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Reproductive Processes Do Not Constrain the Western Range Limit of *Gelsemium sempervirens* (Gelsemiaceae)

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Abstract

Range limits are often hypothesized to arise from reduced reproductive success at distributional margins, yet direct tests integrating pollination and post-pollination processes remain uncommon. Whether reproductive failure constrains the distylous *Gelsemium sempervirens* at its western range edge in eastern Texas was investigated by quantifying flowering phenology, floral visitation, pollinator effectiveness, and seed fate over two flowering seasons. Flowering timing differed markedly between years due to freeze events, but flowering effort and morph synchrony remained high. Although multiple floral visitors were recorded, fruit set was overwhelmingly associated with the southeastern blueberry bee (*Habropoda laboriosa*), which dominated visitation and remained active throughout the flowering period. No evidence of autonomous self-pollination or breakdown of functional distyly was detected. Seed set in unattacked fruits was high and comparable to values reported from central-range populations. In contrast, post-pollination seed loss due to cryptic fruit herbivory substantially reduced seed survival, though herbivory patterns did not differ qualitatively from those documented elsewhere in the species' range. Together, these results indicate that reproductive failure does not explain the abrupt western range limit of *G. sempervirens* and instead suggest that ecological transitions associated with the forest–prairie ecotone, rather than pollination or early seed development, may play a more important role in shaping the species' distribution.

Keywords: biogeographic limits; pollen limitation; floral phenology; heterostyly; post-pollination processes; fruit herbivory; ecotonal boundaries

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1. Introduction

Understanding the ecological and evolutionary factors that restrict species' geographic distributions remains a central goal of plant ecology and biogeography [1,2]. Range limits often occur where demographic rates—particularly reproduction—decline to levels insufficient to sustain populations [3,4]. For flowering plants, reproductive failure at range edges may arise from multiple mechanisms, including pollen limitation (through phenological mismatch with pollinators), breakdown of mating systems, or increased post-pollination seed loss [5,6]. As shown in previous studies, these processes may act independently or in combination, making direct tests of reproductive performance essential for evaluating whether reproduction constrains a species' distribution [7,8].

Plants with specialized mating systems may be especially vulnerable to reproductive failure near ecological margins [9]. Distylous species require legitimate pollen transfer between long-styled and short-styled morphs to produce fruit and seed [10,11]. Because autonomous self-pollination is typically absent and intramorph crosses are incompatible,

successful reproduction depends on reliable pollinator service and temporal synchrony between morphs [12,13]. Numerous studies have documented pollen limitation, reduced fruit set, or partial breakdown of heterostyly in marginal populations, suggesting that mating-system failure can contribute to range limits under some conditions [14–16].

Gelsemium sempervirens (L.) J.ST.-Hil. (Gelsemiaceae) is a distylous, woody vine widely distributed throughout the southeastern United States, where it is abundant in the Coastal Plain and Piedmont (Figure 1). Its native range extends from the Atlantic Coastal Plain westward into eastern Texas, where populations reach the western edge of the species' distribution (Figure 1). The species occurs primarily in pine-dominated forests, forest margins, and adjacent woodland habitats, and its distribution in the southeast broadly corresponds with transitions among forest types. Flowers are tubular, nectariferous, and bloom in early spring; successful seed production requires legitimate pollen transfer between floral morphs [17,18]. Neither long-styled (LS) nor short-styled (SS) flowers are capable of autonomous self-pollination, and distyly has been shown to function consistently across multiple populations [18,19]. Fruits are two-locule capsules that mature through late summer and dehisce in autumn, dispersing winged seeds. In addition to its ecological role as a dominant early-spring flowering vine, *G. sempervirens* is pharmacologically notable due to its production of bioactive indole alkaloids [17,18]. Because seed set depends on legitimate pollen movement, *Gelsemium* provides a powerful system for testing whether pollination failure contributes to geographic range limits.

In the outer Coastal Plain of Georgia, early-spring bee communities provide abundant effective pollinators. The southeastern blueberry bee, *Habropoda laboriosa*, is among the most efficient visitors to *Gelsemium* and other early-flowering species and plays a disproportionate role in fruit and seed production [20–25]. Importantly, *H. laboriosa* itself approaches its western geographic limit near the western distributional boundary of *G. sempervirens* [26,27]. This geographic coincidence has led to the hypothesis that pollination failure—specifically reduced visitation by this highly effective pollinator or absence of this bee species—could limit reproduction and contribute to the species' western range edge. Under this model, populations near the range margin would experience reduced fruit set, increased pollen limitation, or altered pollinator assemblages insufficient to maintain reproduction [1–4].

Herbivory at the floral stage on *Gelsemium sempervirens* has been studied extensively, where damage to corollas and nectaries can alter pollinator behavior and fruit initiation [28–30]. In contrast, herbivory affecting developing fruits has received little attention. To date, only a single study has reported fruit herbivory in *Gelsemium*, documenting reduced reproductive outcomes in suburban landscapes but without identifying the herbivore or characterizing its feeding mode [31]. This latter study primarily identified herbivory through external pericarp holes. Whether this form of seed predation is widespread, whether it intensifies toward the western range edge, and whether it contributes meaningfully to range limitation remain unresolved.

The western limit of *Gelsemium sempervirens* occurs abruptly in eastern Texas, near the transition from pine-dominated forest (Pineywoods) to post-oak savanna and prairie (Oak Woods and Prairies). This distributional boundary is evident in county-level occurrence maps and regional floristic treatments [32,33] and corresponds to a well-recognized ecoregional transition in eastern Texas [34,35] (Figure 2). However, this boundary is not associated with a sharp climatic discontinuity at the regional scale [34], raising the possibility that biological or ecological constraints, rather than abiotic tolerances alone, define the species' range edge. If reproductive processes fail in western populations, reduced fruit set, lower pollination efficiency, or increased seed developmental failure would be expected [19,36]. Alternatively, if reproduction remains intact, ecological factors such as forest structure, host-tree availability, soil characteristics, or disturbance regimes (in-

cluding fire) or constraints on the distribution of the primary pollinator itself may better explain the termination of the species' distribution across the Pineywoods–oak savanna transition [34,35].

