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Growth–defense trade-offs shape population genetic composition in an iconic forest tree species

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All organisms experience fundamental conflicts between divergent metabolic processes. In plants, a pivotal conflict occurs between allocation to growth, which accelerates resource acquisition, and to defense, which protects existing tissue against herbivory. Trade-offs between growth and defense traits are not universally observed, and a central prediction of plant evolutionary ecology is that context-dependence of these trade-offs contributes to the maintenance of intraspecific variation in defense [Züst and Agrawal, *Annu. Rev. Plant Biol.*, 68, 513–534 (2017)]. This prediction has rarely been tested, however, and the evolutionary consequences of growth–defense trade-offs in different environments are poorly understood, especially in long-lived species [Cipollini *et al.*, *Annual Plant Reviews* (Wiley, 2014), pp. 263–307]. Here we show that intraspecific trait trade-offs, even when fixed across divergent environments, interact with competition to drive natural selection of tree genotypes corresponding to their growth–defense phenotypes. Our results show that a functional trait trade-off, when coupled with environmental variation, causes real-time divergence in the genetic architecture of tree populations in an experimental setting. Specifically, competitive selection for faster growth resulted in dominance by fast-growing tree genotypes that were poorly defended against natural enemies. This outcome is a signature example of eco-evolutionary dynamics: Competitive interactions affected microevolutionary trajectories on a timescale relevant to subsequent ecological interactions [Brunner *et al.*, *Funct. Ecol.* 33, 7–12 (2019)]. Eco-evolutionary drivers of tree growth and defense are thus critical to stand-level trait variation, which structures communities and ecosystems over expansive spatiotemporal scales.

Populus tremuloides | competition | herbivory | intraspecific variation | eco-evolutionary dynamics

Attack by herbivores and competition with other plants are the most significant biotic pressures faced by plants (1). Allocation to defense against herbivory often negatively covaries with plant growth rate and thus with competitive ability, but the likelihood and mechanistic basis of such growth–defense trade-offs are scale-dependent (2). When observed among or within individual plants, growth–defense trade-offs are driven mainly by costs of defense that are either regulatory in nature [arising from inhibitory cross-talk among pathways (3)] or metabolic in nature [arising from multiple demands for limited substrates and enzymes (4)]. At a broader regional scale, growth–defense covariance tends to be absent or positive among populations due to increases in expression of both types of traits along gradients of increasing resource availability (5). When observed among plant genotypes within a population, however, growth–defense trade-offs arise from genetic costs related to underlying genotypic variation (4). A key feature of genetic costs of defense is that they are sensitive to selection regimes: A selective pressure favoring growth and disfavoring defense, or vice versa, is strong evidence for a genetic trade-off. In turn, genetic costs of defense are uniquely important for the evolutionary dynamics of plant populations.

Among-genotype trade-offs between growth and defense are commonly, but not universally, observed. This lack of consistency has been the subject of much research and debate, and one prominent explanation is that the magnitude and direction of growth–defense trait covariance depends on the biotic and abiotic context (4, 6, 7). Context dependence of growth–defense trade-offs is thought to maintain intraspecific variation in defense traits because it leads to different levels of defense being favorable for growth and fitness in different environments (1). Exceedingly few studies, however, have tested this prediction in trees, and those that have typically used growth as the sole proxy for fitness rather than the more evolutionarily relevant metrics of survival or reproduction (8). No research to date has evaluated the evolutionary consequences of context-dependent growth–defense trade-offs in trees. Investigating these consequences is critical to our understanding of how trait variation and diversity are maintained within and among forest stands.

When multiple traits covary, environmentally mediated selection may act on them in tandem, although this is rarely studied (9). It follows that, in the presence of a growth–defense trade-off, selection on growth rate due to competitive interactions may lead to eco-evolutionary dynamics wherein population composition shifts toward dominance by fast-growing genotypes that are correspondingly less defended against herbivores. Eco-evolutionary dynamics can occur when selection-driven evolutionary change occurs on a sufficiently short time scale to feed back upon and influence subsequent ecological interactions (10). Several cases of eco-evolutionary

Significance

Genetic diversity is critical for ecological resilience and is maintained when different traits are advantageous in different environments. Traits are not entirely independent, however: When trade-offs occur, selection on one trait may indirectly act on another. Here we examine how environmentally mediated selection for growth interacts with a trade-off between growth and herbivore defense in experimental aspen stands. We show that even an environmentally fixed trait trade-off can lead to real-time divergence in population genetic composition between environments. The underlying growth–defense trade-off led to an eco-evolutionary dynamic wherein high-competition environments selected for fast-growing trees and thus ultimately selected against herbivore resistance. This discovery reveals how patterns of genetic covariation, coupled with environmental variation, can link ecological and evolutionary processes.

