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Migration Patterns of Epiphyllous Bryophyte Metapopulations in Amazonian Fragmented Landscape Inferred From Census and Genomic Data

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ABSTRACT

Habitat fragmentation affects metapopulation dynamics by reducing patch (discrete area occupied by a local population) size and connectivity, but its long-term genetic consequences are confounded by species-specific traits and limitations of sequencing techniques. Studies of terrestrial plants with relatively short generation times, combined with high-throughput sequencing, provide valuable insights into the demographic and genetic effects of land-use change. We integrate long-term censuses and genotyping data from epiphyllous bryophyte metapopulations in experimentally fragmented Amazonian forests. We focused on two bryophyte species with contrasting mating systems across 11 populations in small (1- and 10-ha) and large (100-ha and continuous) habitats. We aim to assess how long-term reductions in colony numbers in small fragments affect population genetic diversity and differentiation compared to larger habitats. We also explore how species' mating systems influence migration patterns across forest sites, with bisexual species expected to exhibit a higher likelihood of sexual reproduction and spore output than their unisexual counterparts. Our results reveal contrasting patterns of genetic structure between the two species, with no consistent effects of forest fragmentation detected across the landscape. The bisexual species showed notably lower genetic diversity and slightly higher differentiation in small fragments, suggesting a non-equilibrium metapopulation driven by limited migration. In contrast, the unisexual species exhibited minimal genetic impact from fragmentation, maintaining symmetrical migration among fragments regardless of size, indicative of patchy metapopulation dynamics. This study highlights how contrasting mating systems in epiphyllous bryophytes influence migration patterns and underscores the species-specific responses to habitat fragmentation.

RESUMO

A fragmentação do habitat afeta a dinâmica das metapopulações ao reduzir o tamanho e a conectividade dos patches (áreas discretas ocupadas por populações locais), mas suas consequências genéticas de longo prazo são influenciadas por características específicas das espécies e pelas limitações das técnicas de sequenciamento. Estudos com plantas terrestres de ciclos de vida

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relativamente curtos, combinados com sequenciamento de alto rendimento, fornecem perspectivas valiosas sobre os efeitos demográficos e genéticos das mudanças no uso da terra. Integramos dados de censos de longo prazo e genotipagem de briófitas epífilas em florestas amazônicas fragmentadas experimentalmente. Focamos em duas espécies de briófitas com sistemas reprodutivos contrastantes, analisando onze populações em habitats pequenos (1 e 10 ha) e grandes (100 ha e floresta contínuas). Nosso objetivo foi avaliar como as reduções prolongadas no número de colônias em pequenos fragmentos afetam a diversidade genética populacional e sua diferenciação, em comparação com habitats maiores. Também exploramos como os sistemas reprodutivos das espécies influenciam os padrões de migração entre os fragmentos, considerando que espécies bissexuais tendem a apresentar maior probabilidade de reprodução sexual e produção de esporos do que suas contrapartes unissexuais. Nossos resultados revelaram padrões contrastantes de estrutura genética entre as duas espécies, sem efeitos consistentes da fragmentação florestal em toda a paisagem. As populações da espécie bissexual apresentaram diversidade genética significativamente menor e diferenciação ligeiramente maior em pequenos fragmentos, sugerindo uma metapopulação fora de equilíbrio, devido a migração limitada. Em contraste, as populações da espécie unissexual exibiram impacto genético mínimo da fragmentação, mantendo migração simétrica entre os fragmentos, independentemente do tamanho, o que indica uma dinâmica metapopulacional mais estável. Este estudo destaca como sistemas reprodutivos contrastantes em briófitas epífilas moldam os padrões de migração e reforça as respostas espécie-específicas à fragmentação do habitat.

1 | Introduction

Anthropogenic land-use change is transforming worldwide landscape configuration (Haddad et al. 2015; Taubert et al. 2018; Fischer et al. 2021). The Amazon Forest is changing toward a mosaic of small forest patches, with deforestation increasing at a 0.5% rate per year (Taubert et al. 2018). The Amazon has lost an estimated 17% of its original forest cover in the past half-century, while more than 50% of the remaining forests are degraded (Lovejoy and Nobre 2018; Matricardi et al. 2020; Lapola et al. 2023; Albert et al. 2023). These rapid changes disrupt gene flow between populations and impair species' ability to adapt to spatial disturbances (Aguilar et al. 2008; Vranckx et al. 2012; Daskalova et al. 2020). The compounding effects of forest fragmentation, leading to ecosystem decay, may drive metapopulations into non-equilibrium states and increase species extinction risk (Thrall et al. 2000; Wang and Altermatt 2019; Chase et al. 2020; Carley et al. 2022).

Habitat (patch) size and connectivity are fundamental factors shaping the ecological and evolutionary dynamics of metapopulations, influencing their persistence and genetic structure (Thrall et al. 2000; Wang and Altermatt 2019). Small, isolated patches exhibit reduced migration and higher genetic differentiation due to increased extinction rates, compared to large and connected patches (Figure 1A–D; Hanski and Gaggiotti 2004; Whittaker et al. 2008). Moreover, in isolated patches, migration appears area-dependent, altering source-sink metapopulation dynamics (Wang and Altermatt 2019) with small patches contributing fewer migrants and restricting gene flow to other populations (Aycrigg and Garton 2014; Hanski and Gaggiotti 2004; Hanski 2012; Hanski et al. 2017). Therefore, understanding the effects of patch size on effective propagule dispersal and gene flow is essential for the conservation of metapopulation genetics (Auffret et al. 2017; Hanski et al. 2017; Vellend et al. 2017; Gargiulo et al. 2025).

Predicting the relationship between demographic dynamics and the standing genetic diversity of metapopulations remains a complex challenge (Figure 1; Vellend and Geber 2005; Aycrigg and Garton 2014; Vranckx et al. 2012; Carvalho et al. 2019;

Gargiulo et al. 2025). Typically, genetic diversity declines with decreasing patch size and connectivity, as observed in oceanic islands (Figure 1C: island-mainland metapopulation; Whittaker et al. 2017; Costanzi and Steifetten 2019); however, exceptions exist (see Laenen et al. 2011). In patchy metapopulations, genetic diversity can be maintained regardless of patch size due to ongoing gene flow (Figure 1D; Aycrigg and Garton 2014). Conservation genetic theory suggests that diversity patterns within a metapopulation are shaped by migration and extinction rates among patches (Lowe et al. 2005; Aguilar et al. 2008; Vellend et al. 2014; Vellend and Geber 2005), with these effects varying according to the number of generations since isolation (Young et al. 1996; Aguilar et al. 2008; Mona et al. 2014; Gargiulo et al. 2025).

Human-induced habitat loss, though recent on an evolutionary timescale, poses unique challenges. Long-lived species often experience delayed genetic consequences, such as extinction debts, characterized by allele loss due to increased extinction rates and limited migration (Hamilton 1999; Aldrich et al. 1998; Vranckx et al. 2012; Figueiredo et al. 2019; Gargiulo et al. 2025). Addressing these confounding effects requires incorporating multiple genetic markers and spanning multiple generations under conditions of reduced habitat size and connectivity (Carvalho et al. 2019; Gargiulo et al. 2025).

