Defaunation is associated with increased fine-scale spatial genetic structure in a small-seeded palm despite high abundances of small-bodied seed dispersers

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Abstract

Anthropogenic pressures such as hunting are increasingly driving the localized functional extinctions of all or most large and medium-sized wildlife species in tropical forests, a phenomenon broadly termed defaunation. Concurrently in these areas, smaller-bodied wildlife species benefit from factors such as competitive release and experience population increases. This transformation of the wildlife community can impact species interactions and ecosystem services such as seed dispersal and seed-mediated gene flow with far reaching consequences. Evidence for negative genetic effects following defaunation is well-documented in large-seeded plants that require large frugivores for long distance seed dispersal. However, how defaunation affects small-seeded (<1.5cm diameter) plants, which are dispersed by frugivores with a wide range of body-sizes and responses to anthropogenic threats, is not well understood. To better understand the reach of defaunation’s impacts on tropical plant communities, we investigated spatial and genetic patterns in a hyperabundant small-seeded palm, Euterpe precatoria in three sites representing distinct defaunation levels. We found significantly higher fine-scale spatial genetic structure among nearest-neighbor seedlings in the defaunated site and in the recovering, partially defaunated site relative to the faunally-intact site. Defaunation was associated with shorter distances between seedlings and adults and lower genetic distance between adult and seedling cohorts. No effects were detected on inbreeding and genetic diversity; however, we caution that trends we detected indicate that defaunation influences the spatial distribution of genetic variation even in small-seeded plants that inherently have a broad suite of seed dispersal agents, and this could lead to negative downstream effects on genetic diversity.

INTRODUCTION

Understanding the consequences that biodiversity loss will have on ecosystem functioning is a longstanding focus of ecological and conservation research, particularly in light of ongoing global species declines (Ceballos et al., 2020; Gonzalez et al., 2020; van der Plas, 2019). In tropical forests, biodiversity loss in the form of defaunation, or the decline and local extirpation of wildlife species, presents a multi-faceted threat to ecosystem functioning by affecting species interactions (e.g., seed dispersal), changing the relative abundances of large- versus small-bodied animals, and decreasing wildlife diversity. In particular, defaunation is associated with decreases in the abundances of large-bodied animals and increases in smaller-bodied vertebrates that benefit from release from predators and competition as well as supplementary resources from
nearby human settlements (Dirzo et al., 2014; Peres & Dolman, 2000; Pires & Galetti, 2023). While defaunation is often intertwined with disturbances such as fragmentation and logging, it can be independently pervasive when heavy hunting and poaching have impacted animal communities while the plant community remains structurally intact. Some estimates posit that hunting-driven defaunation affects a greater area of tropical forests than logging and fragmentation combined (Benítez-López et al., 2019; Harrison et al., 2016; Pires & Galetti, 2023). Despite the ubiquity of defaunation, it remains unclear (1) the extent to which animals remaining in defaunated forests compensate for interactions and services previously performed by the larger extirpated species and (2) the functional outcomes of these altered or lost interactions (Bueno et al., 2013; Culot et al., 2017; Fricke et al., 2018; Sekar & Sukumar, 2013). Developing nuanced insight into how defaunation per se impacts ecological processes is an important step to understanding the consequences of anthropogenic change in tropical forests. Further, this offers insight into the functional roles that frugivores differentially impacted by defaunation (e.g., small versus large-bodied species) play in shaping tropical forest plant communities.

Seed dispersal is a co-evolutionary, mutualistic relationship between plants and animals that is often disrupted by defaunation. In exchange for important food resources, the consumption of fruit and/or seeds by animal species can result in the deposition of seeds away from maternal plants. Many specialized pathogenic and invertebrate seed predators are associated with soil communities beneath maternal plants, making the dispersal of seeds to new microhabitats an important aspect of increasing the survival of seeds and forest regeneration as a whole (Chesson, 2000; Connell, 1971; Hazelwood et al., 2021; Janzen, 1970; Swamy & Terborgh, 2010). From a micro-evolutionary perspective, seed dispersal across a large spatial scale can promote migration between populations to minimize the effects of drift and inbreeding and increase genetic diversity in populations (Aguilar et al., 2008; Dick et al., 2008; Oddou-Muratorio et al., 2001; Pérez-Méndez et al., 2016). At a more local scale, the movement of seeds by diverse frugivore assemblages to a variety of deposition sites serves to decrease the relatedness of neighboring plants and thereby limiting fine-scale spatial genetic structure as well as biparental inbreeding (Browne et al., 2015; C. da S. Carvalho et al., 2021; Choo et al., 2012; Karubian et al., 2010). As a result, seed dispersal is a critical ecosystem function carried out by fruit-eating animals and is especially important in tropical forests where the majority of plant species rely on animals to disperse their seeds (Howe & Smallwood, 1982).

Large-bodied frugivores are capable of moving seeds across large distances and are most likely to promote long distance dispersal between plant populations (Fragoso et al., 2003; Goebel et al., 2023; Link & Fiore, 2006; Naniwadekar et al., 2019; Ong et al., 2022). In some instances, there are close mutualistic relationships between plants with large seeds and large-bodied frugivore species with gape sizes large enough to swallow the seeds whole (Brockelman et al., 2022; Giombini et al., 2016, 2017; Landim et al., 2022). Most research investigating anthropogenic effects on seed dispersal services in tropical forests has focused on large seeded plants because they are seen as the most vulnerable to losing dispersal services as the large-bodied mutualistic partners they specialize on to disperse their large seeds tend to disappear first after human disturbances (Dirzo et al., 2014; Galetti et al., 2013; Koerner et al., 2017; Kurten, 2013). Such studies have linked the loss of large-bodied frugivores to decreased dispersal and recruitment success of larger seeded plants (Bagchi et al., 2018; Holbrook & Loiselle, 2009; Vanthomme et al., 2010), changes in allele frequencies and lower allelic richness (C. S. Carvalho et al., 2016; Giombini et al., 2017), as well as higher spatial genetic structure and lower genetic diversity (Browne et al., 2015; Diaz-Martin & Karubian, 2021; Giombini et al., 2017). However, generalist relationships are much more common in tropical forests where most plants have small- to medium-sized fruits and seeds that can be consumed by small-, medium-, and large-bodied animals (Howe & Smallwood, 1982; Malhado et al., 2015; McConkey & Brockelman, 2011). Relatively little research has used a population genetics lens to evaluate the impact of defaunation on generalist plants (Kurten, 2013), which limits our comprehensive understanding of the stability of tropical plant communities.

