Received: 19 February 2020 | Revised: 19 May 2021 | Accepted: 11 June 2021

DOI: 10.1111/mec.16060

ORIGINAL ARTICLE

MOLECULAR ECOLOGY WILEY

Forest cover at landscape scales increases male and female gametic diversity of palm seedlings

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Funding information
National Science Foundation: GRFP to ZDM; Disney Conservation Fund; U.S. Fish and Wildlife Service, Grant/Award Number: NMBCA # 6318; Tulane University Department of Ecology and Evolutionary Biology; Conservation, Food and Health Foundation; American Philosophical Society; Andrew W. Mellon Foundation; National Geographic Society; National Science Foundation, Grant/Award Number: EAGER #1548548

Abstract

Genetic diversity shapes the evolutionary potential of plant populations. For outcrossing plants, genetic diversity is influenced by effective population size and by dispersal, first of paternal gametes through pollen, and then of paternal and maternal gametes through seeds. Forest loss often reduces genetic diversity, but the degree to which it differentially impacts the paternal and maternal contributions to genetic diversity and the spatial scale at which these impacts are most pronounced are poorly understood. To address these questions, we genotyped 504 seedlings of the animal-dispersed palm *Oenocarpus bataua* collected from 29 widely distributed sites across Ecuador and decomposed the contribution of paternal and maternal gametes to overall genetic diversity. The amount of forest cover at a landscape scale (>10 km radius) had an equally significant positive association with both male and female gametic diversity. In addition, there was a significant positive association between forest cover and effective population size. Stronger fine-scale spatial genetic structure for female versus male gametes was observed at sites with low forest cover, but this did not scale up to differences in male versus female gametic diversity. These findings show that reductions in forest cover at spatial scales much larger than those typically evaluated in ecological studies lead to significant, and equivalent, decreases of diversity in both male and female gametes, and that this association between landscape level forest loss and genetic diversity may be driven directly by reductions in effective population size of *O. bataua*, rather than by indirect disruptions to local dispersal processes.

KEYWORDS
alpha, beta and gamma diversity, conservation genetics, effective population size, genetic diversity, seed and pollen dispersal

1 | INTRODUCTION

Genetic diversity increases plant populations' ability to respond to changing environments (Koehn & Hilbish, 1987), such as diseases outbreaks (Altizer et al., 2003), extreme weather events (Reusch et al., 2005), or changing climates (Jump & Peñuelas, 2005). Plant species with large effective population sizes, or N_e, often have higher levels of genetic diversity due in part to reduced impacts of stochasticity and inbreeding (Ellstrand & Elam, 1993; Hoban et al., 2021; Nei & Takahata, 1993). Genetic diversity can also be promoted through the movement of alleles across populations, which similarly counteracts the effects of genetic drift and inbreeding (Ellstrand, 2014). In outcrossing plants, gene flow occurs sequentially through the movement of pollen, comprised of haploid, paternally inherited male gametes, and then seeds, which are diploid and a combination of male gametes and maternally inherited female gametes. Many flowering plant species rely on mutualistic relationships in which animals provide effective dispersal of genetic material in both dispersal

phases (Corrêa Côrtes & Uriarte, 2013; Ollerton et al., 2011). This often results in the movement of alleles between genetically distinct groups of plants across the landscape (Klein et al., 2006; Nathan, 2008). Together, effective population size and dispersal processes are key factors in sustaining genetic diversity for wild plant species.

Land-use change may alter patterns of genetic diversity for many plant species by decreasing the amount of habitat, changing the configuration and connectivity of forests through fragmentation, or both (DiLeo & Wagner, 2016; Fahrig, 2013, 2017; Fahrig et al., 2019). In the Tropics and many other regions of the planet, conversion of forest to agricultural land is widespread (Crowther et al., 2015) and while it may increase biodiversity or long-distance dispersal (Fahrig, 2017; Kramer et al., 2008), many studies have documented negative outcomes. From the perspective of forest-dwelling animals that serve as dispersal vectors, decreasing forest cover can alter the abundance, behavior, or composition of disperser communities (Fontúrbel et al., 2015; Hadley & Betts, 2012; Kremen et al., 2007; McConkey et al., 2012; Walter et al., 2017), which can then impact dispersal and patterns of genetic structure in seedlings (Aguilar et al., 2019; Browne & Karubian, 2018). Decreases in forest cover can also have direct impacts on effective population sizes of plants, and associated reductions in the number or density of individuals can result in genetic bottlenecks (Aguilar et al., 2008; Honnay & Jacquemyn, 2007; Vranckx et al., 2012). The cumulative impacts of forest loss can increase isolation between populations, which may expose populations to increases in inbreeding (Lowe et al., 2005; Manoel et al., 2012) and correlated paternity (Breed et al., 2012; Browne & Karubian, 2018; Ewédjè et al., 2017), as well as decreased reproductive output (Quesada et al., 2004; Suarez-Gonzalez & Good, 2014) and outcrossing rates (Dick et al., 2008).

Despite considerable research, our understanding of how forest loss impacts the genetic diversity of plant populations remains incomplete in two main ways. First, it is unclear if forest loss asymmetrically influences the male and female contributions to genetic diversity at the level of individual seedlings. To address this question, researchers can genotype diploid seedling leaf tissue (maternal + paternal gametes) and pericarp seed tissue (only maternal gametes) of the same seedling (Gelmi-Candusso et al., 2019; Godoy & Jordano, 2001; Jordano et al., 2007). Using both genotypes, one can match the maternally inherited female alleles and infer the paternally inherited male alleles (Smouse et al., 2012; Sork & Smouse, 2006). This allows for the estimation of α diversity, or the effective number of alleles inherited paternally (i.e., male gametes) and those inherited maternally (i.e., female gametes), providing insight into the independent impacts of paternal and maternal gametes to overall α diversity of alleles in diploid seedlings (Grivet et al., 2005; Sork et al., 2015). Using this direct approach in relatively pristine habitats, research has found that pollen dispersal is typically more extensive than seed dispersal and male gametes have been shown to contribute more to gene flow (Iwaizumi et al., 2010) and overall genetic diversity of offspring (Browne et al., 2018; Grivet et al., 2009; Sork et al., 2015; but see Iwaizumi et al., 2013). Similarly, in continuous habitat, male gametes typically exhibit weaker fine-scale spatial genetic structure compared to female gametes (Browne et al., 2018; Nakanishi et al., 2009).

However, the relative influence of forest loss on male vs. female allelic diversity remains uncertain. Forest loss could impact genetic diversity directly (e.g., by reducing population size of focal tree species that in turn reduces N_e), or indirectly (e.g., by disrupting dispersal processes), or both. As pollen and seed disperser communities are likely to differ in key features such as diversity, abundance, specificity, and foraging behaviour, their responses to the amount of remaining forest cover is also likely to vary. For example, if decreasing forest cover has a particularly strong effect on seed dispersal vectors, then female gametes may show strong fine-scale spatial genetic structure despite robust levels of pollen movement (e.g. Browne & Karubian, 2018; Grivet et al., 2009). Such a reduction in localized seed, but not pollen, dispersal could scale up to dampen seed dispersal-mediated gene flow at greater spatial scales (Matlack, 2005), so that maternally inherited female gametes have a stronger association with the amount of remaining forest cover compared to paternally inherited male gametes. Available research has been conducted at local spatial scales and provides mixed results, with either pollen (Parejo-Farnés et al., 2017) or seed flow (Browne & Karubian, 2018) being more heavily impacted by forest fragmentation.