Bryophytes offer a unique system to study the genetic consequences of habitat fragmentation. Their rapid generation times allow tracking metapopulation dynamics within decades of habitat fragmentation (Pharo and Zartman 2007; Spagnuolo et al. 2007; Zartman et al. 2006; Sierra, Toledo, Nascimento, et al. 2019). Additionally, their diverse mating systems and capacity for asexual reproduction provide opportunities to predict gene flow patterns based on trait variability (Snäll et al. 2004; Wang et al. 2012; Obbard et al. 2006; Patiño et al. 2013). For instance, monoicous bryophytes, which have both male and female reproductive organs on the same gametophyte, are more likely to reproduce sexually, enhancing their spore dispersal potential. In contrast, dioicous species, where male and female organs occur on separate gametophytes, require spatial proximity for

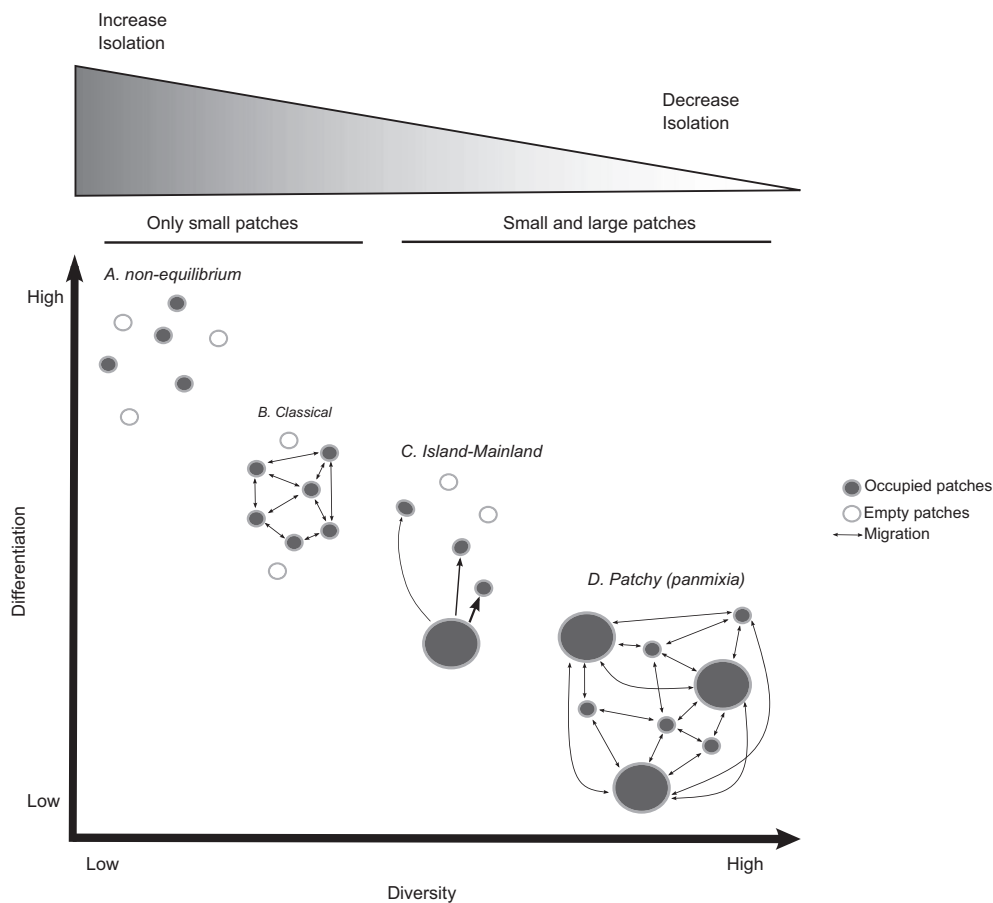


FIGURE 1 | Expected population genetic outcomes under different metapopulation structure models with variable degrees of isolation (connectivity) and patch size. (A) In the non-equilibrium metapopulation, patches of equal size are highly isolated, because there is no exchange of migrants between populations. (B) In the classical metapopulation model, patches of equal size present a high probability of extinction but have enough connectivity to allow (re)colonization of unoccupied patches allowing metapopulation persistence. (C) The mainland-island metapopulation presents small and large patches, where unidirectional migration to small patches is dependent on the mainland population where the extinction rate is low (Island-Mainland). Distances from the mainland will determine the rate of migration represented by the arrow size. (D) In patchy metapopulation, patches of variable size are highly connected (patchy) with a high rate of migration among all populations. In the metapopulation models following a patch size and connectivity continuum, a high degree of genetic differentiation will be observed in highly isolated small patches, and highly connected patches of varying size, the genetic differentiation will be lower (figure adapted from Aycrigg and Garton 2014).

sexual reproduction, potentially limiting spore output (Laenen et al. 2016).

The metapopulation dynamics of epiphyllous bryophytes (epiphylls) are closely tied to the lifespan of their host leaves, which typically last between 6 and 12 months (Zartman et al. 2015). New colonies of epiphylls arise from the dispersal of microscopic spores or asexual propagules (Zartman et al. 2012; Sierra, Toledo, Salazar Allen, and Zartman 2019; Mežaka et al. 2020). As water-dependent organisms, epiphylls require moisture for establishment and reproduction, making them highly sensitive to microenvironmental changes (Zartman et al. 2015). Their sensitivity makes them valuable indicators of biodiversity loss linked to habitat fragmentation and climate change (Alvarenga et al. 2009; Sierra, Toledo, Nascimento, et al. 2019; Zartman et al. 2015). Epiphylls have persisted at low abundances for over four decades in small forest fragments (< 10 ha) within the Amazon Basin, as observed through long-term monitoring at the Biological Dynamics of Forest Fragmentation Project (BDFFP) (Sierra, Toledo, Nascimento, et al. 2019). Despite reduced

colonization rates over 20 years (Zartman and Shaw 2006), studies using amplified fragment length polymorphisms revealed evidence of linkage disequilibrium between loci but no signs of genetic drift (Zartman et al. 2006). However, a broader assessment of Amazonian bryophyte species using high-throughput genomic sequencing indicated significant geographic isolation across regional spatial scales, suggesting limited gene flow (Ledent et al. 2020).

In this study, we integrate demographic and genetic data to investigate the impacts of forest fragmentation on metapopulation dynamics over multiple generations. We sampled 11 populations of two epiphyllous bryophyte species across a 10,000-km² experimentally fragmented Amazonian landscape in the BDFFP. Our study addresses the following questions: (1) Are demographic changes (observed reduced number of colonies) reflected in population genetic drift in small and isolated patches? Additionally, (2) does a species' mating system confer differences in migration rates between forest fragments? Considering these questions, we hypothesized: (H1) that populations in smaller fragments with