Accurately predicting the net effect of defaunation on seed dispersal and population genetic patterns in generalist plants is difficult. Generalist plants may be robust to vertebrate losses associated with defaunation thanks to redundant seed-disperser roles played by multiple small-, medium-, and large-bodied frugivore mutualists. Animals that persist in high densities in defaunated forests such as some small primates, small
or medium frugivorous birds, and agoutis or other rodents can facilitate effective seed dispersal in defaunated tropical forests (C. da S. Carvalho et al., 2021; Culot et al., 2010; Godó et al., 2022; Heymann et al., 2022; Hirsch et al., 2012; Mittelman et al., 2020). Indeed, rats can be important seed dispersers in tropical forests because they have the ability to handle small and large seeds and occupy central positions within seed-dispersal networks (Ong et al., 2021). In addition, small and medium-sized frugivores, particularly birds, may remain and sometimes thrive in defaunated forests where they can serve as important seed dispersers capable of maintaining local plant genetic diversity and the movement and mixing of maternal genotypes (C. da S. Carvalho et al., 2021; Heymann et al., 2019; Mittelman et al., 2020). However, smaller frugivores remove seeds in smaller numbers and typically disperse across shorter distances than their larger counterparts (Bagchi et al., 2018; Heymann et al., 2022). Larger-bodied frugivores are often predicted to be disproportionately important within seed-dispersal networks even for generalist and small-seeded plants because they facilitate long distance seed dispersal and consume large numbers of seeds in a single foraging bout (Donoso et al., 2020; Goebel et al., 2023; Naniwadekar et al., 2019; Vidal et al., 2013). Because defaunation causes downsizing in the size and diversity of the frugivore community (Koerner et al., 2017; Poulsen et al., 2013), it may effectively eliminate long distance dispersal events for animal-dispersed plants in defaunated forests (Donoso et al., 2020). Distinguishing empirical genetic and spatial patterns resulting from seed dispersal in defaunated relative to faunally intact forests from the myriad of theoretical outcomes will advance our understanding of how defaunation impacts seed-mediated gene flow and genetic structure of generalist plant populations.

Here we investigate potential genetic consequences for a small-seeded generalist palm, *Euterpe precatoria*, following defaunation. Across three comparable continuous forest sites impacted by varying levels of hunting pressures we compared (1) inter-cohort (i.e. adult to seedling) spatial and genetic distances, (2) fine-scale spatial genetic structure, and (3) genetic diversity and inbreeding. We predicted that if defaunation does remove a suite of frugivores that play significant roles in seed dispersal and seed-mediated gene flow for small-seeded species, we will find defaunation to be associated with decreased inter-cohort spatial distances as seeds are moved shorter distances or fail to be dispersed at all from parent plants; further, we predict this may also result in lower genetic differentiation between adults and seedlings in defaunated relative to the faunally-intact or intermediately-intact sites. We also expect an increase in fine-scale spatial genetic structure associated with defaunation due to damped seed movement and increased spatial aggregations of related individuals. However, we expect differences in genetic diversity and inbreeding related to defaunation may not be detected as these measures are often robust to anthropogenic change over short time scales. Examining the effects of defaunation on a generalist plant will further our understanding of how changes in animal communities impact micro-evolutionary processes in the plants that rely on their ecosystem services.

**MATERIALS AND METHODS**

**Study species**

*Euterpe precatoria* Mart. (Arecaceae) (Figure 1) is a widespread palm spanning from the edge of the southwestern Amazon Basin in Bolivia through Peru, Ecuador, Colombia and Brazil (Ramos et al., 2021). The species is adapted to both nutrient-poor, dry soils as well as seasonally flooded alluvial soils and has been classified as the most abundant palm in the Amazon Basin (ter Steege et al., 2013). Because of this, *E. precatoria* represents an important resource for frugivorous animals. Although extraction by humans can affect *E. precatoria* population demography and size (Avalos et al., 2013), it has not been harvested by humans across our study sites. *E. precatoria* is nonmorous and while self-pollination may occur, existing studies document temporally distinct male and female flower phases (Ramos et al., 2019). Pollination can occur with wind, but primarily a mixed-species guild of beetles (primarily in the Curculionidae, Chrysomelidae, and Staphylinidae families) and bees (primarily in the Halictidae family) pollinate *E. precatoria* (Küchmeister et al., 1997). Individuals in our study areas reached heights of approximately 20-30m. The species is long lived and takes 50 or more years to become reproductive (V. Swamy, personal communication). *E. precatoria* seed diameters can range from < 1cm to ~1.5cm and are surrounded by a thin dark purple or black mesocarp (Figure 1c). Fruits are dispersed by a range of small and large frugivores birds, primates, and rodents (Avalos et al., 2013; Bagchi et al., 2018; Ramos et al., 2021).
Seed size is a functional trait that determines the range of frugivore species that can swallow and thereby disperse a species (Galetti et al., 2013; Holbrook & Loiselle, 2009). Because of this, seed size is a trait used to categorically group plant species when considering what frugivores are likely to comprise their primary seed-dispersal partners. In general, ‘small’ seeded species are considered generalists because a wide range of frugivores can swallow and disperse their seeds, and plants assigned to this category in tropical forests are generally those with seeds < 1.5 cm diameter, although specific size cutoffs for ‘small’ seed categories vary across studies (Galetti et al., 2013; Kurten, 2013; Malhado et al., 2015).

**Study sites and field sampling**

Our study was conducted in the Madre de Dios River Basin located in the southeastern corner of the Peruvian Amazon (Figure 2). Our study system includes robust data on the frugivore community that documents the transition from a diverse seed disperser community that includes several large-bodied frugivores in our faunally-intact site into a downsized and depauperate community in our defaunated site, which has been subject to frequent hunting (Table 1). Our sites are long-term forest dynamics plots established in 2008 and measuring four hectares (200m x 200m) each. All sites are unlogged primary floodplain forest with similar soil types and which historically hosted similar communities of frugivores (Bagchi et al., 2018). Rainfall in the Madre de Dios River Basin is typically 2,500-3,500 mm annually punctuated by a dry season from June through September (Gentry, 1993; Tobler et al., 2009). Euclidean distances between sites range from 82 km to 113 km. Importantly, the processes and effects of defaunation often occur at landscape scales creating logistical constraints that limit our ability to intensively sample multiple sites across remote and rugged regions and as such we note that, like other studies examining the effects of defaunation (Nuñez-Iiturri and Howe 2007; Bagchi et al., 2018; Boissier et al., 2020; Hazeldwood et al. 2020; Aliaga-Rossel et al., 2022; Boiten et. al. 2023), our work is not able to include multiple replicated sites.