A second major limitation is that very little research, and no decomposing male versus female gametic diversity, has explicitly evaluated the spatial scale at which forest cover impacts genetic diversity. Instead, most study designs focus on plant populations restricted to isolated forest fragments (DiLeo & Wagner, 2016) by sampling a series of nearby plots (i.e., separated by tens or hundreds of meters) that are all embedded within a single landscape or "patch" that frequently spans a few square kilometres or less (Aguilar et al., 2019). While this design provides useful insights into dynamics at relatively fine spatial scales, it does not address the degree to which forest cover at larger spatial scales (e.g., the landscape scale) impacts patterns of genetic diversity. Yet, there are good reasons to believe that forest cover at a broader spatial scale may have important impacts on genetic diversity (Anderson et al., 2010; Robledo-Arnuncio et al., 2014). For example, despite the majority of pollen and seeds being dispersed at local scales, long-distance dispersal events at much larger spatial scales are likely to disproportionately contribute to gene flow (Corrêa Côrtes & Uriarte, 2013; Ellstrand, 2014). In addition, population size may vary for a given species across different landscapes at a broad scale (Prunier et al., 2017).

In the current study, we address how forest cover at varying spatial scales asymmetrically influences the contribution of paternal and maternal gametes to overall genetic diversity. The novelty of this work lies in decomposing the impact of forest cover on the male and female contributions to gametic diversity separately, at geographical scales that far exceed the relatively restricted scale used by most ecological studies. This approach also allows new insights into how effective population size and local dispersal may mechanistically contribute to observed patterns of genetic diversity. To do so, we collected seedlings of the neotropical palm, *Oenocarpus bataua* (Mart.) across a total area of 147,853.72 km^2 in the country of Ecuador (Figure 1a), with an average pairwise distance of 282.05 $\pm$ 156.96 km between sampling localities. *Oenocarpus bataua* is well suited to address this

topic because it is common and widespread across the landscape (Henderson et al., 1995) and seedlings remain attached to seeds for up to 2 years after germination, allowing the decomposition of male and female gametes and the estimation of their direct contribution to diploid genetic diversity. We used this regional sampling design in combination with information about surrounding forest cover to identify at what spatial scale (i.e., from local to landscape scale) the relationship between forest cover and genetic diversity is strongest. We then investigated impacts of the relative contribution of male and female gametes to overall allelic diversity at this scale. We predicted that the area encompassing the main distances at which dispersal typically occurs for this species (e.g,. an area with a radius of 1-km or 309-ha; Browne et al., 2018; Ottewell et al., 2012) would best explain all measures of genetic diversity. We also predicted that α diversity would be highest for male gametes, which would also have a weaker relationship with forest cover than female gametes, as insect pollinators may be less impacted by lower levels of forest cover compared to vertebrate seed dispersers. Finally, we evaluated the degree to which low forest cover is associated with dampened effective population size and disruptions in local dispersal processes that may mechanistically influence observed patterns in genetic diversity, with the expectation that both factors will be impacted by forest loss.

2 | MATERIALS AND METHODS

2.1 | Study system

Oenocarpus bataua var. *bataua* (Mart.; Arecaceae) is a widespread, hyperdominant, long-lived, canopy palm (Henderson et al., 1995; ter Steege et al., 2013). In Ecuador, the species is distributed on the western slope of the Andes mountain range in the Tumbes-Chocó biogeographic zone as well as on the eastern side of the Andes in Amazonian lowland and foothill forests (Browne & Karubian, 2016; Escobar et al., 2018). It is highly outcrossed with low rates of selfing (Ottewell et al., 2012). Curculionidae and Nitidulidae beetles play important roles as pollen dispersers, but pollinator communities are diverse (Borchsenius et al., 1998; Núñez-Avellaneda & Rojas-Robles, 2008) and may change across *O. bataua's* range. Fruits take approximately 2 years to mature (Ramirez-Parada et al., 2020; Rojas-Robles & Stiles, 2009). In northwest Ecuador, seed dispersal is provided primarily by large birds (Mahoney et al., 2018) and rodents, while in Amazonia, seeds are dispersed primarily by primates (*Ateles belzebuth*) (Karubian et al., 2015; Link & de Luna, 2004), tapirs, large terrestrial and arboreal birds, and rodents. In continuous and fragmented forest, pollinators disperse pollen relatively far distances and pollen dispersal exceeds seed dispersal, but fragmentation impacts both dispersal processes (Browne et al., 2015; Browne & Karubian, 2018; Browne et al., 2018; Ottewell et al., 2012).

In the wild, *O. bataua* exclusively grows in lowland and foothill ecosystems, suggesting that it would be present throughout its natural range in Ecuador if free of human interference (aee Figure S1B). However, Ecuador has among the highest rates of forest loss in South America (Food & Agriculture Organization of the United Nations, 2012). From 2000–2010, Ecuador lost 1.8% of its forest cover per year, translating to a yearly loss of 198,000 ha (Food & Agriculture Organization of the United Nations, 2012; Figure S1A), driven by commercial and subsistence agricultural practices, illegal logging, oil exploitation, and mining (Ministerio del Ambiente, 2013; Sierra, 2013). Coastal Ecuador has experienced particularly intensive forest loss and retains only 5% of original forest cover as of 2013 (Ministerio del Ambiente, 2013).

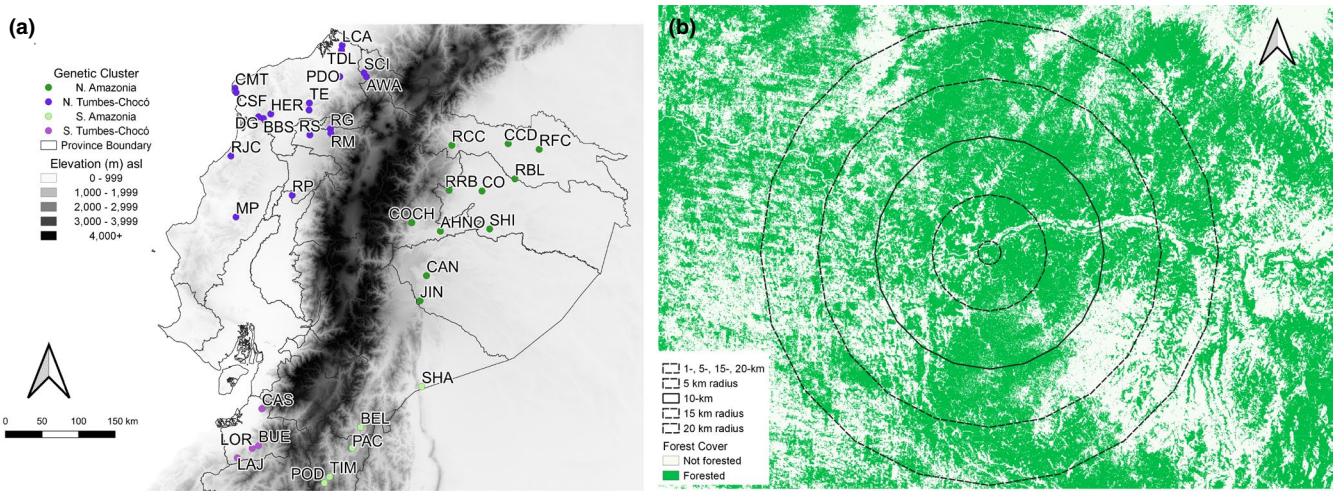

FIGURE 1 Sampling locations for 641 seedlings of *Oenocarpus bataua* across 29 sites in Ecuador as well as surrounding forest cover for one illustrative sampling site (RG). Map of study area showing (a) each sample site location as well as their assigned genetic cluster including north Amazonia (NAM), north Tumbes-Chocó (NTC), south Amazonia (SAM), and south Tumbes-Chocó (STC). Also shown is a (b) map of sampling site RG, with 5 circular areas in which forest cover was measured. Areas considered have radii with 1-, 5-, 10-, 15-, and 20-km and forest cover within each distance band was measured based on pixels with ≥90% cover represented in dark green. The solid band in bold is the area with a 10-km radius [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Genetic sampling and genotyping

