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Informative title: Extensive clonal reproduction drives liana proliferation following forest fragmentation.

Concise title: Liana clonal proliferation in fragmented forests.

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ABSTRACT

- **Background and Aims:** As forest landscapes become increasingly fragmented worldwide, concerns are growing over the cascading effects on biodiversity and ecosystem functioning. While such fragmentation often promotes liana proliferation, the role of clonal reproduction in this process remains poorly understood. In this study, we investigated how a temperate liana, *Wisteria floribunda*, reproduces and expands its distribution through clonal growth in fragmented forests.
- **Methods:** Using DNA analyses in fragmented forests (21.6 ha) and in a continuous forest plot (6 ha) in central Japan, we examined the distribution and structure of genets to evaluate their contribution to the dominance of *W. floribunda*.
- **Key Results:** Our findings revealed that 94% of the apparent individuals (ramets, N = 273 in total) in the fragmented forests, were derived from clonal reproduction, significantly exceeding the 45% observed in the continuous forest. These clonal genets collectively covered 57% of the study area in the fragmented forests, compared to only 7% in the continuous forest. Notably, three large genets in the fragmented forests spanned multiple patches, with the largest covering 9.5 ha across seven patches. These genets were predominantly located in areas historically covered by forests, suggesting that they likely expanded through clonal reproduction before fragmentation. Furthermore, stem density in fragmented forests was approximately three times higher than in the continuous forest.
- **Conclusions:** These results demonstrate that extensive clonal reproduction drives liana proliferation in fragmented forests. This study underscores the importance of considering clonal strategies when assessing and predicting liana dynamics in fragmented landscapes,

where historical and ongoing clonal reproduction play critical roles in their dominance. (250 words)

Keywords: Woody vines; fragmented forest; anthropogenic disturbance; habitat fragmentation; vegetative reproduction; clonal reproduction; forest fragmentation; lianas; *Wisteria floribunda*

INTRODUCTION

In recent decades, deforestation has escalated rapidly, driving widespread forest fragmentation on a global scale and prompting concerns over its profound impacts on biodiversity and ecosystem functioning (Hansen et al., 2013; Liu et al., 2018). Such fragmentation disrupts habitat structure and connectivity, altering ecological processes across diverse taxa, including plants, animals, and microorganisms (Haddad et al., 2015; Li et al., 2022; Kiesewetter et al., 2023) and ultimately affecting species interactions and ecosystem functions (Fahrig, 2003; Wilson et al., 2016). Among these impacts, increased liana (woody vine) abundance is particularly noteworthy, with fragmented forests often exhibiting higher liana density and dominance (Schnitzer and Bongers, 2011; Campbell et al., 2015; Ladwig and Meiners, 2015). Lianas thrive in disturbed conditions, especially in edge habitats where they benefit from greater light availability and suitable small trees for colonisation (Laurance et al., 2001; Londré and Schnitzer, 2006; Jones et al., 2017; Campbell et al., 2018). This proliferation is considered a major factor in their global rise relative to trees (Schnitzer and Bongers, 2011; Ngute et al., 2024), yet the specific ecological mechanisms—particularly at the species level—that drive liana expansion in fragmented landscapes remain poorly understood.

Clonal reproduction is an important mechanism influencing the abundance and spatial distribution patterns of lianas at the stand scale. In natural continuous forests, the substantial contribution of clonal reproduction to liana abundance and distribution has been reported in previous studies (Yorke et al., 2013; Ledo and Schnitzer, 2014; Mori et al., 2018; Schnitzer et al., 2021). In contrast, under bright-light environments such as gaps and edges, several studies have reported relatively higher occurrence rates (Yuan, 2024) and survival rates (Mori et al., 2020) of seed-origin liana seedlings compared to those

under closed canopies. In addition, forest fragmentation may limit the spatial expansion of clonal reproduction beyond the edges of fragmented stands, reducing its role in liana proliferation compared to continuous forests, where clonal growth enables wider distribution within a stand (Putz, 1984; Mori et al., 2018). Simulation studies also suggest that fragmentation, which reduces patch size, favours long-distance dispersal strategies, while clonal reproduction is less effective in small patches (Travis and Dytham, 1998; Hiebeler, 2004; Fukui and Araki, 2014). However, the extent to which clonal reproduction contributes to liana proliferation in fragmented forests remains largely unexamined, leaving a critical gap in understanding the ecological mechanisms underlying liana proliferation in these altered landscapes.

Wisteria floribunda (Fabaceae) is a liana species that is widely distributed across temperate forests in the Northern Hemisphere (GBIF Secretariat, 2023). It reproduces clonally by producing apparent individuals (hereafter referred to as ramets) through the extension of stolons (Sakai et al., 2002; Mori et al., 2021). This species is known as a dominant liana species in Japanese temperate forests; In a 6-ha permanent plot established in natural continuous forests in the same region as the study area (Ibaraki Prefecture, Japan), *W. floribunda* accounted for 69% of the number of liana stems and 85% of the total basal area (Mori et al., 2016a, 2024a). In addition, a previous study conducted in the same 6-ha plot have revealed the clonal structure of this species, showing that more than half of its stems are derived from clonal reproduction, with ramets up to 180 m apart belonging to the same clone (Mori et al., 2018). As a representative temperate liana species with well-documented genetic structure and abundance in natural continuous forests, *W. floribunda* offers valuable insights for understanding the influence and mechanisms of clonal reproduction on liana proliferation in fragmented forests.

The primary objective of this study was to investigate how clonal reproduction contributes to the proliferation of the liana *W. floribunda* in fragmented forests. We focused on a 21.6-ha area comprised of multiple forest fragments in Ibaraki Prefecture, Japan (hereafter, "Fragmented Forest Site"), where *W. floribund*a is a dominant species. Using DNA analyses, we assessed the impact of forest fragmentation on the role of clonal reproduction. For comparison, we utilised data from a 6-ha permanent plot in a continuous natural forest covering 103.51 ha (Ogawa Forest Reserve; Nakashizuka and Matsumoto, 2002; Mori et al., 2018, 2024a) approximately 100 km from the Fragmented Forest Site, within the Ibaraki Prefecture (hereafter, "Continuous Forest Site").

