 months or less as determined by comparison with known-age seedlings so that they represented dispersal activity from the previous season. Samples were stored in individually labelled envelopes in dry conditions until laboratory analyses were conducted.

DNA isolation and amplification

We used the Mixer Mill MM301 (Retsch, Newtown, PA, USA) with a tungsten ball to grind ∼50 mg of maternally inherited husk tissue (from dispersed seeds) or leaf tissue (from adults) to powder, and the DNeasy Plant Mini Kit (QIAGEN) to extract the DNA. We followed the polymerase chain reaction profiles in Montufar *et al.* (2007) for each of the seven microsatellite loci used in this study. We amplified husk and leaf tissue, as well as negative DNA isolation control (tissue replaced with water) and a negative PCR control (PCR mixture without DNA) to check for contamination. The authors re-ran a subset of 50 samples to check for reliability of the genotypes; average per locus genotype error rates were 7.4 ± 1.7% for husk tissue from seeds and 4.0 ± 1.4% for leaf tissue from adults. We analysed each aliquot of each PCR product with an ABS 3700 automatic sequencer, and genotyped them based on the statistical packages of the UCLA Sequencing and Genotyping Core Facility (for details, see http://www.genetics.ucla.edu/sequencing/index.php).

Direct parentage assignment

We conducted direct parentage analyses for all sampled dispersed seeds against the genotypes of all adults in the 30-ha study parcel. For these analyses we included all seeds for which we obtained genotypes. Because each adult had a unique genotype, maternity assignment was conducted by simple exclusion comparing multilocus genotypes of seedlings with those of adults. Potential mothers were rejected if alleles at any of the seven loci did not match respective seedling values and samples were re-run if only one locus did not match at one allele in the first analysis. Analyses were conducted using GeneAlEx 6.2 software (Peakall & Smouse 2006). We characterized all loci for observed heterozygosity (H_O), number of alleles and the multilocus probability of identity (P_{ID}, the probability that any two adult trees share the same multilocus genotype; Waits *et al.* 2001).

Seed pool structure

We calculated PMI, the probability that two random seeds drawn from the same seed pool have identical seed donors (i.e. mothers), using methods in Grivet *et al.* (2005). In these analyses, we used only those plots with eight or more genotyped progeny and used the
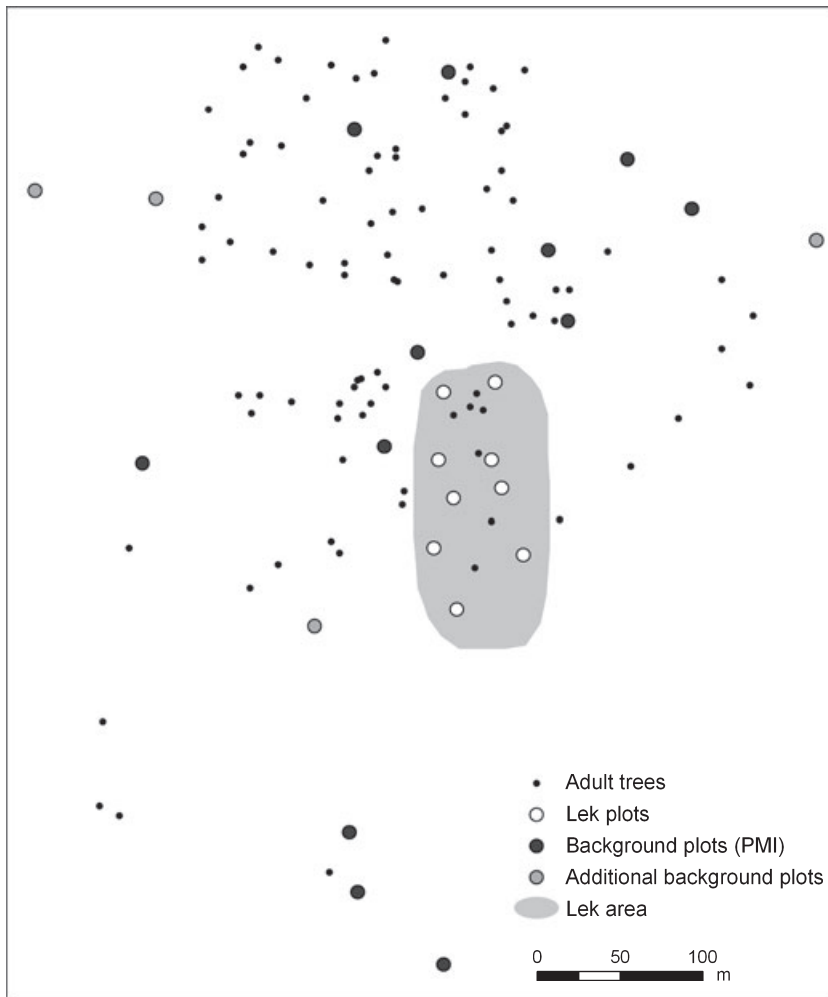
Fig. 1 Map of 30-ha study parcel, located within the Bilsa Biological Reserve in northwest Ecuador. The location a focal lek of the long-wattled umbellabird, of all adult *Oenocarpus bataua* individuals, and of all seed sampling plots (lek plots, background plots used for probability of maternal identity and direct parentage analyses, and additional background plots used only for direct parentage assignment) are denoted.