We sampled *O. bataua* seedlings across Ecuador from January through May 2017 in forested areas on both sides on the Andes mountain range (Figure 1a). Sampling sites were selected by identifying areas known to, or likely to, include *O. bataua*. Within each site, we opportunistically sampled seedlings at varying distances from adult trees (1 to >20 m) by collecting the entire seedling and seed tissue. If multiple seedlings were found within a 1 m radius of one another, we collected a maximum of three individuals in the group (see Table S1). The mean pairwise distance between seedlings sampled per site was 269.27 ± 913.46 m (Table S1). Leaf and seed tissue were dried in plastic bags with silica and stored in envelopes until genetic analysis.

We used Qiagen DNeasy 96 kits to extract DNA from leaf and the outer seed coat. We then amplified 11 microsatellite loci using polymerase chain reaction (PCR) and scored microsatellite genotypes using the program GENEMARKER v. 1.85 (SoftGenetics) using a protocol previously used for *O. bataua* in Ecuador (e.g., Browne et al., 2018; Karubian et al., 2010, 2015; Ottewell et al., 2012). We extracted DNA from leaf and seed tissue from 641 seedlings (average = 22.10 ± 2.79 per site, range = 17–25) from 29 sites across Ecuador (Figure 1a). 138 seed samples did not amplify well and were omitted from analyses, leaving 504 samples with both leaf and corresponding seed tissue (average = 17.40 ± 4.48 per site, range = 6–23); the mean pairwise distance between these samples per site was 80.38 ± 104.90 m (Table S1). There was no significant correlation between average within site pairwise sample distance and α diversity of male and female gametes or diploid leaf tissue ($p > .30$ for all analyses; Table S1).

Of the 11 microsatellite loci amplified, Ob11 and Ob10 did not amplify well and were excluded from analyses. We used the program GENEPOP v. 4.7.0 to evaluate Hardy-Weinberg Equilibrium across loci at each site using the default parameters and to determine linkage disequilibrium between loci (Raymond & Rousset, 1995). We used FreeNA (Chapuis & Estoup, 2007) to estimate the presence of null alleles at each site. We assessed genotyping error rate by regenotyping a subset of samples. We found eight out of 36 pairs of loci to be in genotypic linkage disequilibrium ($p < .05$; see Table S2). Most loci showed low average estimates of null alleles (see Table S3) and the F_{ST} estimates calculated by FreeNA did not greatly differ before (0.234) and after (0.232) correction for null alleles (range of average null alleles for loci = 0.0044–0.0287). Genotyping error rate was relatively low for most loci (<8% for all loci but one). We found locus Ob23 to be out of HWE at two sites (SHA and SHI), in genotypic linkage disequilibrium with four other loci, and had a substantially higher than average rate of null alleles (0.05). Ob23 was therefore omitted from all subsequent analyses leaving an array of eight microsatellite loci (Table S3). The marker Ob22 was excluded from analyses for the three populations for which it was out of HWE (COCH, JIN, and SHA).

2.3 | Population genetics

We used all of the diploid genotypes obtained from leaf tissue ($n = 641$) to determine the genetic structure of *O. bataua* across Ecuador. To do so, we used a Bayesian clustering method implemented in STRUCTURE v. 2.3.4 (Pritchard et al., 2000) to assign individuals and sites to genetic clusters (see Figure S2). We used Structure Harvester (Earl & vonHoldt, 2012) to find ΔK, or the optimal number of *K* (Evanno et al., 2005). As STRUCTURE results can be biased towards indicating $K = 2$ (Janes et al., 2017), we also determined lower orders of hierarchical structuring. We used a scaled and centred principal components analysis (PCA) to evaluate genetic similarity between samples and their genetic clusters using the R package adegenet (Jombart, 2008). Once the genetic clusters were determined, we also used adegenet to calculate pairwise F_{ST} between them. In addition, we calculated G_{st}' between genetic clusters, the inbreeding coefficient (F_{IS}), the number of effective alleles (A_e), expected heterozygosity (H_e) and observed heterozygosity (H_o) for each site as well as each genetic cluster using gstudio (Dyer, 2009).

2.4 | Genetic diversity metrics and effective population size

Once genetic clusters were identified, we estimated the relative paternal and maternal genetic contribution to offspring for those samples in which both leaf and seed tissue amplified ($n = 504$). To determine maternally and paternally inherited alleles for each locus, we used a modified TwoGener gametic extraction (Smouse et al., 2001; Sork et al., 2015) as described by Browne et al. (2018). When both leaf and seed tissue were heterozygous at the same allele (~13%), we assigned a 50% probability that the allele was inherited maternally or paternally.

We then used the analogues of species level diversity, α, γ, ß, and δ, to describe genetic diversity of male, female, and diploid gametes following Scofield et al. (2012) and Sork et al. (2015). These metrics provide a framework to estimate genetic diversity across scales such as within, between, and across sites and can directly be compared between studies as well as between taxa, such as the diversity of animal communities in the same system. Site-level allelic diversity, or α diversity, estimates the effective number of alleles per locus per sampling site and is robust to extreme bias that may be introduced by small sample sizes (Grivet et al., 2005; Scofield et al., 2012; Smouse & Robledo-Arnuncio, 2005; Sork et al., 2015). Cumulative allelic diversity (γ diversity) estimates effective number of alleles per locus across all seedlings in the sample; ß diversity estimates the number of genetically nonoverlapping sites, with higher values suggesting more turnover between sites; δ (delta) estimates between-site divergence on a scale from 1 (no overlap) to 0 (complete overlap) (Sork et al., 2015). To facilitate comparison with other studies, we also present scaled metrics, α', γ', and $ß'$ (Sork et al., 2015), but only unscaled α diversity was used in subsequent analyses.

We estimated effective population size (N_e) at each site using the program NEESTIMATOR v2.1 (Do et al., 2014). We estimated N_e using the same leaf genotypes used in the population genetics analyses (n = 641), the linkage disequilibrium model, and the lowest allele frequency of 0.01. NEESTIMATOR uses a jackknifing approach to generate 95% confidence intervals (CI) to decrease bias (Do et al., 2014). Negative or infinity values of N_e were found for two sites and the upper CI for 11 sites (see Table S4), indicating a large population size or limited data is leading to the genetic results being explained entirely by sampling error (Waples & Do, 2010). However, even in these cases, a finite lower bound of the CI can provide useful information about the lower limit of N_e (Waples & Do, 2010), which we use as the estimate of N_e in downstream analyses (Table S4). Because the lower CIs for N_e and α diversity were positively correlated (R = 0.62, p < .001) and generated using the same genetic data, we were unable to build linear mixed models with N_e as the predictor variable and α diversity as the response term. The lower 95% CI for N_e was not correlated with sample size (R = 0.27, p = .15) or the average pairwise distance (m) between samples at each site (R = −0.07, p = .72).