Tambopata Research Center (‘TRC’, our faunally-intact site) is located within ~17,000 km² of protected forest at a junction between the Tambopata National Reserve and Bahuaja-Sonene National Park. The area has been formerly protected from hunting since the early 1990s; however, before that time, hunting was limited due to the station’s remote location (> 50 km from human settlements and difficult to access). Because of this, TRC hosts a faunally-intact vertebrate community consisting of large frugivorous primates (Table 1). Los Amigos Biological Field Station (‘LA’, our intermediately-defaunated site) is situated in a 453-ha reserve adjoined by a 46,000-ha conservation concession. Los Amigos is 2 km from a human settlement and until the early 1990s hosted a large gold mining camp during which time it was subject to heavy hunting (Bagchi et al., 2018; Rosin & Swamy, 2013). The area has been officially protected since 2001 and monitoring efforts have nearly eliminated hunting in the area since 2003 (Tobler et al., 2009). Los Amigos now hosts a semi-depauperate, recovering vertebrate community that does include some large primates and avian frugivores (Table 1). Reserva Amazonica (‘RA’, our defaunated site) has experienced intense and ongoing hunting since the 1980s. It is a small private reserve of about 1,500 ha that consists of structurally undisturbed mature forest but is surrounded by human settlements as close as 1 km away. RA hosts a defaunated disperser community lacking large frugivores and dominated by high densities of smaller vertebrates including secondary seed dispersers such as agouties, bird species not heavily affected by hunting, and a hyperabundance of saddleback tamarins (Saguinus fuscicollis) which have benefitted notably from competitive release in the area (Rosin & Swamy, 2013). The defaunation status of these sites can be ranked based on the densities of three key primary disperser groups: large primates (e.g., spider and howler monkeys), medium primates (e.g., capuchins), and large frugivoruous birds (e.g., guans, toucans, trumpeters) (Table 1).

We mapped and sampled all *E. precatoria* individuals in each 4-ha plot in each site. We collected genetic tissue from individuals in two cohorts: adults (≥10 cm dbh) and seedlings (<1 m tall). We consider the seedling individuals to have likely been dispersed by the frugivore community currently persisting in these sites. While we expect genetic effects of defaunation in the seedling cohort, we do not anticipate this to be the case in the adult cohort because hunting only began affecting our defaunated and recovering sites in the early- to mid-1980s. Given that adult *Euterpe* palms are likely to take several decades to attain reproductive status (V. Swamy, personal communication), it is unlikely that the current population of reproductive adult
palms at any of the sites were significantly affected by defaunation.

Genotyping

We collected and dried leaf tissue from all *Euterpe precatoria* individuals. However, we only included adults and seedlings in genetic analyses because we expect signatures of defaunation to be most detectable in seedlings relative to sapling or juvenile cohorts, and we use adults to control for pre-existing genetic differences in individuals between sites. We randomly selected 125 seedlings from each site to genotype, while all adults in each plot were genotyped. We extracted genomic DNA using Qiagen DNeasy 96 Plant Kit following the manufacturer’s instructions (Qiagen, Germany). We used polymerase chain reaction (PCR) to test 11 microsatellite loci developed for *E. precatoria* (Arias et al., 2016). After evaluating the size range of each primer separately, we create two PCR multiplexes, one with forward and reverse primers for Ep03, Ep05, Ep08, Ep13, Ep25, and Ep30; and the other with forward and reverse primers for Ep02, Ep06, Ep32, Ep35, Ep36. Each PCR multiplex master mix was prepared in an eppendorf tube with 315 μl deionized water, 525 μl Multiplex PCR Qiagen Master Mix, and 105 μl of the multiplexed primer mixture. We then aliquoted 9 μl of the PCR multiplex master mix across a 96-well plate with 1 μl template DNA. PCR was run on an Eppendorf ProS thermal cycler following programming outlined in the Qiagen Multiplex PCR Kit, with annealing temperatures of 60°C for the first multiplex and 61.1°C for the second multiplex. Post PCR, multiplexes were pooled and run on an ABI 3100 capillary sequencer. We then analyzed amplified fragments and genotyped samples using the program GENEMARKER v. 1.85 (SoftGenetics).

Of the 11 microsatellites, two were not polymorphic in our sampled sites and were excluded from subsequent analyses, leaving a set of nine loci. We evaluated marker quality for the remaining nine loci using GenePop (Rousset et al., 2023) in R v. 4.2.2 (R Core Team, 2022) (all subsequent analysis were conducted in R unless otherwise noted). First, we excluded all individuals with missing data in >30% of loci. Then in each site we tested each locus for departure from Hardy-Weinberg Equilibrium (HWE) using exact tests with a Markov chain method and Bonferroni correction (Benjamini & Hochberg, 1995; Guo & Thompson, 1992). No markers significantly deviated from HWE across all sites and 4 of the 21 marker x site combinations showed significant HWE departure within a site (Ep06 in RA, Ep35 and Ep32 in LA, and Ep32 in TRC) (Supplementary Materials Table S1). We estimated null allele frequencies through maximum likelihood (Dempster et al., 1977). Null allele frequency estimates ranged from 0 to 0.24 (average = 0.058) (Supplementary Materials Table S2). One marker, Ep25, had high null allele frequencies (>0.9) and was excluded from all analyses. We then tested for linkage disequilibrium between pairs of loci at each site to avoid pseudoreplication (Hill & Weir, 1994). No marker pairs showed significant linkage disequilibrium in all 3 sites. Potential linkage was detected between Ep32 and Ep02 in LA (p = 0.01) and in TRC (p = 0.04), and between Ep03 and Ep06 in RA (p = 0.04). We re-amplified and re-genotyped approximately 7% of our samples (n = 28) to assess allele identification error rates. Mean allele typing error per locus was low (average = 0.44%; Supplementary Materials Table S3), a rate lower than or consistent with data used in similar studies (Browne et al., 2015; Giombini et al., 2017). In addition, we found marker Ep36 to have a high percentage of missing data (>25%) in the adult cohort due to amplification failure. We excluded Epr36 leaving a final panel of 7 microsatellites markers that were used in our subsequent analyses.