We hypothesised that clonal reproduction plays a more significant role in the Continuous Forest Site due to its low-light environment, which suppresses the establishment of seedlings derived from seed reproduction of *W. floribunda* in the Continuous Forest Site (Mori et al., 2020), and its spatial continuity, which facilitates clonal growth and expansion. In contrast, seed reproduction is expected to become more prominent in the Fragmented Forest Site, where higher light availability and spatially constrained conditions could limit the relative contribution of clonal reproduction. Specifically, we addressed two key questions: (1) Does clonal reproduction—quantified by the proportion of multiple-ramet genets and clonal patch size—contribute less to *W. floribunda* proliferation in the Fragmented Forest Site compared to the Continuous Forest Site? (2) Could clonal reproduction have contributed to spatial expansion prior to forest fragmentation? To address the second question, we examined whether single genets spanned multiple fragments and whether they were predominantly located in areas historically covered by forests. By answering these questions, this study aims to advance our understanding of the ecological mechanisms underlying *W. floribunda* proliferation

in fragmented landscapes and to provide broader insights into the ways in which forest fragmentation may affect liana dynamics and dominance.

MATERIALS AND METHODS

Study Sites

The study site comprises multiple fragmented forests within a 21.6-ha area located on the campus of the University of Tsukuba (36°06'40"N, 140°06'17"E) located in the Ibaraki Prefecture, Japan (Figs. S1; S2). The forest area in 1959 was estimated to be 15.1 ha, representing approximately 70% of the study area (Figs. 1 and S3), based on aerial photographs (1959–2008) provided by the Geospatial Information Authority of Japan and Copernicus Sentinel data (2018, 2024). Forest areas were defined as regions with visible tree canopies. Historically, these forests were likely used as traditional woodlands.

Over 65 years, forests in the region became increasingly fragmented into multiple smaller patches (Figs. 1, 2, and S4). This fragmentation occurred due to large-scale development during the 1960s-1980s, which significantly reduced the forest area (Figs. 1 and S3). By 1975, the forest area had decreased to 4.6 ha (30% of the original size). Subsequently, the forest began to recover through secondary succession and afforestation, reaching 12.5 ha by 1998. By that time, the forest area and the number of forest patches had reached a stable state, with no significant changes observed thereafter (Fig. 1).

Currently, areas with frequent human access, primarily along roads, are subject to ongoing management, including 2-3 rounds of mowing annually between May and November (Fig. S5, hereafter referred to as "managed areas"). In contrast, most other

forest areas remain unmanaged.

Study Species

The focal species of this study is *Wisteria floribunda* (Fabaceae), a temperate deciduous liana (Fig. S6) (Ohashi, 1989). *Wisteria floribunda* is reported to be a dominant species with high abundance in old-growth temperate forests in the same region as the study site (Ibaraki Prefecture, Japan; Suzuki, 2002; Mori et al., 2016a; 2024a), making it a representative liana species in the region. This species is characterised by its relatively large stems, with individuals reaching a maximum of approximately 40 cm in diameter under natural conditions (Mori et al., 2018). *Wisteria floribunda* reproduces clonally through the extension of stolons (Sakai et al., 2002), which increases the number of ramets (clonal individuals). Genetic analyses in a 6-ha plot of the Continuous Forest Site revealed that clonal reproduction contributed up to 71% of the total number of ramets of the study species (Mori et al., 2018). This species is also a major problematic liana in forestry, as it entwines around planted trees, reducing the quality of harvested timber (Suzuki, 1989). Furthermore, many liana species native to East Asia, including *W. floribunda*, are invasive in regions such as North America, where they pose significant ecological challenges, such as competition with native species (Trusty et al., 2007; Leicht-Young, 2015).

Given these characteristics, focusing on *W. floribunda* offers valuable insights that range from fundamental ecological knowledge to applied perspectives on management and conservation in liana species. As such, *W. floribunda* serves as an ideal model species for investigating the role of clonal reproduction in the proliferation of lianas under forest fragmentation.

Liana Inventory

To estimate the abundance and community structure of lianas within the study site, a liana census was conducted. The study area was divided into 20 × 20 m grid cells (Fig. S7). Lianas attached to trees (hereafter on-tree stage) were almost absent in the managed areas, likely due to management activities, although ground-creeping lianas (hereafter on-floor stage) were present. Therefore, fifteen grid cells (total area: 0.6 ha) were randomly selected within forested areas outside the managed areas (Fig. S7). Species and diameter at breast height (DBH) of all lianas (DBH > 0 cm) attached to trees (DBH > 1 cm) in these grid cells were recorded following Mori et al., (2024a), which is basically the same method described in Gerwing et al., (2006) except that the diameters were measured at 1.3 m above ground. Species names followed the nomenclature of Yonekura and Kajita, (2003).

Sampling, DNA extraction, and Genotyping

The study area, divided into 20 × 20 m grid cells as described above, was used for sampling. One sample of the target species was randomly selected per grid cell. In the managed areas, few on-tree lianas were present; however, ground-creeping individuals were occasionally found. Sampling was conducted as follows: if ramets attached to trees (DBH > 1 cm) were present, they were randomly selected for sampling. If such on-tree ramets were not available, ramets in the on-floor stage were randomly sampled.

Samples were first stored at 4°C and then frozen at −30°C until DNA extraction. DNA extraction was performed using the modified 2× CTAB (cetyltrimethylammonium bromide) protocol (Murray and Thompson, 1980). Genotypes were determined through

PCR amplification of 10 microsatellite loci described in Mori et al., (2016b). The PCR products were analysed using a 3130 Genetic Analyzer (Applied Biosystems, CA, USA). Electropherograms from each marker were meticulously examined for peak patterns using GeneMarker v1.95 (https://softgenetics.com/products/genemarker/).