2.5 | Forest cover, spatial scale, genetic diversity, and effective population size

We built linear and linear mixed models to assess how the amount of forest cover at differing spatial scales may influence genetic diversity and effective population size (N_e). To do so we first estimated the amount of forest cover at varying scales by calculating the centroid of the area in which seedlings were sampled at each site. We then generated a series of 5 circular areas around the centroid, with the radii of these areas ranging from 1-, 5-, 10-, 15-, and 20-km (Figure 1b). We limited the areas to 20 km radii to minimize overlapping areas between sites, although four pairs of sites overlapped in area (Table S1). We then used the Global Forest Change database, which has a spatial resolution of approximately 30 m per pixel, to measure forest cover in each area of interest (Hansen et al., 2013). This database uses Landsat satellite images from the year 2000 to define forest cover and for each subsequent year binary maps of forest loss and gain are used to calculate the area with contemporary forest cover for that given year. Pixels were considered forested if they had ≥90% forest cover in 2014, which corresponds to the time frame that dispersal processes were occurring given that collected seedlings are at most 2 years old and seeds take up to 2 years to mature. We used the gfcanalysis (Zvoleff, 2015) package in R, which calculates the amount of forest cover (ha) from pixels at each spatial scale at each site.

Next, for each of the five spatial scales considered, we used a model selection approach to build linear mixed models with two response variables: log transformed alpha diversity and square root transformed lower 95% CI of N_e. First, we fit models with different random effects including overlapping area, site, a nested effect of site within overlapping area, as well as a model with no random effects. For α diversity, the models with a random effect of site had the lowest AICc and were used in all subsequent models for all spatial scales (see Table S5). The N_e models with no random effects has the lowest AICc and was used in all subsequent models for all spatial scales (Table S5). We then fit fixed effects. For α diversity we included forest cover (ha), gamete type (male, female, diploid), genetic cluster (to account for population structure), and an interaction between forest cover and gamete type. We also included elevation as a fixed effect since high elevation sites may be at the elevation range limit and could experience decreased gene flow and genetic diversity. For N_e, we included forest cover (ha), genetic cluster, and elevation as fixed effects. Next, we determined if including a correlation structure would improve the models in accounting for spatial autocorrelation in model residuals. For each scale, we fit a model with no correlation structure and models with exponential, gaussian, linear, and spherical correlation structures. All the models without a correlation structure was the best fitting model.

For genetic diversity at each of the five spatial scales considered, a "final" model included the log of α diversity as a response variable, fixed effects of forest cover, gamete type, genetic cluster, elevation, and a random effect of site (Table S6). For N_e, a "final" model included the square root of the lower 95% CI of N_e as a response variable and forest cover as the predictor variable for all scales except the 1-km scale which also included elevation and genetic cluster as fixed effects (Table S6). All models were then validated and met the assumptions of normality in residuals, equal variance, and we did not detect multicollinearity in model terms (variance inflation factor <3). We then used model selection to compare these "final" models for each spatial scale to determine at which scale forest cover best explains allelic diversity and N_e and to evaluate the relationship between them at that scale. We also used Pearson's correlation to correlate the amount of forest cover at each spatial scale with alpha diversity of each gamete type to evaluate the scale with the highest correlation (e.g., Mendenhall et al., 2011; San-José et al., 2019). Finally, we noted that if using sites with 15 or more samples (n = 22), we attained qualitatively similar results with a near significant positive relationship between α diversity and forest cover at the ~30,000-ha scale (ANOVA results of model terms: F = 4.19, p = .057).

All models were fit using the lme() function in the R package nlme (Pinheiro et al., 2020). Model selection was performed using the model.sel() function in the MuMIn package (Bartoń, 2020). We evaluated model fit by comparing Akaike information criterion for small sample sizes (AICc), the model weight, and ΔAICc. We also used a type III analysis of variance (ANOVA) to test for the significance of model terms. We show partial residual plots of the model using the visreg package in R set to "conditional", which holds all variables constant while plotting the variable on the x-axis and the corresponding change on the y-axis (Breheny & Burchett, 2017). All analyses were conducted in R v. 3.6 (R Core Team, 2020).

2.6 | Landscape scale forest cover and fine-scale spatial genetic structure

We also evaluated the relationship between forest cover and spatial genetic structure of paternal and maternal gametes and diploid seedlings. To do so we first categorized sites as having high (>75%) or low (≤75%) forest cover at the scale identified to be the most important for genetic diversity (see above). High and low categories had similar number of sites (n_{high} = 16, n_{low} = 13) and seedlings (n_{high} = 250, n_{low} = 254) for each analysis. Analyses for diploid seedlings included all genotyped leaf to increase sample size (n_{high} = 357, n_{low} = 285). Sites in the "high" category had significantly higher forest cover than those in the 'low' group (t = −2.71, df = 26.36, p = .011). We then used the program SPAGEDI v.1.5d (Hardy & Vekemans, 2002, 2004) to estimate the kinship coefficient F_{ij} (Loiselle et al., 1995). Pairwise comparisons between individuals occurred within sites and reference allele frequencies were calculated separately for each site. We chose distance classes based on recommendations by Hardy and Vekemans (2002, 2004) to include ~100 pairwise comparisons, a percent participation (*% partic*) ~50%, and a coefficient of variation of the number of times each individual/population is represented (*CV partic*) <≈ 1, when possible (see Table S7). As such, we used the distance classes of 1–5, 5–10, 10–15, 15–20, 20–30, 30–40, 40–50, 50–100, 100–200, and 1,200 + metres. Measures were jackknifed over loci and we permuted individuals among locations 9,999 times to assess the significant of spatial genetic structure at each distance class. In addition, we evaluated spatial genetic structure when restricting analyses to a maximum of 100 m.

To estimate the strength of fine-scale spatial genetic structure, we calculated the *Sp* statistic as $-b_{Flog}/(1 - F_1)$ for each locus in all analyses. Here, b_{Flog} is the log mean slope of the regression coefficient of F_{ij} and F_1 is the mean kinship coefficient at the first distance class. We then tested for differences in the *Sp* statistic between sites with high and low forest cover as well as for differences between gamete types. These tests were conducted using a paired Wilcoxon rank sum test with loci as the paired factor.

3 | RESULTS

3.1 | Population genetics

Using all genotyped leaf tissue, we identified four geographically distributed genetic clusters with the Tumbes-Chocó and Amazonia, each having a northern and southern cluster (Figure 1a; Figure S2; Figure S3); this is also supported by the first three axes of the PCA (Figure 2a–b). Intermediate levels of genetic structuring exist between the northern and southern clusters in Amazonia and the northern Tumbes-Chocó, as measured by F_{ST} (Table 1). Measures of G_{ST}' followed similar patterns (see Table S8). Overall, the number of effective alleles was higher in Amazonia than in the Tumbes-Chocó, as were expected and observed heterozygosity (Table S4).