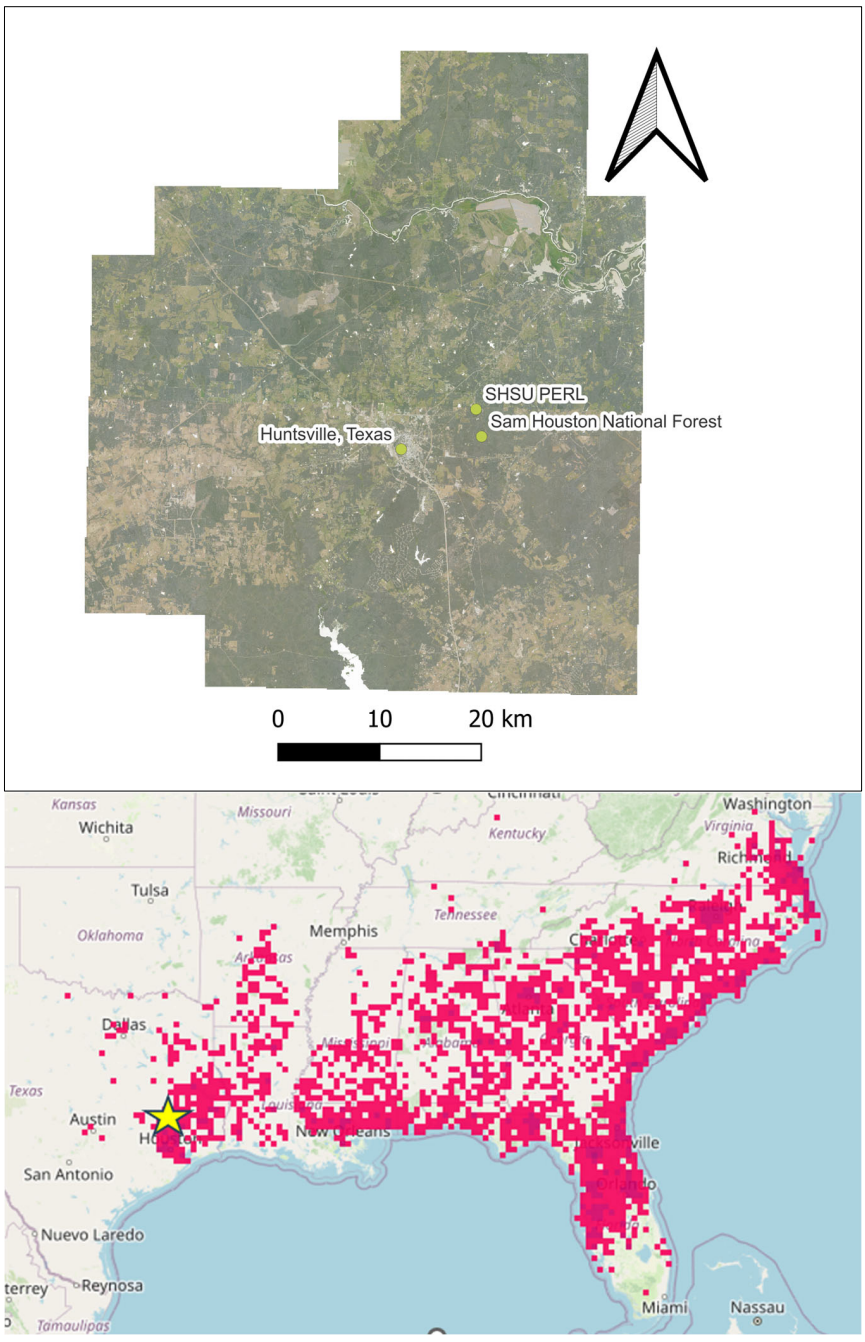

Figure 1. Location of the study population of *Gelsemium sempervirens* at the western edge of the species' native range in eastern Texas. The Sam Houston State University Piney Woods Environmental Research Laboratory (SHSU PERL), Walker County, TX, USA, lies within a contiguous pine-dominated forest matrix of the Pineywoods ecoregion and near the forest–prairie ecotone marking the species' western distributional limit. Surrounding land cover illustrates increasingly open landscapes associated with the Oak Woods and Prairies to the west. Background imagery is 2024 USDA National Agriculture Imagery Program (NAIP) aerial imagery (60 cm resolution). Inset: Distribution of *G. sempervirens* in the southeastern United States based on data from the GBIF records present on iNaturalist. The yellow star indicates the location of the study population.

Figure 2. Flowering vine of *Gelsemium sempervirens* at the study site on 27 February 2024.

In this study, the hypothesis that reproductive failure contributes to the western range limit of *Gelsemium sempervirens* was tested using two years of data from a natural population at the Piney Woods Environmental Research Laboratory (PERL) in Walker County, which is exactly the western edge range in eastern Texas. Integrated analyses of flowering phenology, floral visitation, pollinator effectiveness, and fruit and seed predation were used to evaluate whether (1) pollen limitation or breakdown of functional distyly occurs at the range edge, (2) effective pollinators are present and temporally synchronized with flowering, and (3) post-pollination seed loss is unusually severe. By focusing on a single site across two years, this study analyzes natural interannual variability while providing a direct test of whether reproduction constrains the western distribution of this ecologically specialized distylous vine.

2. Materials and Methods

2.1. Study Site

All fieldwork was conducted at the 91 ha Sam Houston State University Piney Woods Environmental Research Laboratory (PERL) (30.746348° N, −95.474865° W, 78–80 m elevation), Walker County, Texas, located at the western range edge of *G. sempervirens* (Figure 1). The study population occurs within a secondary loblolly pine (*Pinus taeda*) forest approximately 35 years old, situated within the forest–prairie ecotone of eastern Texas and bordered on the south and east by the Sam Houston National Forest. This region marks an abrupt transition from pine-dominated forest to post-oak savanna and prairie farther west [34,35], a boundary that coincides with the western limit of the native distribution of *G. sempervirens* (Figure 1). Climatic conditions are characterized by high interannual variability in winter and early spring temperatures. Weather data for both years were obtained from the

National Weather Service station at Huntsville Municipal Airport (KHTV; 10.65 km west of the Piney Woods Environmental Research Laboratory, PERL). Because 2024 was a leap year, the 2024 dataset included one additional day (91 vs. 90 days).

2.2. Plant Sampling and Census

Plants were monitored for flowering phenology beginning in January of each year (Figure 2).

No flowers were open during January; flowering commenced in February, at which time plants were formally measured and permanently marked. In 2024, 40 flowering individuals were randomly selected and permanently marked within the PERL population. For each plant, vine height on the host tree and horizontal canopy width were measured to characterize plant size. In July 2024, an additional 62 plants were added to the census population to increase sample size for phenological monitoring. Only well-developed, reproductively mature vines climbing into the sub-canopy or canopy were included in the census. Floral morph (LS or SS) was determined for all plants based on anther and stigma positions during anthesis.

2.3. Flowering and Fruiting Phenology

Flowering phenology was monitored weekly from 1 January through the end of April in both 2024 and 2025. On each census date, the number of open flowers was recorded for every marked plant. Total flower production per plant was determined by summing the number of newly opened flowers recorded for each plant across all weekly census dates within a flowering season. Observations began prior to anthesis and continued until no open flowers remained in the population. For each year, population-level flowering curves were generated by aggregating the number of open flowers across all plants by Julian day. Peak flowering was defined as the Julian day with the maximum number of open flowers. Flowering duration for individual plants was calculated as the number of days between the first and last observed open flower. Morph synchrony was quantified as the proportion of flowering days on which both LS and SS morphs were simultaneously in bloom within the population. Fruit production for the 2023 flowering season was recorded in January 2024, whereas fruit production for the 2024 and 2025 flowering seasons was recorded in November of those respective years by counting all fruits on each plant. *Gelsemium sempervirens* produces dry, dehiscent capsules with wind-dispersed seeds, and intact fruits can persist on vines for up to two years if undisturbed, permitting retrospective assessment of prior-year fruit production. Open-pollination fruit set was quantified in 2024 and 2025 as the proportion of flowers that developed into fruits.

2.4. Floral Visitation

Floral visitors were observed directly throughout the entire bloom period in both 2024 and 2025. Floral visitation observations were conducted on marked plants. Individual plants were observed multiple times within a flowering season, with the number of observation periods per plant varying depending on flowering availability. Observations were conducted in 10 min intervals between 07.00 and 18.00 under suitable weather conditions (no precipitation, low wind). During each observation period, the number of open flowers observed (focal group size), the identity of each floral visitor, the number of flowers visited per visit, the plant identification number, observation time, and local climatic variables (air temperature, mean wind speed, relative humidity, and sky conditions) was recorded. To increase sampling coverage and document visitor behavior, direct observations were supplemented with digital video recordings using Nikon and GoPro (Nikon Corporation, Tokyo, Japan; GoPro, Inc., San Mateo, CA, USA) cameras positioned to capture floral activity. Video footage was reviewed to identify additional visits, confirm visitor iden-

tity, and quantify flower-probing behavior. Floral visitors were identified to the lowest taxonomic level possible using direct observation, photographs, and voucher specimens. Representative specimens were collected when feasible and deposited in the Sam Houston State University Natural History Collections.