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dynamics have been documented for single plant functional traits, including herbivore defenses (11, 12) and growth rate (13). A real-time interaction between context-dependent selection and trait covariance promises to transform our understanding of intraspecific trait variation in trees and to expand the array of potential drivers of variation in herbivore defense. To date, no research has explored whether competitive environment drives either selection on plant defense traits over time or changes in defense expression at the population level in long-lived woody plants.

Understanding intraspecific dynamics of growth- and defense-related traits may be particularly important for predicting the ecological trajectories of tree populations. Although plant traits often show more variance among than within species, increasing evidence has revealed that intraspecific variation can cover much of the same range in trait expression (14, 15) and have similar ecological consequences (16, 17). Intraspecific variation is especially important in foundation plant species, such as trees, that often have high genetic variability and structure larger communities and ecosystems (18–20). In forest systems, tree growth traits play a key role in the carbon cycle (21), and tree defense traits structure both terrestrial and aquatic food webs (22–24).

In this study, we established an experimental common garden of trembling aspen (*Populus tremuloides*) to test the context dependence of genetic growth–defense trade-offs and to track eco-evolutionary dynamics of tree populations at unprecedented spatial and temporal scales. Aspen is an ideal study system for this type of selection experiment, as it exhibits high heritable genetic variability in many traits, including growth and defense (25, 26). Our common garden simulates the aftermath of an aspen seeding event, where multiple genotypes of uniform age establish on disturbed soil (27, 28). Intraspecific competition is the most important driver of mortality in young aspen stands (29), and outcomes of competitive interactions at this phase set the stage for stand genotypic composition for decades to centuries into the future, as clones spread vegetatively (27). Aspen is also a widespread foundation species, for which intraspecific trait variation is exceptionally ecologically important (30).

Within the aspen common garden, experimental stands were established with identical genotypic composition and subjected to two different intensities of intraspecific competition. We then measured expression of, and selection on, growth and defense traits over the course of 5 y (tree ages 5 to 9 y). The main foliar defenses of aspen against herbivory by both insects and mammals are salicinoid phenolic glycosides (PGs), which tend to be genetically canalized and are minimally inducible (31). Genotypic growth–defense trade-offs have been observed previously in aspen, which may allocate upward of 30% of assimilated carbon to PG metabolism (32). We quantified allocation to herbivore defense as the combined concentration, per unit leaf mass, of PGs.

Results

Throughout the 5-y study period tree relative growth rate exhibited an among-genotype trade-off with level of herbivore defense, regardless of competitive environment or year (Fig. 1 and *SI Appendix*, Table S1). That is, the genetic cost of defense in terms of growth rate reduction was not context-dependent.

Although competition intensity did not alter the covariance between growth and defense traits, it did affect the strength of selection pressure on both growth and defense. Over the course of the study, high competition intensity led to lower survivorship of slow-growing genotypes compared with fast-growing genotypes, whereas stands with low competition intensity supported higher survivorship for tree genotypes across the range of growth rates (Fig. 2*A*). Selection differentials for growth rate were >0 in both competitive environments, meaning that trees that ultimately survived to 2019 had higher growth rates in 2015 than the population average at that time (Fig. 3*B* and *SI Appendix*, Fig. S3). This selection differential was stronger, however, in high-competition