3.2 | Forest cover, spatial scale, and genetic diversity

Within site allelic diversity (α) for all sites was higher for male gametes than female gametes and diploid genotypes, and α diversity for diploid leaf tissue was higher than α diversity for female gametes (Table 2; Table S4). Similarly, cumulative allelic diversity across plots (γ) was higher for male gametes, intermediate for diploid leaf tissue,

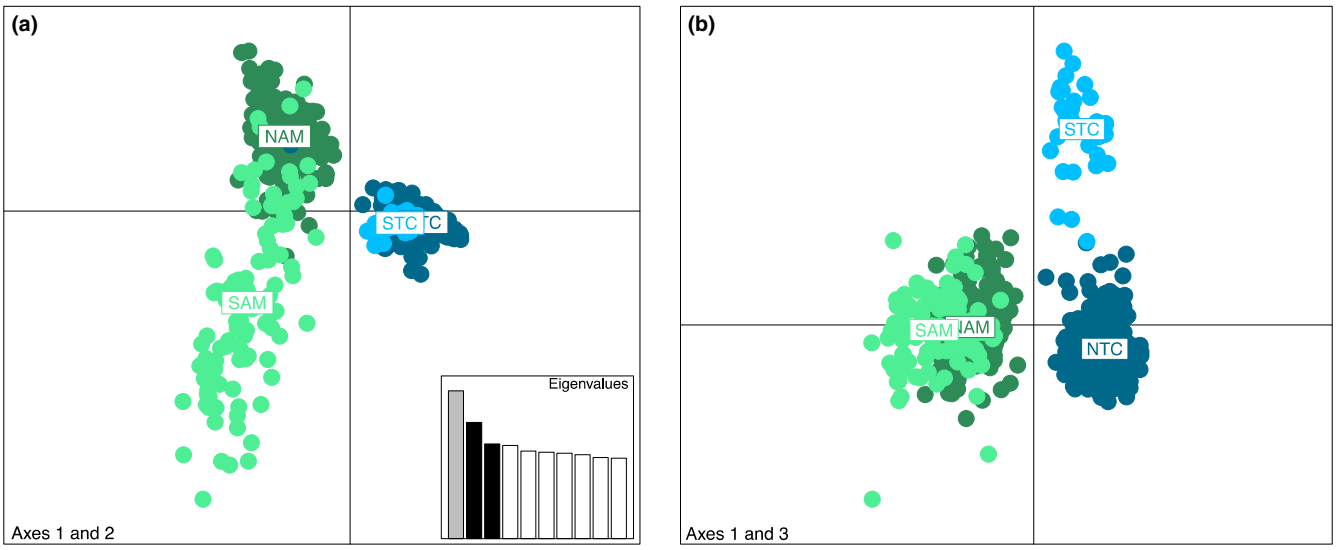

FIGURE 2 Population genetic structure of 641 seedlings of *Oenocarpus bataua* across 29 sites in Ecuador. A scaled and centred principal components analysis (PCA) shows that (a-b) genetic clusters in the Tumbes-Chocó and Amazonia vary along axis 1, while (a) the south Amazonia (SAM) and north Amazonia (NAM) clusters vary along axis 2 and (b) clusters in the south Tumbes-Chocó (STC) and north Tumbes-Chocó varying along axis 3. In both panels axis 1 is the x-axis [Colour figure can be viewed at wileyonlinelibrary.com]

and lowest for female gametes (Table 2). Between plot turn over (ß) and divergence (δ) were lowest for male gametes, intermediate for diploid leaf tissue, and highest for female gametes in all genetic clusters (Table 2). Genetic clusters in Amazonia exhibited higher α and γ than those in the Tumbes-Chocó, with the south Tumbes-Chocó being notably low (Table 2).

Models of genetic diversity and forest cover including areas with radii of 5-, 10-, 15-, and 20-km had ΔAIC <2, which indicates they are all equally plausible models that perform better than the model with a radius of 1 km (Table 3). While the model with a radius of 5-km had the lowest ΔAIC and greatest weight, the 10-km area was nearly indistinguishable from the 5-km area in its ability to explain the data (Table 3). In addition, when correlating the amount of forest cover from areas of each size class with male, female, and diploid allelic diversity, we found correlations reached a plateau between these spatial scales (see Figure S4). Therefore, we present the model for the area with the 10-km radius to facilitate comparisons with the N_e model (below). An area with a 10-km radius totals 30,901.70-ha and we found substantial variation in the amount of surrounding forest cover in that area areas across ranging from 25% to 97% forest cover (Table S1). The four models with radii >1-km have significant associations between forest cover and α diversity (see Table S9).

TABLE 1 Pairwise F_{ST} between four genetic clusters identified in Ecuador using 641 *Oenocarpus bataua* seedlings collected from 29 sites across Ecuador

	NAM	SAM	NTC
SAM	0.025	–	–
NTC	0.058	0.052	–
STC	0.099	0.14	0.062

Note: Genetic clusters were identified in north Amazonia (NAM), south Amazonia (SAM), north Tumbes-Chocó (NTC), and south Tumbes-Chocó (STC).

We found a significant positive association between surrounding forest cover at the 10-km scale and α diversity ($F = 6.61$, $p = .017$; Figure 3a), with every one-ha increase yielding a 0.0017% increase in α diversity, meaning that a 1,000-ha increase in forest cover (i.e., approximately 3% of the nearly 30,000-ha area) would increase α diversity by 1.68% (Table S9). There was a significant difference in the allelic diversity of different gamete types ($F = 59.77$, $p < 0.001$). Male gametic diversity was significantly higher than both other gamete types (Figure 3b; Table S9). In addition, there was a significant effect of genetic cluster on gametic diversity ($F = 11.25$, $p < .0001$), with genetic clusters in Amazonia having higher allelic diversity than those in the Tumbes-Chocó (Figure 3c). We also observed a significant effect of elevation ($F = 54.78$, $p = .039$), with sites at lower elevation having higher genetic diversity (Figure 3D).

3.3 | Forest cover, spatial scale, and effective population size

The lower 95% confidence interval for N_e varied across sites (average = 15.04 ± 13.02; range = 0.1–53.5). The model including forest cover at the 15-km scale had the lowest AICc value, but again the 10- and 20-km scales were nearly indistinguishable in explaining the data (Table 3). All models with forest cover in radii >1-km showed a positive association between forest cover and the lower 95% CI for N_e (Table S4). Therefore, we present the results from the model with a 10-km area to facilitate comparison with allelic diversity model (above). The model at the 10-km scale indicated a positive association between forest cover and the lower 95% CI for N_e ($F = 20.18$, $p < .001$) with a one-ha increase in forest cover yielding a 0.018% increase in effective population size (Table S9) (Figure 4). As such, a 1,000-ha increase in forest cover at this scale, which is ~3% of the total area, would translate to a ~17.62% increase in the lower 95% CI for N_e. Models at the 15- and 20-km scales show qualitatively similar positive associations between forest cover and effective population size (Table S9).

TABLE 2 Allelic diversity in male and female gametes and diploid leaf tissue of 504 *Oenocarpus bataua* seedlings collected from 29 sites and four genetic clusters across Ecuador

	North Amazonia			South Amazonia			North Tumbes-Chocó			South Tumbes-Chocó		
	Male	Female	Diploid	Male	Female	Diploid	Male	Female	Diploid	Male	Female	Diploid
α	4.35	2.54	3.73	4.01	2.28	3.54	2.79	1.88	2.55	1.39	1.18	1.41
α'	0.83	0.65	0.76	0.84	0.63	0.75	0.66	0.49	0.62	0.38	0.21	0.33
γ	4.92	3.94	4.7	4.67	3.62	4.51	3.35	2.62	3.11	1.53	1.25	1.51
γ'	0.8	0.75	0.8	0.8	0.73	0.78	0.71	0.62	0.68	0.36	0.20	0.34
ß	1.13	1.55	1.26	1.16	1.59	1.27	1.20	1.39	1.22	1.11	1.05	1.08
ß′	0.13	0.41	0.24	0.16	0.42	0.25	0.19	0.32	0.21	0.11	0.06	0.08
δ	0.16	0.44	0.27	0.23	0.51	0.31	0.20	0.34	0.24	0.20	0.12	0.16

Note: North and south Amazonia represents sites from the genetic cluster on the eastern side of the Andes mountain range, and the north and south Tumbes-Chocó are from the genetic cluster on the western coast. Shown above are within-site allelic diversity (α), across-site allelic diversity (γ), between site allelic turnover (ß), and across site allelic divergence (δ). Also shown are scaled counterparts of each metric (α', γ', ß′).