2.5. Pollinator Effectiveness

Pollinator effectiveness was assessed in 2025 using single-visit and limited multiple-visit observations [20]. The marked census population used for phenological monitoring (n = 102; Sections 2.2 and 2.3) served as the source population for this experiment. To facilitate pollination treatments, developing floral buds were bagged with fine-mesh pollination bags on 3 February 2025. Bags were placed over vine tips encompassing one or more adjacent nodes, resulting in a variable number of flower buds per bag. The number of buds enclosed within each bag was recorded at the time of bag placement.

Bags were checked weekly from 10 February through 30 March 2025. Upon flower opening, bags were removed and the number of flowers that opened within each bag was recorded. Flowers were then observed continuously for 10–60 min until one or more visits occurred. Visitor identity and number of visits were recorded. Although the intent was to document single visits, some flowers received multiple visits by the same individual, multiple individuals of the same species, or multiple species during a single observation period. Only flowers receiving visits from a single pollinator taxon were included in pollinator effectiveness analyses; flowers receiving visits from multiple taxa were excluded. Observations were conducted between 09.00 and 19.00 h when air temperatures exceeded 16 °C. Following visitation, flowers were rebagged to prevent additional visits. Floral visitation was monitored on 39 individual plants (21 short-styled, 18 long-styled) across 27 observation days (8 in February and 19 in March), representing approximately 1560 min of observation conducted by four observers.

Pollination bags had a mesh size of 0.37 mm, measured using a Keyence digital microscope (Keyence Corporation, Osaka, Japan), effectively excluding floral visitors while allowing airflow and light penetration. In April, approximately one month after flowering, fruit set was scored as 1 for developing fruits and 0 for aborted flowers. Fruits were marked at initiation and monitored through development. Mature fruits were harvested in August 2025 for measurement and seed analysis. Due to storm events and tree falls, some fruits that initiated development in April were unavailable for harvest.

2.6. Test for Autonomous Self-Pollination

To test for autonomous self-pollination, flowers were bagged prior to anthesis in 2025 to exclude pollinators. This assay was used to evaluate whether reproductive assurance via autonomous selfing occurs at the western range edge, which would indicate potential relaxation or breakdown of obligate outcrossing associated with distyly. Between one and nine flowers were bagged on each of 10 randomly selected plants (6 long-styled, 4 short-styled). Bags remained in place through anthesis and early fruit development. Fruit initiation was monitored weekly following corolla abscission. Flowers on the same plants that were left open for natural pollination were monitored concurrently. This approach does not test compatibility relationships among floral morphs or pollen-tube interactions; these aspects of the breeding system have been extensively characterized in previous studies [18,19] and were not re-evaluated here.

2.7. Fruit Phenology

Fruits were collected on 29 August 2025 from a subset of plants monitored for flowering phenology at the Piney Woods Environmental Research Laboratory (PERL). Fruits were mature and dry at harvest. Only closed fruits (pericarp intact, seeds retained) were used to

quantify pollination efficiency and seed production. Fruit size was measured as a proxy for developmental investment, allowing assessment of whether herbivory effects varied across fruit growth trajectories rather than being restricted to final fruit set alone. Additional details on fruit classification and herbivory assessment are provided in Supplementary S1 Methods.

2.8. Herbivory Detection and Classification (See Figures S2–S4)

Methods used to detect and classify fruit and seed damage from herbivory are described in the Supplementary S1 Methods.

2.9. Seed Scoring and Pollination Efficiency

Fruits were dissected and seeds were classified as good (fully developed), damaged, tiny green (developmentally arrested), or unfertilized ovules. Seed set was calculated as the proportion of ovules that developed into seeds, assuming a maximum of 20 ovules per fruit. Seed survival was calculated as the proportion of good seeds relative to total seeds. Additional details on seed classification and damage categories are provided in the Supplementary Materials.

2.10. Statistical Analyses

All statistical analyses were conducted in R (version 4.3.3, R Core Team, Vienna, Austria). Statistical procedures, including Fisher's exact tests, chi-square tests, generalized linear models, and nonlinear phenology models, were implemented using base R functions. Niche overlap metrics were calculated using the vegan package, and bootstrap procedures were conducted using the boot package. Figures were generated using ggplot2.

Population-level flowering curves were summarized by Julian day and fitted with Gaussian and Weibull functions using nonlinear least squares to estimate peak bloom timing and curve spread. Both Gaussian and Weibull functions were evaluated because flowering phenology distributions may be symmetric or skewed, with final model selection based on goodness-of-fit. Differences in individual-plant flowering duration between years were assessed using Welch's t-tests. Peak bloom timing was compared between years using bootstrap resampling (10,000 iterations) to generate 95% confidence intervals around the difference in peak Julian day.

Temporal overlap in flowering phenology between long-styled (LS) and short-styled (SS) floral morphs was quantified using Pianka's niche overlap index. Daily flowering distributions were constructed for each morph by summing the number of open flowers per day across all monitored plants within a year. Pianka's index was then calculated as

$$O = \frac{\sum p_{i,SS}}{\sqrt{\left(\sum p_{i,LS}^2\right)\left(\sum p_{i,SS}^2\right)}}$$

where p_i represents the proportion of flowers of a given morph observed on day i. The index ranges from 0 (no temporal overlap) to 1 (complete overlap). Overlap was calculated separately for 2024 and 2025 using daily flowering data.

For pollinator effectiveness analysis, fruit set was treated as a binary response variable. Differences in fruit set between observation periods with and without *Habropoda laboriosa* visitation were evaluated using Fisher's exact tests. Temporal comparisons focused on periods with and without *Habropoda laboriosa* because it was the only pollinator present across the full flowering period; other visitors occurred too infrequently to support meaningful temporal analysis. Because multiple flowers were often observed on the same plant within a single day, observation periods were used as the unit of analysis for hypothesis

testing to reduce pseudo replication and provide a conservative assessment of pollinator effectiveness; flower-level data are presented descriptively.

Pollination efficiency of closed fruits was analyzed using linear models with herbivory category as a predictor. Proportions of good seeds were analyzed using binomial generalized linear models with logit links. Planned contrasts compared unattacked fruits with those exhibiting internal wall feeding or hole presence. Additional analyses related to fruit herbivory and seed damage are described in the Supplementary Materials. Model assumptions were evaluated using residual diagnostics.

3. Results

3.1. Flowering Phenology

3.1.1. Weather Conditions and Freeze Events

Precipitation differed markedly between years. Total precipitation from January–March was substantially higher in 2024 (53.5 cm) than in 2025 (21.4 cm), with 2024 exceeding and 2025 falling below the long-term average. Mean air temperatures were modestly warmer in 2024 than in 2025, including average daily temperature (13.2 vs. 11.9 °C), average maximum temperature (18.7 vs. 17.6 °C), and average minimum temperature (7.7 vs. 6.2 °C). However, thermal conditions varied strongly by month in both years. January temperatures were cooler than the long-term average in both years, whereas February and March were warmer than average. Because insect activity is sensitive to temperature, the number of days exceeding 16 °C—the previously reported minimum flight temperature for the southeastern blueberry bee (*Habropoda laboriosa*) [20]—was quantified. In 2024, the proportion of days exceeding 16 °C was higher in January (41.9%) and February (86.2%) than in 2025 (25.8% and 60.7%, respectively), whereas March was warm in both years.

Freezing events differed markedly between years. During the 2024 flowering period at PERL (14 February–20 March), only two nights had minimum temperatures below 0 °C, and 32 of 36 days exceeded 16 °C, with most warm days occurring after 20 February. In contrast, during the 2025 flowering period (17 February–31 March), eight consecutive nights of freezing temperatures occurred between 17 and 24 February, including a hard freeze on 21 February (minimum −7.8 °C). Despite these freezes, 35 of 43 flowering-period days exceeded 16 °C, with most warm days occurring after 25 February.

