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# Early fitness consequences of cultivar gene escape in flowering dogwood (Cornus florida L., Cornaceae)

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**Research Article**

**Keywords:** cultivar-to-wild gene flow, cultivar gene escape, narrow-sense heritability, common garden, introgression, Cornus florida

**Posted Date:** November 27th, 2026

**DOI:** https://doi.org/10.21203/rs.3.rs-11816232/v1

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**Additional Declarations:** No competing interests reported.

## Abstract

Ornamental cultivars of native plants are increasingly abundant in urban landscapes, creating large domestic reservoirs adjacent to wild populations. Whether cultivar alleles that escape into wild stands persist depends on how cultivar-origin offspring perform during early recruitment into natural habitats. We tested two competing hypotheses for flowering dogwood (*Cornus florida*): that cultivar ancestry imposes an early fitness penalty under wild conditions (maladaptation), or that cultivar-origin seedlings perform at least as well as wild seedlings, leaving early viability selection unable to restrain gene escape (cultivar persistence). We monitored survival, growth, and biomass over two growing seasons for 569 open-pollinated seedlings from 36 maternal families (20 managed landscape, 16 second-growth forest) grown in an unmanipulated, deeply shaded forest understory common garden. We classified seedlings by landscape provenance (maternal origin) and neutral genetic ancestry (admixture percentage with commercial voucher lines). Overall survival was high (~ 82%) and did not differ by origin or admixture score. While origin explained little growth variation, maternal family accounted for substantial variation among cultivar-origin seedlings, yielding moderate narrow-sense heritabilities for height, above-ground biomass, and stem biomass ( $h^2 \approx 0.3\text{-}0.5$) alongside heterogeneous family survival. Native families, in contrast, exhibited no heritable variation across any measured trait. Cultivar-origin seedlings were not disadvantaged in a deeply shaded understory, suggesting that early viability selection is unlikely to limit the establishment of escaped cultivar alleles. These results highlight the potential for long-term introgression and genetic homogenization in declining wild *C. florida* populations.


## Introduction

The flowering dogwood (*Cornus florida* L., Cornaceae) is an ecologically important understory tree in mesic forests of eastern North America. Populations of native *C. florida* currently face several demographic pressures, the most important of which include the fungal pathogen *Discula destructiva* (Redlin 1991; Sherald et al. 1996; Carr and Banas 2000; Jenkins and White 2002), which thrives in the moist and shaded understories, resulting in significant mortality, and exotic invasive species such as *Microstegium vimineum* (Trin.) A. Camus, whose dense groundcover significantly limits seedling recruitment (Flory and Clay 2010; Schmit et al. 2020). Changes in forest successional composition toward more shade-tolerant species increase both disease severity and competition from such invasives (Pierce et al. 2008; Suchecki and Gibson 2008). Since the mid-1700s, dogwoods have been cultivated for their copious floral displays, striking bract color, and exceptional growth vigor in open spaces, and multilocus genotyping can identify many recognized cultivars (Wadl et al. 2008). In residential and commercial landscapes, these trees are commonly grown with significant canopy openings, are completely free from overstory competition, and benefit from extensive human provisioning, including irrigation, fertilization, and pest control. This long-standing commercial demand, with an estimated annual sales rate of $31 million (USDA 2020; Hamm et al. 2026), has created a highly managed suburban and urban reservoir of cultivar genotypes in close contact with remnant natural forests.

This spatial proximity suggests that the potential for asymmetric gene escape of cultivars into native forest populations is substantial. *Cornus florida* possesses several life-history traits that facilitate either pollen- or seed-mediated gene flow across the urban-native interface. This species has a predominantly outcrossing mating system with strong prezygotic barriers to selfing (Reed 2004; Dyer et al. 2012). Although evidence supports environmental influence on flowering time (Reader 1975), significant phenological overlap remains in the approximately 2–4 week flowering window between urban cultivars and native *C. florida* individuals. A broad suite of insect pollinators provides pollination services, spanning at least 11 insect families, many of which are commonly found in both forest and urban habitats (Carr 2010; Rhoades et al. 2011). It produces bright red drupes in the fall, an important food resource for a variety of forest species, and they may be dispersed via endozoochory (Dyer et al. 2012). These dispersal mechanisms have historically maintained high levels of genetic diversity within the species (Hadziabdic et al. 2010, 2012; Pais et al. 2017).

The long-term demographic and evolutionary consequences depend heavily on how cultivar-origin offspring perform when they recruit into natural habitats. Cultivated dogwoods have been selected to maximize reproductive output and thrive in open, high-light environments so that these traits may represent a severe physiological mismatch in native forest conditions. Artificial selection to persist in human-managed environments, where resources are abundant, has essentially no native recruitment through the seed pool, resource competition is reduced during early growth stages, and canopy competition is largely absent. These conditions may relax selection on traits related to resource-use efficiency, early growth, and shade tolerance. These trade-offs may make cultivar-origin offspring less able to establish in deeply shaded, resource-competitive, and unmanaged forest understories. If cultivar-origin genotypes carry such maladaptive traits, early-stage viability selection will likely weed them out, mitigating the evolutionary impact of gene escape. However, if cultivar-origin seedlings perform as well as or better than native forest genotypes despite these novel selection pressures, cultivar genes are expected to establish and persist, raising the long-term consequences of genetic introgression and the loss of unique, locally adapted wild genotypes.

In this study, we tested two competing hypotheses regarding the consequences of cultivar gene escape into proximate native populations of flowering dogwood. If human selection for copious floral displays and vigor in open, high-light environments has relaxed selection for shade tolerance, understory competitiveness, and early seedling growth, cultivar-origin seedlings are expected to exhibit a fitness penalty under wild forest canopy growing conditions, manifested as reduced survival, growth, and/or biomass accumulation compared to seedlings with non-cultivar heritage. We will refer to this as the *maladaptation hypothesis*. Conversely, if the vigor and physiological growth traits selected under cultivation result in non-negative consequences in native environments, then early-stage viability selection would not restrain gene escape, signaling that cultivar alleles can readily establish and persist. This scenario sets the stage for long-term genetic introgression of cultivar genotypes into surrounding native populations—the *cultivar persistence hypothesis*.

To differentiate between these two hypotheses, we sampled offspring arrays from maternal trees from managed landscapes and native second-growth forests surrounding the metropolitan region of Richmond, Virginia, USA. We classified offspring in two ways. First, we used the location of the maternal tree in the landscape to designate cultivar if the tree was located in a landscaped and managed location (commercial and residential properties in Richmond, Virginia) or as native if the maternal tree was sampled from second-growth forests (Pocahontas State Park and the Rice Rivers Center). To correct for potential pollen-mediated gene flow from native populations into cultivar trees, or longer-term introgression of cultivar genes into native populations, we also used multilocus genotyping to compare genetic admixture in offspring genotypes from well-known cultivar varieties planted in the Mid-Atlantic region. We germinated seeds and transplanted 569 seedlings into a common garden in the deeply shaded understory of a second-growth mixed hardwood forest at the VCU Rice Rivers Center. We monitored all seedlings across two growing seasons for survival, growth (height and stem diameter), and dry above- and below-ground biomass. Crucially, because we did not experimentally manipulate light, our common garden provides a direct empirical test of early seedling performance under natural forest understory conditions, allowing us to evaluate whether cultivar-origin seedlings face a viability bottleneck when recruiting into deeply shaded, natural environments.

# Methods

## Study species

*Cornus florida* is a common understory tree native to the forests of eastern North America, with a natural range extending from northern Florida to southern New York and eastward to Michigan, Missouri, and parts of eastern Texas. Cultivated varieties of *C. florida* can be found in residential landscaping throughout the native range. Native *C. florida* individuals are common in second-growth forests throughout its range, competing as subcanopy trees and typically reaching no more than 10 m in height. Flowering occurs over approximately 2–4 weeks in early spring, with inflorescences containing 20–30 perfect flowers subtended by four large white bracts. Insects from 11 taxonomic families pollinate the plant, depending on the surrounding habitat (Carr 2010; Rhoades et al. 2011).