	Alpha (α) diversity			Effective population size (N_e)		
Radius of area	AICc	ΔAIC	Weight	AICc	ΔAIC	Weight
1-km	−21.2	5.32	0.025	114.4	10.14	0.003
5-km	−26.5	0	0.36	110.4	6.17	0.019
10-km*	−26.1	0.47	0.28	105.1	0.81	0.28
15-km	−25.3	1.28	0.19	104.2	0	0.42
20-km	−24.7	1.87	0.14	105.1	0.87	0.27

TABLE 3 Model selection summary for 10 models evaluating the relationship between forest cover and alpha diversity and effective population size for *Oenocarpus bataua* seedlings collected from sites across Ecuador

Note: For each model, we varied the scale at which forest cover was considered (radius of area). For alpha diversity, the models included the log of α diversity and forest cover, gamete type, genetic cluster, and elevation with a random effect of site for each model. For effective population size (N_e), models included the square root transformed lower 95% confidence interval of N_e as the response variable and forest cover as the predictor variable, except for the 1-km area that included genetic cluster, and elevation. *Indicates the model used in final analysis

3.4 | Landscape scale forest cover and fine-scale spatial genetic structure

Across all sites, fine-scale spatial genetic structure was significantly lower for paternal compared to female gametes ($V = 4$, $p < .001$) and higher for maternal gametes compared to diploid seedlings ($V = 136$, $p < .0001$); there was no difference in male gametes compared to diploid seedlings ($V = 38$, $p = .13$) (Table 4). Fine-scale spatial genetic structure was significantly higher for maternal gametes and diploid seedlings in sites with lower forest cover compared to sites with higher forest cover, especially in near distance classes ($V = 33$, $p = .039$; $V = 34$, $p = .023$, respectively; Table 4; Figure 5b–c). Also, kinship for female gametes was significantly higher than zero at distances <15 m for sites with low forest cover, but not high forest cover (see Table S6). In contrast, there was no significant difference in the strength of fine-scale spatial genetic structure of kinship for male gametes at sites with low compared to high cover ($V = 24$, $p = .46$, Table 4; Figure 5a). When restricting analyses to 100 m, the effect of spatial genetic structure tended to be higher for sites with low forest cover for all gametes types, though this effect was not statistically significant (see Figure S5).

4 | DISCUSSION

The extent of surrounding forest cover is expected to shape patterns of genetic diversity among animal-dispersed plants directly by decreasing effective population sizes or indirectly by disrupting dispersal processes, or both (Aguilar et al., 2019). Efforts to understand these relationships have been slowed by (a) difficulties associated with isolating the effect of forest cover on the independent genetic contribution of paternal versus maternal gametes to overall genetic diversity, and (b) uncertainty about the appropriate spatial scale at which to investigate these effects. We employed the same set of genetic markers in the same individual seedlings of *Oenocarpus bataua* to assess how forest cover at a range of spatial scales influences the asymmetric maternal and paternal contributions to overall genetic diversity. Notably, this work was conducted at a regional scale covering 29 sites across two genetic clusters in Ecuador, spanning nearly 150,000 km^2 and an average pairwise distance between sites of 282.05 ± 156.96 km, while statistically accounting for the impacts of population genetic structure on genetic diversity.

The regional sampling approach used in this study provides novel insights into how forest cover contributes to the maintenance of genetic diversity in natural populations of palms. Not surprisingly, we found that the male contribution to genetic diversity exceeds the maternal contribution, corroborating previous studies that identify the extensive movement of pollen as key in maintaining genetic diversity (Browne & Karubian, 2018; Ennos, 1994; Hamrick, 2004; Parejo-Farnés et al., 2017; Petit et al., 2005; Sork et al., 2015). However, by calculating the area that best explains allelic diversity across sites, we found that α diversity for all gamete types is most strongly associated with forest cover at a landscape scale (>5 km radius) rather than more localized spatial scales that ecological studies typically investigate. Moreover, in contrast to our expectations, we found that the paternal and maternal contributions to genetic diversity were equally sensitive to landscape scale forest cover; that is, the effect of forest cover was symmetric across gamete types. We also found a significant impact of genetic cluster on genetic diversity, highlighting the importance of regional population genetic structure in shaping patterns of genetic diversity at a regional scale. Finally, we detected a significant negative association between elevation and α diversity, probably due to high elevation sites being at the species' range limit (Eckert et al., 2008). This research suggests that, after accounting for regional population genetic structure and potentially confounding effects of site, contemporary forest cover at large spatial scales has significant consequences for microevolutionary processes that shape observed patterns of genetic diversity.

Many of our findings contrast with other studies that have decomposed the male and female gametic contributions to overall allelic diversity, many of which report asymmetric impacts of forest loss on male vs. female gametes. We suggest that this may be due to the distinctive spatial scale of the study design we employed. For example, our findings differ from a 2018 study on *O. bataua* conducted within a single landscape (maximum distance between sites ~10-km) that found overall α diversity and female and diploid diversity had