3.1.2. Flower Response to Freezing Temperatures

At PERL, 6 of 8 (75%) plants suffered freeze damage. 14/15 (93%) flowers in the bagged autogamy experiment that were in late bud or open during the late-February freeze period exhibited visible damage, including shriveling, swelling, or water-soaked tissue and were aborted within a week. Overall, 14 of 119 flowers (11.8%) used for the breeding system experiment were killed by freeze events and were excluded from fruit-set analyses.

3.1.3. Flowering Phenology

In 2024, 31/40 plants flowered (77.5%) and 29/31 fruited yielding a plant-level fruiting frequency of 93.5%. In contrast, in 2025, 91/102 monitored individuals flowered (89.2%) but only 40 (44%) produced fruit. Using only the 2025 flowering population, the proportion of floral morphs did not deviate significantly from a 1:1 expectation (short-styled = 37, long-styled = 31; $\chi^2_1 = 0.53$, $p = 0.47$). Flowering phenology varied between the two years. Population-level flowering curves showed that peak bloom occurred markedly earlier in 2024 than in 2025 (Table 1). In 2024, peak flowering occurred in early March, whereas in 2025 flowering was delayed until late March (Figure 3). Absolute flowering abundance peaked at 747 open flowers in 2024 and 1759 open flowers in 2025.

Table 1. Flowering phenology of *Gelsemium sempervirens* at the Piney Woods Environmental Research Laboratory (PERL), Walker County, TX, USA, in 2024 and 2025. Peak bloom values were estimated from Gaussian and Weibull fits to population-level flowering curves.

Year	First Flower	Peak Bloom (Gaussian)	Peak Bloom (Weibull)	Last Flower	Flowering Duration (Days, Mean ± SE)
2024	54	61.5	62.5	74	11.3 ± 1.2
2025	69	75.6	77.5	90	14.1 ± 1.5

Notes: Days are Julian. Peak bloom occurred approximately 14 days later in 2025 than in 2024 (bootstrap 95% CI: 13.6–14.4). Flowering duration did not differ significantly between years (Welch's *t*-test, $p = 0.156$).

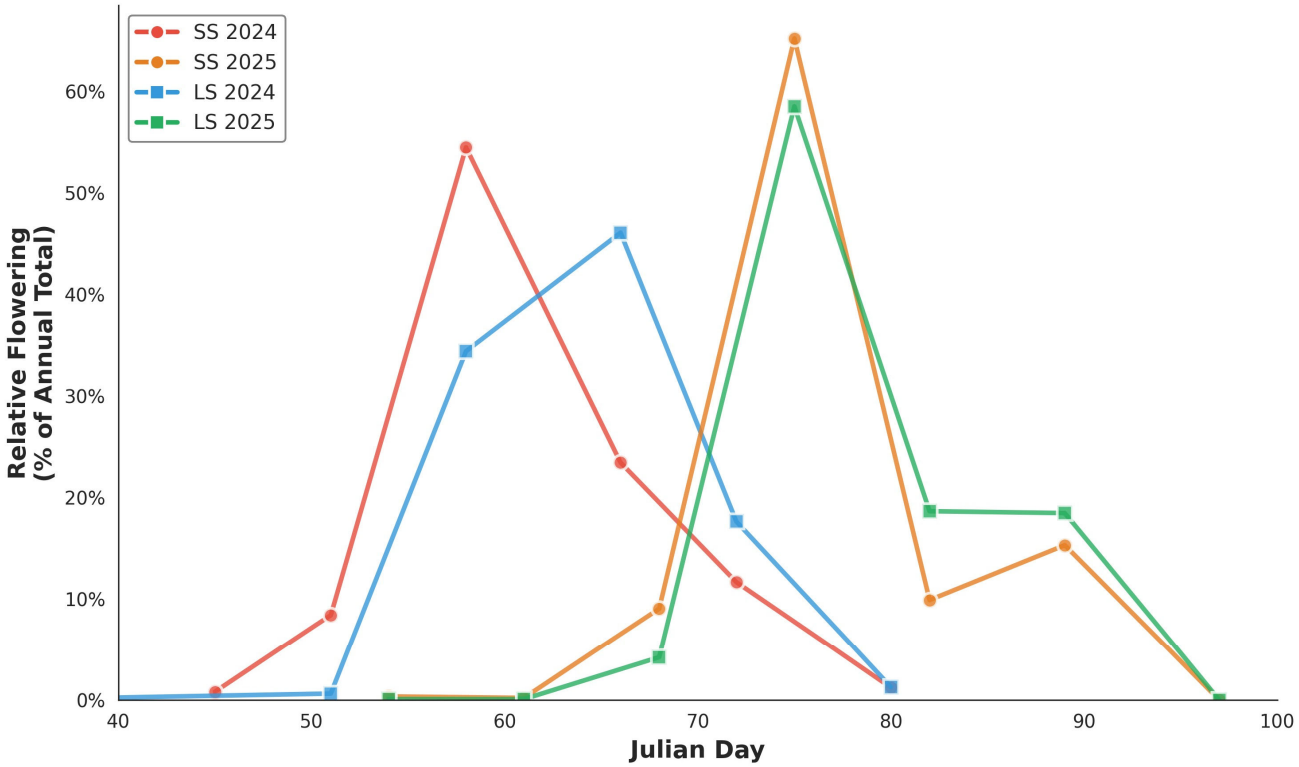

Figure 3. Population-level flowering curves for *Gelsemium sempervirens* at the Piney Woods Environmental Research Laboratory (PERL) in 2024 and 2025, shown separately for short-styled (SS) and long-styled (LS) floral morphs. Curves show the relative (normalized) abundance of open flowers by day of the flowering season, with points representing observed values and lines representing Gaussian fits used to estimate peak flowering timing.

Gaussian and Weibull fits to aggregated flowering curves yielded consistent estimates of peak bloom timing. In 2024, peak flowering occurred on Julian day 61.5 based on the Gaussian fit and Julian day 62.5 based on Weibull fit. In contrast, peak flowering in 2025 occurred on Julian day 75.6 (Gaussian) and Julian day 77.5 (Weibull), representing a delay of approximately 14 days. Bootstrap resampling confirmed a strong interannual shift in peak flowering (difference = 13.9 days; 95% CI: 13.6–14.4) (Table 1, Figure 3). Although peak timing differed sharply between years, flowering duration did not differ significantly. Mean flowering duration was 11.3 days in 2024 and 14.1 days in 2025 ($p = 0.156$). However, flowering curves in 2025 were more temporally compressed than in 2024, as indicated by a narrower Gaussian spread (SD ≈ 3.8 days in 2025 versus 5.5 days in 2024).

The SS and LS floral morphs exhibited consistently high flowering synchrony across both study years. Pianka's niche overlap index indicated substantial temporal overlap in flowering phenology, with values of 0.86 in 2024 and 0.99 in 2025, representing a 14.7% increase in overlap between years. In 2024, SS flowers peaked on Julian day 58 and

LS flowers on day 66 (8-day separation), although their flowering curves overlapped broadly. In 2025, both morphs reached peak flowering on Julian day 75, indicating complete convergence. Weighted mean flowering dates were also similar between morphs: in 2024, SS and LS means were day 61.1 and day 64.4 (difference = 3.3 days), and in 2025 they were day 77.1 and day 78.4 (difference = 1.3 days). Despite pronounced interannual shifts in flowering timing and concentration, morph overlap remained high in both years.