Defaunation and inter-cohort spatial distance

In order to estimate the effect of defaunation on seed dispersal distances, we use a Kruskal-Wallis test to compare pairwise spatial distances between *E. precatoria* adults and seedlings (‘inter-cohort distances’). We then ran a post-hoc Dunn test to evaluate which pairs of sites differed significantly in inter-cohort distances. If defaunation is reducing seed dispersal services, seedlings should be nearer to adults in defaunated sites compared to faunally intact sites (Bagchi et al., 2018; Giombini et al., 2017; Ismail et al., 2017). While nearest adult conspecifics are considered to have a higher probability of being the parent plant relative to farther conspecific adults, this is not always the case and our results should be interpreted with this in mind (Sezen et al., 2009).

Defaunation and inter-cohort genetic distance
We estimated pairwise genetic distance between adult and seedling cohorts within each site using the pairwise.neifest function in the hierfstat package (Goudet, 2005) according to Nei (1987) and defined as \( D = - \ln \frac{J_Y}{\sqrt{J_X J_Y}} \), where \( J_i \) represents the mean probability of two individuals in group \( X \) having identical alleles from the same locus, \( J_Y \) represents this probability in group \( Y \), and \( J_{XY} \) is this probability of an individual in \( X \) and one of \( Y \) sharing an allele at the same locus (Meirmans & Hedrick, 2011; Nei, 1987). We then performed a scaled and centered Principal Component Analysis (PCA) to present genetic distances between individuals and groups (i.e., cohorts within sites) using the first two axes via the package adegenet (Jombart, 2008; Patterson et al., 2006; Price et al., 2006). Again, if defaunation is reducing seed dispersal services, seedlings, and adults at defaunated sites will be more genetically similar (i.e., have lower genetic distance) than those at the faunally intact site.

**Defaunation, genetic diversity, and inbreeding**

We used the function basic.stats in the package heurisfstat to compute allelic richness (Ar, the raw number of alleles present per loci) to n =115 seedlings and n = 22 adults), observed heterozygosity (Ho), gene diversity (Hs), and the inbreeding coefficient (Fis) in each cohort at each site. Ho measures the observed genetic variability as \( H_o = 1 - \sum_k \sum_i \frac{P_{ki} n_i}{np} \) where np is the number of individuals in the sample, and \( P_{ki} \) is the proportion of homozygote \( i \) in sample \( k \). Gene diversity (Hs) is also often referred to as expected heterozygosity and was calculated based on what would be predicted for a population in Hardy-Weinberg equilibrium (HWE) (Goudet, 2005; Nei, 1987; Nei & Chesser, 1983). These heterozygosity measures are used to evaluate study site subpopulations for evidence of events such as a significantly reduced breeding population size (i.e., a population bottleneck) which would result in very low Ho. Evaluating Ho relative to Hs, or, the heterozygosity expected under HWE, also helps gain information regarding factors at play in a site’s subpopulation such as inbreeding, which can contribute to lower than expected heterozygosity (Nei, 1987; Ritland, 1996). We calculate inbreeding according to Nei (1987) as \( F_{is} = 1 - \frac{H_o}{H_s} \). We also report the number of effective alleles (Nae) computed through the program SPAGeDi (Spatial Pattern Analysis of Genetic Diversity) (Hardy and Vekemans 2002), which estimates the number of alleles with equal frequencies needed for the specific gene diversity (Hs) observed; with Nae, frequent alleles contribute little and Nae helps facilitate comparisons between subpopulations even if allelic richness and frequencies vary widely (Nielsen et al., 2003).

The population genetics metrics described above were computed for each locus in each cohort in each site and we analyzed the effects of defaunation status on each of these using linear mixed effects models. Models contained the random effect of locus and the fixed effect of site (i.e., defaunation status) and were subsequently evaluated using the dharma package to ensure model assumption were met (Brooks et al., 2022; Hartig & Lohse, 2022). Model formats were M ~ site|ID + (1| locus|ID) were M stands for a given population genetics Metric (Ar, Ho, Hs, Fis, orNae). Finally, we used the Anova function in the car package to report simplified model outputs (Fox & Weisberg, 2019).

**Defaunation and fine-scale spatial genetic structure**

We evaluated if defaunation impacts the fine-scale spatial genetic structure of *Euterpe precatoria* seedlings by analyzing spatial autocorrelation of the pairwise kinship coefficient \( F_{ij} \) (Browne et al., 2015; Loiselle et al., 1995). The kinship coefficient \( F_{ij} \) is computed between pairs of mapped individuals and gives the correlation in the frequencies of like alleles, \( F_{ii} \), and \( F_{jj} \) at a given locus in pairs of individuals \( i \) and \( j \) (Loiselle et al., 1995). If defaunation is reducing the dispersal of individuals within sites, we would expect to find that seedlings that are near neighbors are also related or have high kinship coefficients. Fewer medium- and long-distance seed dispersal events should also contribute to this pattern by resulting in less mixing of genotypes across the landscape and reducing the deposition of less-related propagules to an area.

We used the program SPAGeDi (S patial P attern A nalys is of G enetic D iversity, version 1.5) (Hardy & Vekemans, 2002) to compute pairwise kinship coefficients, \( F_{ij} \), between pairs of individuals in a given cohort and site for specified pairwise distance intervals. For example, the first (shortest) pairwise distance interval for which \( F_{ij} \) was computed in seedling cohorts for each site was 45m, meaning pairwise \( F_{ij} \) was...
calculated between all possible pairs of seedlings within 45m of each other, for which we report the mean $F_{ij}$ and standard errors estimated via Jackknifing across loci. In specifying distance intervals, we followed recommendations from Hardy and Vekemans (2002) and selected distance intervals that included a minimum of 100 pairwise comparisons between individuals in a given cohort and site, involved >50% of individuals, and resulted in a coefficient of variation of participation that was < 1.0 (Supplementary Materials Table S5). The exception being the adult cohorts, which had smaller sample sizes than seedlings as there were fewer adults in each site. As a result, the number of pairs included in $F_{ij}$ computation for each distance interval dips below 100 pairs in some cases, with a minimum of 74 pairs. As such we recommend interpreting our spatial genetic structure estimates for adults and their comparisons across sites with caution.