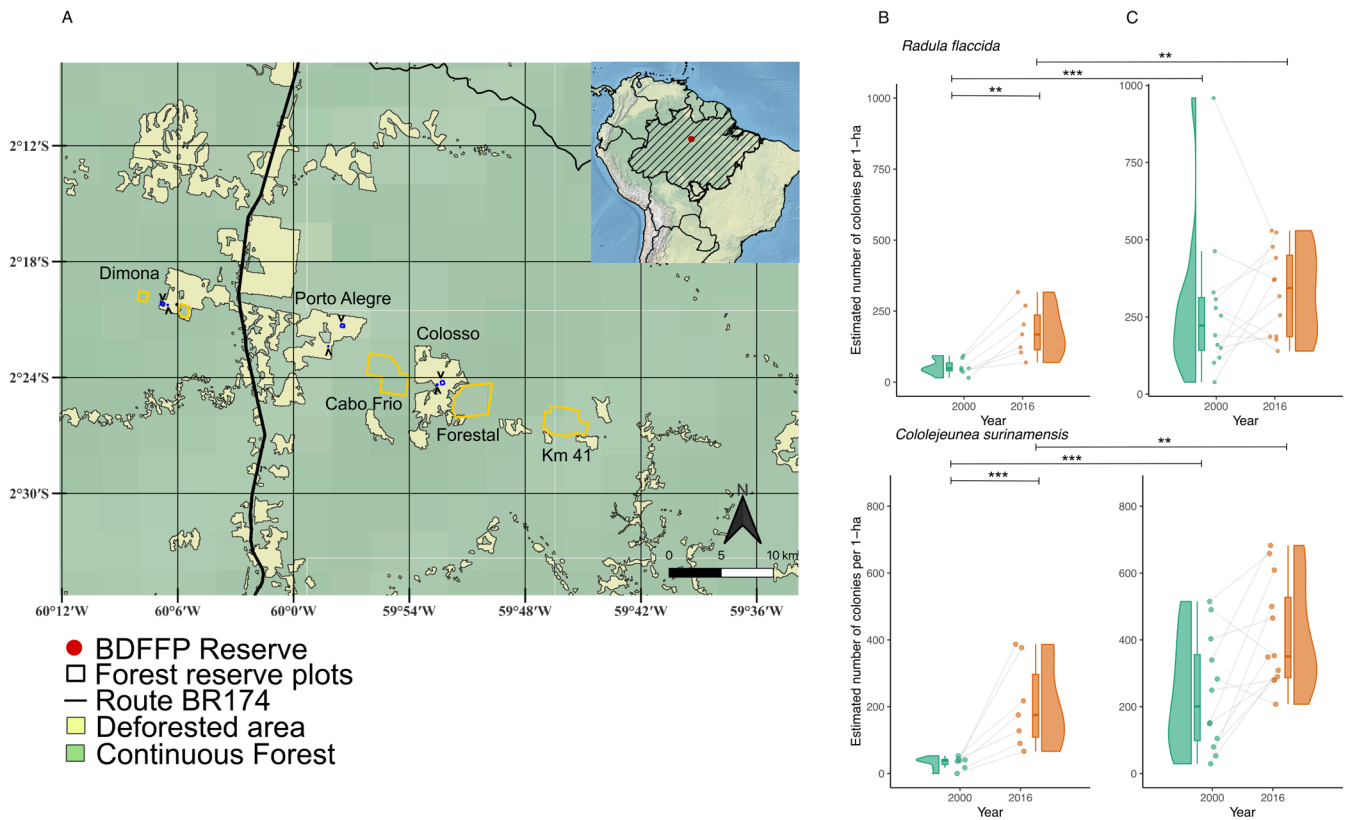


FIGURE 2 | (A) Study site: The Biological Dynamics of Forest Fragmentation Project (BDFFP) along the highway BR-174 ~80 km north of Manaus, Amazonas (Brazil). Forest fragments of 1- and 10-ha (blue polygons), and 100-ha (yellow polygons) replicates inside three reserves (Dimona, Porto Alegre, and Colosso), separated by deforested areas from mature continuous forests. Study plots inside continuous forest sampled for this study are highlighted as yellow polygons. (B, C) Population size as the estimated number of colonies for the species *Radula flaccida* and *Cololejeunea surinamensis* per 1-ha study plot in (B) small forest patches (1- and 10-ha), and (C) in large forest patches (100-ha and continuous forest). Cloud plot showed the temporal variation (connecting line) in the number of colonies between the years 2000 and 2016 for each 1-ha study plot. Significant differences are given for p -value $** = <0.01$ and $*** = <0.001$.

a reduced number of colonies show signs of genetic drift over 40 years, with observable lower values of genetic diversity and higher differentiation compared to continuous forests. Secondly (H2), habitat fragmentation affects the species' genetic profile in relation to the species' mating systems. Bisexual species may have a higher probability of sexual reproduction and spore output and may exhibit higher migration rates across patches, regardless of size and degree of isolation (Figure 1D: patchy metapopulation). In contrast, unisexual species, with a lower probability of sexual reproduction and spore output, are expected to show restricted migration from the continuous forest to nearby small forest fragments (Figure 1C: island-mainland metapopulation).

2 | Methods

2.1 | Study Area and Population Sampling

The BDFFP is located in central Amazonia (2°30'S, 60°02'W) along the BR-174 highway, ~80 km north of Manaus, Brazil. The BDFFP consists of *terra firme* (non-flooded), lowland rainforest of nutrient-poor soils, with elevations ranging between 50 and 150 masl (Laurance et al. 2018). The annual rainfall in nearby climatic stations at the ZF2 and Reserva Ducke ranges between 1900 and 2550 mm (Ferreira et al. 2005; Aleixo et al. 2019). The

rainy season extends mainly from November to June, with a period of reduced rainfall from July to October. In the BDFFP, forest fragment patches were experimentally delimited and isolated in 1980 among three adjacent cattle ranch reserves (i.e., Dimona, Porto Alegre, and Colosso in the Esteio farm). Forest fragment patches vary in size, with replicates of 1-, 10-, and 100-ha, separated by 70–1000 m from continuous forest (Figure 2A). The matrix in the BDFFP landscape was composed of cattle pasture from 1980 to 1995. As pasture creation slowed down and ceased in the 1990s, *Vismia* spp. and *Cecropia* spp. dominated secondary forests that have overtaken the matrix by the year 2015 (Laurance et al. 2018). For this study, we selected seven forest fragment patches of 1-, 10-, and 100-ha in three reserves, and sampled four surrounding continuous forests for a total of 11 sites (hereafter referred to as the assigned populations) (Table S1; Figure 2A).

We selected two regionally and locally abundant epiphyllous leafy liverworts, *Radula flaccida* Lindenb. & Gott. (Radulaceae) and *Cololejeunea surinamensis* Tixier (Lejeuneaceae), predominantly inhabiting leaves of young trees, shrubs, and understory palms (Figure S1A,E). These species have a comparatively higher frequency relative to the other epiphyllous species known from BDFFP and showed a negative effect of fragmentation on their local abundances, a characteristic that they share with a

vast majority of the other epiphylls (Sierra, Toledo, Nascimento, et al. 2019). The species are typically found producing sexual reproductive structures (male: androecia or/and female: gynoecia, Figure S1B,C,F,G) and specialized asexual propagules (gemmae, Figure S1D). *Radula flaccida* has a unisexual mating system, with male and female organs in separate individuals. In contrast, *C. surinamensis* is a bisexual species, with both male and female organs in the same individual (Figure S1), allowing us to compare species dispersal potential within the premises of the long-term effects of reduced patch size and connectivity.

2.2 | Estimates of Epiphyllous Colonies

We used spatial and temporal occupancy data as a baseline of species demographic changes across the BDFFP landscape censused in the years 2000 and 2016 (Sierra, Toledo, Nascimento, et al. 2019). In this study, we considered a host plant as a suitable host for epiphyllous bryophytes, hereafter epiphyllous colony. We estimated the number of colonies as the proportion of occupied host plants with the focal species to the total number of host plants with any epiphyllous bryophyte species in the BDFFP long-term 1-ha study plot. This approach led us to accurately study the temporal changes in the estimated number of colonies between fragmented and continuous forests, avoiding spatial and sampling size bias. For 10-, 100-ha, and continuous forests, we sampled three separate 1-ha study plots and calculated the mean estimated number of colonies and the standard error. These multiple 1-ha study plots per site correspond to plots on the opposite edges of the forest fragments and one in the center of the forest fragments, or three separate plots in continuous forests (Sierra, Toledo, Nascimento, et al. 2019). We estimated the number of colonies within the 11 assigned populations (Table S1; Figure 2A). Our sampling includes six small forest fragments: 1-ha ($n=3$) and 10-ha ($n=3$), one 100-ha fragment, and four continuous forests. Using the non-parametric Wilcoxon rank sum exact test, we tested for statistical differences in the estimated number of colonies between two habitat size classes: populations in small (1- and 10-ha) and large (100-ha fragments and continuous forests) in the years 2000 and 2016.

2.3 | Genetic Sampling

We sampled a total of 142 colonies of *R. flaccida* and 135 of *C. surinamensis* across the 11 assigned populations between April and May 2017 at regularly spaced intervals of < 10m (Table S1). In the laboratory, using a dissecting scope, we carefully separated 0.5–1g of the bryophyte gametophyte from the leaf surface, avoiding contamination from host plant tissue or other epiphyllous organisms. Bryophyte specimens were dried using silica gel. The number of specimens sampled varied from 8 to 15 in each forest site. Detailed information is presented in Table S2.

2.4 | DNA Extraction and Genotyping

We flash-froze the samples in liquid nitrogen before pulverizing them for genomic DNA extraction using the E.Z.N.A. Plant DNA DS Mini kit (Omega Bio-tek Inc., Norcross, GA, USA). A double digest genotyping by sequencing (GBS) library with the enzymes

PstI/MspI (Abed et al. 2019) was prepared and sequenced on the Ion Proton instrument by the Plateforme d'analyses génomiques (Institut de Biologie Intégrative et des Systèmes, Université Laval, Québec City, QC, Canada). We identified each sample using unique forward and reverse 13–15 base-pair barcodes at the 5' and 3' ends when multiplexing.