# Sampling Design

We identified maternal trees in both managed urban environments and second-growth forests around Richmond, Virginia. In urban areas, researchers sampled maternal trees from residential yards (with landowner permission) and public spaces. We sampled native maternal dogwood trees in the deciduous and pine second-growth forests of Pocahontas State Park in Chesterfield, VA, and at the Virginia Commonwealth University (VCU) Rice Rivers Center in Charles City County, VA. We found no evidence that native tree sampling location affected survival or any phenotypic trait (Table S1, Supplementary Materials), so we felt justified in combining samples from the Rice Rivers Center and Pocahontas State Park trees into a single native category.

We sampled open-pollinated seeds from 36 focal maternal individuals in both urban and native environments in fall 2017. We depulped individual seeds and subjected them to an acid wash (following Carr 2010), and used average seed weight per mother as a surrogate for material provisioning. We then planted seeds in a 2:1 sphagnum-perlite mixture and sealed them in gas-permeable bags (Garner Enterprises, Willis, TX). After stratification at 4°C for at least 90 days, we monitored seeds for signs of germination. Germination occurred over an extended period, and we recorded the germination date for each seed to account for differences in developmental time between germination and subsequent trait measurements. After cotyledon expansion, we planted seedlings in 4-inch nursery pots and grew them indoors before transplanting them into the common garden.

## Common Garden

We established a common garden in the understory of a second-growth mixed hardwood forest at the VCU Rice Rivers Center (Charles City Count, Virginia). We deliberately situated the garden under a deeply shaded canopy to evaluate seedling establishment under natural, unmanipulated understory light regimes. To prevent seedling loss to deer browsing (Long et al. 2007), we surrounded the common garden with an 8-ft exclusion fence (Redick and Jacobs 2020). At planting, we had 20 family arrays (n= 395 seedlings) collected from maternal trees classified as cultivar and 16 family arrays ( $n$ n= 174 seedlings; see Table S2, Supplementary Materials) whose maternal location was designated as native. We transplanted each seedling into a 2-gallon plastic nursery pot randomly placed within the garden.

We monitored seedling growth and survival over two growing seasons, with survival censuses conducted each year at peak growth (May/June) and at the end of the growing season before leaf drop (September/October). We measured height from the base of the plant to the apical meristem, and stem diameter just below the cotyledons (when present) or the cotyledon scar (thereafter).

To control for confounding effects of foliar pathogens during growth measurements, we treated seedlings biweekly with fungicides (Cleary's 3336F, neem oil, milk solution) upon the first emergence of powdery mildew (*Erysiphe pulchra*) in spring of Year 2. Powdery mildew represents a common foliar disease affecting nursery seedlings in this study region (Hamm et al. 2026). Managing fungal pressure uniformly across all seedlings ensured that growth and allocation metrics reflected understory shade and microclimate performance, independent of differential foliar disease defoliation. At the end of the second growing season, before leaf drop, we harvested all plants. We separated stem and leaf tissue from the roots, placed them in brown paper bags, and dried them at 62°C for 72 hrs. We then weighed samples to determine above- and below-ground biomass (AGB and BGB, respectively). We further separated above-ground biomass into leaf biomass (LB) and stem biomass (SB).

## Genetic Analyses

We collected leaves from maternal individuals and froze fresh tissue at–20°C until DNA extraction. We collected seedling leaf tissue after seedlings were established in the common garden. We also collected samples from known *C. florida* cultivars provided by the Rutgers University horticultural program and from individuals in commercial nurseries in the greater Richmond, VA, metropolitan area. These individuals provided the cultivar panel for admixture analysis (see below).

We extracted genomic DNA from approximately 50 mg of plant tissue following standard Qiagen DNeasy Plant Kit protocols and standardized concentrations using a NanoDrop 8000 (NanoDrop, Wilmington, DE, USA). We used Qiagen Type-It Microsatellite PCR kits to perform 20 µL amplification reactions with ~ 20 ng of DNA. We amplified samples at 9 microsatellite loci identified as diagnostic for cultivar strains: cf213, cf273, cf581, cf585, cf597, cf634 (Table 2, Wadl et al. 2008), cf020, cf125, cf701 (Table 3, Wang et al. 2009). Polymerase Chain Reaction (PCR) amplification settings were: 5 min at 95°C, 90s at 60°C, 30s at 72°C, x 34, then 30 min at 60°C. We sent amplicons to the Nevada Genomics Center for fragment analysis. Peaks were called in Geneious Prime (v. 2021.0.3). The presence of null alleles was assessed with the nulls function in the genepop R package (v. 1.2.17; Rousset 2008), which returns a maximum-likelihood estimate of null-allele frequency and its confidence interval for each locus. Genetic diversity of maternal trees and offspring arrays was quantified across the nine microsatellite loci as number of alleles per locus ( $A$), effective number of alleles ( $A_e$), observed and expected heterozygosity ( $H_o$, $H_e$ ), and single-locus and combined multilocus exclusion probabilities ( $P_e$) using the gstudio R package (v. 1.14; Dyer 2009).

Table 2

Model selection and latent-scale quantitative-genetic parameters for seedling survival, from binomial generalized linear mixed models (logit link). Subsets: Total, Native, and Cultivar (split by maternal-tree location) compare family, origin + family, and fixed-only (germination timing + seed weight, no random effects) models; AP (seedlings with a genotype) instead compares the family model with and without Admixture Percentage as an additional fixed covariate (family vs. AP + family). Variance components, proportion of latent-scale variance, and half-sib heritability ($h^2$) with 1000-replicate bootstrap 95% CIs; residual variance fixed at $\pi^2/3$.

| Subset | Model | AICc | ΔAICc | wAICc | $V_{origin}$ | $V_{family}$ | $P_{family}$ | $h^2$ |
|---|---|---|---|---|---|---|---|---|
| Total | family | 409.8 | 0.0 | 0.54 | — | 0.29 [0.00, 0.78] | 0.08 | 0.32 [0.00, 0.77] |
| Total | fixed only | 411.2 | 1.4 | 0.27 | — | — | — | — |
| Total | origin + family | 411.9 | 2.0 | 0.19 | 0.00 [0.00, 0.00] | 0.29 [0.00, 0.75] | 0.08 | 0.32 [0.00, 0.74] |
| Native | fixed only | 157.2 | 0.0 | 0.74 | — | — | — | — |
| Native | family | 159.3 | 2.1 | 0.26 | — | 0.00 [0.00, 0.48] | 0.00 | 0.00 [0.00, 0.51] |
| Cultivar | family | 252.7 | 0.0 | 0.68 | — | 0.48 [0.00, 1.21] | 0.13 | 0.51 [0.00, 1.07] |
| Cultivar | fixed only | 254.2 | 1.5 | 0.32 | — | — | — | — |
| AP | family | 130.4 | 0.0 | 0.73 | — | 0.00 [0.00, 1.08] | 0.00 | 0.00 [0.00, 0.99] |
| AP | AP + family | 132.4 | 2.0 | 0.27 | — | — | — | — |

Likelihood-ratio tests: family effect $\chi^2 = 3.427$, $p = 0.032$ (Total) and $\chi^2 = 3.522$, $p = 0.030$ (Cultivar); origin effect $\chi^2 = 1.431 \times 10^{-7}$, $p = 0.500$.