Data Analysis

Identification of clones

Clones were identified based on the methods proposed by Arnaud-Haond et al., (2007). The ability of the microsatellite markers to distinguish multilocus genotypes (MLGs) was tested by calculating the number of MLGs for all combinations of a given locus, and the results were then verified based on the plateaus of the genotype accumulation curve (Fig. S8). To ascertain whether stems of the same MLG belonged to the same clone, the probability of a given MLG occurring in a population under Hardy-Weinberg equilibrium was calculated using the equation $p_{gen} = \prod_{i=1}^{l}(f_i)2^h$ (Parks and Werth, 1993), where f_i is the frequency of each allele at the i-th locus estimated with a round-robin method, and h is the number of heterozygous loci. Then, the probability of obtaining n repeated MLGs from a population more than once by chance in N samples (p_{sex}) was calculated using the equation $p_{sex} = \sum_{i=n}^{N} \frac{N!}{i!(N-i)!}[p_{gen}]^i[1-p_{gen}]^{N-i}$ (Parks and Werth 1993). Both p_{gen} and p_{sex} were calculated using the R package "RClone" (Bailleul et al., 2016). To distinguish each distinct MLG that belonged to a distinct clone, multilocus lineages (MLLs) were defined based on pairwise genetic distances that have been genotyped in this study (Fig. S9). This procedure was necessary to prevent the false detection of clones due to slightly different MLGs resulting from somatic mutation or genotyping errors. The

pairwise genetic distance threshold was determined with the cutoff_predictor function of the R package "poppr" (Kamvar et al., 2014, 2015). MLLs are equivalent to genets (clones) in ecological studies, and we will use "genets" hereafter for MLLs.

Comparative analysis of liana abundance

To compare whether the abundance (stem density and basal area) observed in the Fragmented Forest Site differs from that in the Continuous Forest Site, we performed the following analysis using a bootstrap method. We used the liana census data of *W. floribunda* (DBH > 0 cm) attached to trees (DBH > 1 cm), as reported by Mori et al., (2024a). These data were collected from a 6-ha plot (300 m × 200 m) of Continuous Forest Site (Fig. S1). The plot was divided into a grid of 20 × 20 m cells (15 × 10 grid cells), following the same methodology as this study. We randomly selected 15 grid cells from the Continuous Forest Site and obtained the stem density and basal area of the study species.

To account for the effects of random selection, we repeated this process 1,000 times using a bootstrap approach to calculate mean values and 95% confidence intervals (CIs). We defined the abundance in the Fragmented Forest Site as significantly different from that in the Continuous Forest Site if it fell outside the 95% CI derived from the bootstrap for the Continuous Forest Site. In our study, random sampling avoided managed areas, such that each selected grid cell in the Fragmented Forest Site contained at least one *W. floribunda* individual. To ensure comparability, the bootstrap procedure for the Continuous Forest Site also restricted the selection to grid cells that contained at least one *W. floribunda* individual.

We then fitted generalised linear models (GLMs) for each bootstrap iteration to

estimate the magnitude of differences in abundance between the Fragmented Forest Site and the Continuous Forest Site. Stem density and basal area were used as the response variables, with site (fragmented or continuous) as the explanatory variable. Stem density was modelled using a Poisson distribution, whereas basal area was modelled using a normal distribution. Residual diagnostics via the R package "DHARMa" (Florian, 2022) revealed non-uniformity and overdispersion ($P < 0.001$) for the Poisson GLM; hence, we employed a Poisson generalised linear mixed model (GLMM) with grid cell as a random effect.

Comparative analysis of contribution of clonal reproduction

To test whether the contribution of clonal reproduction observed in the Fragmented Forest Site differs from that in the Continuous Forest Site, we conducted a bootstrap analysis using two metrics: (1) the percentage of ramets derived from clonal reproduction (% Clonal ramet), calculated as the proportion of clonal ramets (multiple-ramet genets) relative to the total number of ramets, and (2) the percentage of genet area (% Genet area), calculated as the proportion of the total study area covered by genets. For comparison between the two sites, both metrics were calculated based on liana individuals in the on-tree stage. We used clonal structure data for *W. floribunda* from the Continuous Forest Site (the 6-ha plot), as reported by Mori et al., (2018), which included all *W. floribunda* individuals (DBH > 0 cm) attached to host trees (DBH > 5 cm) throughout the 6-ha area. To ensure comparability, the site was divided into 20 × 20 m grid cells (15 × 10 grid cells), and one sample was randomly selected from each grid cell. The contribution of clonal reproduction was calculated for each site, and the bootstrap method was used to repeat this process 1,000 times, providing mean values and 95% confidence intervals (CIs). The

observed values from the Fragmented Forest Site were considered significantly different from those in continuous natural forests if they fell outside the 95% CI derived from the Continuous Forest Site.

Although the minimum host tree size thresholds differ between the Fragmented Forest Site (DBH > 1 cm) and the Continuous Forest Site (DBH > 5 cm), a previous census of *W. floribunda* in the Continuous Forest Site (Mori et al., 2024a) suggests that this discrepancy has minimal impact on our comparison. In that census, 93.4% of individuals attached to smaller host trees (DBH 1–5 cm) co-occurred in the same 20 × 20 m grid cells as those on larger trees (DBH > 5 cm). Moreover, individuals on larger trees appeared in 13 additional grid cells, indicating a broader spatial distribution. The pairwise nearest-neighbour distance between *W. floribunda* on smaller vs. larger host trees averaged 5.2 ± 4.4 m, with 95% of occurrences within 14.8 m. These findings (Fig. S9) demonstrate that, despite using different size thresholds, the spatial overlap is sufficient to ensure that the lower threshold of 1 cm in the Fragmented Forest Site has minimal impact on our comparative analysis.