2.5 | Bioinformatic Pipeline for Sequences Assembly

We trimmed raw sequence reads to 130 base pairs, representing the best quality length distribution observed in FastQC v0.11.3 using the default phred33 parameter (Andrews 2010). We demultiplexed the libraries and cluster loci with a minimal percentage of identity of 85% within and among individuals with the Stacks v2.4 pipeline (Rochette et al. 2019). Subsequently, we searched for the optimal value for the maximum distances between stacks ($-M$), coverage depth ($-m$), and the number of mismatches ($-n$) for assembling loci (Supporting Information: Methods), following Rochette and Catchen (2017) and Paris et al. (2017). We assembled the sequenced reads by species separately with the optimal parameters as described in Supporting Information: Methods with the *de novo* Stacks v.2.4 pipeline (Rochette et al. 2019).

The program *populations* of the software Stacks v.2.4 (Catchen et al. 2013; Rochette and Catchen 2017) was used to produce an unfiltered dataset of the GBS assembled loci considering each specimen as a single population. Requiring a minor allele frequency was set to > 0.05, and maximum observed heterozygosity was set for haploid organisms with a value of 0. We explored the impact of the number of missing loci in the sample sequences by excluding the samples with a high percentage of missing data (> 90%–98%). Afterward, we produced two filtered genomic datasets, differing in the percentage of missing data and the number of specimens (Table S2). We conducted a comparison to assess if the differences in missing data or the sample size in our two datasets biased downstream analyses of genetic summary statistics, clustering, and spatial analyses (Hodel et al. 2017; Yi and Latch 2022). In summary, both datasets yielded consistent patterns; for the sake of conciseness, we exclusively present the results from the dataset with filtered loci in > 15% of the individuals, prioritizing a higher number of genotyped individuals (Supporting Information: Methods).

2.6 | Population Genetic Diversity

We calculated the following genetic diversity metrics for the 11 populations: variant sites, polymorphic sites, private alleles, and nucleotide diversity (π_T) with program *populations* (Catchen et al. 2013). Overall summary statistics per locus and gene diversity (h) and allelic richness estimates (A_r) by rarefying allelic counts per population were calculated with the R-package *hierfst* (Goudet and Jombart 2022). Genotype diversity (MLG) and richness indexes, including Shannon-Weiner Diversity index (H), Stoddard and Taylor's Index (G), and Simpson's index (λ), were calculated using the *poppr* R-package (Kamvar et al. 2014, 2015). We fitted linear regressions with the *stats* R-package (R Core Team 2022) to explore the relationship between population

genetic diversity metrics and habitat size, small fragments (1- and 10-ha) and large (100-ha and continuous forests).

2.7 | Population Structure Analyses Using Individual-Based Clustering

For subsequent analyses, we imputed missing genotypes within populations based on the mean allele frequency of the known genotype observed as a reference. Imputing missing genotypes helps to prevent inflation in Type I error rates and ordination bias (Yi and Latch 2022). We inferred the genetic relatedness of the individuals within study plots in small (1- and 10-ha) and large (100-ha and continuous forests) using a multivariate statistical approach. We used the discriminant analysis of principal components (DAPCs) to partition the genetic variance into between-group and within-group components, to maximize discrimination between groups without making assumptions of panmixia (Jombart et al. 2010). This approach is more convenient for populations assumed to be partially clonal and genetically related due to relatively recent isolation events. DAPC integrates principal component analysis (PCA) identified through discriminant analysis (DA) to infer the optimal number of clusters in the metapopulation. We performed a stratified cross-validation of DAPC to select the optimal number of principal components (PCs) to retain, considering most sources of variation. Following cross-validation, we performed a DAPC assigning samples to their populations corresponding to their geographical site and habitat size as cluster population priors ($n = 11$), with the optimal number of PCs axes and using the five first axes retained in the DA. Following the same workflow, we ran a DAPC now grouping the 11 forest patches into four size categories (1-, 10-, 100-ha, and continuous forests).

To assess whether populations in small and large habitats exhibit significant genetic differentiation within and between populations, we computed a pairwise genetic differentiation index for each population pair (F_{ST} ; Weir and Cockerham 1984), using the *hierfst* R-package (Goudet and Jombart 2022). Furthermore, we applied the hierarchical analysis of molecular variance (AMOVA) with 999 permutations to the F_{ST} calculations. We evaluated differences in the total genetic variation observed between assigned populations in two class sizes, small vs. large, and within small fragments or large 100-ha fragments and continuous forests separately. All calculations were performed using *hierfst* (Goudet and Jombart 2022) and *poppr* (Kamvar et al. 2014) R-packages.

2.8 | Spatial Autocorrelation Analyses

We conducted spatial autocorrelation analyses to explore the relationship between genetic distances ($F_{ST}/1 - F_{ST}$; Rousset 1997) and their geographical distance [$\log(\text{Euclidean distance})$] of the 11 populations, using the *dartR* R-package (Gruber et al. 2018). To address potential limitations of statistical power at the population level, we also conducted isolation-by-distance analyses at the individual level (j) by calculating individual kinship coefficients as genetic distance $[(1 + F_j)/2]$. Subsequently, we assessed spatial genetic differences attributed to isolation by distance (IBD) using a Mantel test and Pearson's product-moment

correlation (Mantel 1967) with 999 random permutations, using the *vegan* R-package (Oksanen et al. 2016). We examined for significant IBD for all population pairs, and within pairs of populations in small and large classes, allowing for a thorough understanding of the spatial patterns of genetic differentiation across the landscape.

2.9 | Migration Network Analyses

We used network analyses to estimate the relative migration levels (G_{ST} and Nm parameters) based on neutral SNPs (Sundqvist et al. 2016), implemented in the *diveRsity* R-package (Keenan et al. 2013). This approach allowed us to quantify the proportion and direction of recent migration, which is essential for understanding metapopulation dynamics where deterministic extinction and density-dependent processes govern source-sink dynamics (Sundqvist et al. 2016). We determined significant migration events based on 1000 bootstrap interactions, with a filter threshold of 0.35. We observed similar results with the G_{ST} and estimated the effective number of migrants (Nm) parameters. Therefore, we summarized the direction and magnitude of recent migration with Nm using network graphics with the *qgraph* R-package (Epskamp et al. 2012). Analyses were done with the software (R Core Team 2022).

3 | Results

3.1 | Epiphyllous Colonies in Forest Patches

We observed changes in the estimated number of colonies censused for *R. flaccida* and *C. surinamensis* within the study plots between 15 years censused (from 2000 to 2016) (Figure 1B,C; Table 1). Specifically, the mean number of *R. flaccida* colonies in small fragments showed an increase from 53.03 (± 10.3) to 176.89 (± 33.9) colonies; like *C. surinamensis* from 33.04 (± 6.8) to 198.27 (± 40.2). In both years censused, the estimated number of colonies in small patches was lower when compared to larger habitats (Figure S2, Table 1). A lower number of colonies was observed in 10-ha compared to 100-ha fragments and continuous forests in 2000. However, by 2016, small patches reached a similar number of colonies compared to large habitats (Figure S2, Table 1).