Table 3

Variance components (origin, family, residual), proportion of phenotypic variance, and narrow-sense heritability ($h^2$) for the end-of-experiment growth traits, from the origin + family and family models, with 1000-replicate bootstrap 95% CIs. Each panel shows results for the original data and after a sensitivity pass: removing individual observations with |standardized residual| > 3 (obs), or removing the single most influential maternal family (fam; family shown). Random-effect significance from ranova: · p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001.

| Trait | Model | Sensitivity | Dropped | $V_{origin}$ | $V_{family}$ | $V_{residual}$ | $h^2$ |
|---|---|---|---|---|---|---|---|
| Plant height | origin + family | original | — | 0.023** [0.000, 0.127] | 0.005*** [0.001, 0.011] | 0.050 [0.043, 0.057] | 0.276 [0.000, 0.641] |
| Plant height | origin + family | obs | 2 | 0.021* [0.000, 0.109] | 0.006*** [0.002, 0.011] | 0.047 [0.040, 0.054] | 0.311 [0.061, 0.676] |
| Plant height | origin + family | fam | urb09 | 0.012* [0.000, 0.062] | 0.002· [0.000, 0.006] | 0.050 [0.043, 0.058] | 0.142 [0.000, 0.380] |
| Plant height | family | original | — | — | 0.009*** [0.004, 0.017] | 0.050 [0.043, 0.056] | 0.626 [0.254, 1.051] |
| Plant height | family | obs | 2 | — | 0.009*** [0.004, 0.016] | 0.047 [0.041, 0.053] | 0.652 [0.295, 1.061] |
| Plant height | family | fam | urb09 | — | 0.004*** [0.001, 0.009] | 0.050 [0.044, 0.057] | 0.325 [0.050, 0.641] |
| Stem diameter | origin + family | original | — | 0.003 [0.000, 0.020] | 0.002* [0.000, 0.005] | 0.043 [0.037, 0.049] | 0.163 [0.000, 0.396] |
| Stem diameter | origin + family | obs | 4 | 0.003 [0.000, 0.015] | 0.002** [0.000, 0.005] | 0.038 [0.032, 0.043] | 0.195 [0.000, 0.425] |
| Stem diameter | origin + family | fam | urb09 | 0.000 [0.000, 0.006] | 0.001 [0.000, 0.003] | 0.044 [0.038, 0.050] | 0.079 [0.000, 0.290] |
| Stem diameter | family | original | — | — | 0.003** [0.000, 0.006] | 0.043 [0.037, 0.048] | 0.226 [0.000, 0.504] |

| Trait | Model | Sensitivity | Dropped | $V_{origin}$ | $V_{family}$ | $V_{residual}$ | $h^2$ |
|---|---|---|---|---|---|---|---|
| Stem diameter | family | obs | 4 | — | 0.003** [0.000, 0.005] | 0.038 [0.033, 0.043] | 0.251 [0.021, 0.523] |
| Stem diameter | family | fam | urb03 | — | 0.002* [0.000, 0.005] | 0.043 [0.037, 0.050] | 0.193 [0.000, 0.443] |
| Number of leaves | origin + family | original | — | 0.000 [0.000, 0.024] | 0.012* [0.000, 0.030] | 0.275 [0.240, 0.314] | 0.168 [0.000, 0.412] |
| Number of leaves | origin + family | obs | 5 | 0.000 [0.000, 0.029] | 0.016** [0.001, 0.034] | 0.234 [0.202, 0.265] | 0.250 [0.010, 0.509] |
| Number of leaves | origin + family | fam | urb09 | 0.000 [0.000, 0.023] | 0.004 [0.000, 0.019] | 0.280 [0.242, 0.319] | 0.052 [0.000, 0.266] |
| Number of leaves | family | original | — | — | 0.012* [0.000, 0.031] | 0.275 [0.237, 0.316] | 0.168 [0.000, 0.431] |
| Number of leaves | family | obs | 5 | — | 0.016** [0.001, 0.034] | 0.234 [0.201, 0.268] | 0.250 [0.015, 0.550] |
| Number of leaves | family | fam | urb09 | — | 0.004 [0.000, 0.017] | 0.280 [0.242, 0.320] | 0.052 [0.000, 0.248] |
| Above-ground biomass | origin + family | original | — | 0.127** [0.000, 0.666] | 0.022** [0.000, 0.048] | 0.380 [0.330, 0.433] | 0.165 [0.000, 0.436] |
| Above-ground biomass | origin + family | obs | 6 | 0.119** [0.000, 0.627] | 0.024*** [0.003, 0.053] | 0.313 [0.273, 0.356] | 0.207 [0.025, 0.527] |
| Above-ground biomass | origin + family | fam | urb09 | 0.058* [0.000, 0.294] | 0.004 [0.000, 0.025] | 0.384 [0.333, 0.436] | 0.039 [0.000, 0.235] |
| Above-ground | family | original | — | — | 0.041*** | 0.380 | 0.392 |

| Trait | Model | Sensitivity | Dropped | $V_{origin}$ | $V_{family}$ | $V_{residual}$ | $h^2$ |
|---|---|---|---|---|---|---|---|
| biomass | | | | | [0.009, 0.081] | [0.329, 0.435] | [0.082, 0.713] |
| Above-ground biomass | family | obs | 6 | — | 0.041*** [0.012, 0.078] | 0.313 [0.272, 0.360] | 0.463 [0.151, 0.821] |
| Above-ground biomass | family | fam | urb09 | — | 0.013 [0.000, 0.038]· | 0.384 [0.330, 0.438] | 0.130 [0.000, 0.380] |
| Below-ground biomass | origin + family | original | — | 0.089 [0.000, 0.482]· | 0.029* [0.000, 0.065] | 0.541 [0.467, 0.618] | 0.175 [0.000, 0.421] |
| Below-ground biomass | origin + family | obs | 7 | 0.076 [0.000, 0.393] | 0.047*** [0.011, 0.091] | 0.425 [0.367, 0.485] | 0.341 [0.083, 0.673] |
| Below-ground biomass | origin + family | fam | urb09 | 0.025 [0.000, 0.147] | 0.007 [0.000, 0.032] | 0.546 [0.468, 0.618] | 0.046 [0.000, 0.223] |
| Below-ground biomass | family | original | — | — | 0.043*** [0.008, 0.094] | 0.541 [0.471, 0.616] | 0.295 [0.053, 0.607] |
| Below-ground biomass | family | obs | 6 | — | 0.054*** [0.014, 0.106] | 0.437 [0.377, 0.501] | 0.441 [0.121, 0.814] |
| Below-ground biomass | family | fam | urb03 | — | 0.042*** [0.006, 0.090] | 0.533 [0.462, 0.616] | 0.290 [0.045, 0.607] |
| Leaf biomass | origin + family | original | — | 0.241** [0.000, 1.295] | 0.010 [0.000, 0.046] | 0.794 [0.690, 0.905] | 0.039 [0.000, 0.211] |
| Leaf biomass | origin + family | obs | 8 | 0.160** [0.000, 0.854] | 0.017 [0.000, 0.050]· | 0.537 [0.463, 0.612] | 0.093 [0.000, 0.316] |
| Leaf biomass | origin + family | fam | urb09 | 0.131** [0.000, 0.667] | 0.000 [0.000, 0.034] | 0.812 [0.702, 0.920] | 0.000 [0.000, 0.154] |

| Trait | Model | Sensitivity | Dropped | $V_{origin}$ | $V_{family}$ | $V_{residual}$ | $h^2$ |
|---|---|---|---|---|---|---|---|
| Leaf biomass | family | original | — | — | 0.045** [0.000, 0.104] | 0.796 [0.691, 0.909] | 0.215 [0.000, 0.469] |
| Leaf biomass | family | obs | 7 | — | 0.044*** [0.007, 0.096] | 0.551 [0.475, 0.631] | 0.295 [0.051, 0.610] |
| Leaf biomass | family | fam | urb13 | — | 0.043** [0.000, 0.100] | 0.741 [0.646, 0.848] | 0.218 [0.000, 0.505] |
| Stem biomass | origin + family | original | — | 0.093* [0.000, 0.461] | 0.031*** [0.007, 0.064] | 0.316 [0.275, 0.362] | 0.282 [0.066, 0.641] |
| Stem biomass | origin + family | obs | 5 | 0.087* [0.000, 0.455] | 0.032*** [0.008, 0.061] | 0.273 [0.237, 0.311] | 0.328 [0.076, 0.689] |
| Stem biomass | origin + family | fam | urb09 | 0.033 [0.000, 0.179] | 0.010 [0.000, 0.032] | 0.319 [0.276, 0.364] | 0.113 [0.000, 0.359] |
| Stem biomass | family | original | — | — | 0.046*** [0.016, 0.089] | 0.316 [0.274, 0.362] | 0.512 [0.191, 0.907] |
| Stem biomass | family | obs | 4 | — | 0.046*** [0.016, 0.085] | 0.278 [0.241, 0.320] | 0.567 [0.213, 0.956] |
| Stem biomass | family | fam | urb09 | — | 0.016* [0.000, 0.038] | 0.318 [0.276, 0.368] | 0.188 [0.000, 0.441] |