3.2. Floral Visitation

3.2.1. Autogamy Experiment vs. Open Flowers on Same Plants

Bagged flowers were used to test for autonomous self-pollination. None of the bagged autogamy control flowers produced fruits (0 of 38 flowers; fruit set = 0.00). In contrast, open-pollinated flowers exhibited substantial fruit production (31 of 104 flowers; fruit set = 0.30; 95% CI: 0.21–0.39). Open-pollinated fruit set did not differ between long-styled and short-styled plants ($\chi^2 = 0.02$, $p = 0.88$).

During pollinator effectiveness trials, bags were temporarily removed to allow controlled visitation; flowers that received no visits during these exposure periods effectively functioned as additional autonomous controls. Across all such unvisited bagged flowers (50 flowers on 26 LS and 24 SS plants in 2025), no fruits were produced, regardless of morph, plant identity, bag type, or flowering date.

3.2.2. Composition of Floral Visitors

Through both years, floral visitation at PERL was strongly dominated by a single bee species, *Habropoda laboriosa* (Table 2, Figure S1). In 2024, *H. laboriosa* accounted for approximately 70% of all visits. In 2025, dominance by *H. laboriosa* was even more pronounced, accounting for approximately 78% of all visits across the flowering season (Table 2). *H. laboriosa* was present throughout the entire flowering period in both years.

Table 2. Relative abundance (%) of floral visitors to *Gelsemium sempervirens* at the Piney Woods Environmental Research Laboratory (PERL), Walker County, TX, USA, in 2024 and 2025. Values represent the percentage of total recorded visits per year. The final column summarizes the temporal distribution of visits across the flowering period and highlights the sustained activity of the primary pollinator relative to other visitors.

Flower Visitor	2024 (% Visits)	2025 (% Visits)	Flight Period (Combined)
Habropoda laboriosa	69.8	77.8	14 February–24 March
Apis mellifera	14.2	10.0	20 February–14 March
Osmia spp.	10.3	9.5	20 February–14 March
All other Apoidea	—	0.6	16 February–10 March
Total Apoidea	93.4	97.9	—
Papilio polyxenes asterius	6.5	0.3	6 March–19 March
Other Lepidoptera	0.1	1.6	20 February–19 March
Total Lepidoptera	6.6	1.9	—
Other visitors †	0.0	0.2	10 March–24 March

Notes: † Includes Syrphidae (*Toxomerus* spp.) and *Archilochus colubris*. Percentages may not sum to exactly 100 due to rounding.

Other bee taxa were observed intermittently and contributed substantially less to total visitation. *Apis mellifera* accounted for approximately 10%–14% of visits across years, while *Osmia* spp. contributed approximately 9%–10%. Both species were primarily active during the first half of the bloom period. Carpenter bees (*Xylocopa*) and other apoids (*Bombus*, *Ceratina*) were rare. Lepidopteran visitors occurred sporadically and collectively accounted for less than 2% of visits in 2025 and less than 7% in 2024 and were primarily active in

the latter half of the bloom period. Total flowering visiting species were 7 in 2024 and 11 in 2025. However, the pollinator assemblage for both years was characterized by low functional redundancy and strong numerical dominance by *H. laboriosa* (Table 2). Floral visitation rates in both years are presented in Supplemental S2 Results.

3.3. Pollinator Effectiveness

Because *Habropoda laboriosa* dominated floral visitation across both years and exhibited strong temporal overlap with flowering, its effectiveness relative to other visitors was evaluated directly in controlled pollination trials in 2025. A total of 39 individual plants (21 short-styled, 18 long-styled) were observed across 27 observation days (8 in February and 19 in March), representing approximately 1560 min of observation by four observers. Floral visitation was rare in February and limited to *Xylocopa*, whereas visitation by *Habropoda laboriosa* began in early March and accounted for nearly all visits thereafter.

Across 75 flower-level observations in which at least one floral visit occurred, fruit set was overwhelmingly associated with visitation by *H. laboriosa*. To account for non-independence among flowers observed on the same plant and within the same day, observation periods were treated as independent sampling units for statistical inference. Fruit set occurred in 20 of 38 observations that included *Habropoda*, compared with only 1 of 11 observations in which *Habropoda* was absent (Table 3). Fruit set was therefore significantly more likely during *H. laboriosa* visits than during periods without *Habropoda* visitation (Fisher's exact test, $p = 0.014$). Observation periods, rather than individual flowers or plants, were treated as independent sampling units for statistical inference.

Table 3. Association between *Habropoda laboriosa* visitation and fruit set using observation periods as independent sampling units.

Habropoda Present	Samples (*n*)	With Fruit Set	Without Fruit Set	Proportion with Fruit
No	11	1	10	0.091
Yes	38	20	18	0.526

Notes: Statistical test: Fisher's exact test, $p = 0.014$.

Other bee visitors (*Apis*, *Bombus*, *Xylocopa*) were observed infrequently and were not associated with fruit set in this dataset. Lepidopteran visitation was rare and did not contribute to fruit production. Mixed-species visitation events were not treated as an independent pollination category because all mixed visits included at least one *H. laboriosa* visit; therefore, fruit set following mixed visits reflects the presence of *H. laboriosa* rather than pollination by other taxa.

When summarized at the flower level for descriptive purposes, flowers visited by *H. laboriosa* exhibited substantially higher fruit set (0.42 ± 0.06, mean $\pm$ SE, $n = 59$) than flowers visited by other bee taxa, none of which produced fruit ($n = 11$; Table 4). Flowers receiving two or more visits showed higher observed fruit set (0.50 ± 0.16, $n = 10$) than flowers receiving a single visit (0.32 ± 0.06, $n = 65$). Observed fruit set following *Habropoda* visitation also differed between floral morphs, with long-styled flowers exhibiting higher fruit set (0.59 ± 0.12, $n = 17$) than short-styled flowers (0.36 ± 0.07, $n = 42$).

Once fruits developed, however, seed production did not differ between morphs. Fruits produced following *H. laboriosa* visitation contained a mean of 11.6 ± 1.5 seeds ($n = 17$), corresponding to approximately 57% seed set. Seed number did not increase with increasing numbers of visits, and mixed-species visits did not result in higher seed production than visits involving *Habropoda* alone. Because flowers were bagged before and after pollination trials, no fruit herbivory was observed in these fruits.

Table 4. Fruit set and seed production following floral visitation by different visitor categories at the Piney Woods Environmental Research Laboratory (PERL), Walker County, TX, USA. Values are mean ± SE.

Visitor Category	Flowers Observed (*n*)	Fruit Set (Proportion ± SE)	Seeds per Fruit (Mean ± SE)
Habropoda laboriosa	59	0.42 ± 0.06	11.6 ± 1.5
Other bees (*Apis*, *Bombus*, *Xylocopa*)	11	0.00 ± 0.00	—
Lepidoptera	5	0.00 ± 0.00	—
Mixed visits ‡	10	0.50 ± 0.16	11.2 ± 2.1

Notes: ‡ All mixed visits included at least one *Habropoda laboriosa* visit. Fruit set was observed only in flowers receiving at least one *Habropoda laboriosa* visit; other visitor categories were too infrequent to permit reliable assessment of pollination effectiveness.

3.4. Fruit and Seed Predation

3.4.1. Fruit Production in the Phenology Census Plants

Fruit production varied strongly among years. In 2023, plants produced a mean of 26.8 ± 6.0 fruits per plant (range 0–459), with 69 of 102 monitored individuals producing at least one fruit. As in subsequent years, fruit production exhibited strong right-skew, reflecting substantial among-plant variation in realized reproductive output. In 2024, 29 of 31 flowering plants fruited (93.5%) while, in 2025, only 40 of 91 flowering plants (44%) produced fruit. Mean fruit production per plant differed strongly between years. Plants produced substantially more fruits in 2024 (20.95 ± 6.02 fruits per plant) than in 2025 (3.82 ± 1.08 fruits per plant). Restricting analyses to fruiting individuals only yielded a similar pattern, with higher fruit production per plant in 2024 than in 2025 (Mann–Whitney *U* test, $p = 0.00077$).