To test the null hypothesis of no spatial genetic structure, we created null models in SPAGeDi using 20,000 random permutations within each specified pairwise distance intervals by which genotypes were randomly assigned to the locations of mapped individuals to construct a 95% confidence interval that was compared to the observed values for a given distance interval within a cohort and site, and we report p-values for this computed in SPAGeDi based on one-tailed tests (Browne et al., 2015; Choo et al., 2012).

In each site, we also used SPAGeDi to compute the mean slope of observed $F_{ij}$ over the natural logarithm of pairwise distances within each specified distance interval. This slope, denoted as $b_{Flog}$, is expected to be negative if spatial genetic structure is present, meaning, mean $F_{ij}$ should decrease as pairwise distance intervals increase. Significance of $b_{Flog}$ was also determined through one-tailed tests of the observed values compared to the null model’s 95% confidence intervals. Finally, we calculated the statistic $Sp$, which was proposed by Vekemans & Hardy (2004) and has been used to summarize the strength of fine-scale spatial genetic structure in a subpopulation and can be used for comparisons across groups (Vekemans & Hardy, 2004). $Sp$ is calculated as $-b_{Flog}/(1-F_{ij \ 1})$ where $F_{ij \ 1}$ is the mean observed kinship coefficient of the first pairwise distance interval (i.e., between nearest conspecific neighbors). We ran our spatial genetic structure analysis and computed $Sp$ statistics across varying distance interval specifications and found consistent results. We tested if defaunation status was a significant predictor of $Sp$ through linear mixed effects models (one per cohort) with the same model structure as described above for testing for the effects of defaunation on genetic diversity and inbreeding.

RESULTS

Adult densities in each plot ranged from 23-33 individuals per 4-ha plot, and seedling densities ranged from 172-427 individuals (Table 2). To a lesser extent, there was variation in the number of individuals successfully genotyped (Table 2). Mean distances between seedlings and between adults were comparable across sites (Table 2).

Inter-cohort spatial and genetic distance

Distance between an E. precatoria seedling and the nearest conspecific adult varied significantly with defaunation status (Kruskal-Wallis rank sum test $X^2 = 48.73$, $p < 0.001$) (Figure 3). Median distance from E. precatoria seedlings to nearest conspecific adults in the defaunated site (RA) was 17.76m (mean 18.78m, 10.73m SD) and 14.70m (mean 15.56m, 9.04m SD) in the recovering site (LA), while in the faunally-intact site (TRC) the median distance was 22.03m (mean 22.78m, 12.80m SD), significantly greater than both other sites (Figure 3a). Post-hoc Dunn tests indicate significant differences between the faunally-intact site and the defaunated site (TRC vs. RA $Z = -4.16$, $p < 0.001$) as well as between the recovering and defaunated sites (LA vs. RA $Z = -2.84$, $p < 0.01$) and the faunally-intact and recovering site (TRC vs. LA $Z = -6.67$, $p < 0.001$).

Genetic distance between adult and seedling cohorts was also lowest in the defaunated site (RA; $F_{ST} = 0.0012$) and higher in both the faunally-intact site (TRC; $F_{ST} = 0.0036$) and in the recovering site (LA; $F_{ST} = 0.0046$) (Figure 3b). Due to low replication, we were unable to statistically test for differences between these metrics.

Defaunation, genetic diversity, and inbreeding
Genetic diversity and inbreeding metrics did not vary greatly across sites (Table 3, Supplementary Materials Figures S1-2) and linear mixed effects models showed no significant effects of defaunation on any of the genetic diversity metrics or inbreeding values analyzed. (Table 3, Supplementary Materials Figures S1-2, Table S4).

**Defaunation and fine-scale spatial genetic structure**

In all sites, the adult cohorts had mean pairwise kinship coefficients $F_{ij}$ in the first pairwise distance interval (in which spatial genetic structure is most likely to be detected as this interval captures nearest neighbors) that did not differ significantly from the null model of no spatial genetic structure, nor did mean $F_{ij}$ in the first distance class differ significantly between sites (Figure 4a) (Supplementary Materials Table S6). Potential spatial genetic structure existed for the defaunated and faunally-intact sites among adults, however, with adults in the farthest pairwise distance interval (126-227m apart) being less related than expected by the null model within the defaunated site, and also in the faunally-intact site for adults in the mid-distance interval (those 74-125m apart). In the adult cohorts, $b_{\log}$ (the slope of the kinship coefficient $F_{ij}$ over the natural logarithm of pairwise distances between individuals) declined with increasing pairwise distances more so than expected under the null model only in the defaunated site (Figure 4a). Defaunation was nearly significant as a predictor of $Sp$ (a measure of fine scale spatial genetic structure strength) in adults (linear mixed effects model, $X^2 = 5.64$, $p = 0.06$) (Table 4); however, $Sp$ values for the adult cohorts could not be calculated in two instances: loci Ep02 in TRC and Ep35 in LA, where no variation in genotypes occurred (limited sample size of adults contributed to this issue). Results were qualitatively unchanged if these loci were included or omitted in final analysis and $Sp$ calculations; however, we conservatively omit these loci from the $Sp$ analysis of adults.

In the seedling cohorts, mean pairwise kinship in the first distance class in the defaunated site was significantly greater than expected by chance (null model of no spatial autocorrelation of kinship, one-tailed test, $p = 0.03$), but not in the recovering ($p = 0.21$) or faunally-intact sites ($p = 0.71$) (Supplementary Materials Table S6) (Figure 4b). Mean $F_{ij}$ was also significantly higher in the first distance class (higher relatedness between nearest neighbors) in the defaunated site relative to the faunally-intact site, while the recovering site had mean values between the two (Figure 4b). The second pairwise distance class (46-70m apart) showed significant spatial genetic structure for only the seedlings in the recovering site ($p = 0.03$, one-tailed test with 95% confidence interval of null model assumption of no spatial autocorrelation of kinship), and overall mean kinship was significantly higher in this second distance class in the recovering site compared to either of the other two sites. The third pairwise distance class (71-90m apart) showed marginally significant spatial genetic structure only for the seedlings in the faunally-intact site ($p = 0.49$, one-tailed test against 95% confidence interval of null model), and mean overall kinship was significantly higher among seedlings in the third pairwise distance class in the faunally-intact site relative to the defaunated and recovering sites. In the seedling cohorts, $b_{\log}$ reflected a decrease in $F_{ij}$ with increasing pairwise distances and was significantly lower than expected by the null model in the defaunated site ($p = 0.03$) and the recovering site ($p = 0.03$), but not in the faunally-intact site ($p = 0.54$) ($p$-values based on one-tailed tests against the 95% confidence intervals obtained from the null model of no spatial autocorrelation of kinship) (Table 4, Figure 4b). Finally, seedlings showed lowest $Sp$ values (fine-scale spatial genetic structure strength) in the faunally-intact site, and our linear mixed effects model indicated defaunation was marginally insignificant as a predictor for $Sp(X^2 = 4.97$, $p = 0.08$).