Multilocus genotypes of maternal trees and offspring arrays were used to develop a secondary classification system based on shared ancestry with cultivar varieties, following the approach of Wadl et al. (2008), who reported six of the loci in our panel (cf213, cf273, cf581, cf585, cf597, cf634) and used four of them (cf213, cf581, cf585, cf597) as a diagnostic key for identifying specific named cultivar lineages. We instead used the full nine-locus panel, including five loci not part of that original key (cf273 and cf634, which Wadl et al. 2008 reported but did not include in the key, and cf020, cf125, and cf701; Wang et al. 2009), for a broader, similarity-based admixture score rather than exact lineage matching. We

compared each seedling with every cultivar voucher genotype, scored it at each locus, and classified it by the proportion of alleles shared with known cultivar varieties yielding an Admixture Percentage (AP) score. We did not have enough samples to distinguish among individual cultivar varieties, so we treated all cultivars lineages the same. We used both maternal sample location (cultivar vs. native) and admixture percentage as covariates in the following analyses.

## Cultivar Impact Analysis

After harvest and tissue processing, we evaluated the following traits intended to differentiate between the *cultivar persistence* and *maladaptation hypotheses*. We evaluated germination date (GD) as an early indicator of vigor. We used seedling survival (SS) to estimate how origin and admixture affect early seedling viability. Quantitative plant traits included plant height (PH), stem diameter (SD), number of leaves (NL), below-ground biomass (BGB), and above-ground biomass (AGB), which was further partitioned into leaf biomass (LB) and stem biomass (SB). These traits were used to evaluate quantitative genetic differences in performance expressed by seedlings growing in a native understory environment.

We fitted mixed-effects models with continuous response variables using the lme4 package (version 2.0.6; Bates et al. 2015), and evaluated fixed-effect significance using t-tests with Satterthwaite degrees of freedom (lmerTest; Kuznetsova et al. 2017). We fitted survival with a binomial error distribution and logit link ( lme4 ; Bates et al. 2015). We estimated variance components and heritability from models fit by restricted maximum likelihood (REML); we compared models by Akaike Information Criterion (AIC) and fit them by maximum likelihood. Under the location-based classification, the full model for each trait was

$$y_{ij} = \beta_0 + \beta_1 Days_{ij} + \beta_2 S_{w,j} + f_j + o_{k(j)} + \epsilon_{ij}, \text{[1]}$$

where $y_{ij}$ is the response of the $i^{th}$ seedling from the $j^{th}$ family, $Days_{ij}$ is the scaled developmental time since germination (a proxy for germination timing), $S_{w,j}$ is the scaled mean seed weight of the maternal family (included as fixed covariates to account for early developmental and maternal effects), with coefficients $\beta_1$ and $\beta_2$ and intercept $\beta_0$; $f_j \sim N(0, \sigma^2_{family})$ is the random effect of maternal family; $o_{k(j)} \sim N(0, \sigma^2_{origin})$ is the random effect of the origin class $k$ (native or cultivar) within which family $j$ is nested; and $\epsilon_{ij} \sim N(0, \sigma^2_{\epsilon})$ is residual error. Candidate models dropped the origin effect (family model) or both random effects (fixed effects only). Under the admixture-based classification, we replaced the origin random effect with a fixed term, $\beta_3 AP_{ij}$, for the seedling's scaled admixture percentage. Traits measured repeatedly across the two growing seasons (height, stem diameter, number of leaves), indexed by census $m$, additionally included a fixed effect of census, $\beta_4 Census_m$, and a random effect of individual plant, $p_i \sim N(0, \sigma^2_{plant})$, added to the model above. For each trait, we compared models with and without origin (or *AP*) using AIC to assess whether cultivar ancestry explained variation in seedling performance beyond what maternal family alone explained.

We estimated narrow-sense heritability ( $h^2$) assuming open-pollinated maternal arrays represent half-sib families ( $h^2 = \frac{4V_{family}}{V_{total}}$). Because open-pollinated seed arrays in natural and/or urban environments may contain fractions of full-sibs, selfed offspring, or correlated paternity (e.g., Gardiakos, 2009), this standard formulation represents an upper-bound estimate of narrow-sense heritability. Here $V_{family}$ is the among-family variance component and $V_{total}$ is the sum of all estimated variance components (origin, family, and residual, plus among-plant variance for repeated measures). Estimates for each trait came from the best-supported model, using both the combined sample and, separately, for each putative origin subset. Maternal family is nested within origin — no family contributed both native and cultivar offspring — so a model fit to the combined sample yields a single family-variance estimate shared across all families, which need not represent either origin class individually; fitting the family model separately within each origin subset instead lets family-level variance differ freely between native and cultivar lineages, allowing origin-specific heritability to be estimated directly. We estimated survival heritability on the latent liability scale following Gilmour et al. (1985). Uncertainty in variance components, proportions of variance, and heritabilities was quantified with 95% confidence intervals from 1,000 parametric bootstrap replicates (new responses, including new random-effect draws, simulated from each fitted model with bootMer ; Bates et al. 2015), taking the 2.5$^{th}$ and 97.5$^{th}$ percentiles of the bootstrap distribution; the significance of random effects was additionally evaluated with likelihood-ratio tests ( ranova, lmerTest ; Kuznetsova et al. 2017). The Supplementary Materials provide the full model structure, variance decomposition, and heritability derivations, along with model diagnostics and sensitivity analyses. We performed all statistical analyses in R (version 4.5.3; R Core Team 2026), and all code and data are available in the online supplementary materials.

## Results

# Genetic Analysis

Only 28 of the potential 36 families were genotyped completely and for admixture-based analyses numbering 9 native and 19 cultivar families with 397 total offspring. The nine microsatellite markers assayed showed moderate to high polymorphism (5–21 alleles per locus) in maternal individuals and comparable diversity among offspring genotypes (Table S3, Supplementary Materials). Maximum-likelihood estimates of null-allele frequency were generally low (point estimates ≤ 0.12, highest in the native sample at cf020 and cf634), and their confidence intervals excluded zero in both the native and cultivar samples at three loci (cf020, cf597, cf634; Table S4, Supplementary Materials). Genetic marker panels, including either the full set of loci or only the subset not indicated as having any null alleles, retained almost identical discriminatory power ( $P_{excl,multi,full} > 0.9999$ vs $P_{excl,multi} = 0.9998$).

The sampled cultivar voucher panel comprised 21 named accessions, spanning the disease-resistant Appalachian series, the Cherokee series, and several other commercial lines (Table S5, Supplementary Materials). These individuals were genotyped alongside the target maternal and offspring arrays and serve as the reference key for admixture scoring.

Admixture percentage (AP), the proportion of alleles shared with the best-matching cultivar voucher, was broadly distributed rather than clustering into two discrete groups. Among the maternal trees, AP averaged 49.8% (range 33.3–88.9%), and across all offspring it averaged 50.4% (range 27.8–75.0%), with the offspring distribution largely overlapping that of the maternal generation. Restricting the comparison to the six loci reported by Wadl et al. (2008), which include their four-locus cultivar-identification key, gave a similar picture: AP averaged 53.3% (range 33.3–91.7%) among maternal trees and 54.0% (range 25.0–100.0%) among offspring under this reduced panel. These are slightly higher and somewhat more variable than under the full nine-locus panel, but showing the same broad overlap between generations rather than a sharper separation (Table S6, Supplementary Materials). This diffuse pattern of allele sharing with cultivar vouchers, evident under both marker sets and across both maternal and offspring generations, suggests that the diagnostic loci, while collectively providing strong discriminatory power (above), are not individually fixed to cultivar lineages.