r-estimator (r_{gg}) to calculate the effective number of mothers per gene pool because it relatively unbiased by small sample sizes (Grivet *et al.* 2005). We calculated $\bar{r}_0$ by averaging the r-estimator across seed pools, and divided 1 by $\bar{r}_0$ to estimate N_{em}, the effective number of mothers per seed pool, separately for leks and background plots.

Modelling interplot overlap

Also following methods in Grivet *et al.* (2005) and using the same plots as before, we calculated pair wise maternal overlap r_{ij}, defined as the probability that two seeds collected from two different plots share the same maternal source. To model r_{ij} as a function of interplot distance, we tested commonly used nonlinear models (e.g. exponential, exponential power and inverse power functions following Klein *et al.* 2006) but found that standard linear regression on log-transformed values of r_{ij} [$\ln(r_{ij}+0.0001)$] best fit our data. We used an interaction term between plot type and distance in our regression model to test for a difference in how r_{ij} varies with distance among lek vs. background plots. We used robust standard error to correct for mild heteroscedasticity of the residuals and scaled distance by dividing by 100. We restricted our analyses to pairwise interplot distances of ≤140 m, which corresponds to the maximum distance between any two lek plots. Analyses were conducted using the PROC REG procedure in the statistical package SAS (SAS Institute, Cary, NC, USA).

Spatial genetic autocorrelation

To assess the impact of dispersal by lekking males on fine-scale genetic structure, we conducted spatial autocorrelation analysis using distance classes of 35-m intervals that maximize sample size within each distance class. We set the first distance class at 0–10 m to account for within-plot variation (plots were 10-m diameter). Changing the size of the distance classes did not qualitatively alter the outcome of the analyses. We restricted our analyses of spatial genetic structure to

Table 1 Number of alleles, size range (base pairs), observed heteroygosity (H_O) and multilocus probability of identity (P_{ID}) for seven microsatellite loci used in this study. Values for a sample of 98 adult *Oenocarpus bataua* collected at Bilsa Biological Station, northwest Ecuador are shown. Combined P_{ID} = 0.0000013

Locus	OB3	OB4	OB6	OB7	OB10	OB11	OB16
# Alleles	8	5	4	7	8	4	6
Range	94–112	129–143	185–195	166–182	142–156	133–139	128–140
H_O	0.81	0.57	0.57	0.82	0.85	0.43	0.55
P_{ID}	0.07	0.28	0.24	0.08	0.06	0.23	0.24

seedlings because a prohibitively small number of adult trees (n = 6) were present in the lek and because of uncertainty about the history of lek movement (see next). Analyses were conducted using GeneAlEx 6.2 software (Peakall & Smouse 2006).

Results

Long-distance dispersal

The study parcel contained 98 reproductive *Oenocarpus* adults (Fig. 1), each of which had a unique genotype across the seven microsatellite markers used in this study (Table 1). Approximately half the seeds we sampled (176/313 = 56%) directly matched one of these 98 adult genotypes; the remaining 44% were 'immigrants' whose source trees were located beyond the parcel boundaries. The proportion of immigrant seeds was higher in the lek than background (80/157 = 51% vs. 57/156 = 37%; Fisher Exact test, two-tailed P = 0.017). This suggests a higher rate of long-distance dispersal from outside the parcel's boundaries into the lek than into the background plots, despite the fact that the background plots were located closer to the parcel's boundaries (Fig. 1).

Seed pool structure

The PMI analysis of *Oenocarpus* from nine lek plots (n = 157 total seedlings; 17.44 ± 0.38 seedlings/plot; range 16–19) and 12 background plots (n = 131 total seedlings; 10.92 ± 0.47 seedlings/plot; range 8–12) indicated that the lek plots had lower values of r_{gg} (Table 2), with the mean lek value ($\bar{r}_0$ = 0.037) much lower than the mean background plot value ($\bar{r}_0$ = 0.191). These values translate into 27 effective seed sources per plot in the lek vs. 5.2 effective seed sources in the background plots, for an average of five times more maternal seed sources in lek than background plots.