**DISCUSSION**

We evaluated the effects of defaunation on seed dispersal services, fine-scale spatial genetic structure (FSGS), and population genetics of a hyperabundant small-seeded palm. We found that defaunation was associated with decreased spatial and genetic distances between *Euterpe precatoria* seedlings and nearest conspecific adults, indicating reduced dispersal services relative to the faunally-intact site. In addition, our FSGS analysis shows that at the site most impacted by defaunation, seedlings that are near-neighbors are significantly related while seedlings that are further away from one another are less related- a trend not observed in seedlings at the faunally-intact site. While our results should be interpreted with caution due to the lack of
replication, our findings generally suggest that defaunation is reducing seed dispersal services for our focal species, despite it being a generalist small-seeded palm. Although viable small-bodied terrestrial, avian, and arboreal frugivore dispersers persisted in our defaunated site, our results indicate defaunation-induced seed dispersal limitation is affecting the fine-scale spatial genetic structure of seedling cohorts in the short term, which may affect population genetics and consequently demographic dynamics in the long term. Because our work could indicate that defaunation affects not only large-seeded species, but also small-seeded plants rarely considered in related research, we urge further studies to incorporate plant species representing a wider range of functional groups to gain a more comprehensive and community-level understanding of defaunation’s downstream effects.

Consequences of defaunation on spatial/genetic distance and fine-scale spatial genetic structure

The downsizing of the frugivore community through defaunation is a well-documented phenomenon and may explain the observed decrease in spatial and genetic distances between seedlings and adults at the defaunated site. The defaunated site lacked species such as toucans, guans, and trumpeters; large- and medium-sized primates such as spider monkeys and capuchins, and large terrestrial secondary dispersers such as tapirs and brocket deer. Relative to other frugivores, these species disperse the greatest diversities and quantities of seeds across the longest distances and their foraging behaviors are known to shape spatial and genetic patterns in animal-dispersed plant populations (Browne & Karubian, 2018a; Choo et al., 2012; Giombini et al., 2016; Link & Fiore, 2006; Wehncke & Dominguez, 2007). For example, spider monkeys disperse seeds over 1250m, with an average distance estimated to be ~450m and tapirs disperse seeds >2km from maternal trees (Fragoso, 1997; Karubian et al., 2015; Link & Fiore, 2006) and both species shape genetic patterns for plants whose fruits they consume (Giombini et al., 2016; Karubian et al., 2015). In the defaunated site in our study, these extirpated frugivore groups have been replaced by high abundances of tamarins and rodents (such as agoutis). Although tamarins are highly frugivorous and can disperse seeds upwards of 500m, most of their seed dispersal is over much shorter distances, generally under 200m (Culot et al., 2010; Heymann et al., 2022). Agoutis can also be effective short distance secondary dispersers and will cache seeds in clusters, although they are also seed predators (Cao et al., 2011; Mittelman et al., 2021). The loss of large bodied frugivore has likely dampened long distance seed dispersal to explain why seedlings nearer to adults were less genetically differentiated from adults in the defaunated site compared to the other two sites. However, this result should be treated with caution due to the low level of replication and overall small difference in pairwise $F_{ST}$.

Less well studied are the effects of defaunation through decreasing the diversity of the frugivore community through decreasing the abundance and evenness of species. We posit that this may be an additional facet behind the increased seedling FSGS we found in the defaunated site. Decreased frugivore diversity should lead to a decrease in the diversity of seed deposition sites given that different frugivore species vary in their movement patterns, habitat use, and foraging behaviors, all of which can create differential seed dispersal services and variation in dispersal to different microhabitats (C. da S. Carvalho et al., 2021; Razafindratsima & Dunham, 2015; Rumeu et al., 2020). For example, small terrestrial vertebrates tend to re-use paths and particular sections of the forest as they forage and move throughout the day while larger vertebrates are more wide ranging (Cao et al., 2011; Lichti et al., 2017; Russo et al., 2006). While the loss of large frugivores may also impact the movement of seeds at smaller spatial scales, we posit that the reduced diversity of the frugivore community coupled with the shift to smaller body sizes dampens dispersal at small scales such that near neighbors become more related. If the current seedlings establish and become reproductively active adults, bi-parental inbreeding could increase in subsequent generations and increase the expression of deleterious alleles (Jones & Hubbell, 2006; Quesada et al., 2011; Sebbenn et al., 2011). Partitioning the effects of the downsizing of the frugivore community versus the decrease in diversity would significantly advance our understanding of how defaunation impacts animal mediated seed dispersal.

No short-term consequences of defaunation for genetic diversity

Defaunation was not associated with a decrease in genetic diversity (including allelic richness, effective number of alleles, observed heterozygosity, or gene diversity) nor an increase in inbreeding, suggesting that
processes such as continued pollen flow may be sufficient to maintain these metrics, at least for the timescale our study captures. The extensive nature of pollen dispersal makes it a key ecological process that maintains gene flow and therefore genetic diversity in many tropical and temperate plant species (Browne & Karubian, 2018a; Ennos, 1994; Hamrick, 2004; Parejo Farnés et al., 2017; Petit et al., 2005; Sork et al., 2015). As our study sites were in contiguous forest, we do not anticipate that defaunation has impacted pollinator communities making it so that pollination services have likely remained intact. Indeed, beetle and bee pollinators of another South American palm have been found to maintain gene flow even across severely deforested landscapes (Diaz-Martin & Karubian, 2021). In addition to continued pollen-mediated gene flow from an intact effective population size, a ‘time lag effect’ may have buffered the recruiting seedlings in our defaunated site from decreases in genetic diversity. This could at least in part be because defaunation alone does not cause a severe genetic bottleneck and associated decrease in effective population size, which would result in a rapid decrease in genetic diversity (Aldrich et al., 1998; C. da S. Carvalho et al., 2021; Kettle et al., 2008; Kramer et al., 2008). The combined negative effects of forest loss and fragmentation on genetic diversity have been found to take 50 to 100 years to become detectable (Aguilar et al., 2008; Vranckx et al., 2012), while increases in fine-scale spatial genetic structure serve as early warning signs that seed-mediated geneflow is being interrupted (C. da S. Carvalho et al., 2021). One study examining another canopy palm species, *Oenocarpus bataua*, found that forest loss has a direct, negative effect on genetic diversity, most likely by decreasing effective population size $N_e$, and that this effect was much greater than minor disruptions to seed dispersal services (Diaz-Martin & Karubian, 2021). Although we do not find that defaunation has a direct effect on genetic diversity, we similarly caution that damped seed dispersal could increase inbreeding over time to eventually impact genetic diversity.