## Cultivar Impacts

To evaluate whether early seedling performance was shaped by landscape provenance and/or continuous genetic ancestry, we tested seedling survival and growth traits under two parallel frameworks: a categorical maternal origin (urban/cultivar vs. forest/native), which reflects the seed tree's landscape location, and a continuous admixture percentage (AP), which quantifies neutral allele sharing with commercial voucher lines based on previous cultivar identification markers in this species.

Maternal origin did not account for significant variation in the timing of germination in either group: adding origin did not improve model fit for germination date over maternal family alone ($\Delta$AICc = 2.036; likelihood-ratio test p = 0.475), although germination timing was itself heritable among families ($h^2$ = 0.421; 95% CI 0.145, 0.722; Table 1). Similarly, maternal origin did not affect seedling survival through the end of the second growing season. Mortality remained relatively consistent across the entire experiment in both groups (Fig. 1). Adding native/cultivar origin to the generalized linear mixed model did not improve fit over maternal family alone (family: $\Delta$AICc = 0.000; fixed-effects only: $\Delta$AICc = 1.398; origin + family: $\Delta$AICc = 2.036; Table 2), and the origin random effect explained little of the unexplained variance (likelihood-ratio test, $\chi^2 = 1.431 \times 10^{-7}$, p = 0.500).

Table 1

Model comparison and quantitative-genetic parameters for germination timing (developmental time since germination), testing whether origin predicts germination timing itself. Origin was fit as a random effect; the germination-timing covariate is omitted because it is the response, so the fixed-only model here contains seed weight alone (no random effects). 1000 replicate bootstrap 95% CIs.

| Parameter | Model | Value |
|---|---|---|
| AIC | family | AICc = 4636.503, ΔAICc = 0.000, *w*AICc = 0.735 |
| AIC | origin + family | AICc = 4638.538, ΔAICc = 2.036, *w*AICc = 0.265 |
| AIC | fixed only | AICc = 4662.576, ΔAICc = 26.073, *w*AICc = 0.000 |
| Variance | $V_{origin}$ | 10.665 [0.000, 71.826] |
| Variance | $V_{family}$ | 23.303 [7.617, 42.205] |
| Heritability | $h^2$ | 0.421 [0.145, 0.722] |
| LRT | origin random effect | $p = 0.475$ |
| LRT | family random effect | $p < 0.001$ |

For plant growth traits, the family and family + origin models were within ΔAICc ≤ 2 of one another for plant height (PH), stem diameter (SD), number of leaves (NL), above-ground biomass (AGB), below-ground biomass (BGB), and stem biomass (SB). These results suggest that origin added little beyond family alone (see also Table S7, Supplementary Materials). The bootstrap confidence interval for the variance attributed to origin included zero for every trait except leaf biomass (LB; Table 3) where the origin-inclusive model was clearly favored (ΔAICc = 4.886, wAICc = 0.916 vs. 0.080; Table S7, Supplementary Materials) despite its origin variance component's confidence interval also including zero (Table 3). Repeated-measures models showed the same pattern (Table S8 and Table S9, Supplementary Materials). Together, these results indicate that, except for leaf biomass, origin contributed little to trait variation under the location-based classification and we retain considerable uncertainty about the magnitude of any effect.

Under the admixture-based classification, adding Admixture Percentage as a fixed covariate also did not improve model fit over maternal family alone for any trait (family alone favored or tied in every case; Table S7, Supplementary Materials). The estimated AP coefficient was not significant for any trait. Comparing model support across classification schemes in (Table S7, Supplementary Materials) highlights this contrast: while models incorporating categorical maternal origin are competitive with, or favored over, family-only models (ΔAICc ≤ 2 for six of seven traits), adding admixture percentage as a continuous covariate consistently reduced model support relative to family alone. We therefore found no evidence that cultivar ancestry, whether inferred from either maternal location or genetic admixture, meaningfully affected seedling survival, growth, or persistence.

## Family-Level Variation and Trait Heritability

Because admixture percentage forms a continuous, broadly overlapping distribution across maternal trees rather than discrete genetic clusters, we partitioned family-level trait variance ( $h^2$) across all families and then within each categorical maternal-origin class. Based on the same location-based origin split described above, maternal families explained substantially more variation in survival and growth among putative cultivar-origin seedlings than among native-origin seedlings. The family model was the best model for the cultivar offspring for every growth trait except leaf biomass, whereas the fixed-effects-only model was best supported for every trait in the native set (Table S7 and Table 4). For survival, the same split showed that adding family improved model fit in the cultivar subset (ΔAICc = 1.481, wAICc = 0.677 vs. 0.323; likelihood-ratio test $\chi^2 = 3.522$, df = 1, p = 0.030) but not in the native subset, where the fixed-effects-only model remained best supported (ΔAICc = 2.096, wAICc = 0.740 vs. 0.260; Table 2). While there was evidence for family-level variance in survival among cultivar-origin families, the heritability estimate was highly uncertain ($h^2 = 0.510$; 95% CI 0.000-1.072). However, family-specific conditional modes (analogous to BLUPs in linear models) extracted from the putative cultivar-survival GLMM show that survival variation varied across cultivar-origin families (Fig. 2).

Table 4

Within-origin variance components and narrow-sense heritability (family model only), analyzed separately for putative native and putative cultivar seedlings, with 1000-replicate bootstrap 95% CIs and the same sensitivity pass as Table 3. Significance from ranova: · p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001.

| Trait | Subset | Sensitivity | Removed | $V_{family}$ | $V_{residual}$ | $h^2$ |
|---|---|---|---|---|---|---|
| Plant height | Native | original | — | 0.003 [0.000, 0.014] | 0.055 [0.042, 0.069] | 0.238 [0.000, 0.877] |
| Plant height | Native | obs | 1 | 0.004 [0.000, 0.013] | 0.051 [0.040, 0.064] | 0.275 [0.000, 0.832] |
| Plant height | Native | fam | nat19 | 0.005 [0.000, 0.017] | 0.049 [0.037, 0.064] | 0.356 [0.000, 1.053] |
| Plant height | Cultivar | original | — | 0.006*** [0.001, 0.014] | 0.047 [0.040, 0.055] | 0.474 [0.112, 0.933] |
| Plant height | Cultivar | obs | 1 | 0.006*** [0.001, 0.014] | 0.045 [0.038, 0.052] | 0.501 [0.113, 0.975] |
| Plant height | Cultivar | fam | urb09 | 0.002 [0.000, 0.006] | 0.047 [0.039, 0.055] | 0.163 [0.000, 0.458] |
| Stem diameter | Native | original | — | 0.000 [0.000, 0.006] | 0.052 [0.039, 0.064] | 0.008 [0.000, 0.457] |
| Stem diameter | Native | obs | 1 | 0.000 [0.000, 0.007] | 0.045 [0.035, 0.056] | 0.040 [0.000, 0.539] |
| Stem diameter | Native | fam | nat19 | 0.000 [0.000, 0.007] | 0.047 [0.035, 0.060] | 0.040 [0.000, 0.542] |
| Stem diameter | Cultivar | original | — | 0.003* [0.000, 0.006] | 0.038 [0.032, 0.044] | 0.247 [0.000, 0.592] |
| Stem diameter | Cultivar | obs | 3 | 0.002* | 0.035 | 0.193 |