To compare differences in proportions (% Clonal ramet and % Genet area) between the sites, we used odds ratios, defined as $\{p/(1-p)\}/\{q/(1-q)\}$, where p represents the proportion in the Fragmented Forest Site and q represents the proportion in the Continuous Forest Site. An odds ratio of 1 indicates no difference in the odds of clonal reproduction contribution between the two sites. If the 95% CI of the odds ratio was significantly greater than 1, it indicated higher odds in the Fragmented Forest Site, whereas a 95% CI significantly below 1 indicated higher odds in the Continuous Forest Site. The mean odds ratio and its 95% CI were calculated using the bootstrap method.

Previous research in the Continuous Forest Site suggested that large genets of *W.*

floribunda (genets with N ≥ 3 ramets) exhibit mutually exclusive distribution patterns (Mori et al., 2018). To test whether the genet distribution patterns observed under natural conditions in the Continuous Forest Site differ from those in the Fragmented Forest Site, we evaluated the distribution exclusivity in both sites. Large genets (N ≥ 3 ramets) were randomly placed within the study area, and the total overlapping area of their convex hull polygons was calculated using the R package "sf" (Edzer 2018; Edzer and Roger 2023). This process was repeated 1,000 times for each site to obtain 95% CIs. If the observed value fell significantly below the 95% CI, genets were considered significantly mutually exclusive, while values above the 95% CI indicated significantly overlapping distributions.

Distribution of genets across fragmented forests

To examine whether genets expanded their distribution solely through clonal reproduction after forest fragmentation or whether some genets had already expanded their distribution before fragmentation, we asked the following questions: (1) Do genets occur in multiple fragmented forest patches? (2) If so, are such genets disproportionately distributed in areas covered by forest in 1959, prior to fragmentation? These questions were examined as follows:

Fragmented forest patches were defined as forest units isolated by roads or other artificial structures where forest canopies no longer connect, based on aerial photographs (Fig. S4). If a genet was found exclusively within a single forest patch, it was defined as having expanded its distribution through clonal reproduction within that patch after fragmentation. To test whether genets occurring in multiple patches were

disproportionately distributed in areas covered by forest before fragmentation, we compared their distribution to that of genets confined to a single patch using Fisher's exact test.

If genets were distributed across multiple forest patches and were significantly more likely to occur in areas covered by forest before fragmentation, the present study considered that these genets had most likely expanded their distribution through clonal reproduction before fragmentation. All analyses were performed using R version 4.3.2 (R Core Team, 2023).

RESULTS

Stem Density and Basal Area

A total of 9 liana species were recorded during the census conducted in the 0.6-ha (15-grid cell) area, comprising 573 stems and a basal area of 0.287 m^2 (Table S1). Among these, *W. floribunda* was the most abundant species, with 393 stems and a basal area of 0.258 m^2. This accounted for 69% of the total stem density and 90% of the total basal area of all liana species. The next most abundant species in terms of stem density and basal area were *Parthenocissus tricuspidata* (Vitaceae; 75 stems) and *Toxicodendron orientale* subsp. *orientale* (Anacardiaceae; 0.012 m^2), which corresponded to 13% and 4% of the total stem density and basal area, respectively. These results indicate that *W. floribunda* is the dominant species, contributing the majority of liana abundance in these fragmented forests.

In the Continuous Forest Site, subsampling over a comparable area of 0.6 ha (15-grid cells) yielded a mean stem density of *W. floribunda* of 126.1 (95% CI: 75.0–192.0)

and a basal area of 0.282 m^2 (95% CI: 0.106–0.504) (Fig. 3). Compared to the Continuous Forest Site, the Fragmented Forest Site exhibited a statistically significant higher stem count of *W. floribunda*, with an estimated site effect coefficient mean of 1.14, corresponding to exp(1.14) = 3.12 times higher stem density (95% CI: 2.07–4.86, $P < 0.001$). In contrast, the difference in basal area between the sites was not statistically significant (mean estimated site effect coefficient = -0.003, 95% CI: -0.019–0.009, $P = 0.51$).

Clonal Structure in Fragmented Forests

Genetic analysis revealed that the 273 ramets belonged to a total of 47 genets (Fig. 4). Among these, 257 ramets (94% of all ramets) were part of multiple-ramet genets, which are definitively derived from clonal reproduction. The probability of the study species obtaining a given genotype ($p_{gen} < 0.001$) or obtaining repeated genotypes that originated from distinct sexual reproductive events by chance ($p_{sex} < 0.001$) were low; thus, it was assumed that errors in the identification of clones were unlikely. When one ramet was excluded from each multi-ramet genet (under the assumption that each multi-ramet genet contains a single ramet derived from seed reproduction), the proportion remained 93%. Of the 273 ramets, 231 were in the on-tree stage and 42 in the on-floor stage. Among these, 94% of on-tree ramets (217/231) and 95% of on-floor ramets (40/42) were part of multiple-ramet genets, with no significant difference between the two groups (Fisher's Exact Test; Odds ratio: 1.29; 95% CI: 0.279–12.12; $P = 1.00$). This indicates that the proportion of ramets derived from clonal reproduction does not differ significantly between growth stages (on-tree versus on-floor).

The area of the 47 genets estimated using convex hull polygons was 12.5 ha, accounting for 58% of the total study area (21.6 ha). When considering only on-tree ramets, the genet area was 12.3 ha, equivalent to 57% of the study area. The largest genet (Genet ID = 1; Fig. 4) consisted of 105 ramets (39% of all ramets) and occupied an area of 9.5 ha, which accounted for 77% of the total genet area (Fig. 5).

Comparison of Contribution of Clonal Reproduction

The proportion of on-tree ramets derived from clonal reproduction (% Clonal ramet) was 94% in the Fragmented Forest Site, compared to 45% (95% CI: 38–52%) in the Continuous Forest Site (Fig. 6). The odds ratio was 18.2 (95% CI: 13.2–24.0), indicating that the proportion was significantly higher in the Fragmented Forest Site, by 49% (odds 18.2 times greater), compared to the Continuous Forest Site.