Seed pool overlap

We used standard linear regression to model pairwise interplot maternal overlap r_{ij} as a function of interplot

Table 2 Probabilities of maternal identity (PMI) for *Oenocarpus bataua* seedlings collected from plots located within (lek) or outside (background) a lek of the long-wattled umbrellabird in northwest Ecuador. Number of seedlings sampled per plot is given between parentheses. The probability that any two seedlings from a given seed pool come from the same seed source is given by the r-estimator for each sampling plot, and the averages and root mean-squared errors (rMSE) are provided for lek and random plots. The average number of effective seed sources (N_{em}), estimated by $1/\bar{r}_0$, is shown for the lek and background plots

Lek		Background	
Plot ID (n)	r_{gg}	Plot ID (n)	r_{gg}
101 (18)	0.052	3 (8)	0.214
102 (16)	0.067	12 (12)	0.015
103 (19)	0.047	13 (9)	0.056
104 (16)	0.050	14 (12)	0.106
105 (17)	0.015	17 (12)	0.424
106 (17)	0.000	19 (11)	0.018
107 (18)	0.000	20 (12)	0.076
108 (19)	0.058	22 (8)	0.036
135 (17)	0.044	34 (12)	0.242
		38 (12)	0.833
		39 (12)	0.030
		41 (11)	0.055
$\bar{r}_0$	0.037		0.191
rMSE	0.004		0.007
N_{em}	27.0		5.2

distance and included an interaction term in our model to compare the spatial scale of seed movement via lek vs. background dispersal processes (overall model results: $F_{3,49}$ = 7.78, P = 0.0002, r^2 = 0.32). Background plots exhibited high r_{ij} at short distances but r_{ij} rapidly decreased as interplot distance increased (intercept = −0.06 ± 1.39, slope = −7.03 ± 1.45), whereas lek plots exhibited low r_{ij} values even at short distances and a relatively slow rate of decline as interplot distances increased (intercept = −4.04 ± 0.52, slope = −1.70 ± 0.87; Fig. 2). The difference among the two plot types was statistically significant (interaction term = 5.33 ± 1.66; $F_{1,52}$ = 6.75, P = 0.002), suggesting limited gene movement and high genetic structure among background
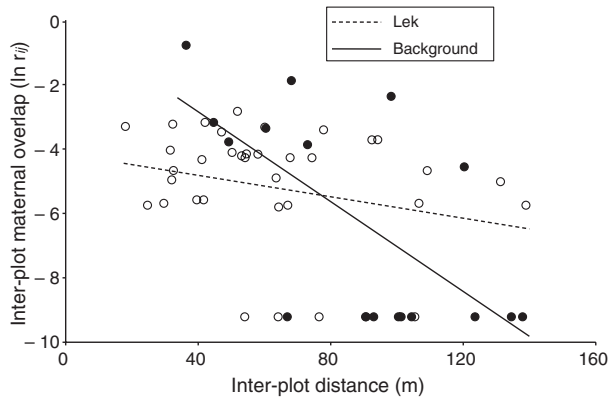
Fig. 2 Linear regressions of pairwise seed source overlap (log-transformed r_{ij}) of the palm *Oenocarpus bataua* in relation to interplot distance in an Ecuadorian rainforest. Separate fits are provided for seed plots in a lek of the long-wattled umbrella-bird (open circles fit by the hashed line) and background plots located outside the lek (closed circles, solid line). Among background plots r_{ij} decreases rapidly as interplot distance increases, consistent with limited source-based dispersal around fruiting trees. Among lek plots the function decreases more gradually, consistent with more frequent long-distance dispersal events and extensive mixing of gene pools in leks.

plots and high levels of gene movement and mixing among lek plots.

Fine-scale genetic structure

To quantify how umbrellabird lekking behaviour affects fine-scale spatial genetic structure of *Oenocarpus* seeds, we calculated spatial autocorrelation for seed genotypes collected in lek or background plots, and used a non-parametric heterogeneity test (Smouse *et al.* 2008) to compare fine-scale genetic structure of these two classes of seedlings. Fine-scale genetic autocorrelation was significantly lower among seedlings from lek plots than seedlings from background plots at all distance classes and across the entire correlogram (Fig. 3 and Table 3).