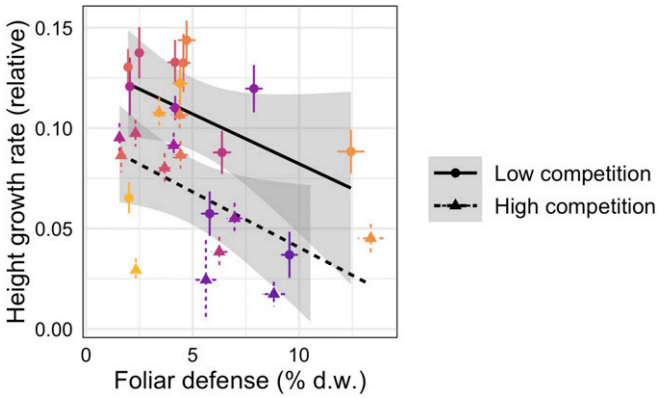

Fig. 1. Genetic costs of defense. Relationship between genotype-level growth and defense traits over time in low-competition (solid line) and high-competition (dashed line) environments, averaged across the 5 y of the study. Growth is quantified as the relative growth rate in terms of height; defense is quantified as the total foliar concentration of PGs (percent dry weight). Points are genotype means in each environment and whiskers are ±1 SEM. Colors denote unique genotypes. Shaded areas are 95% confidence intervals for the linear regression lines. Slopes do not differ significantly between competition treatments or years (see *SI Appendix*, Table S1).

stands than in low-competition stands (Fig. 3*B* and *SI Appendix*, Fig. S3). Because of the underlying negative genetic covariance between growth rate and PG defenses, the selection pattern detected for allocation to herbivore defense was opposite that observed for growth rate. At high competition intensity, survivorship was low for well-defended genotypes relative to less-defended genotypes, whereas at low competition intensity survivorship was largely unrelated to defense (Fig. 2*B*). Selection differentials were <0 for foliar PG concentrations in high-competition stands, indicating directional selection against high levels of defense (Fig. 3*C*). Trees that survived all 5 y to 2019 under high competition intensity had defense levels that were 14% lower than the stand average at the onset of the study (2015) (Fig. 3*C*).

As a result of competition-mediated selection, the genotypic composition of the experimental stands diverged over time (Fig. 3*A*). Mean cumulative survivorship varied widely among genotypes, from 6.5 to 88.2% in high-competition stands and from 22 to 100% in low-competition stands, in accordance with the genotypes' growth–defense phenotypes (Fig. 2 *A* and *B*). This evolutionary divergence occurred within the 5 y of the study, an ecologically relevant timescale that represents a fraction of the lifespan of a single generation of trees. Trees in this study were not yet reproductively mature, so we did not measure genotype fitness in terms of sexual reproduction. However, given the high mortality rates in young aspen stands and the tendency toward aggressive vegetative reproduction by surviving genotypes (27, 29), survivorship is a key fitness metric in this system.

At the end of the 5-y study, low-defense genotypes dominated high-competition aspen stands in terms of basal area (*SI Appendix*, Fig. S1*A*), due to a combination of faster growth and higher survivorship. Low-competition stands exhibited more even representation across genotypes (*SI Appendix*, Fig. S1*B*). Stand-level averages for foliar PGs and herbivory, weighted by relative basal area, did not significantly differ between treatment groups (PGs: $t_{16} = 0.65$, $P = 0.53$, herbivory: $t_{16} = -0.32$, $P = 0.75$; *SI Appendix*, Fig. S2). Over time, however, competition-mediated changes in the number and relative size of trees belonging to each genotype can be expected to produce parallel shifts in distributions of ecologically relevant traits at the forest stand level. This is especially likely in aspen, for which most traits are strongly genetically determined (25).