The proportion of the study area covered by on-tree genets (% Genet area) was 57% in the Fragmented Forest Site, compared to 7% (95% CI: 4–10%) in the Continuous Forest Site, with an odds ratio of 18.6 (95% CI: 11.9–31.6) (Fig. 6). This indicates that the proportion was significantly higher in the Fragmented Forest Site, by 50% (odds 18.6 times greater), compared to the Continuous Forest Site.

The total area of overlapping genets (N ramet ≥ 3) was 0.46 ha in the Fragmented Forest Site and 0.05 ha in the Continuous Forest Site (Fig. 5). In both sites, the observed values were significantly smaller than their respective 95% CIs (0.96–4.97 for the Fragmented Forest Site and 0.06–0.23 for the Continuous Forest Site). This indicates that large genets (N ramet ≥ 3) exhibited mutually exclusive distribution patterns in both sites.

Distribution of Genets Across Fragmented Forests

Three genets (Genet IDs: 1, 9, and 10; Fig. 4) were distributed across multiple fragmented forest patches, while the remaining 44 genets (94% of all genets) were found exclusively within a single forest patch. The total number of ramets belonging to these three genets was 117, accounting for 43% of all ramets. Among the nine forest patches where *W. floribunda* was present, the largest genet (Genet ID = 1) spanned seven patches, while the other two genets were each distributed across two different patches (Fig. 4).

Of the 117 ramets belonging to genets distributed across multiple forest patches, 10 were located in areas not covered by forest prior to fragmentation (6.5 ha), while 107 were in areas covered by forest (15.1 ha). In contrast, among the 156 ramets confined to a single forest patch, 61 were in areas not covered by forest, and 95 were in areas covered by forest. The proportion of ramets in areas covered by forest was significantly higher for genets distributed across multiple patches (91%) compared to those confined to a single patch (61%) (Fisher's Exact Test; Odds ratio: 6.83; 95% CI: 3.24–15.8; $P < 0.001$).

DISCUSSION

We initially hypothesised that clonal reproduction would be more prominent in the Continuous Forest Site, whereas seed reproduction would prevail in the Fragmented Forest Site, due to the differences in light conditions and spatial continuity. Contrary to this expectation, our genetic analyses revealed that clonal reproduction played a substantial role in liana proliferation, with large clonal patches evident throughout the fragmented forests. Moreover, these clonal expansions appeared to have been established even before forest fragmentation, suggesting that both current and historical clonal

structures underpin the species' proliferation in these landscapes. In the following sections, we discuss how these findings refine our understanding of liana species' ecological strategies in response to fragmentation, and consider broader implications for liana dominance in human-altered forests.

Liana Abundance in Fragmented Forests

In the Fragmented Forest Site, stem density was approximately three times higher. This is likely due to substantial anthropogenic disturbances that altered forest structure, increased edge effects, and the presence of young forest patches within the Fragmented Forest Site. Such increases in liana abundance following forest fragmentation have been widely reported in temperate (Ladwig and Meiners, 2015) and tropical forests (Laurance et al., 2001; Jones et al., 2017). The elevated stem density of the study species observed here is consistent with these findings. Genetic analyses further suggest that this high stem density in fragmented forests is primarily due to clonal reproduction, which enables rapid population expansion under forest disturbance.

Despite the higher stem density, the maximum stem diameter of the study species in the Fragmented Forest Site was about 14 cm (Table S1), whereas stems reaching 40 cm have been documented in the Continuous Forest Site (Mori et al., 2018). This difference in stem diameter likely reflects variations in forest structure (e.g., tree density) and successional stage. Although the maximum diameter in the Fragmented Forest Site is smaller, the overall basal area of lianas remains comparable to that of the Continuous Forest Site, presumably due to their greater density. Larger lianas are more common in non-fragmented forests, consistent with findings in tropical forests (Campbell et al., 2018).

However, as succession progresses in the Fragmented Forest Site, it is plausible that lianas already reaching the canopy will continue to grow, potentially leading to further increases in the basal area (Ladwig and Meiners, 2010).

Role of Clonal Reproduction in Fragmented Forests

This study hypothesised that in fragmented forests, where edge effects increase light availability and fragmentation reduces spatial continuity, seed reproduction may play a more prominent role compared to continuous forests. However, the proportion of clonal ramets and the genet area in fragmented forests were significantly higher than in continuous forests (both approximately 50%, with an odds ratio of 18), which indicated that the proliferation of lianas in fragmented forests cannot be fully explained by improved light conditions and spatial continuity alone, but is likely driven by other factors related to large-scale disturbances that enhance clonal growth. One possible explanation is the inherent characteristics of clonal plants, which allow them to share resources such as water and nutrients through stolons or rhizomes, enabling rapid recovery from partial damage and facilitating extensive distribution (Fahrig et al., 1994; Winkler and Fischer, 2002; Saitoh et al., 2006). Moreover, previous studies have shown that improved light conditions alone cannot account for the abundance of lianas in temperate forests (Carrasco-Urra and Gianoli, 2009; Mori et al., 2024a). Instead, factors such as clonal reproduction and host tree availability may play a more critical role in their proliferation.

The exclusive distribution patterns of genets observed in fragmented forests closely resemble those found under natural conditions in continuous old-growth forests. This suggests that the clonal spread of genets operates in a similar way in both fragmented and non-fragmented forests. Clonal reproduction likely promotes the dominance of

certain genets by enabling them to occupy suitable habitats in forest patches, potentially suppressing the spread of others (Schmid and Harper, 1985; van Groenendael et al., 1996). As structural parasites, lianas rely on external biomechanical support (i.e., host trees) as an essential habitat for their growth and survival (Putz and Holbrook, 1991; Sakai and Suzuki, 1999). Such exclusivity in the distribution of the studied genets may therefore be a consequence of competition among genets for suitable host trees. Studies in continuous forest sites (Mori et al., 2016a, 2024a) have shown that lianas, including *W. floribunda*, exhibit a strong preference for host tree size, while small-scale natural disturbances (e.g., canopy gaps caused by one or a few fallen trees) and landforms play only a minor role in their distribution. Specifically, stem-twining and tendril-climbing lianas are more likely to establish on small host trees when their stems are small and shift to larger host trees as they grow. These findings highlight that host-tree availability—and the resulting competition for host trees—strongly shapes the spatial distribution of lianas by determining their ability to establish and grow on suitable hosts. This supports our hypothesis that clonal reproduction and genet exclusivity are tightly linked to host-tree competition.