3.2 | Genetic Diversity and Patch Size Relationship

Divergent patterns in some of the genetic diversity metrics estimates were observed between the two species concerning patch size (Figures S6 and S7; Tables S3 and S4). *Radula flaccida* in small habitats exhibited a similar proportion of variant sites, polymorphic sites, allelic richness, private alleles, and nucleotide diversity compared to those in large habitats (Figure S6; Table S5). In contrast, *C. surinamensis* tends to show lower genetic diversity in small habitats compared to populations in large habitats (Figure S6; Table S5). This difference was more pronounced and statistically significant for polymorphic sites ($R^2 = 0.47$, $p\text{-value} \leq 0.05$) and nucleotide diversity ($R^2 = 0.45$, $p\text{-value} = 0.01$) (Table S5). The observed genotype diversity (MLG), the Shannon-Weiner diversity index (H), Stoddard and Taylor's

TABLE 1 | Summary statistics results of the Wilcoxon rank sum exact test of differences in the estimated number of colonies between categories considering 1- and 10-ha forest fragments as small patches, and 100-ha and continuous forests as large patches; and compared between the 2 years sampled (2000 and 2016). Significant differences with p -value < 0.01 and < 0.001 are highlighted in bold.

Categories	W	p
<i>Radula flaccida</i>		
Small vs. large in the year 2000	86	0.0005
10-ha vs. large in the year 2000	49	0.0059
Small vs. large in the year 2016	112	0.0067
10-ha vs. large in the year 2016	53	0.1974
1- and 10-ha (small) between 2000 vs. 2016	2	0.0023
100-ha and continuous forest (large) between 2000 vs. 2016	47	0.16
<i>Cololejeunea surinamensis</i>		
Small vs. large in the year 2000	85	0.0007
10-ha vs. large in the year 2000	47	0.0151
Small vs. large in the year 2016	113	0.0054
10-ha vs. large in the year 2016	53	0.1974
1- and 10-ha (small) between 2000 vs. 2016	0	0.0005
100-ha and continuous forest (large) between 2000 vs. 2016	33	0.0242

index (G), and Simpson's index (λ) suggested that *R. flaccida* and *C. surinamensis* populations in small and large habitats have similar genetic diversity (Figure S7, Table S5).

3.3 | Individual-Based Clustering and Pairwise Differentiation

The DAPC based on posterior genotype probabilities revealed one overlapping cluster with all populations from different size classes (Figure S5) but with certain individual genotypes diverging from this cluster. In the DAPCs with populations prior assigned to fragment sizes: 1-, 10-, 100-ha, and continuous forests, we observed that genotypes of *R. flaccida* in 1-ha fragments tended to diverge from the main cluster along Axis 1, which explained over 60% of the genetic variation (Figure 3A). Similarly, genotypes of *C. surinamensis* in the 100-ha fragment diverged along Axis 1 from the clusters of 1-ha, 10-ha, and continuous forest. The clusters with genotypes from the 1-, 10-ha, and continuous forests diverged along Axis 2, which explained 25.9% of the variation (Figure 3B).

Mean pairwise F_{ST} comparison, and F_{ST} comparison over loci are provided in Tables S6 and S7. Global differentiation across populations was low; *R. flaccida* ($F_{ST} = 0.06$) and *C. surinamensis* ($F_{ST} = 0.19$). The mean pairwise F_{ST} values for *R. flaccida* populations indicated no substantial differentiation among

small fragments ($F_{ST} = 0.06$), between small and large size classes ($F_{ST} = 0.07$), or within large 100-ha and continuous forests ($F_{ST} = 0.07$) (Figure 4C). In contrast, *C. surinamensis* populations showed slightly higher mean F_{ST} values for pairwise comparisons among small fragments ($F_{ST} = 0.14$) and between small and large size classes ($F_{ST} = 0.17$), while low mean values were observed within large 100-ha and continuous forests ($F_{ST} = 0.05$) (Figure 4D).

Using the statistical test of AMOVA, we hierarchically grouped populations by specific fragment sizes 1-, 10-, 100-ha, and continuous forests, and within two size classes (small and large). For both species, most of the observed genetic differentiation was explained by within-population variation. The geographic location of the forest patches across the landscape explained to a minor extent the observed genetic variation (Table 2). Genetic variation between small and large classes was statistically significant for *C. surinamensis* (Table 2), indicating some degree of differentiation of populations in small fragments.

3.4 | Spatial Autocorrelation and Migration Patterns

Spatial autocorrelation results for all population pairs and individuals in small and large habitats are summarized in Table S8. Population pairwise genetic differences were not correlated to geographic distances irrespective of habitat size. Isolation-by-distance analyses at the individual level were consistent with the population-based analyses, showing no significant correlation between genetic and geographic distances for populations in either small or large habitat. However, within pairs of populations of *R. flaccida* in small fragments, we observed a positive slope, indicating a slight genetic differentiation with geographical distance ($R^2 = 0.22$, p -value = 0.02).

The relative migration levels estimated between populations suggest a high migration between *R. flaccida* populations irrespective of habitat size and isolation (Figure 4A; Table S9). However, small fragments mostly exhibited migration toward other forest fragments and continuous forest patches across the landscape, acting as source populations. Small fragments did not receive migrants from continuous forests, except for the Dimona 1-ha fragment, which also showed a higher positive change in the number of colonies between the years 2000 and 2016. Populations in continuous forests showed signs of asymmetrical migration among them, as well as significant symmetrical migration observed between Forestal continuous forests and the Dimona 100-ha fragment.

The migration network of *C. surinamensis* was less complex with fewer populations connected by vertices, suggesting low or no migration across the landscape (Figure 4B). Populations in small fragments showed significant relative migration among them, at a higher rate than between continuous forests. Dimona 1-ha fragments exhibited migration from distant fragments of Porto Alegre 1-ha and Colosso 10-ha, reflected in a higher positive change in the number of colonies. The 1- and 10-ha fragments of Porto Alegre and Colosso with a higher number of colonies in the 2016 census showed significant migration toward other surrounding forest fragments (source