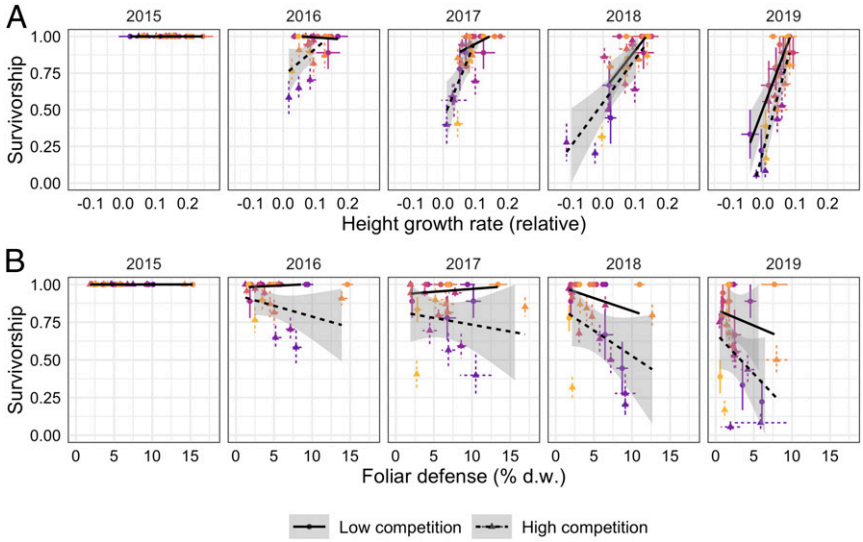

Fig. 2. Competition-mediated selection on growth and defense traits. Relationship between genotype-level cumulative survivorship and (*A*) growth and (*B*) defense traits in low-competition (circles, solid lines) and high-competition (triangles, dashed lines) environments. Growth is quantified as the relative growth rate in terms of height, and defense is quantified as the total foliar concentration of PGs (percent dry weight). Points are genotype means and whiskers are ±1 SEM. Colors denote unique genotypes and are consistent with Fig. 1. Shaded areas are 95% confidence intervals for the linear regression lines. Slopes differ between competition treatments for both traits (growth × competition and defense × competition interactions), and slopes vary significantly by year for growth (growth × year interaction; see *SI Appendix*, Table S2).

Discussion

We found that a genetically fixed growth–defense trade-off coupled with high levels of competition led to simultaneous selection for genotypes with both high growth rates and low herbivore defense levels. Environmental variation in growth–defense trade-offs is often implicated in the maintenance of intraspecific variation in plant defense traits (2); in particular, the likelihood and magnitude of growth–defense trade-offs are predicted to increase with competition intensity. Prior tests of this prediction, however, have produced mixed evidence (33–36), and our results show that genetic trade-offs can in fact have fixed expression across divergent environments. Our results provide strong evidence for the perspective that although plant defense traits evolved in response to herbivore pressure, covariance with other ecologically important traits renders the evolution of defense traits sensitive to selection pressures other than herbivory. Our results also help explain nonintuitive patterns of defense allocation across populations where herbivory is not the principal selective force.

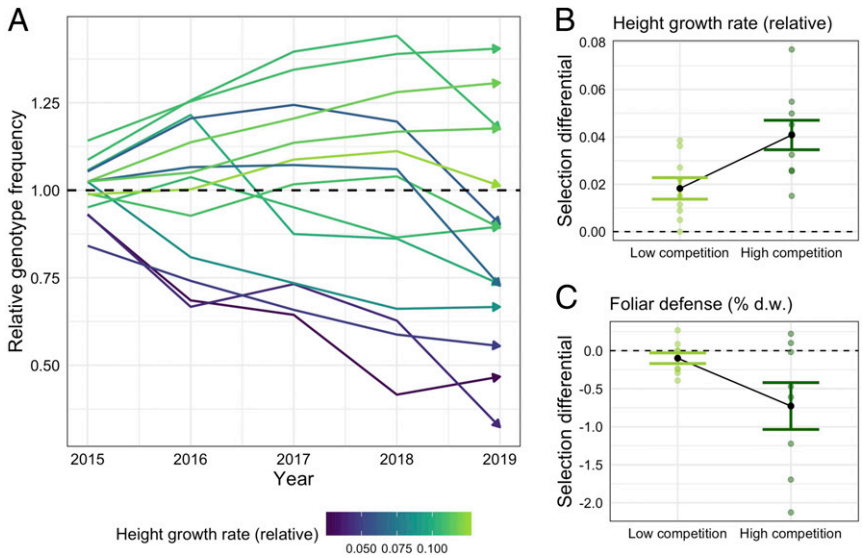

Fig. 3. Competition-mediated changes in stand genotypic composition. (*A*) Relative frequency of genotypes in high- vs. low-competition environments. Values above 1 indicate higher frequency for an individual genotype in high-competition stands and values below 1 indicate higher frequency in low-competition stands. Trajectories of relative frequency over time vary among genotypes (genotype × year interaction; see *SI Appendix*, Table S3). Genotype trajectories are colored based on their 5-y average relative growth rate in terms of height. (*B* and *C*) Selection differentials (how survivors' trait values differed from the initial population mean) in low- vs. high-competition environments for (*B*) growth rate ($F_{1,16} = 8.58$, $P = 0.010$) and (*C*) defense ($F_{1,15} = 1.67$, $P = 0.053$). A selection differential >0 indicates selection for higher values of a trait in that plot, and a selection differential <0 indicates selection for lower values of a trait. Each point represents a plot and error bars are ±1 SEM across plots.