Discussion

The genetic composition of seedling populations in umbrellabird lek sites is far more heterogeneous than randomly sampled patches of seedlings: seed pools in the lek originated from an average of five times more source trees than equivalent seed pools in background areas. Incidence of long-distance dispersal, as measured by 'immigrant' seeds originating beyond the boundaries of our study parcel, was also higher in the lek despite the fact that the background plots were located closer to the parcel's boundaries. Extending these findings to a spatially explicit framework, we found that, relative
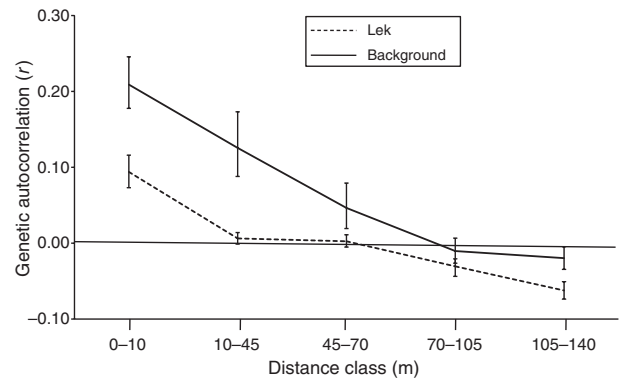

Fig. 3 Fine-scale correlogram for *Oenocarpus bataua* seedlings within (hatched line) and outside (solid line) a lek of the long-wattled umbrellabird in northwest Ecuador. Seedlings within the lek show significantly lower genetic structure at all distance classes.

to background plots, lek plots exhibited a more gradual decline in interplot maternal overlap (r_{ij}) as interplot distance increased and significantly lower spatial genetic autocorrelation at all distance classes analysed. Thus, destination-based dispersal driven by male umbrellabird display behaviour promotes gene movement and homogenizes local genetic structure of *Oenocarpus* seedlings.

Our findings contrast with recent molecular studies of animal-dispersed plants and with a long-held belief that vertebrate dispersal should yield genetically homogenous seed pools characterized by high genetic structure. Ecological observations of frugivores making repeated trips between source trees and roosting (Jordano & Schupp 2000), resting (Russo & Augspurger 2004) or displaying sites (Wenny & Levey 1998) have led to the assumption that destination-based dispersal should result in strong clustering of maternal genotypes at these sites. Molecular studies have largely corroborated this expectation, but have tended to focus on dispersed seeds or seedlings without definitive knowledge of how the seeds arrived in that location in the first place. Two notable exceptions to this generality are the work on acorn woodpeckers in California and the frugivore community in Spain. In the acorn woodpecker, group foraging and territorial behaviour results in limited dispersal distances and a low number of seed sources per seed pool for both the California valley oak *Quercus lobata* and the coastal live oak *Quercus agrifolia* (N_{em} = 2–6 across studies; Grivet *et al.* 2005; V. L. Sork, unpublished), suggesting that seed dispersers that store their seeds in a single area close to the seed source may exhibit restricted seed dispersal. It is notable, however, that the molecular approach estimates three times more seed sources per granary than a recent observational study of acorn woodpecker dispersal (V.L. Sork,

Table 3 Autocorrelation analysis of fine-scale genetic structure for *Oenocarpus bataua* seedlings collected within and outside the boundaries of a long-wattled umbrellabird lek in northwest Ecuador. Shown are the *r*-values and *P*-values for each of the five distance classes, the intercept value and a global test of departure from the null hypothesis of $r = 0$ for each type of seedling. Also shown are the single-distance class (t^2) and multi-distance class (ω) test criteria, and associated *P*-values, comparing lek vs. background. Both exhibit significant departures from random, but seedlings in the lek have significantly less structure than seedlings from outside the lek

Distance class	1	2	3	4	5	ω-test	Estimated
Interval (m)	0–10	11–45	46–70	71–105	106–140	criterion	*P*-value
Lek intercept = 72.6							
r	0.094	0.006	0.002	−0.031	−0.062	37.500	0.010
n	1296	3295	4251	1805	1599		
P	0.01	0.030	0.240	0.010	0.010		
Background intercept = 98.6							
r	0.209	0.126	0.046	−0.010	−0.020	41.080	0.010
n	731	240	508	1043	758		
P	0.010	0.010	0.010	0.060	0.020		
Lek vs. background							
t^2	31.183	32.890	8.572	4.247	16.814	43.279	0.010
P	0.010	0.010	0.010	0.040	0.010		

unpublished; Koenig *et al.* 2008). The community of frugivorous birds in Spain studied by Garcia *et al.* (2009) dispersed *Prunus mahaleb* seeds long distances from source trees but still yielded strong clustering of maternal genotypes in seed traps. This pattern, which is likely explained by preferences for certain microhabitat types as foraging, resting or roosting sites and/or by the fact that several fruits may be consumed in a single foraging bout and deposited together, shows that genetic bottlenecks can arise despite long-distance movement of seeds.