| Trait | Subset | Sensitivity | Removed | $V_{family}$ | $V_{residual}$ | $h^2$ |
|---|---|---|---|---|---|---|
| | | | | [0.000, 0.005] | [0.029, 0.040] | [0.000, 0.502] |
| Stem diameter | Cultivar | fam | urb11 | 0.002· [0.000, 0.005] | 0.037 [0.031, 0.043] | 0.181 [0.000, 0.493] |
| Number of leaves | Native | original | — | 0.000 [0.000, 0.000] | 0.241 [0.188, 0.300] | 0.000 [0.000, 0.000] |
| Number of leaves | Native | obs | 1 | 0.000 [0.000, 0.000] | 0.223 [0.172, 0.277] | 0.000 [0.000, 0.000] |
| Number of leaves | Native | fam | nat19 | 0.000 [0.000, 0.000] | 0.258 [0.197, 0.329] | 0.000 [0.000, 0.000] |
| Number of leaves | Cultivar | original | — | 0.020** [0.000, 0.051] | 0.289 [0.245, 0.336] | 0.263 [0.000, 0.622] |
| Number of leaves | Cultivar | obs | 4 | 0.025*** [0.003, 0.054] | 0.239 [0.201, 0.276] | 0.378 [0.049, 0.779] |
| Number of leaves | Cultivar | fam | urb09 | 0.009 [0.000, 0.032] | 0.296 [0.246, 0.342] | 0.123 [0.000, 0.405] |
| Above-ground biomass | Native | original | — | 0.000 [0.000, 0.039] | 0.410 [0.307, 0.506] | 0.000 [0.000, 0.365] |
| Above-ground biomass | Native | obs | 2 | 0.000 [0.000, 0.000] | 0.325 [0.252, 0.403] | 0.000 [0.000, 0.000] |
| Above-ground biomass | Native | fam | nat29 | 0.000 [0.000, 0.062] | 0.403 [0.304, 0.491] | 0.000 [0.000, 0.575] |

| Trait | Subset | Sensitivity | Removed | $V_{family}$ | $V_{residual}$ | $h^2$ |
|---|---|---|---|---|---|---|
| Above-ground biomass | Cultivar | original | — | 0.032*** [0.003, 0.078] | 0.366 [0.310, 0.424] | 0.322 [0.030, 0.720] |
| Above-ground biomass | Cultivar | obs | 4 | 0.031*** [0.004, 0.073] | 0.310 [0.264, 0.358] | 0.364 [0.047, 0.779] |
| Above-ground biomass | Cultivar | fam | urb09 | 0.009 [0.000, 0.032] | 0.369 [0.310, 0.428] | 0.090 [0.000, 0.327] |
| Below-ground biomass | Native | original | — | 0.017 [0.000, 0.113] | 0.630 [0.468, 0.778] | 0.103 [0.000, 0.666] |
| Below-ground biomass | Native | obs | 1 | 0.023 [0.000, 0.109] | 0.529 [0.409, 0.657] | 0.165 [0.000, 0.722] |
| Below-ground biomass | Native | fam | nat19 | 0.028 [0.000, 0.117] | 0.512 [0.378, 0.657] | 0.209 [0.000, 0.821] |
| Below-ground biomass | Cultivar | original | — | 0.031 [0.000, 0.082]* | 0.496 [0.420, 0.574] | 0.233 [0.000, 0.589] |
| Below-ground biomass | Cultivar | obs | 5 | 0.040*** [0.004, 0.089] | 0.398 [0.336, 0.459] | 0.363 [0.038, 0.776] |
| Below-ground biomass | Cultivar | fam | urb09 | 0.005 [0.000, 0.038] | 0.494 [0.409, 0.571] | 0.042 [0.000, 0.291] |
| Leaf biomass | Native | original | — | 0.000 [0.000, 0.095] | 0.817 [0.605, 1.003] | 0.000 [0.000, 0.440] |
| Leaf biomass | Native | obs | 2 | 0.000 [0.000, 0.083] | 0.647 [0.490, 0.797] | 0.000 [0.000, 0.494] |
| Leaf biomass | Native | fam | nat19 | 0.000 | 0.789 | 0.000 |

| Trait | Subset | Sensitivity | Removed | $V_{family}$ | $V_{residual}$ | $h^2$ |
|---|---|---|---|---|---|---|
| | | | | [0.000, 0.106] | [0.578, 1.001] | [0.000, 0.493] |
| Leaf biomass | Cultivar | original | — | 0.026 [0.000, 0.091] | 0.775 [0.655, 0.898] | 0.130 [0.000, 0.427] |
| Leaf biomass | Cultivar | obs | 6 | 0.031 [0.000, 0.079]* | 0.484 [0.406, 0.560] | 0.238 [0.000, 0.585] |
| Leaf biomass | Cultivar | fam | urb09 | 0.002 [0.000, 0.042] | 0.809 [0.678, 0.936] | 0.010 [0.000, 0.204] |
| Stem biomass | Native | original | — | 0.008 [0.000, 0.060] | 0.349 [0.259, 0.431] | 0.090 [0.000, 0.635] |
| Stem biomass | Native | obs | 2 | 0.019 [0.000, 0.077] | 0.279 [0.213, 0.349] | 0.252 [0.000, 0.936] |
| Stem biomass | Native | fam | nat19 | 0.019 [0.000, 0.076] | 0.311 [0.229, 0.399] | 0.235 [0.000, 0.861] |
| Stem biomass | Cultivar | original | — | 0.037 [0.006, 0.083]*** | 0.304 [0.258, 0.353] | 0.438 [0.072, 0.891] |
| Stem biomass | Cultivar | obs | 3 | 0.035*** [0.006, 0.073] | 0.273 [0.231, 0.315] | 0.450 [0.081, 0.883] |
| Stem biomass | Cultivar | fam | urb09 | 0.011 [0.000, 0.035] | 0.303 [0.254, 0.355] | 0.141 [0.000, 0.431] |

Confidence intervals for the family variance component in the native subset spanned zero for all plant growth traits (Table 4). While cultivar families showed statistically significant heritable variation for height, above-ground biomass, and stem biomass ( $h^2 \approx 0.32$\- $- 0.47$), native families had low point estimates of $V_{family}$ with wide bootstrap confidence intervals that spanned zero. This pattern indicates either reduced standing genetic variance for understory growth traits in local wild stands or limited

statistical power to resolve small family variance components given the smaller array sizes and lower seed availability in native maternal trees. In the cultivar offspring arrays, family variance was significant, though modest, for plant height (PH; 11.853% of phenotypic variance), above-ground biomass (AGB; 8.061%), and stem biomass (SB; 10.946%; Table 4). In the putative cultivar set, heritabilities were also significant for the same three traits, ranging from $h^2 = 0.322$ (95% CI: 0.030–0.720) for AGB to $h^2$ = 0.474 (CI: 0.112–0.933) for PH (Table 4), consistent with heritable variation among cultivar families, leaving the potential for evolutionary responses to selection when seedlings are grown in understory conditions.

Sensitivity tests included removing influential observations at the family and individual levels. Results for putative cultivar families were robust to removing outlier individual observations; if anything, the family effect strengthened (e.g., NL and BGB; Table 4), and the largest heritability shift was in BGB ($h^2 = 0.233 \rightarrow 0.363$). Removal of the single most influential maternal family had a larger effect on variance-component and heritability estimates. In most growth traits, this family was urb09. For stem biomass in the overall family model, removing urb09 reduced the family variance component ($V_{family} = 0.046 \rightarrow 0.016$) and heritability ($h^2 = 0.512 \rightarrow 0.188$), weakening but not eliminating support for the family random effect (likelihood-ratio test $\chi^2 = 5.251, df = 1, p = 0.022$; Table 3). A similar pattern occurred within the cultivar subset (Table 4), where excluding urb09 again reduced cultivar height heritability ($h^2 = 0.474 \rightarrow 0.163$) and above-ground biomass heritability ($h^2 = 0.322 \rightarrow 0.090$).