Although genetic costs of defense in terms of growth rate were not context-dependent, the ultimate survivorship cost of high defense levels could be considered a context-dependent ecological cost, because it is incurred only in the presence of a high density of interacting competitors (4, 36). Herbivory occurred at low background levels during the study (3.4% leaf area lost overall), and we would expect defense variation to be more important for reducing herbivory in outbreak years (31), when potential damage exceeds those levels by twofold or more (37) up to complete defoliation (38). Such changes in stand genotypic composition due to competitive interactions affect not only current defense levels but also patterns of defense allocation into the future, because allocation to chemical defense changes in a genotype-specific manner as trees proceed through ontogenetic development (26).

Dynamics of aspen growth and defense traits such as those documented here are expected to have pervasive and enduring repercussions for ecological processes in forest systems across scales. First, previous research has documented that variation in aspen growth and defense traits influences the performance, distribution, and abundance of aspen-associated herbivores (31, 39, 40) and pathogens (41). The dominance of less-defended genotypes in highly competitive environments will likely increase aspen stand vulnerability to pests and pathogens that can cause major damage (29), and those threats are expected to increase with climate change (42). Second, variation in aspen defense traits will influence community-level structure and function, including multitrophic interactions (22), canopy arthropod communities (43), and soil microbial communities (44, 45). As the genotypes used in this study have previously been shown to support different arthropod communities (42), our results provide insight into the eco-evolutionary mechanisms that create these community-level "extended phenotypes" (18). Third, variation in aspen traits will affect processes at the ecosystem level, such as litter decomposition, nutrient cycling, and carbon sequestration in woody biomass (19, 32, 46). Ecosystem-level studies have revealed genotype-specific effects even among groups of aspen genotypes with less trait variation than seen in our study (19).

Our work provides unique and compelling evidence of eco-evolutionary dynamics in forest trees. Such dynamics have been empirically tested only a handful of times in plants (11, 47), and rarely under field conditions. Our results also highlight the relevance of eco-evolutionary dynamics across scales, because the evolutionary effects of interactions at the within-population level drove changes in traits that are relevant to interactions among species. The relevance of population-level dynamics for trophic interactions underscores the pressing need to move beyond species means in trait-based community ecology. Consideration of the cross-scale nature of eco-evolutionary dynamics, via the currency of plant traits, will enhance our understanding of higher-order biological systems and their resilience to environmental change (10, 48).

This work challenges a key assumption of plant–herbivore ecology: that growth–defense trade-offs must be context-dependent to have context-dependent evolutionary consequences. Our findings show that, to the contrary, genetic trade-offs can differentially affect population composition in different environments—and thus maintain intraspecific variation across environments—even if the trade-offs themselves are fixed. This discovery significantly advances our understanding of eco-evolutionary trait dynamics in plants generally and in trees more specifically. By linking stand genotypic composition to the outcomes of biotic interactions, genetically controlled trait trade-offs in trees can govern trajectories of forest structure and function over time. Stand-scale patterns of growth and defense expression created by these dynamics have the potential to define the resilience of forests to the increased magnitude and frequency of stressors predicted for the future.

Materials and Methods

Study Site and Experimental Design. The experimental garden consisted of a set of 18 aspen stands planted on a 0.2-ha site at the University of Wisconsin Arlington Agricultural Research Station (Arlington, WI; 43°18′9.47″ N, 89°20′ 43.32″ W). The soil at the site is a Huntsville silt loam (mesic Cumulic Hapludoll), which supported a grass-dominated old field prior to plowing for this study.

The experiment was a 2 (competition intensity) × 14 (genotype) split-plot design, with competition intensity manipulated at the stand level and genotype nested within competition intensity. Each stand consisted of replicate individuals from each of the 14 genotypes, plus a border of nonexperimental trees. Half of the stands ($n = 9$) were randomly assigned to the high-competition-intensity treatment while the other half ($n = 9$) were assigned to the low competition intensity.