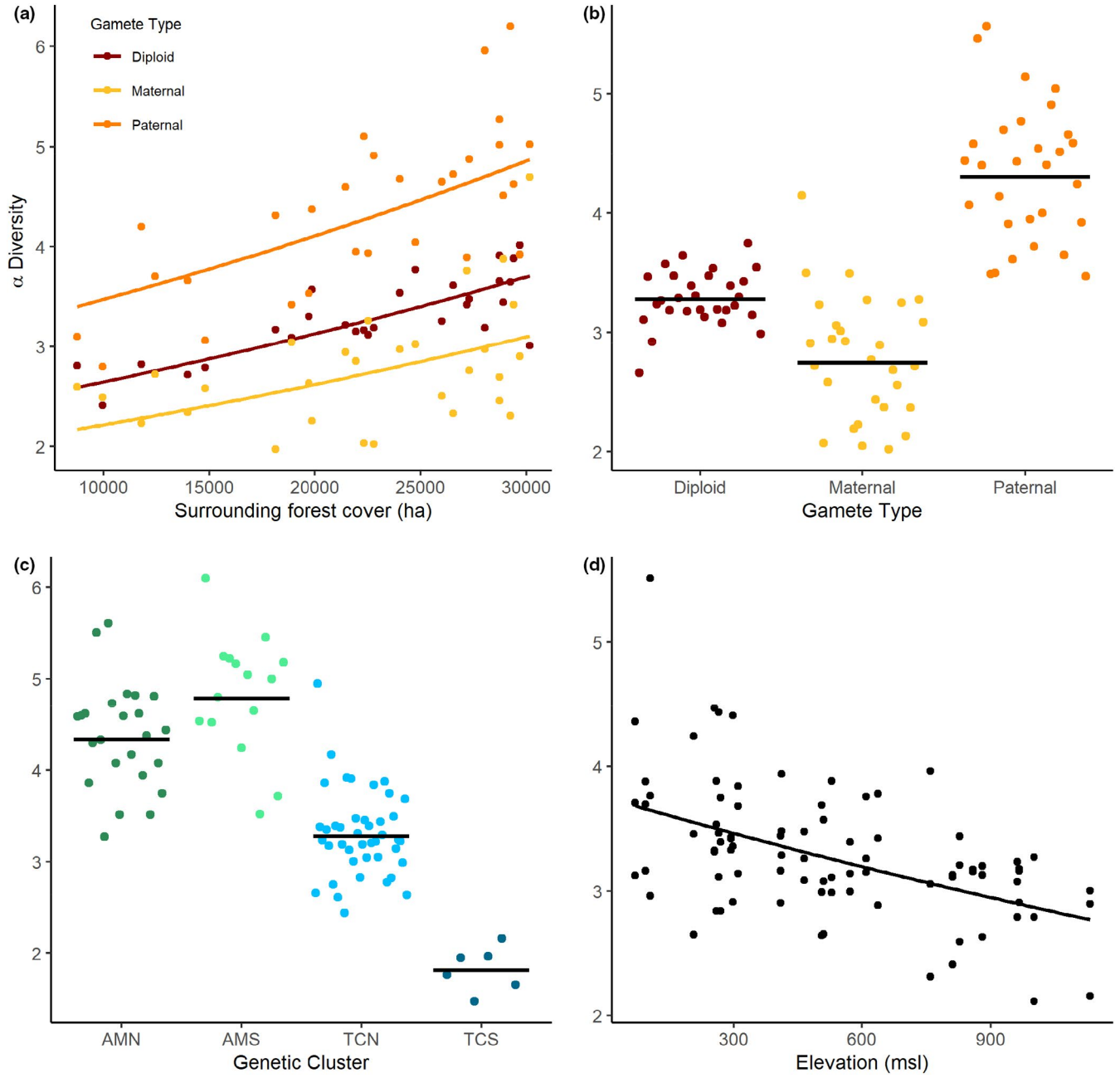

FIGURE 3 Relationship between α diversity and surrounding forest cover, gamete type, and longitude for 504 *Oenocarpus bataua* seedlings collected from 29 sites across Ecuador. Panel (a) shows a partial residual plot with a significant positive association between α diversity and surrounding cover in a ~30,000-ha area; the lack of an interaction between forest cover and gamete type suggests a qualitatively similar impact of forest cover on both male and female gametic diversity. Panel (b) illustrates α diversity for different gamete types with male gamete being significantly more diverse than female gametes and diploid alleles, and female gametes being significantly less diverse than diploid alleles. Panel (c) indicates a partial residual plot with significant differences in α diversity between genetic clusters. Panel (d) shows a partial residual plot with a significant negative relationship between α diversity and elevation [Colour figure can be viewed at wileyonlinelibrary.com]

a significant positive association with surrounding forest cover in a 2-km area around each site, whereas no relationship was detected with male gametes (Browne & Karubian, 2018). In our own data set, modeling the effects of forest cover at this localized scale would not have uncovered the significant associations we detected at a landscape scales: a model fit with forest cover at a 2-km scale using the data in the current study would have shown a non-significant relationship with α diversity ($F = 3.32$, $p = .08$) and would have been the second worst fit model after the 1-km area if included in the model selection approach. This suggests that the relatively restricted spatial scales typically employed in studies of this type to date may not be broad enough to capture the full relationship between forest cover and male gametic diversity. Instead, sampling regionally across multiple "landscapes", while taking into account the effect of genetic

structure, may be necessary to accurately document the full effect of forest cover on all measures of genetic diversity. In our study, the areas with 5-, 10-, 15-, and 20-km radii were all capable of explaining our data, suggesting that once a certain threshold is reached, then the influence of the factors that shape patterns of genetic diversity are sufficiently captured. Alternatively, it is possible that our models are not able to determine the scale at which forest cover is most associated with genetic diversity for other reasons such as: a lack of resolution regarding the explanatory variable, insufficient genetic data, confounding factors, or large variance in the processes that generate the observed patterns. We encourage future studies to address this question in more depth.

What factors might mechanistically drive the symmetric relationship we uncovered between landscape scale forest cover and diversity across gamete types? Although resolving this question was not the main focus of our study, our data enabled us to explore two potential factors: the direct influence of reductions in effective population size (N_e) and the indirect impact of disruptions to local dispersal processes. The significant positive association between forest cover at the 10-km scale and N_e is consistent with the idea that forest loss directly decreases N_e by removing trees from the landscape, leading to reduced standing genetic variation of paternal and maternal sources (reviewed in: Aguilar et al., ,2008, 2019; Honnay & Jacquemyn, 2007; Vranckx et al., 2012). *Oenocarpus bataua* probably has a historically large population size given it is a hyperdominant palm throughout lowland Ecuador (Montufar & Pintaud, 2006; ter Steege et al., 2013) and although we were unable to directly measure population sizes across the large study area, it is reasonable to assume that decreasing forest cover decreases N_e for this species (Figures S1A–B). At the same time, we found significant fine-scale spatial genetic structure (SGS) for female, but not male, gametes at short distance classes (<15 m) in sites with lower surrounding forest cover. This is consistent with other studies reporting that forest loss has driven declines of seed dispersers (Markl et al., 2012; McConkey et al., 2012) and dispersal services, leading to increased fine-scale SGS in a variety of plant populations (Breed et al., 2015; Carvalho et al., 2016; Giombini et al., 2017). On the other hand, invertebrate pollinators are generally less impacted by forest fragmentation (Aguilar et al., 2019). However, the outcomes of these local dispersal dynamics do not scale up to an overall asymmetric association between landscape level forest cover and male versus female gametic diversity in *O. bataua*. This may be because forest loss at landscape scales does not meaningfully affect longer distance seed and pollen dispersal processes, that both modes of dispersal are equally impacted by forest loss, or that not enough time has passed for changes in SGS associated with dispersal reductions to translate to changes in overall genetic diversity (i.e., the time lag effect; Kramer et al., 2008; Vranckx et al., 2012). Taken together, our findings support the idea that decreases in gametic diversity are associated with the direct effects of low forest cover through declines in N_e, instead of the indirect effects of disrupted local dispersal services, but are ambiguous about the role of dispersal at larger scales. We suggest that future research evaluate the association between landscape level forest cover and gene flow using a landscape genetics approach in combination with

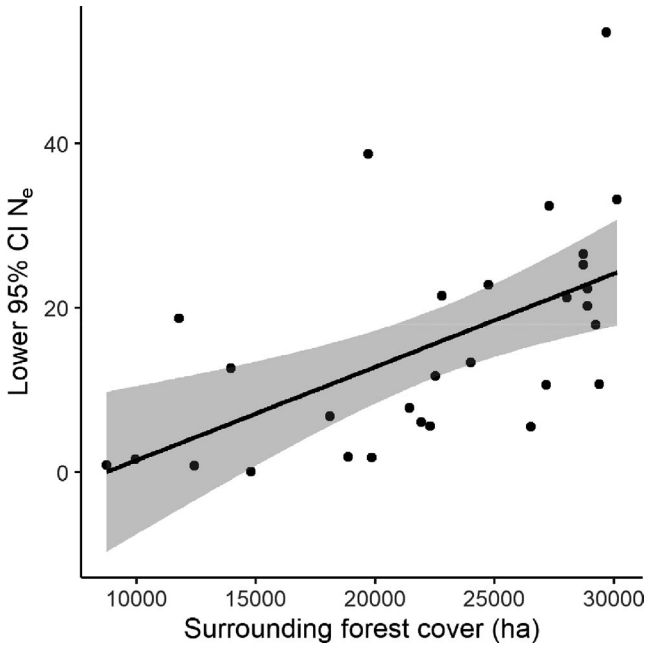

FIGURE 4 Relationship between the lower 95% CI for effective population size (N_e) and surrounding forest cover in 10-km radius area for 641 *Oenocarpus bataua* seedlings collected from 28 sites ($n = 1$ site with no estimate) across Ecuador. The 95% confidence interval is shown in grey

Gamete type	Forest cover level	F_{ij1}	b_{Flog}	b_{Flog} SE	*Sp*
Paternal	High	0.002	−0.007	0.003	0.007
	Low	−0.006	−0.01	0.005	0.01
Diploid	High	0.027	−0.008	0.001	0.008
	Low	0.053	−0.0003	0.003	0.003
Maternal	High	0.12	−0.03	0.004	0.04
	Low	0.19	−0.08	0.01	0.10

TABLE 4 Details of the fine-scale spatial genetic structure for paternally and maternally inherited gametes and diploid *Oenocarpus bataua* seedlings in landscapes with high and low levels of forest cover from 29 sites across Ecuador

Note: Shown is the kinship coefficient of the first distance class (F_{ij1}), the natural log of the slope estimate of the regression of the kinship coefficient (b_{Flog}), the standard error (b_{Flog} SE), and the overall strength of fine-scale spatial genetic structure for each (*Sp*).