Total fruit production occurred in all study populations but varied strongly among years. At PERL, population-level fruit production exceeded 2500 fruits in both 2023 and 2024 but declined sharply in 2025 (378 fruits). At the plant level, fruit set ratios further illustrate this contrast. In 2024, ranging from approximately 0.4–0.7. In contrast, ratios in 2025 were often <0.1.

3.4.2. Seed Set and Seed Production in Fruits

Seed set (pollination efficiency) did not differ among herbivory categories (Table 5). Pollination efficiency remained uniformly high in fruits with no herbivory and internal wall feeding. Closed fruits with no herbivory produced an average of 12.14 ± 0.6 seeds (mean ± SE), corresponding to a mean seed set of 0.74 (Table 5). No fruit exceeded the assumed ovule number of 20, and several produced the full complement of seeds.

Table 5. Pollination efficiency and seed survival in closed fruits of *Gelsemium sempervirens* at the Piney Woods Environmental Research Laboratory (PERL), Walker County, TX, USA. Values are mean ± SE. Fruits exhibiting external wall feeding without internal damage were pooled with the no-internal-herbivory category. Comparisons between categories were conducted using Welch two-sample *t*-tests.

Variable	No Internal Herbivory (*n* = 69)	Internal Wall Feeding (*n* = 50)	Test Statistic
Pollination efficiency [1]	0.74 ± 0.02	0.72 ± 0.03	$t_{97} = 0.57$, $p = 0.57$
Good seeds per fruit	12.14 ± 0.58	4.82 ± 0.62	$t_{104} = 9.03$, $p < 0.0001$
Proportion good seeds [2]	0.88 ± 0.02	0.36 ± 0.04	$t_{83} = 11.6$, $p < 0.0001$

Notes: [1] Pollination efficiency calculated as min (TotalSeeds/20, 1.0) for each fruit. [2] Proportion good seeds calculated as TotalGood/TotalSeeds for each fruit.

Fruit herbivory was common in the PERL population, with 48.6% of fruits attacked (51/105). In contrast to pollination efficiency, seed survival differed strongly among herbivory categories (Table 5, Figure S3). Fruits without herbivory (Figure S4) exhibited the highest seed survival (Good/Total Seeds ≈ 0.88), with few damaged or developmentally arrested seeds. Fruits with external wall feeding showed similar seed survival and did not differ significantly from unattacked fruits.

Fruits with internal wall feeding exhibited marked reductions in viable seed production (Table 5, Figures S3, S5 and S6) (an approximate 60% reduction). Good seed numbers declined to <5 seeds per fruit, while the proportion of tiny green seeds increased sharply (Figure S6). Fruits with pericarp holes exhibited the most severe seed loss (Figure S5), with good seed survival often below 0.30 and extensive secondary damage (Figure S6). Hole presence therefore represented the terminal stage of herbivore attack, associated with extensive secondary feeding and near-complete loss of viable seed production. Binomial generalized linear models confirmed that internal wall feeding and hole presence significantly reduced seed survival relative to unattacked fruits ($p < 0.001$). Fruit length and width did not differ significantly among herbivory categories (ANOVA, $p > 0.10$), indicating that herbivores did not preferentially target fruits based on size.

4. Discussion

4.1. Reproductive Failure Does Not Explain the Western Range Limit of Gelsemium sempervirens

This study tested the hypothesis that reproductive failure constrains *Gelsemium sempervirens* at its western geographic boundary. Across two flowering seasons at the Piney Woods Environmental Research Laboratory (PERL), reproductive outcomes did not show progressive deterioration consistent with intrinsic reproductive failure at a range edge. Fruit initiation following successful pollination occurred in both years, distyly remained fully functional, and no evidence of autonomous self-pollination or morph-specific reproductive depression was detected. Closed fruits routinely produced viable seeds in numbers comparable to those reported from central-range populations in the Coastal Plain and Piedmont [19–22,31]. Together, these results demonstrate that breakdown of the mating system or failure of fertilization does not explain the abrupt western distributional limit of *G. sempervirens*.

These findings are consistent with recent syntheses arguing that range limits often emerge from eco-evolutionary constraints and trade-offs, rather than intrinsic failure of reproduction per se [36,37]. In particular, frameworks that emphasize species' capacity to track environments through colonization ability and phenotype–environment matching predict that populations may persist at margins when reproductive functions remain intact but other ecological axes become limiting [37].

Because *Gelsemium* is obligately outcrossing and depends on legitimate pollen exchange between floral morphs, pollination would be expected to decline if effective pollinators declined toward the range edge [11,12]. In much of the species' range in the Coastal Plain, the southeastern blueberry bee (*Habropoda laboriosa*) is among the most effective early-spring pollinators [22,24]. At PERL, *H. laboriosa* was present in both study years and dominated the floral visitor assemblage throughout the flowering period. Fruit set following visitation was overwhelmingly associated with *Habropoda*, whereas visits by other bee taxa rarely resulted in fruit production, although sample sizes were too small to fully evaluate their potential for pollination. These observations indicate that the primary effective pollinator of *Gelsemium* remains present and functionally dominant at the western range edge, and that pollinator absence is unlikely to explain reduced reproduction in this population.

Viewed broadly, the persistence of effective pollination at a range boundary accords with evidence that demographic performance at margins can remain robust when key mutualists are present, and that adaptive limits—rather than reproductive collapse—often structure edges in space and time [38].

4.2. Stability of Distyly and Implications for Range-Edge Theory

Breakdown of heterostylous mating systems is a well-documented mechanism of reproductive failure at ecological margins, particularly when pollinator services become unreliable [10,11]. However, *Gelsemium sempervirens* shows no evidence of such breakdown at its western range edge. Functional distyly remains intact, morph synchrony is high, and legitimate pollination is common. The persistence of an obligate outcrossing system at the range edge suggests that selection has not favored autonomous selfing or partial compatibility as reproductive assurance, likely because pollination remains sufficiently reliable. This result highlights the importance of directly measuring pollinator effectiveness and fruit set rather than inferring reproductive limitation from geographic coincidence or pollinator range overlap alone. More broadly, intraspecific trait variation can mediate how mating systems function across gradients and how edge populations match local environments [39], while eco-evolutionary limits to adaptation help explain why some margins remain sharp despite adequate reproduction [38].

4.3. Phenological Variability, Visitation Dynamics, and Pollination Opportunity

Although pollination was effective, flowering phenology and pollinator activity exhibited pronounced interannual variability. Peak flowering occurred approximately two weeks later in 2025 than in 2024 and was more temporally compressed, consistent with sensitivity to early-season climatic conditions. Despite these shifts, flowering overlap between long-styled and short-styled morphs remained high at the population level, indicating that phenological asynchrony between morphs did not compromise opportunities for legitimate pollination.

Reproductive success was substantially lower in 2025 than in 2024. The most parsimonious explanation for this reduction is direct abiotic damage associated with severe freezing events rather than pollination failure. Early season freezes in 2025 eliminated or damaged developing buds and flowers, reducing the number of reproductive structures available for successful fruit development. Such direct effects of cold stress on floral tissues can strongly constrain reproduction independently of pollinator activity. Importantly, no evidence from this study indicates that reduced reproduction in 2025 resulted from pollinator absence or failure of fertilization processes.