Clonal Reproduction Before and After Forest Fragmentation

The proliferation of lianas through clonal reproduction in fragmented forests reflects the combined influences of both pre- and post-fragmentation processes. Our results indicate that most genets were confined to single forest patches, suggesting that the expansion of genet distribution primarily occurred after forest fragmentation. This may be because clonal offspring face difficulties migrating to fragmented patches (Fukui and Araki, 2014). However, three specific genets were found across multiple forest patches and were

469 significantly more abundant in areas historically covered by forest before fragmentation.
470 This pattern indicated that these genets had already expanded across multiple patches
471 prior to fragmentation. Notably, these three genets accounted for 43% of all recorded
472 ramets, highlighting the substantial role of pre-fragmentation clonal structures in driving
473 the pronounced proliferation of lianas in fragmented forests.

474 Increased liana abundance following forest fragmentation is a well-known
475 phenomenon in temperate and tropical forests (Schnitzer and Bongers, 2011; Campbell
476 et al., 2015; Ladwig and Meiners, 2015). However, our findings suggest that a key factor
477 underlying this trend may lie in the clonal structures established prior to fragmentation.
478 As discussed earlier, the adaptive traits and life-history strategies of clonal plants enable
479 them to thrive under disturbance and environmental change, facilitating the proliferation
480 of these clonal species in fragmented landscapes (Fahrig et al., 1994; Winkler and Fischer,
481 2002; Saitoh et al., 2006). It is likely that a small number of successful genets,
482 characterised by high adaptability or favourable traits, drive the post-fragmentation
483 proliferation of liana species in response to altered environmental conditions. Indeed, in
484 warm temperate forests of Japan, the dominant liana *Trachelospermum asiaticum* var.
485 *asiaticum* (Apocynaceae) was reported to establish a few genets via seed dispersal during
486 early successional stages. These genets rapidly expanded through clonal reproduction in
487 forests recovering from large-scale natural disturbances caused by volcanic eruptions
488 (Mori et al., 2024b).

489

490 Implications of Clonal Reproduction for Liana Management

491 *Wisteria floribunda* is a problematic liana species requiring management and control in

forestry (Suzuki, 1989). At our study site, small pre-climbing ramets were found even in managed areas subjected to multiple rounds of mowing annually. The present study found that most of these ramets were derived from clonal reproduction. Mature *W. floribunda* individuals are known to expand their distribution by producing numerous ramets through stolon growth (Sakai et al., 2002; Mori et al., 2021). However, in managed areas, pre-climbing small ramets were observed even in the absence of mature individuals in the on-tree stage. This finding suggests that clones established during periods when the forest was continuous have persisted underground and remained viable despite repeated mowing. This finding aligns with previous studies on kudzu (*Pueraria montana* var. *lobata*) in North America, which reported that mowing enhances clonal diversity (Kartzinel et al., 2015), and on *Clematis vitalba* in New Zealand, which reported the ability to regenerate from severed stems (Jarvis-Lowry et al., 2024). These results suggest that for lianas with strong clonal growth capabilities, conventional mowing and liana cutting practices may be insufficient to effectively suppress the number of genets. This highlights the need for a precise understanding of the life history strategies of lianas at the species level to effectively manage and conserve them in forests.

CONCLUSIONS

This study elucidates the impact of forest fragmentation on liana proliferation through the lens of clonal reproduction. Our findings strongly suggest that clonal reproduction serves as a key mechanism driving the spatial expansion and dominance of lianas in fragmented forests. Additionally, the distribution patterns of large genets indicate that the proliferation of lianas following fragmentation heavily depends on pre-existing clonal structures established before fragmentation. These results clarify that forest fragmentation not only

promotes new clonal growth but also highlights the significant influence of historical clonal structures on the current distribution and abundance of genets. Furthermore, this study suggests that the proliferation of lianas in fragmented forests may be driven by a limited number of successful genets belonging to a few clonally dominant species, highlighting the critical role of species-specific reproductive strategies and life histories in facilitating the dynamic population expansion of lianas following forest fragmentation. This study also underscored the necessity of considering clonality and life history strategies at the species level when developing management and conservation approaches for lianas. Overall, the findings of this study indicate that lianas, due to their sensitivity to environmental changes, serve as valuable ecological indicators (Schnitzer, 2018) for assessing the impacts of human-induced disturbances, such as deforestation and habitat fragmentation. While this study provides significant insights, it is limited to a single study site. Future research with similar designs across multiple sites is necessary to generalise these findings and gain a more comprehensive understanding of how forest fragmentation influences liana proliferation.

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FIGURE CAPTIONS

Figure 1. Temporal changes in forest area and the number of forest patches over 65 years at the study site following forest fragmentation. Forest area and the number of patches were estimated from aerial photographs (1959-2008) and satellite images (2018-2024).

Figure 2. Approximate forest patch age (in years) of the fragmented forests in the study site, estimated from the temporal changes in forest area over 65 years.

Figure 3. Stem density and basal area of the study species in 15 quadrats (20 x 20 m grid cells; 0.6 ha) of the Fragmented Forest Site (this study; vertical red line) and Continuous Forest Site (Mori et al. 2024a; shaded bars). Stem density and basal area at the Continuous Forest Site were obtained by subsampling 15 quadrats with 1000 bootstraps.

Figure 4. Clonal structure of the study species in fragmented forests of the study site. Each number indicate ramets; same numbers indicate genetically identical individuals (i.e., genets/clones). Orange polygons with solid lines indicate genet area obtained as convex hull polygons. Filled green background represent area currently covered by forest.