Caveats

While restricted seed movement is among the most cited explanations for the presence of a high spatial genetic structure, inferring mechanisms from observed patterns can be challenging and we recommend a conservative interpretation of our results (Grimm & Railsback, 2005; Levin, 1992). It should also be noted that our study uses a limited number of microsatellite markers and alleles, which may reduce the robustness of our genetic results. Additionally, we note that while the strength of fine-scale spatial genetic structure, $Sp$, and kinship coefficients were higher in the adult cohorts relative to the seedling cohorts, however, comparison of estimated kinship coefficients between the two populations is not a reliable gauge of relative spatial genetic structure. This is primarily because mean pairwise kinship coefficients were calculated between pairs of adult individuals for markedly different, as well as fewer, distance classes compared to the seedling FSGS analysis due to relatively small adult sample sizes caused by lower overall adult densities relative to seedling populations. Consistency was kept in FSGS within a cohort across sites to facilitate comparison between defaunation levels, but not between cohorts. With these caveats in mind, recommend our results be viewed as impetus for further research into the explicit effects of defaunation on the dispersal and resulting genetic patterns of generalist plants. This is particularly important because the small-seeded functional group has generally been assumed to be relatively less vulnerable to changes in seed dispersal services following defaunation and so has been the focus of few or no related studies. We recommend that future work investigate the effects of defaunation *per se* on small-seeded generalist plant species using more genetic markers and replication.

Conclusion

Our results corroborate recent works that suggest defaunation may increase the importance of small- and medium-bodied frugivores, but that they will likely not be able to compensate fully for the loss of ecological functions performed by extirpated species (C. da S. Carvalho et al., 2021; Fricke et al., 2018; Goebel et al., 2023; McConkey & Brockelman, 2011). The effect of defaunation may be particularly damaging for rare plants which represent a large portion of tropical plant species, as they may rely on farther ranging dispersers to regenerate in isolated habitat niches. In a broader context, the results reported here are an indication of how defaunation may interact with other ongoing global change patterns by damaging plant’s abilities to persist with multiple threats. For example, increased spatial genetic structure in the absence of long distance dispersal events can eventually affect genetic diversity and increase inbreeding in a population,
which are tied to a species’ population-level ability to maintain robust immune systems and mount effective
defenses against plant pathogens and adapt to threats such as climate change (Aguilar et al., 2008; Browne &
Karubian, 2018b; C. S. Carvalho et al., 2016; Fricke et al., 2022). Over multiple generations spanning several
decades into the future, these consequences could become more severe and have long-term and irreversible
effects on fitness and demography of affected tree species, with cascading ecosystem-level effects on higher
and lower trophic levels.

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Dispersal success of a specialized tropical tree depends on complex interactions among diverse mammalian

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**DATA ACCESSIBILITY AND BENEFIT-SHARING**

**Data Accessibility:** Upon manuscript acceptance for publication, all data (e.g. individual genotype data and spatial data) and accompanying metadata along with the analysis R script, formatted in Rmarkdown, will be uploaded and published in a public GitHub repository.

**Benefit-Sharing:** All coauthors acknowledge the importance of international scientific partnerships and capacity building, particularly in tropical countries in which average income is often low and rural areas where opportunities are limited, such as where work for this research was conducted. We conducted this work under the required regulations and permits and worked with Peruvian university students (or recently graduated individuals) throughout the project to provide experience, mentorship, and employment. We provide a second abstract in Spanish and will disseminate work to all research stations and assistants involved in the project and summarize main take-aways (in Spanish) regarding potential impacts of over-hunting. Finally, our data and results are to be publicly available and will be presented at internationally and nationally attended meetings.

**AUTHOR CONTRIBUTIONS**

T.L. conceived of project idea and initial study design, carried out field data collection, lab work, genetic and statistical analyses, and manuscript writing. ZDM contributed to lab work, genetic analysis, and manuscript writing and revisions. V.S. contributed to study design, field data collection, and manuscript revision. J.K. contributed reagents and materials to lab work and contributed to study design and manuscript revision. J.C. contributed reagents and materials to lab work and contributed to genetic analysis, results interpretation and troubleshooting, and manuscript revision. A.E.D. contributed to project framing, study design, and manuscript revision.

**CONFLICTS OF INTEREST STATEMENT**

The authors have no conflicts of interest to declare.

**TABLES AND FIGURES (with captions)**

Tables:
Table 1. Information on relative densities of major primary seed disperser groups in the three study sites (adapted from Bagchi and Swamy 2018).

<table>
<thead>
<tr>
<th>Site</th>
<th>Location</th>
<th>Hunting period</th>
<th>Large primates</th>
<th>Medium primates</th>
<th>Small primates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tambopata Research Center (faunally-intact)</td>
<td>13°7'S, 69°36'W</td>
<td>-</td>
<td>15.9</td>
<td>11.1</td>
<td>7.4</td>
</tr>
<tr>
<td>Los Amigos (recovering)</td>
<td>12°34'S, 70°4'W</td>
<td>1982-2003</td>
<td>3.9</td>
<td>19.8</td>
<td>18.2</td>
</tr>
<tr>
<td>Reserva Amazonica (defaunated)</td>
<td>12°32'S, 69°3'W</td>
<td>1985-present</td>
<td>0</td>
<td>3.7</td>
<td>3.0</td>
</tr>
</tbody>
</table>

Table 2. The density of adult and seedlings in each site within the 4-ha plots, the total number of individuals successfully genotyped, and the mean intracohort pairwise distances followed by the pairwise distance range and standard deviation (SD).