Taken together, these results indicate that reproductive output at the western range edge of *G. sempervirens* is shaped primarily by episodic abiotic stress rather than by pollinator decline or breakdown of the mating system. Interannual variation in climate, particularly extreme cold events, can substantially influence reproductive success even when fertilization processes remain intact. Such environmentally driven variability is consistent with contemporary range-limit theory emphasizing phenotype–environment matching and limits to adaptive responses under fluctuating conditions [37,38]. While trait variation and mutualistic interactions may influence persistence at margins in other systems, the present results demonstrate that reduced reproduction at this western range edge reflects environmental filtering rather than intrinsic reproductive failure.

4.4. Pollination, Reproductive Limitation, and the Eastern Texas Range Margin

Fruit production at the PERL site varied markedly among years, providing important interannual context for interpreting reproductive performance at the western range edge of *Gelsemium sempervirens*. In 2023, plants produced a mean of 26.8 fruits per individual,

with more than two-thirds of monitored plants fruiting, indicating that high reproductive output is possible at this site under favorable conditions. Fruit production declined in 2024 but remained substantial, whereas in 2025 both the proportion of flowering plants that fruited and mean fruit production per plant were sharply reduced. Importantly, this decline occurred despite high flowering frequency, intact distyly, and the continued presence of effective pollinators. Together, these patterns indicate that interannual variability in realized fruit production reflects sensitivity to year-specific environmental conditions rather than chronic reproductive limitation at the western range margin.

Although flowering phenology and visitation rates varied among years, the present study does not provide evidence that reduced reproduction resulted from insufficient pollination intensity or pollen delivery. Visitation rates were low and temporally uneven, but fruit initiation occurred in both years, and no threshold level of visitation associated with reproductive failure was identified. Accordingly, variation in reproductive output is best interpreted as arising from stochastic exposure of flowers to favorable conditions rather than from consistent pollination limitation.

This interpretation contrasts with models of pollination quantity limitation that invoke reduced visit frequency as a primary constraint on reproduction. While such mechanisms may operate in other systems or under different demographic contexts, the present data do not demonstrate that low visitation intensity imposed a systematic constraint on reproduction in this population. Instead, environmental filtering—particularly freeze damage and its effects on floral availability—appears sufficient to explain the observed interannual variation in fruit production.

Although *H. laboriosa* itself approaches a range boundary in East Texas, its continued presence and dominance indicate that a coupled plant–pollinator range limit is not imposed by pollinator disappearance. Rather, the eastern Texas range margin of *G. sempervirens* likely reflects the cumulative effects of environmental variability and episodic reproductive shortfall, rather than a discrete threshold driven by pollinator availability or pollination opportunity. Post-pollination processes quantified in this study, including fruit herbivory and seed loss, further reduced realized reproductive output and contributed to interannual variation in recruitment potential. Together, these results indicate that reproduction at this range margin is shaped by multiple sequential filters acting after flowering, rather than by failure of pollination or breakdown of the mating system.

4.5. Geographic Variation in Pollinator Assemblages and Ecological Context

The pollinator composition in East Texas is nearly identical to that in the coastal plain of South Georgia [21–23] but differs substantially from that observed in the Piedmont of North Georgia and North Carolina (Figure 4). This pattern is consistent with regional variation in soil types and climate regimes between the coastal plain and Piedmont, as *Habropoda laboriosa* is strongly associated with sandy soils for nesting [27] and flowering in the Piedmont typically occurs later in the season (often by approximately a month [26,31] potentially allowing later emerging bee species to contribute more strongly to visitation.

Geographic variation in pollinator assemblages is expected where climatic regimes, soil properties, and vegetation structure vary across a species' range, even in the absence of strong physiological constraints on reproduction. Across the southeastern United States, *Gelsemium sempervirens* occupies habitats that differ markedly in soil texture, moisture availability, forest structure, and disturbance history, all of which can influence the composition and activity of early-season pollinators. Coastal Plain populations typically occur on sandy, well-drained soils within relatively open pine-dominated forests, whereas Piedmont populations occupy more heterogeneous landscapes characterized by finer-textured soils, greater topographic relief, and mixed hardwood–pine forests. These environmen-

tal differences are expected to influence nesting substrate availability and phenological overlap for early-emerging bees, thereby contributing to observed differences in pollinator assemblage composition.

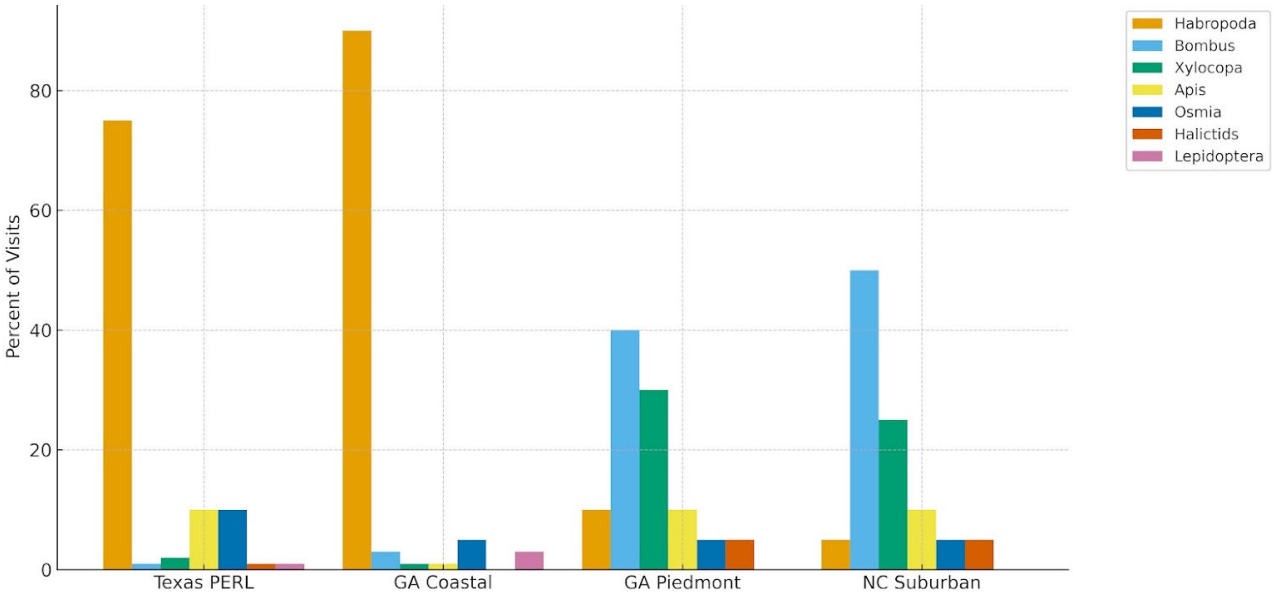

Figure 4. Comparison of pollinator assemblage composition visiting *Gelsemium sempervirens* across regions of the southeastern United States. Relative contributions of major floral visitor groups are shown for eastern Texas (PERL; this study) and for populations in the Coastal Plain and Piedmont regions based on published datasets. Pollinator composition in eastern Texas closely matches that reported from Coastal Plain populations in southern Georgia, where visitation is dominated by *Habropoda laboriosa*, but differs markedly from Piedmont populations in northern Georgia and North Carolina, where visitation is more taxonomically diverse and less strongly dominated by a single effective pollinator. Data for comparison regions are redrawn from Adler and Irwin [19] and Fitch et al. [31].