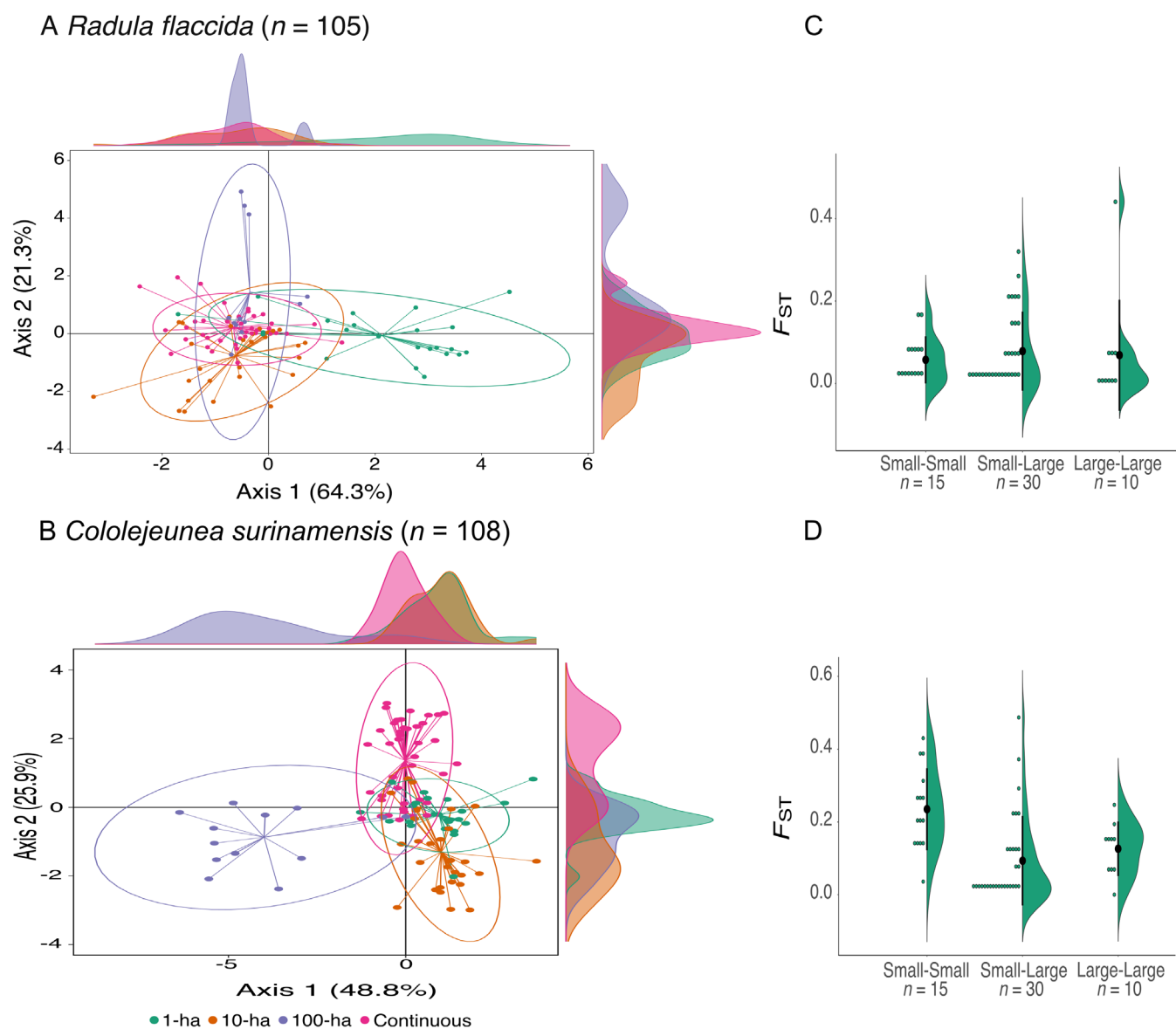


FIGURE 3 | Fine-scale population genetic structure of the species (A) *Radula flaccida* and (B) *Cololejeunea surinamensis* in an experimental Amazonian fragmented landscape. Ordination plot of Discriminant Analysis of Principal Components (DAPC) and density plot depicting the two ordination axis showing the genotype similarity of populations in different forest fragment sizes and continuous forest. Points represent individuals assigned to their respective size category and 95% ellipse showing confidence interval. Population genetic differentiation of the species (C) *Radula flaccida* and (D) *Cololejeunea surinamensis* based on the mean F_{ST} pairwise comparison of populations within small patches, between small and large patches, and within large patches.

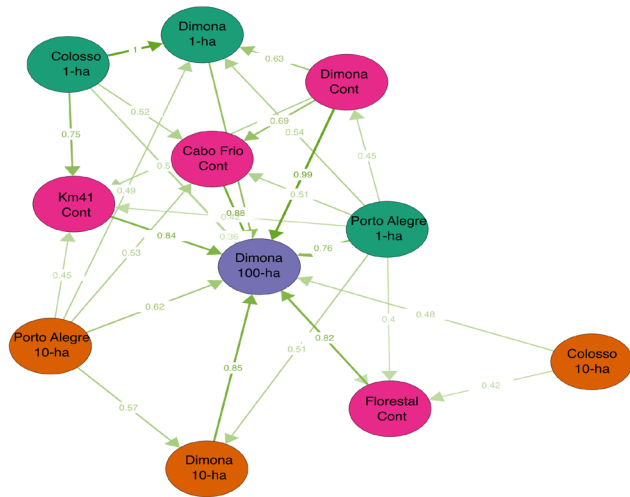
populations). We observed significant migration between continuous forest sites (Forestal, Km 41, and Cabo Frio), but at a relatively low rate. Populations in the Dimona 100-ha fragment and continuous forests seem isolated, with no observed migration (Figure 4B). In the case of the Dimona 100-ha fragment, we observed a decline in the number of colonies from the census data.

4 | Discussion

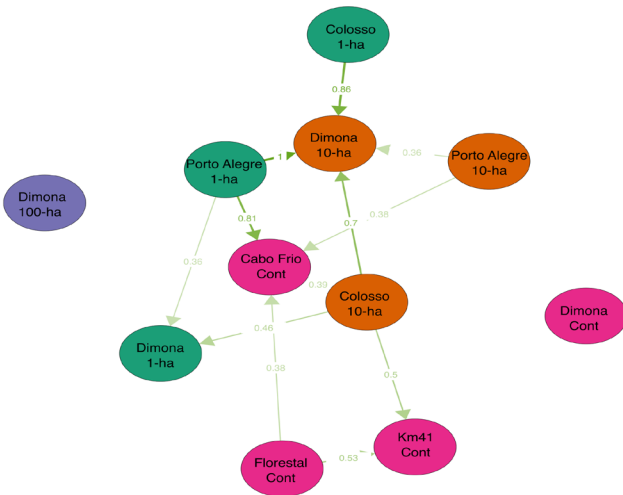
We investigated the effects of habitat fragmentation (e.g., the consequences of reduced size and connectivity) on the demographic and genetic patterns in epiphyllous bryophyte metapopulations. Despite bryophytes being considered highly

vagile organisms (Vanderpoorten et al. 2019), we observed genotype divergence in small patches compared to the surrounding populations in large 100-ha and continuous forests based on ordination analyses and different migration patterns over the long term of experimental reduced size and connectivity (Laurance et al. 2018). However, the limited genetic structure of the population in small patches did not statistically support our hypothesis (H1) of significant genetic drift after decades of reduced habitat size and connectivity. In our study, we observed that *C. surinamensis* (bisexual) experienced genetic diversity loss and limited migration between patches, with predominantly asymmetrical migration between small forest fragments, and with some forest sites completely isolated, non-equilibrium metapopulation. Contrary to our expectations (H2), the lower genetic diversity and migration rates

A *Radula flaccida* ($n = 105$)



B *Cololejeunea surinamensis* ($n = 108$)



● 1-ha ● 10-ha ● 100-ha ● Continuous

FIGURE 4 | Symmetrical relative migration network graph using the Nm parameter among small forest patches (1- and 10-ha), and large forest patches (100-ha and Continuous Forest) for (A) *Radula flaccida* (Dataset $n = 105$, $-R = 15$); and (B) *Cololejeunea surinamensis* (Dataset $n = 108$, $-R = 15$) in an experimental Amazonian fragmented landscape. Filter threshold for the asymmetric values was set to 0.35. Colors correspond to the patch size as in Figure 3.

were more evident in the bisexual species than in the unisexual counterpart. Notably, *R. flaccida* (unisexual) exhibited a patchy metapopulation with a highly interconnected migration network. This observed difference between species with contrasting mating systems should be interpreted cautiously. Genetic diversity meltdown is expected to take a longer time to be apparent than changes in allele frequency in response to habitat fragmentation (Lowe et al. 2005; Gargiulo et al. 2025). The shift in population clustering revealed by DAPC analyses within 1-ha fragments of the unisexual species may indicate early signs of genetic differentiation, consistent with a time-lag effect that emerges across generations following recent habitat fragmentation.

4.1 | Demographic and Genetic Consequences of Forest Fragmentation

The impact of reduced patch size and connectivity in fragmented landscapes is reflected in small local populations and changes in allele frequency in small forest fragments, as observed here for the species *C. surinamensis*. In temperate cryptogams, several studies have observed a lower genetic diversity in a fragmented landscape within approximately 30–50 years following population isolation (Patiño et al. 2010; Wang et al. 2012; Otálora et al. 2011). The forest fragments in the BDFFP were isolated in the year 1980, suggesting that small fragments (1- and 10-ha) over approximately 40 years of isolation have experienced demographic constraint compared to the surrounding continuous forests (Zartman and Shaw 2006). Our migration network analysis demonstrates that even a short distance between forest fragments and from the continuous forest (<1 km) still represents a significant barrier to maintaining connectivity between forest fragments. We did not detect significant population genetic structure in the small and isolated forest fragments, which may indicate that the number of generations since fragmentation occurred has been insufficient for strong genetic divergence to emerge (Mona et al. 2014; Gargiulo et al. 2025). Additionally, occasional dispersal events may be mitigating the genetic impacts of habitat fragmentation. For example, in annual vascular plants, connectivity may be maintained through effective wind-mediated pollen and seed dispersal, despite the population being isolated due to habitat loss (Carvalho et al. 2019).