Figure 5. Distribution of genets in the Fragmented Forest Site (this study) and in the Continuous Forest Site (Mori et al. 2018), shown at the same spatial scale. Genets are shown as convex hull polygons following Figure 4. For visibility purposes, clonal ramets distributed within the genet polygons are not shown in this figure.

Figure 6. Proportion of clonal ramets to the total ramets (% Clonal ramets; upper panel) and proportion of genet area to the total study area (% Genet area; lower panel) of the study species in the Fragmented Forest Site (this study; vertical red line) and Continuous Forest Site (Mori et al. 2018; shaded bars). Proportion of clonal ramets and genet area in the Continuous Forest Site were obtained by subsampling a sample within each 20 x 20 m grid cell with 1000 bootstraps.

APPENDIX

Figure S1. Map of the study sites.

Figure S2. Photographs of the Fragmented Forest Site.

Figure S3. Maps of forest area in the Fragmented Forest Site**.**

Figure S4. Fragmented forest patches in the study site.

Figure S5. Managed zones in the Fragmented Forest Site.

Figure S6. Photographs of the study species.

Figure S7. 20 x 20 m grid cells used in this study.

Figure S8. Genotype accumulation curve.

Figure S9. Pairwise genetic distance.

Figure S10. Distribution map of the study species in the Continuous Forest Site.

Table S1. Liana community structure in the Fragmented Forest Site.

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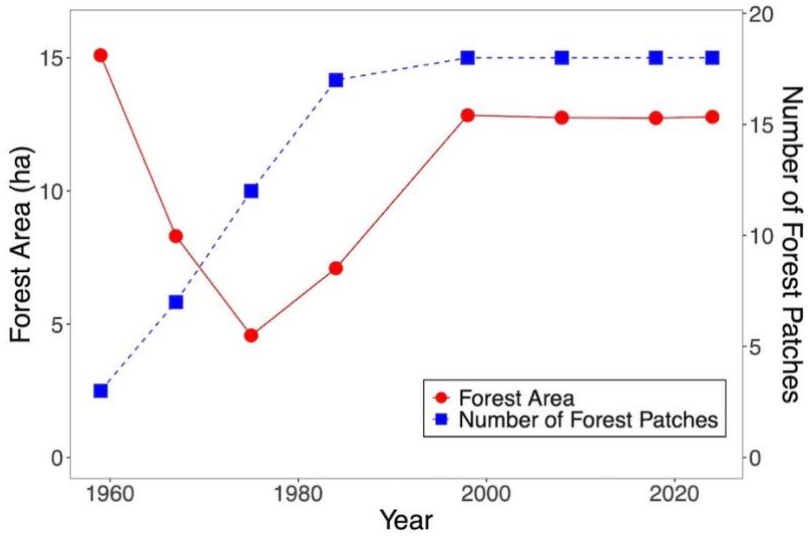

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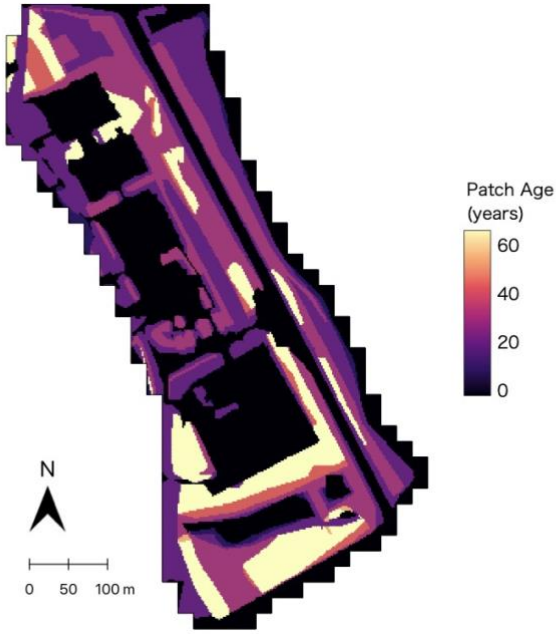

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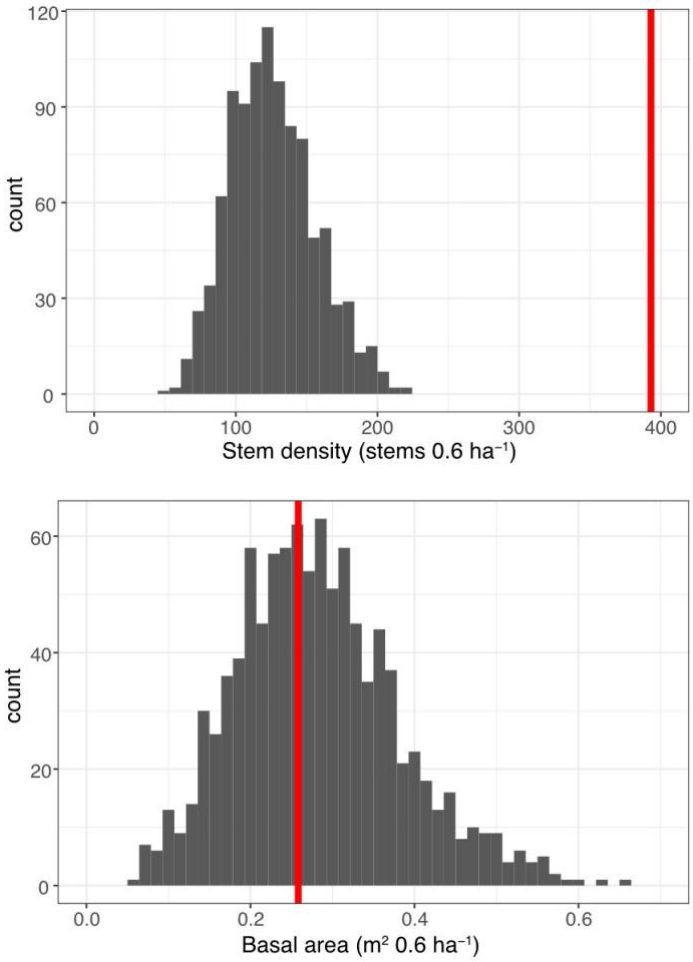