The close similarity between the pollinator assemblage observed at the eastern Texas range edge and those reported from Coastal Plain populations in southern Georgia suggests that regional ecological context, rather than geographic position alone, is a primary determinant of pollinator community composition. In contrast, Piedmont populations in northern Georgia and North Carolina support more taxonomically diverse assemblages with reduced dominance by *Habropoda laboriosa*, reflecting differences in habitat structure and pollinator availability. These patterns indicate that visitation assemblages associated with *Gelsemium* can vary geographically while remaining functionally adequate for pollination without implying uniformity in pollination dynamics across the range.

From an evolutionary perspective, these results align closely with the geographic mosaic theory of coevolution proposed by John N. Thompson [40,41], which predicts that species interactions vary spatially as a function of local ecological conditions, generating a mosaic of interaction outcomes rather than uniform selection pressures across a species' range. Within this framework. Within this framework, variation in pollinator assemblage composition across regions reflects local ecological context rather than a directional weakening of plant–pollinator interactions toward the western range edge.

Importantly, the persistence of a Coastal Plain–like pollinator assemblage in eastern Texas suggests that the western range limit of *Gelsemium* is not associated with a transition to a qualitatively different pollination regime. Rather, the abrupt distributional boundary likely reflects ecological constraints not directly to pollinator assemblage composition, such as reduced availability of suitable habitats, altered fire regimes, or shifts in forest structure

across the pine–oak savanna ecotone. Under this interpretation, geographic variation in pollinator assemblages represents ecological flexibility within the species' interaction network, rather than evidence of mutualistic breakdown at the range edge.

4.6. Cryptic Fruit Herbivory: Detection, Impact, and Range Implications

In contrast to the high efficiency of pollination, post-pollination seed predation exerted strong effects on realized reproductive output. Fruits at PERL exhibited multiple forms of herbivory, ranging from external wall feeding to extensive internal destruction by a concealed midge-like herbivore. Dissections revealed that early larval feeding frequently causes seed destruction without causing the capsule wall to collapse. Estimates of herbivory in *Gelsemium* have likely been substantially underestimated in the literature. Prior studies relied on externally visible "windows" (capsule collapse) to identify damage [31]. However, this study showed that collapsed windows are a late, indirect outcome of heavy infestation; many fruits with extensive internal damage retain their structural integrity. Furthermore, previous studies often terminated sampling at early fruit set or used greenhouse protocols that excluded the specific window of gall-midge oviposition. By extending sampling through maturation and employing dissections, this study reveals that cryptic herbivory is neither rare nor anomalous, but rather a historically overlooked pressure on reproductive output.

Despite its severity, this seed predation does not appear to determine the western range limit of *Gelsemium sempervirens*. The same or a closely related midge attacks developing fruits within the species' range interior (e.g., North Carolina) [31], indicating that herbivory is not geographically restricted to the range margin. The geographic coincidence of this antagonist precludes a simple presence–absence explanation for range limitation. Instead, fruit herbivory acts as a context-dependent demographic modifier of reproductive success. Early larval feeding causes internal seed damage and can induce premature capsule permeability, exposing seeds to secondary predators and decomposers. These cascading effects amplify seed loss, particularly when fruit development is slow. However, unattacked fruits at the range edge consistently produced high numbers of viable seeds. Thus, while cryptic herbivory reduces realized fecundity, it represents a broadly distributed ecological cost on reproduction rather than a unique barrier preventing westward expansion.

This perspective aligns with broader range-edge theory, in which broadly distributed antagonists interact with local environmental conditions to shape population performance without acting as singular causal agents of range limits. From a range-limit perspective, reductions in realized reproduction may still interact with dispersal to influence spread potential; however, recent syntheses indicate that variation in dispersal ability and evolution of dispersal kernels can outweigh moderate reductions in fecundity in determining edge dynamics [42,43].

4.7. Ecological Rather than Reproductive Mechanisms Likely Define the Western Range Edge

Given the absence of evidence for reproductive failure at PERL, the abrupt termination of *Gelsemium sempervirens* in eastern Texas is unlikely to result from failures in pollination, mating-system function, or early seed development. Instead, ecological factors unrelated to reproduction provide a more parsimonious explanation. The transition from pine-dominated forests to post-oak savanna and prairie is associated with reductions in tree density and vertical structure required for vine growth, shifts in soil texture and hydrology, and changes in disturbance regimes, particularly fire frequency [44,45]. *Gelsemium sempervirens* is sensitive to fire and dependent on woody hosts for support, making it poorly suited to open savanna and prairie landscapes even where climatic conditions may otherwise be suitable.

Seed dispersal may also influence population dynamics near the range margin in *Gelsemium sempervirens*. The species produces relatively small, wind-dispersed seeds, but actual dispersal distances in natural habitats remain poorly quantified. Barriers such as forest structure, understory density, and limited availability of suitable microsites could restrict successful establishment beyond parent plants. Although dispersal processes were not evaluated in this study, they represent a plausible ecological filter and a productive direction for future work aimed at understanding the factors shaping population spread and site occupancy.

This interpretation accords with contemporary perspectives that species' range limits often reflect trade-offs among colonization capacity, phenotype–environment matching, and constraints on adaptation, with dispersal and trait expression jointly governing whether populations can track environments beyond current boundaries [37,38,43].

4.8. Future Research Questions

These results highlight several critical avenues for future research on fruit herbivory and seed limitation in *Gelsemium sempervirens*. First, broader geographic sampling is needed to quantify natural variability in fruit herbivory, particularly comparing intact forest interiors with suburban fragments. Such work would clarify whether infestation severity reflects habitat structure, landscape context, or interannual variation in phenology and environmental conditions. Second, the taxonomic identity and life history of the gall-midge herbivore remain poorly resolved. Detailed study of the insect's phenology, host specificity, and associated parasitoids is required to understand the stability of this interaction. Third, the ecological consequences of collapsed capsule "windows" remain largely unexplored. Characterizing the secondary arthropods and fungi that colonize these microhabitats would help disentangle primary herbivore effects from secondary mortality. Finally, integrating fruit herbivory into demographic models is a key next step. Quantifying how reduced seed production translates into seedling recruitment and population growth—particularly at range edges—is essential for evaluating the broader ecological significance of this cryptic seed damage. Ongoing work by the author is addressing these questions across multiple natural and suburban sites in southeastern Texas. These results will be presented separately to provide broader spatial and demographic context.

5. Conclusions

This study provides strong evidence that reproductive failure does not constrain *Gelsemium sempervirens* at its western range edge. Pollination efficiency, functional distyly, and early seed development remain robust, and effective pollinators are present. While post-pollination seed predation reduces final seed numbers, it is not intensified at the range boundary. Instead, the species' geographic limit is best explained by ecological gradients in habitat structure, disturbance regimes, and environmental variability rather than intrinsic reproductive barriers. Together with recent work, these results emphasize that plant range limits are best understood through integrated eco-evolutionary lenses: trade-off frameworks that couple colonization and phenotype–environment matching [37], limits to adaptation and plasticity in time and space [38], and the roles of intraspecific trait variation and dispersal in setting niche positions and facilitating or impeding expansion [39–41]. Within this context, *Gelsemium sempervirens* represents a valuable system for evaluating how reproduction, traits, antagonists, and landscape structure interact to shape plant distributions at biogeographic boundaries.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/f17040413/s1, Supplemental S1 Methods. Fruit herbivory detection and classification. Figure S1: Pollinators of *Gelsemium sempervirens* at the western range limit.

Supplemental S2 Results. Visitation rates and temporal patterns. Figure S2: Seasonal variation in floral visitation rate. Figure S3: Effects of fruit herbivory on seed survival. Figure S4: Unattacked fruits and seeds. Figure S5: External fruit herbivory on *Gelsemium sempervirens*. Figure S6: Internal herbivory damage on fruits and seeds on *Gelsemium sempervirens*.

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