The premise that dispersal limitation in bryophyte metapopulations (Ledent et al. 2020; Campos et al. 2022) will result in stochastic genotype extinction and reduced gene flow should not be generalized. Under future climate scenarios, the ability of bryophyte species to escape local extinction by tracking suitable habitats is of high concern (Zanatta et al. 2020) despite their high dispersal capacities (Vanderpoorten et al. 2019). While a diverse genetic pool of dispersing individuals may reach a disturbed patch, effective colonization is often limited by local environmental conditions (Hedenäs et al. 2021). In the Amazon Forest, spore traps positioned at 325 m height in the Amazon Tall Tower Observatory captured few bryophyte diaspores, suggesting a low frequency of airborne propagules in the atmosphere (Mota de Oliveira et al. 2022). The scarce airborne diaspore challenges the perception of a homogeneous Amazonian bryoflora of highly dispersive species across a regional scale (de Mota Oliveira and ter Steege 2015) and their capacity to maintain gene flow in a highly fragmented landscape (Patiño et al. 2010; Wang et al. 2012; Otálora et al. 2011). However, species intrinsic traits like the mating system, asexual reproduction, and broad range distribution of the studied epiphyllous liverwort might delay genetic loss from local populations (Gargiulo et al. 2025).

4.2 | Consequences of Mating System and Dispersal Potential

Species with different reproductive strategies might present a differential ability to maintain gene flow in a landscape with reduced patch sizes and connectivity (Honnay et al. 2005; Obbard et al. 2006; Nazareno et al. 2013). Bisexual bryophytes are presumed to exhibit high fertilization rates and consequently

TABLE 2 | Analysis of molecular variance (AMOVA) of epiphyllous bryophyte populations in forest fragments and continuous forest patches. Significant differences with p -value < 0.001 are highlighted in bold.

Source of variation	df	Sum sq	Mean sq	Variance σ	% of the total variance	Std obs	p	ϕ statistics
<i>Radula flaccida</i> , dataset $n = 105$, $R = 15$								
Variation within populations	94	5857.46	62.31	62.31	98.44	-3.654	0.001	0.0156
Variation between populations within patch size	7	501.47	71.64	1.015	1.604	2.922	0.006	0.0160
Variation between patch sizes within a size class	2	139.16	69.58	-0.144	-0.228	-0.346	0.597	-0.0023
Variation between size class	1	74.17	74.17	0.115	0.182	-0.007	0.66	0.0018
Total variation	104	6572.27	63.19	63.29	100			
<i>Cololejeunea surinamensis</i> , dataset $n = 108$, $R = 15$								
Variation within populations	97	5904.08	60.86	60.87	95.16	-6.910	0.001	0.0484
Variation between populations within patch size	7	542.32	77.47	1.761	2.754	4.372	0.001	0.0281
Variation between patch sizes within a size class	2	126.25	63.12	-0.717	-1.1207	-0.844	0.801	-0.0116
Variation between size classes	1	167.71	167.71	2.052	3.208	1.469	0.001	0.0321
Total variation	107	6740.36	62.99	63.96	100			

higher spore production, facilitating successful dispersal and colonization (Laenen et al. 2016). In contrast, unisexual species are thought to have lower dispersal potential, as the probability of fertilization depends on the proximity between male and female plants (Snäll et al. 2004; Maciel-Silva et al. 2012; Zartman et al. 2015; Alvarenga et al. 2016). The connected migration network demonstrates the capacity of *R. flaccida* (unisexual) for effective dispersal, maintaining gene flow across fragmented habitats regardless of patch size. Although colonization rates of *R. flaccida* are relatively low, they appear to be sufficient to mitigate genetic diversity loss, as suggested by Zartman et al. (2006). On the other hand, the maintenance of genetic diversity observed in small fragments may be attributed to several factors. First, genetically diverse populations persist in small patches, albeit in a reduced number of colonies, owing to their adaptive potential to cope with environmental change (Lowe et al. 2005), a notion supported by the observed maintenance of linkage disequilibrium in small forest fragments (Zartman et al. 2006). Second, the standing genetic variation has not yet been lost through stochastic demographic events due to constant local recruitment from asexual propagules (Honnay and Bossuyt 2005; Gargiulo et al. 2025). Unisexual bryophyte species may be relying on asexual reproduction for survival to contribute to maintaining population genetic diversity (Pohjamo et al. 2008; Wang

et al. 2012) and ensuring successful sexual reproduction in dioecious organisms (Alvarenga et al. 2016).

Regarding *C. surinamensis*, we found significantly lower genetic diversity and changes in allele frequency that could be related to limited and restricted dispersal among small patches. The low spore output per capsule (250–900 spores) of the genus *Cololejeunea* (He and Zhu 2011) might explain the species' lower dispersal potential. Even if the sporophyte frequencies of the bisexual and unisexual species are similar, the lower spore output per capsule of *C. surinamensis* would limit the species dispersal, as observed for moss species (Snäll et al. 2004). Environmental conditions in degraded forest fragments might further affect reproductive performance by limiting mating availability and colony threshold sizes for sexual expression and sporophyte frequency (Maciel-Silva et al. 2012; Zartman et al. 2015; Alvarenga et al. 2016). Additionally, once a bryophyte is established on a leaf, interactions with environmental conditions and host plant traits (Berrie and Eze 1975) may drive deterministic local extinction prior to leaf senescence, with potential consequences for local metapopulation dynamics (Zartman et al. 2015). However, the trait-related mechanisms underlying the delayed loss of genetic diversity need further exploration to provide species-specific conservation efforts (Gargiulo et al. 2025).

4.3 | Conservation Implications for Metapopulation Genetics in the Amazon Forest

The Amazon faces threat from forest loss and the degradation of 38% of its remaining area, driven by edge effects, logging, fires, and droughts, which jeopardize biodiversity and ecosystem services (Lovejoy and Nobre 2018; Curtis et al. 2018; Chase et al. 2020; Lapola et al. 2023). Even if zero-deforestation policies are achieved by 2030, the fragmented landscape of isolated patches will remain for decades (Fischer et al. 2021), necessitating conservation strategies that prioritize habitat quality, patch size, and connectivity to preserve biodiversity at all levels, including genetic diversity (Fahrig 2019; Fahrig et al. 2022; Watling et al. 2020).

The spatial genetic structure observed in Amazonian plant species (Nazareno et al. 2019; Ledent et al. 2020; Campos et al. 2022), coupled with nonrandom deforestation patterns (Taubert et al. 2018; Matricardi et al. 2020), threatens the persistence of crucial source populations essential for maintaining genetic diversity (Lowe et al. 2005). As ecological barriers proliferate, these disruptions may intensify genetic drift and reduce gene flow, further exacerbating the loss of biodiversity (Taubert et al. 2018; Fischer et al. 2021). However, studies addressing the demographic and evolutionary consequences of fragmentation on long-lived species remain limited due to the constraints of their extended lifespans (Hamilton 1999; Aldrich et al. 1998). In contrast, species with shorter generation times, such as the understory *Heliconia* (Côrtes et al. 2013), endemic savanna herbs (Carvalho et al. 2019), and patch-tracking epiphyllous bryophytes (Zartman et al. 2006), allow for the observation of multiple generations within fragmented landscapes. These species often show resilience by maintaining source-sink dynamics and avoiding significant genetic decay over decades, even in small patches.

Maintaining connectivity between patches is particularly vital for species with asymmetric migration patterns, which enable the rescue of genotypes in small fragments (Hufbauer et al. 2015; Hanski 2015; Auffret et al. 2017; Carley et al. 2022). As observed for the two species studied, small patches remain critical for conservation efforts, acting as sources of migrants for recolonizing unoccupied areas, as seen in this study and on Macaronesian oceanic islands (Laenen et al. 2011; Patiño et al. 2015).

Epiphyllous bryophytes, with their short generation times, offer unique opportunities to investigate long-term metapopulation genetic dynamics in fragmented landscapes. The contrasting genetic responses observed in species with different mating systems underscore the complexity of habitat fragmentation effects, highlighting the need for tailored conservation strategies. Future research utilizing whole genome sequencing will enhance our ability to detect fine-scale specific evolutionary processes and inform conservation strategies to secure biodiversity in the Amazon and other globally threatened ecosystems.