<table>
<thead>
<tr>
<th>Cohort</th>
<th>Site</th>
<th>Collected individuals</th>
<th>N genotyped</th>
<th>Mean pairwise distances (range, standard deviation)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td>Defaunated (RA)</td>
<td>33</td>
<td>25</td>
<td>105m (239-0.5m, 52m SD)</td>
</tr>
<tr>
<td></td>
<td>Recovering (LA)</td>
<td>49</td>
<td>38</td>
<td>104m (245-1m, 52m SD)</td>
</tr>
<tr>
<td></td>
<td>Faunally-intact (TRC)</td>
<td>23</td>
<td>22</td>
<td>99m (227-8m, 51m SD)</td>
</tr>
<tr>
<td>Seedlings</td>
<td>Defaunated (RA)</td>
<td>267</td>
<td>115</td>
<td>91m (195-0.1m, 45m SD)</td>
</tr>
<tr>
<td></td>
<td>Recovering (LA)</td>
<td>172</td>
<td>119</td>
<td>81m (194-0.05m, 39m SD)</td>
</tr>
<tr>
<td></td>
<td>Faunally-intact (TRC)</td>
<td>427</td>
<td>122</td>
<td>79m (226-0.01m, 40m SD)</td>
</tr>
</tbody>
</table>

Table 3. Genetic diversity metrics, and inbreeding means (± standard error) for each cohort and site across loci. Allelic richness (A_r) (rarified to n = 115 seedlings and n = 22 adults), number of effective alleles (NA_e), observed heterozygosity (H_o), gene diversity (H_s), and inbreeding coefficients (F_is) did not differ significantly between sites for either cohort. Per locus values can be found in Supplementary Materials Table S4.

<table>
<thead>
<tr>
<th>Cohort</th>
<th>Site</th>
<th>Rarefied allelic richness (A_r)</th>
<th>Effective number of alleles (NA_e)</th>
<th>Observed heterozygosity (H_o)</th>
<th>Gene diversity (H_s)</th>
<th>Inbreeding (F_is)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult</td>
<td>Defaunated (RA)</td>
<td>3.67 (± 0.35)</td>
<td>1.83 (± 0.17)</td>
<td>0.38 (± 0.02)</td>
<td>0.42 (± 0.04)</td>
<td>0.08 (± 0.07)</td>
</tr>
<tr>
<td></td>
<td>Recovering (LA)</td>
<td>2.98 (± 0.47)</td>
<td>1.98 (± 0.34)</td>
<td>0.34 (± 0.09)</td>
<td>0.39 (± 0.12)</td>
<td>0.71 (± 0.05)</td>
</tr>
<tr>
<td></td>
<td>Faunally-intact (TRC)</td>
<td>3.00 (± 0.49)</td>
<td>1.66 (± 0.37)</td>
<td>0.25 (± 0.11)</td>
<td>0.26 (± 0.10)</td>
<td>0.07 (± 0.12)</td>
</tr>
<tr>
<td>Seedling</td>
<td>Defaunated (RA)</td>
<td>4.86 (± 0.63)</td>
<td>1.92 (± 0.28)</td>
<td>0.40 (± 0.05)</td>
<td>0.43 (± 0.05)</td>
<td>0.07 (± 0.03)</td>
</tr>
<tr>
<td></td>
<td>Recovering (LA)</td>
<td>4.85 (± 0.51)</td>
<td>1.99 (± 0.32)</td>
<td>0.40 (± 0.1)</td>
<td>0.41 (± 0.10)</td>
<td>0.11 (± 0.08)</td>
</tr>
<tr>
<td></td>
<td>Faunally-intact (TRC)</td>
<td>4.85 (± 0.63)</td>
<td>1.78 (± 0.37)</td>
<td>0.30 (± 0.09)</td>
<td>0.33 (± 0.10)</td>
<td>0.12 (± 0.05)</td>
</tr>
</tbody>
</table>

Table 4. The mean slope of the regression of F_g on a logarithm distance scale, b_Flog, for each site and cohort. Significant results are bolded. Sp summarizes spatial genetic structure strength and is shown for each site and cohort with standard errors.

<table>
<thead>
<tr>
<th>Cohort</th>
<th>Site</th>
<th>b_Flog</th>
<th>Sp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult</td>
<td>Defaunated (RA)</td>
<td>-0.03792</td>
<td>0.043 (± 0.024)</td>
</tr>
<tr>
<td></td>
<td>Recovering (LA)</td>
<td>-0.0158</td>
<td>0.013 (± 0.009)</td>
</tr>
<tr>
<td></td>
<td>Faunally-intact (TRC)</td>
<td>-0.01047</td>
<td>-0.007 (± 0.01)</td>
</tr>
<tr>
<td>Seedling</td>
<td>Defaunated (RA)</td>
<td>-0.0048</td>
<td>0.0048 (± 0.003)</td>
</tr>
<tr>
<td></td>
<td>Recovering (LA)</td>
<td>-0.0046</td>
<td>0.0027 (± 0.003)</td>
</tr>
<tr>
<td></td>
<td>Faunally-intact (TRC)</td>
<td>0.00033</td>
<td>-0.0014 (± 0.0007)</td>
</tr>
</tbody>
</table>
Figure 1. Images of the study species showing (a) adult *Euterpe precatoria*, (b) red surface roots characteristic of *E. precatoria*, and (c) *E. precatoria* infructescence with mature fruits. Photo credit: Rainer W. Bussmann & Narel Y. Paniagua Zambrana.

Figure 2. (a) Study region in Peru and (b) enlargement of the Madre de Dios region with study sites labeled (*Google Earth Pro*, 2022).
Figure 3. Spatial and genetic distance between adult and seedling cohorts of each site. Violin-plots (a) show pairwise spatial distances between seedlings and the nearest conspecific adults with horizontal lines showing median distances. Genetic distances between individuals are shown in (b) through a scaled and centered principal components analysis in which points represent individuals and the degree of point overlap represents genetic distance between points (percent variation explained by each axis is shown in parentheses). Lighter points relative to their color counterparts represent seedlings while darker represent adults.

Figure 4. Spatial autocorrelation of pairwise kinship coefficients across defaunation levels for a) adult cohorts and b) seedling cohorts. Points are mean observed kinship coefficients $F_{ij}$ over pairwise distance with standard errors shown by vertical bars. Mean permuted $F_{ij}$ across pairwise distances for the null model is shown as a dashed line and the null model 95% confidence intervals are shown in the shaded regions. Asterisks above standard error bars represent instances where observed values of mean $F_{ij}$ were greater than
the 95% confidence interval computed under the null model (one-tailed test). Plotted values can be found in Supplementary Materials Table S6.