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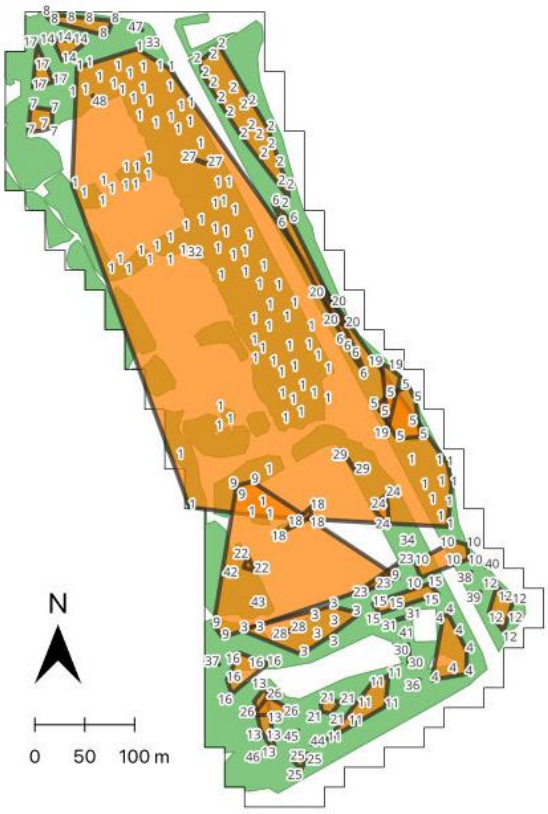

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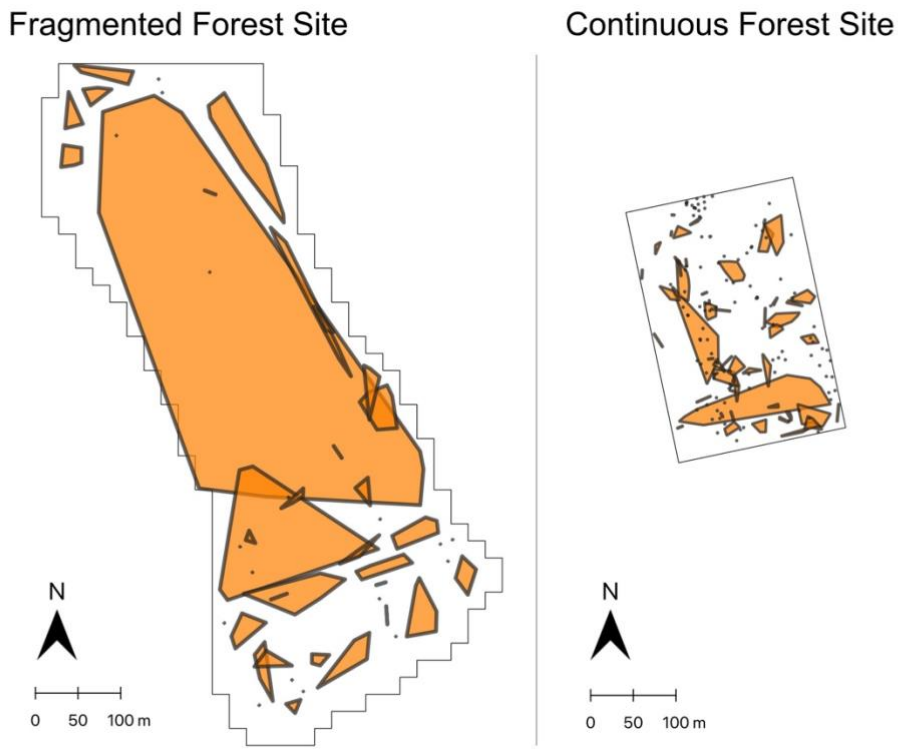
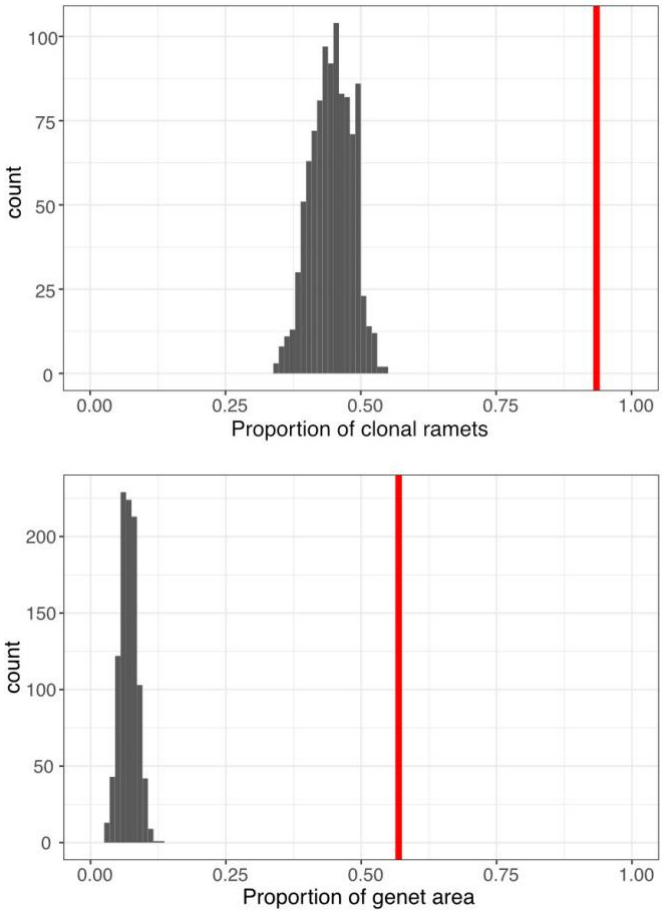
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