Finally, the genomic dataset generated in this study, although valuable, was limited by a relatively low number of SNPs and a high proportion of missing data (~75%–80%). These constraints likely reflect the challenges of applying genotyping-by-sequencing to small non-model bryophytes, including low DNA

quantity and the need for stringent filtering parameters in de novo assembly without a reference genome (Ledent et al. 2020). Although our approach of assessing the data with different proportions of missing values and sample sizes did not reveal potential biases in genetic diversity metrics or ordination, it is true that a high proportion of missing data can inflate estimated F_{ST} values (Hodel et al. 2017). While imputing missing data using the known dominant allele may reduce type I error rates and ordination bias (Yi and Latch 2022), it can also obscure subtle population genetic structure derived from allele frequency metrics due to limited statistical power. Consequently, our findings on genetic differentiation and migration should be interpreted with caution.

Author Contributions

A.M.S., C.E.Z., and J.C.V.A. conceived and designed the study. A.M.S. and C.E.Z. sampled and carried out fieldwork. A.M.S. and J.C.V.A. prepared the specimens and carried out the DNA extraction. A.M.S., M.A.-G., and J.C.V.A. generated and analyzed the genomic data. A.M.S. carried out the statistical analyses. A.M.S. wrote the manuscript with the assistance of all co-authors.

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Disclosure

Benefit-sharing statement: The present work is the result of an international scientific partnership that was developed with scientists from the countries providing data and genetic samples, included as co-authors. The work was done under partnership between research institutions and results will be shared with the provider communities and the broader scientific community.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Genetic data: Raw sequence data were deposited in the NCBI Sequence Read Archive (SRA) with their respective accession numbers under the project [PRJNA980239](https://www.ncbi.nlm.nih.gov/submit/PRJNA980239): Epiphyllous bryophyte genetic structure in fragmented forest. The metadata, individual genotype data, and the scripts used for the analyses that support the findings of this study are openly available at: <https://github.com/adrielsierra/Epiphyllous-bryophyte-demography-and-genetics>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Focal species *Radula flaccida* and *Cololejeunea surinamensis* habit and reproductive strategies. *Radula flaccida*: (A) Macroview of the gametophyte radial growth. (B) Female individual with perianth and mature sporophyte. (C) Microscopic view of the male gametophyte with antheridial branches. (D) Microscopic view of a fully developed cordiform gemmae (Asexual reproduction). *Cololejeunea surinamensis*: (E) Macroview of the gametophyte radial growth. (F) Microscopic view of the sexually reproducing individual bearing both female (perianth) and male structures (short antheridial branches). (G) Detailed view of the female reproductive structure with fertilized archegonia. **Figure S2:** Number of colony distribution

comparison between small and large forest patches for the years 2000 and 2016 for (A) *Radula flaccida* and (B) *Cololejeunea surinamensis*. The mean population size is depicted as follows: orange solid line for 1-ha, orange dashed line for 10-ha, green solid line for 100-ha, and green dashed line for continuous forests. **Figure S3:** Allelic richness rarefaction accumulation curves by the number of genotyped individuals in small forest fragments (1- and 10-ha) and large forest fragments (100-ha) and continuous forests. Curves are given for the two datasets generated for the species *Radula flaccida* and *Cololejeunea surinamensis*, which varied in the number of genotyped individuals and the percentage of missing data. Gray shade corresponds to a 95% confidence interval. **Figure S4:** Multilocus genotype (MLG) accumulation curves by the number of loci randomly sampled. Curves are given for the two datasets generated for the species *Radula flaccida* and *Cololejeunea surinamensis*, which varied in the number of genotyped individuals and percentage of missing data. The red-dashed line indicated the point of the minimum number of loci necessary to discriminate between individuals in a population. **Figure S5:** Fine-scale population genetic structure of the species *Radula flaccida* and *Cololejeunea surinamensis* in Amazon Forest fragments and continuous forest. Ordinations correspond for the two filtered datasets resulting from the minimum percentage of individuals across populations required to process a locus. Ordination plot of discriminant analysis of principal components (DAPC) showing the genotype similarity of populations in different forest fragment sizes and continuous forests. Points represent individuals assigned to their a priori collection locality in forest fragments and continuous forests of different reserves. 95% ellipse showing confidence interval. **Figure S6:** Linear regression of the relationship of population genetic summary statistic and patch class size in small fragments (1- and 10-ha), large fragments (100-ha), and continuous forest for the two epiphyllous species. (A, B) Plots correspond to the two filtered datasets resulting from the minimum percentage of individuals across populations required to process a locus. Gray shade corresponds to a 95% confidence interval. **Figure S7:** Linear regression of the relationship of Table S5. Population genetic indices of heterozygosity, evenness, and linkage. Genetic indices in the y-axis entail for MLG = Multilocus genotypes found, H = Shannon–Weiner diversity index, G = Stoddard and Taylor's index, lambda = Simpson's index for patch class size in small fragments (1- and 10-ha), large fragments (100-ha), and continuous forest for the two epiphyllous species. (A, B) Plots correspond to the two filtered datasets resulting from the minimum percentage of individuals across populations required to process a locus. Gray shade corresponds to a 95% confidence interval. **Table S1:** Sampling design information of epiphyllous bryophyte populations in fragmented forest with their specific geographic information. Small patches include 1- and 10-ha forest fragments, and large patches include a 100-ha forest fragment and continuous forests. The mean estimated number of colonies is given for the two species for the census of 2000 and 2016. Standard error (SE) is given for populations where data of three separate plots were available. NA values correspond to plots that were not sampled in the year 2000. Number of samples for DNA extraction by the study area for both species is given. **Table S2:** General information of the sequence data generated using genotyping-by-sequencing approach. A total of 213 samples (*Radula flaccida* ($n = 105$) and *Cololejeunea surinamensis* ($n = 108$)) are included. For each sample, we provide a detailed information of the collection locality and sequenced read number from the raw files to the number retained after process readtags and after generating the two filtered datasets by the minimum percentage of individuals across populations required to process a locus. **Table S3:** Population genetic summary statistic using the two filtered datasets by the minimum percentage of individuals across populations required to process a locus. **Table S4:** Population genetic indices of heterozygosity, evenness, and linkage for the two filtered datasets by the minimum percentage of individuals across populations required to process a locus. For each population, columns entail for N = number of individuals, MLG = Multilocus genotypes found, eMLG = expected number of MLG, H = Shannon–Weiner diversity index, G = Stoddard and Taylor's index, lambda = Simpson's index. **Table S5:** Linear regression summary statistics of population genetic diversity parameters and patch class size in small fragments (1- and 10-ha) and large fragments (100-ha) and continuous forest for

the two epiphyllous species. Significant relations with p -value ≤ 0.05 are highlighted in bold. **Table S6:** Pairwise F_{ST} comparisons of populations in forest fragments and continuous forest for the two species. F_{ST} calculations are presented for the two filtered datasets by the minimum percentage of individuals across populations required to process a locus. **Table S7:** Pairwise F_{ST} comparison bootstrap over loci of populations in forest fragments and continuous forest for the two species (*Radula flaccida* and *Cololejeunea surinamensis*). F_{ST} calculations are presented for the two filtered datasets by the minimum percentage of individuals across populations required to process a locus. **Table S8:** Mantel test of pairwise genetic distance and geographic distance. The regressions are summarized for pairwise comparisons between populations and individuals in small and large patches in forest fragments and continuous forest for the two species (*Radula flaccida* and *Cololejeunea surinamensis*). **Table S9:** Magnitude of recent asymmetric migration patterns between populations in forest fragments and continuous forest for the two species (*Radula flaccida* and *Cololejeunea surinamensis*) inferred with the function `divMigrate`. Migration inferences with G_{ST} and N_m statistics are presented.