We sampled native-origin maternal trees from two nearby forest sites, whereas cultivar-origin mothers represent potential subsets of independently propagated named lines. We tested whether native mothers are more closely related to one another than cultivar mothers are, which could confound origin with kinship structure rather than a genuine origin effect (Supplementary Materials). We found no evidence of such a difference, suggesting that the family-level variance asymmetry described above is unlikely to reflect unequal relatedness between adults grouped as native or cultivar.

Earlier germination strongly predicted survival and every growth trait except number of leaves in both origin classes ($p < 0.001$; Table S10, Supplementary Materials), suggesting that a developmental head start is an important early advantage regardless of origin. Maternal seed weight had a weaker and more variable effect and was not an important predator of survival in the cultivar subset. However, it was negatively associated with survival overall. In the native subset ($p < 0.05$), and among cultivar-origin seedlings it was negatively associated with above-ground ($p< 0.05$), below-ground ($p < 0.05$), and leaf biomass ($p < 0.01$): seedlings from families with smaller mean seed weight accumulated more biomass. Seed weight did not significantly predict any growth trait in seedlings of native origin.

# Discussion

In this study, we investigated the early fitness consequences associated with cultivar gene escape from urban environments into surrounding native populations of flowering dogwood. We grew seedlings from

maternal individuals sampled in cultivated and natural landscapes under conditions representative of native environments. We classified seedlings by the maternal individual's sampling location (cultivar vs. native) and by estimating admixture percentages with known cultivar lineages. After two years in a common garden, we found that maternal families contributed significantly, though modestly, to variance in plant traits. In contrast, origin explained little variance and did so inconsistently across traits. Likewise, cultivar admixture did not significantly predict any plant trait or survival. Moderate heritability estimates for plant traits among putative cultivar seedlings are consistent with among-family variation upon which selection could act. High overall survival suggests gene flow from cultivated genotypes into native populations may not be self-limiting because early viability selection is weak. Together, these results indicate that, if established, cultivar offspring are unlikely to be disadvantaged compared to native genotypes and therefore may persist in native forested habitats. This has important implications for the evolutionary trajectory and conservation of conspecifics which inhabit the areas adjacent to human-tended cultivars.

Although maternal origin did not differentiate survival and early fitness traits in seedlings, survival and growth traits differed among families within each category (Fig. 2), but family variation among putative cultivar offspring arrays may play an important role. The estimate of narrow-sense heritability for survival among cultivar seedlings was imprecise ($h^2$ = 0.510; CI 0.000-1.072), with differences among families accounting for 12.7% of the latent-scale variance in survival. Conversely, families explained no latent-scale survival variance among putative native families. Our results indicate a similar pattern for growth traits. Evidence that origin contributed significantly to trait variation was weak and inconsistent. However, the origin + family models still predicted consistently higher growth for putative cultivar-origin than native-origin seedlings in height, stem biomass, and above- and below-ground biomass (reflected in the sign of the origin random effect's conditional modes for each group). Because vegetative size is a recognized proxy for fitness in conspecifics (Gross 1984; Younginger et al. 2017) and early juvenile vigor often determines establishment success under competitive conditions, these patterns suggest that cultivar-origin seedlings are not competitively disadvantaged in native understories. Importantly, because we did not experimentally manipulate light availability in our common garden, our setup specifically evaluates performance under natural, deeply shaded understory conditions. These findings suggest that cultivar-origin seedlings show little sign of a physiological trade-off or relaxed shade tolerance associated with their high-light selective history, maintaining equivalent or superior juvenile growth and biomass accumulation under a natural forest canopy. The maternal family contributed more consistently to variance among seedlings of different cultivar origins. Significant family-level variation in growth traits indicates that certain cultivar lineages will outperform others. Selection for vigor and floral display during cultivar development may therefore yield lineages that perform robustly beyond managed urban plantings.

Significant heritability estimates for plant height, above-ground biomass, and stem biomass for putative cultivar-origin seedlings were moderate and consistent with those reported in other tree species (Galeano and Thomas 2023), indicating that some of the variation in seedling growth-related traits may have a genetic basis that can provide variation upon which selection may act. Feurtey et al. (2017) found

increased fitness of domestic × native hybrid apple trees, and significant levels of introgression have led to concerns about the conservation status of European crab apples, while transfer of advantageous alleles may alter native populations, as in frost-resistant ornamental × wild holly that may be driving range expansion in Denmark (Skou et al. 2012). Given the importance of producing anthracnose-resistant lineages in contemporary cultivar strains of Cornus florida, introgression of these genotypes in proximate native populations would not seem to be impacted by early seedling fitness differences.

While our results do not demonstrate disadvantages to cultivar-origin seedlings in native habitats, a general fitness advantage over native seedlings is not strictly necessary for introgression to occur (Lenormand 2002). Pollen migration can be species-, population-, and season-specific, but generally drives gene flow in plant populations (Ellstrand 1992). Evidence of local isolation by distance in *C. florida* indicates that seed migration is likely restricted (Dyer et al. 2012). Thus, in forested habitats, hybridization between cultivar pollen and wild ovules may be more likely, though the forest/urban margin could experience some seed migration from cultivars. Cultivar trees, particularly in adjacent peri-urban locations, may also serve as sources of pollen migrants, supported by human tending and higher-light environments. Additionally, in this system, urban lawns will likely exert strong selective pressure against all seedling establishments other than dispersal into adjacent natural green spaces. Thus, wild pollen flow to cultivar ovules may be less likely to result in successful establishment unless seeds are dispersed into urban-proximate natural areas or the adjacent forest.

The stark asymmetry in heritable variation between origins, where native family arrays exhibited low point estimates of heritable variance while cultivar families harbored substantial heritability ( $h^2 \approx 0.32$\- $- 0.47$), may reflect both statistical and biological factors. Statistically, smaller sample sizes and array sizes among native families ( $n = 174$ across 16 families vs. $n = 395$ across 20 cultivar families) reduce power and tend to pull REML variance component estimates toward zero. Biologically, however, pairwise co-ancestry analyses confirm that native maternal trees are not simply an inbred or highly related cluster (Supplementary Materials). Rather, native forest stands maintain a relatively homeostatic phenotypic response under understory conditions. Conversely, open-pollinated cultivar arrays reflect both the broad phenotypic diversity of domestic selection and the complex spatial structure of urban landscapes. In managed suburban matrices, maternal trees face highly variable microclimates, come from potentially divergent cultivar lineages, and exist in fragmented canopy structures, which may alter local pollinator foraging behavior, effective pollen donor diversity, and outcrossing dynamics relative to contiguous forest understories. Because open-pollinated family variance integrates both maternal genetics and paternal pollen pool composition, evaluating how urban landscape gradients alter contemporary mating systems, pollen pool structure, and gene dispersal remains a critical frontier for predicting the long-term evolutionary trajectories of urban-wild forest boundaries. Specifically, verifying the half-sib assumptions underlying open-pollinated heritability estimates (where we assume $V_A = 4V_{family}$) will require quantifying how urban canopy fragmentation shapes local outcrossing rates, correlated paternity, and effective pollen donor numbers ( $N_{ep}$; Remfert and Dyer, Unpublished).

As a first, more limited step toward that verification, we asked how heritability estimates would change if we relaxed the half-sib assumptions to reflect realized sibship structure rather than the assumed constant. Prior work in this system has shown that canopy openness influences correlated paternity in this species (Gardiakos 2009), and cultivar landscapes are characteristically more open than closed native-forest canopy. We estimated pairwise marker-based relatedness among each mother's own genotyped offspring, pooled within origin, to characterize the realized relatedness distribution for native and cultivar families separately (Figure S2, Supplementary Materials), and re-expressed heritability at each origin's median realized relatedness in place of the assumed $r = 0.25$ (as expected for half-siblings). This shifted point estimates modestly downward for every trait with detectable family variance. Traits whose family-variance estimate was already indistinguishable from zero were, by construction, unaffected. Overall, heritability remained low in the native subset and moderate in the cultivar subset across the complete half-sib-to-full-sib range (Fig. 3; Table S11, Supplementary Materials).