How then can we explain the fact that destination-based dispersal by male umbrellabirds appears to homogenize local genetic structure? Male umbrellabirds leave their display sites on the lek either solitarily or in multimale groups that may travel over 1 km to forage on fruiting trees outside the lek (J. Karubian, unpublished). *Oenocarpus* seeds are relatively large (∼22-mm diameter) and males typically eat fewer than three fruits per foraging bout (J. Karubian, unpublished). Males regurgitate into the lek site over half the seeds they ingest on these foraging trips, and over time a given male can be expected to disperse seeds from many fruiting trees into the lek. This effect is compounded by the fact that leks consist of many males, each following this same pattern. Thus, it appears that the combination of relatively common long-distance dispersal and accumulation over time of seeds from multiple seed sources distributed across the landscape is responsible for high levels of long-distance dispersal and genetic heterogeneity in umbrellabird leks.

This mechanistic understanding of the underlying dispersal process combined with our genetic results can be used to generate predictions about how umbrellabird dispersal may affect *Oenocarpus* seedling recruitment and adult spatial genetic structure. Lekking umbrellabirds may enhance recruitment success via deposition of seeds in favourable microsites (i.e. 'directed dispersal' *sensu* Wenny & Levey 1998) and/or via a 'rare genotype' advantage, in that genetically diverse seed pools may confer resistance to disease or herbivores (Levin 1975). Preliminary results indicate that there is no difference in survival probability from seed to seedling between leks and control sites despite the fact that seed densities are higher in leks and that survival of established seedlings is higher in leks than control sites, but the roles of microhabitat and genetic diversity in explaining these patterns remain to be tested (J. Karubian, unpublished). We would also expect lekking behaviour to generate genetically diverse stands of adults, although landscape consequences for spatial genetic structure (SGS) will depend on the density of leks, the rate at which leks move in space over time, and the degree to which our findings in a single lek apply to other leks. On our study site, the density of leks is ∼1 lek/2.5 km² and we have recorded two instances of leks moving >400 m in 48 lek-years of observation (3–8 years of monitoring each of seven leks; J. Karubian, unpublished). These data indicate that, over time, umbrellabird lekking may have a meaningful impact on forest-wide patterns of SGS for this long-lived palm and also suggest that, with additional data

from continued monitoring, a modelling approach may be employed to estimate this effect. Also, because umbrellabirds consume a wide range of fruits, a similar effect may extend to other tree species beyond *Oenocarpus*. However, lek movement complicates direct tests of umbrellabird dispersal on adult SGS because an adult tree's current location does not necessarily reflect proximity to a lek when it initially recruited into the population.

More broadly speaking, the potential discrepancies between the genetic consequences found in the current study vs. other systems highlight the need to expand the number of studies that explicitly consider the social behaviour of animals when investigating dispersal dynamics. Clearly, animal behaviours directly impacting seed dispersal outcomes can vary dramatically between species and even within a species (e.g. between the sexes or across a geographic range). In our own study system, priorities for future research include determining how degree of habitat fragmentation, tree densities, number of males per lek and sex may impact dispersal outcomes. Incorporating information on the social system of the vertebrate dispersal agent will allow better predictions of the impact of animals on plant populations, and as studies accumulate it may become possible to infer broadly applicable patterns. For example, we predict that lekking behaviour may generally promote gene movement and sharing of seed sources among seed patches, whereas territorial behaviour may generally yield genetically structured seedling populations with restricted dispersal despite the fact that both show destination-based dispersal patterns.

In conclusion, this study demonstrates that making the connection between disperser behaviour, seed movement and resulting genetic structure is key to understanding how vertebrate dispersal affects both reproduction and local genetic structure of plant populations. Establishing this connection will also allow us to take appropriate measures to retain key ecological services such as seed dispersal in the face of current and future anthropogenic perturbations to natural systems such as habitat fragmentation and defaunation. Highlighting this need, the long-wattled umbrellabird is an endangered species whose dispersal services have already been removed from much of its original range (BirdLife International 2000). Linking disperser behaviour to observed patterns of genetic structure provides important insights into natural systems that will aid our efforts to keep them intact into the future.

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