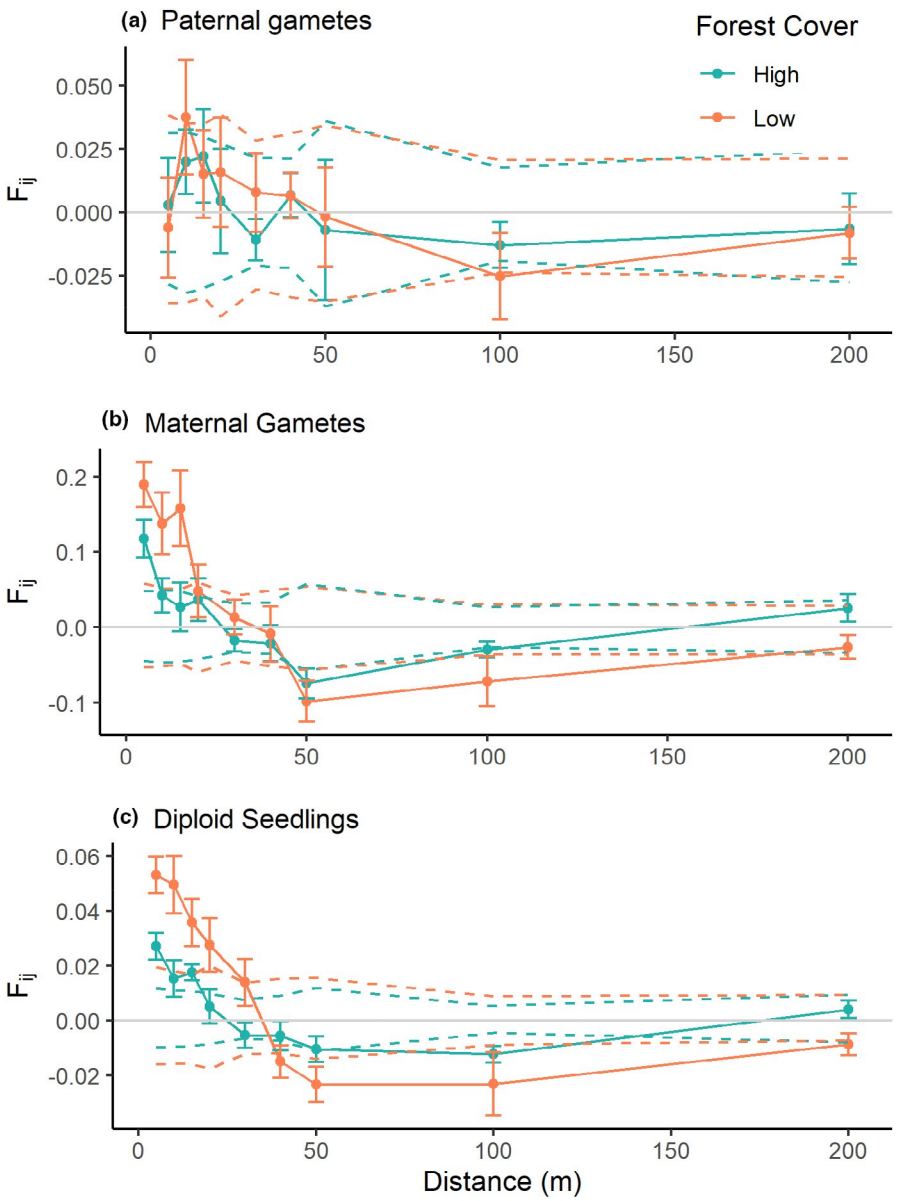

FIGURE 5 Spatial autocorrelation of pairwise kinship (F_{ij}) for (a) paternal gametes, (b) maternal gametes, and (c) diploid leaf tissue of *Oenocarpus bataua* seedlings sampled across 29 sites across Ecuador with high (green) or low (orange) levels of landscape scale forest cover. Dashed lines show the 95% CI range of the null hypothesis that F_{ij} is equal to 0. Error bars show ±2 standard error [Colour figure can be viewed at wileyonlinelibrary.com]

newly developed aerial mapping approaches capable of identifying individual canopy trees over large areas (e.g., Ferreira et al., 2019; Khimoun et al., 2017).

The maintenance of genetic diversity and evolutionary potential in wild plant populations is key to ensuring stability for a variety of ecosystems (Hughes et al., 2008). We show that, after accounting for a strong influence of regional population genetic structure, increased forest cover at the landscape scale is associated with higher α diversity in a widespread tropical palm regardless of gamete type. This work suggests that future studies should focus on evaluating how landscape scale gene flow and effective population size interact at varying spatial scales to mechanistically impact microevolutionary outcomes in plant populations. While theoretical and empirical work suggest that decreasing forest cover also negatively impacts wind pollinated species (Aguilar et al., 2019; Robledo-Arnuncio & Austerlitz, 2006), differences in dispersal modalities may result in varying outcomes for genetic diversity and should be explored. These findings highlight the importance of intact ecosystems in promoting fundamental processes that maintain genetic diversity in natural plant populations.

ACKNOWLEDGEMENTS

We are grateful for the support of FCAT (Fundación para la Conservación de los Andes Tropicales), the Ecuadorian Ministry of the Environment, and the landowners who allowed us to sample their properties. We thank J. Cabrera, F. Castillo, M. Gonzalez, N. Gonzalez, T. Ramirez, A. Russell, S. Ross, M. Furlong, and N. Oleas for assistance with logistics, data collection, and laboratory work. Thanks to L. Browne and the Karubian Laboratory for helpful comments on earlier versions of the manuscript. The manuscript greatly benefited from constructive comments of anonymous reviewers. This project was supported by: the Andrew W. Mellon Foundation (MMUF Program); the American Philosophical Society; the Conservation, Food & Health Foundation; Disney Conservation

Fund; National Science Foundation (EAGER #1548548 and a Graduate Research Fellowship to ZDM); National Geographic Society; Tulane University; and the United States Fish & Wildlife Service (NMBCA # 6318). All research was conducted with approval of the Ecuadorian Ministry of the Environment (MAE – DNB – CM – 2015 – 0017).

AUTHOR CONTRIBUTIONS

Zoe Diaz-Martin contributed to study design, data collection, laboratory work, data analysis and interpretation, and writing the manuscript. Jordan Karubian contributed to study design, interpretation, and writing.

CONFLICT OF INTEREST

There are no conflicts of interest.

DATA AVAILABILITY STATEMENT

Sampling locations and microsatellite genotypes can be found at https://doi.org/10.5061/dryad.tb2rbp016.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Diaz-Martin, Z., & Karubian, J. (2021). Forest cover at landscape scales increases male and female gametic diversity of palm seedlings. *Molecular Ecology*, 30, 4353–4367. https://doi.org/10.1111/mec.16060