With indications that cultivar seedlings can readily survive and perform as well as wild seedlings, an additional factor shaping the persistence of cultivar alleles in native forests is landscape-level parameters that influence gene flow, such as the shape and size of donor populations and the matrix through which gene flow occurs. Much of the contemporary urban landscape genetics research examines whether urban land cover impedes or facilitates gene flow, and the answer is often organism-specific (e.g., Miles et al. 2019). Previous research has found that conspecific canopy cover significantly facilitates pollen flow in *C. florida* (DiLeo et al. 2014), but has provided conflicting evidence on the influence of canopy openings, with scale likely an important factor (Sork et al. 2005; DiLeo et al. 2014). The permeability of the intervening environment will shape whether gene flow can repeatedly facilitate the establishment of cultivar genotypes in forested habitats. Linear landscape elements have been found to promote insect-mediated pollen flow in urban spaces (Van Rossum and Triest 2012), natural areas within cities can experience increased pollen immigration (Noreen et al. 2016) and serve as hybridization zones that facilitate the establishment of hybrid populations (Roe et al. 2014; Hamm et al. 2026). Thus, urban natural areas may serve as a repository for seed and pollen migration.

Some cultivar lines are known to have differential resistance to a variety of diseases, from the susceptibility of Cherokee Chief to canker caused by *Lasiodiplodia theobromae* (Mullen 1991), to the spot anthracnose (*Elsinoë corni*; Jenkins & Bitanc. (1948) resistant Cherokee Brave (Hagan et al. 1998). Powdery mildew (*Erysiphe pulchra* Cooke & Peck, Braun & Takamatsu, 2000) resistance is a highly heritable trait in *C. florida* (Parikh et al. 2016a), with Kay’s Appalachian Mist, Jean’s Appalachian Snow, and Karen’s Appalachian Blush all showing resistance (Windham et al. 2003). Although these diseases are mostly cosmetic in adult trees, they can affect seedlings and inhibit growth (Hagan et al. 1998; Mmbaga and Sauvé 2004; Hamm et al. 2026). *Discula destructiva*, however, has been highly destructive to *C. florida* populations, and resistance could provide significant advantages in the cooler, more humid parts of the *C. florida* range. Appalachian Spring is a cultivar derived from a resistant individual found in Catoctin Mountain, MD, amid a high incidence of conspecific loss to *D. destructiva* (Windham et al. 1998). The vigor and prolific blooming of this strain do not indicate a defense-growth trade-off common

in crop breeding (Gao et al. 2024). Transfer of disease resistance to nearby wild populations of *C. florida* could benefit them, particularly those under disease pressure.

Disease resistance is a major cost-saving trait for nurseries and a desirable trait for home landscaping (Klingeman et al. 2004), so the pursuit of disease resistance will continue to factor into breeding programs (Parikh et al. 2016a, b). This includes interspecific hybrids between *C. florida* and the generally highly resistant *C. kousa*. Artificial methods to overcome non-overlap in flowering timing between species successfully produced hybrids with intermediate phenological characteristics and increased vigor (Mattera et al. 2015). Although *Cornus* × *rutgersensis* hybrids often produce sterile fruits, they can produce some fertile seeds (Mattera et al. 2015). Certain *C. kousa* cultivars and *C. florida* × *C. kousa* hybrids have been assessed as disease-resistant varieties (Ranney et al. 1995; Hagan et al. 1998). Even among *C. florida* cultivars, disease resistance shows high heritability (Parikh et al. 2016a, b). These all pose potential pathways for genetic leakage from urban and peri-urban landscapes into wild *C. florida* populations.

A surprising result in this work was the lack of admixture signal, but several caveats relative to our classification scheme should be noted. First, our voucher panel comprised only the cultivar lines we could obtain (21 named lines), and although it included several popular lines, many remain unrepresented. Next, we do not know the exclusive fidelity of these alleles to specific cultivar lines. Some cultivars are derived from wild individuals through vegetative propagation, so they may share alleles with wild individuals, as those alleles likely existed in the surrounding population at some frequency. Indeed, the broadly overlapping distribution of admixture percentage between maternal trees and their offspring arrays is consistent with this concern, and suggests that the loci identified as cultivar-diagnostic in prior work (Wadl et al. 2008; Wang et al. 2009; Hamm et al. 2026) may not be as exclusively informative for distinguishing cultivar from native ancestry in our sampled populations as originally assumed. As a further check, we tested for non-random multilocus allelic association (linkage disequilibrium) among these nine loci within each origin group, restricted to the 36 unrelated maternal trees to avoid the confounding of family structure present among the offspring arrays. We found no evidence in either the native ( $I_A$ =−0.116, p = 0.607) or cultivar ( $I_A$ = 0.079, p = 0.262) samples (index of association; Agapow and Burt 2001; poppr ; Kamvar et al. 2014; Table S12, Supplementary Materials). As a complementary multivariate test, we also used discriminant analysis of principal components (DAPC; Jombart et al. 2010) to ask whether native and cultivar maternal trees separate on their full nine-locus genotype; even allowing a large number of retained principal components (18 of a maximum 20, chosen by cross-validation), which would tend to favor overfitting and inflate apparent separability, cross-validated classification accuracy (64.4%) did not exceed chance given the sample's class balance (no-information rate 67.9%) and from a permutation null built by re-running the same procedure on 999 relabelings of the same trees (p = 0.237), again finding no evidence that the two groups separate on multivariate genotype combinations (DAPC Classification; mean 0.509, p = 0.237). Finally, while shared neutral alleles may indicate some shared ancestry among individuals, we do not observe any relationship with differences in fitness-related phenotypic traits. This suggests either that seedlings sharing more cultivar alleles

perform similarly to native seedlings under understory conditions or that our marker set lacks the resolution to capture ancestry in genomic regions that influence these traits.

Our current study is limited by its temporal scope, as two growing seasons did not allow us to collect reproductive data. We relied on early fitness traits, which overall have a positive allometric relationship with reproductive output (Gross 1984; Younginger et al. 2017). However, *C. florida* generally does not flower in the first 6 years, making measures of reproductive structures infeasible in this study. Furthermore, a critical component of cultivar × wild gene escape is the breakdown of hybrid vigor after subsequent generations of backcrossing (Hooftman et al. 2007), which we also could not assess here. However, our results do not indicate immediate detrimental impacts for native *C. florida* populations in the Piedmont region of the eastern United States. Cultivar seedlings performed as well as or better than native seedlings and showed no difference in survival. Hybridization may have occurred continuously as urban areas expanded and ornamental *C. florida* became ubiquitous in residential plantings. Deforestation and reforestation in the eastern United States also provide a land-use history that may have included cultivar *C. florida* in rural residential landscaping, which was later abandoned. Together, these results suggest that early viability selection is unlikely to be a barrier to cultivar gene escape in *C. florida*, and that the longer-term consequences — including whether cultivar-derived traits such as disease resistance ultimately benefit or homogenize wild populations — merit continued attention as urban and wild dogwood populations continue to intermix.

## Declarations

# Competing interests

The authors declare no competing interests.

# Ethics and permissions

We sampled maternal trees on private property with landowner permission. Sampling in Pocahontas State Park and at the VCU Rice Rivers Center was conducted under permit PO-RCP–102617.

# Funding

JR received funding from the VCU Rice Rivers Center Research grant 2016, 2018, 2019.

# Author Contribution

Both JR and RJD contributed to the study design, implementation, analysis, and development of this manuscript. This work is a component of the doctoral dissertation for JR, who also conducted the

extraction and genotyping of all samples and all common garden measurements. AJE contributed to statistical analyses, drafting of the manuscript, and critical revision of the manuscript.

# Data Availability

The anonymized data and the annotated R code that reproduce every table and figure are available from the Dyer Laboratory GitHub repository URL (https://github.com/dyerlab/Cornus_Common_Garden).

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