Tree Propagation. Aspen genotypes used in this study were originally collected as root stock throughout south-central Wisconsin and have been maintained since the late 1990s in common gardens (49). Genotype identity was previously confirmed using single-nucleotide polymorphism analysis, and the 14 genotypes used displayed low relatedness (50). Replicate individual trees for this study were propagated via commercial tissue culture (Knight Hollow Nursery). In late summer 2010, individuals were transplanted from propagation trays into conetainers (D40H Deepots; Stueve & Sons) with a 50–50 mix of torpedo sand and MetroMix 366-PSC (Sun Gro Horticulture). The trees were then moved outside and allowed to transition to dormancy. Dormant trees were planted at the study site in late October through early November 2010. All stands were initially planted at the high-competition density (40,000 ha^{-1}, 0.5- m × 0.5-m spacing, four replicate individuals per genotype), which mimics the intense competition often observed in establishing aspen stands when seeds are abundant (27, 28). Then, in early spring 2014 (trees aged 4 y, average 3.65 m tall), the low-competition stands were thinned to 10,000 ha^{-1} (one replicate individual per genotype). The common garden area was fenced, which excluded deer, but otherwise was accessible to herbivores.

Size and Mortality. Size and mortality were surveyed for all trees from 2014 through 2019 (trees aged 4 to 9 y). Surveys were conducted each fall after leaf senescence. Height was measured using telescoping height poles and diameter was measured at breast height (DBH, 1.4 m). Basal area was calculated from DBH, assuming a round trunk. We used height to calculate growth rates, due to its importance for competitive interactions, and we calculated relative growth as the natural log of the ratio of final to initial height. We recorded trees as dead when they had completely dead bark at breast height and calculated survivorship as proportional to the start of the study.

Leaf Collections and Phytochemistry. Leaves were collected from all trees in midsummer (ranging from June to early July) every year from 2015 to 2019 (trees aged 5 to 9 y). Leaves were collected in a systematic manner to reduce potential bias due to positional factors. The leaf collection procedure changed slightly over the course of the study. In 2015, 15 to 20 leaves were collected from each third of the tree crown and chemistry values were averaged across those levels. After 2015, we collected a single pooled leaf sample from the lower two-thirds of each tree's canopy: In 2016 to 2017 we collected four proleptic shoots and kept three leaves per shoot (12 leaves total); in 2018 to 2019 we selected three or four branches per tree depending on tree size, collected two proleptic shoots per branch, and kept two leaves per shoot (12 to 16 leaves total). When proleptic shoots had more than two leaves we kept the most-proximal and third-most-proximal leaves. Petioles were collected along with the leaf blade. We avoided collecting leaves from indeterminate growth and from trees where collection would mean removing half or more of their total foliage. For 2019 herbivory measures we scanned leaves using Canon LiDE 210 and Canon LiDE 700F scanners. Missing leaf edges were reconstructed digitally on scanned images (51), then total leaf area and leaf area removed by herbivores were quantified using WinFOLIA Pro-2007a software (Regent Instruments). After scanning, leaves were vacuum-dried, weighed, and ground on a ball mill for use in phytochemical analyses.

Foliar salicinoid PGs (salicin, salicortin, tremuloidin, and tremulacin) were quantified using ultra-high-performance liquid chromatography (52). Salicortin, tremulacin, and tremuloidin analytical standards were purified from *P. tremuloides* foliage (52) and salicin analytical standard was purchased from Sigma-Aldrich. Additional phytochemical analyses were conducted during the study years, data from which will be reported elsewhere. The current study focuses on genetic variation in herbivore defense and therefore centers on the PGs, compounds of known importance for aspen defense

against herbivory. Condensed tannin data were omitted from this study because condensed tannins are less genetically determined than PGs and are rarely implicated in herbivore resistance (31).

Statistical Analyses. Relationships among growth, defense, and survivorship over time in the two competitive environments were tested using linear mixed models with genotype as a random effect and year as a fixed effect. We used the lme4 package in R to construct mixed models (53, 54) and the car package for significance testing via ANOVA (55). When models contained more than two predictors, we performed model selection to determine which interaction terms to include in the final model. We selected models from all subsets, including interactions, based on the lowest small-sample corrected Akaike information criterion using the MuMIn package (56). We evaluated changes in the relative frequency of genotypes in the different competitive environments over time using a simple linear model with genotype and year as fixed effects. For all models, assumptions of homogeneity and normality of variance were evaluated by plotting residuals against fitted values and by using a QQ plot, respectively. A logit transformation was applied to the survivorship data.

We calculated selection differentials for both growth rate and defense levels. The selection differential provides a metric of how survivors differed from the starting population. Selection differentials were calculated as the difference between the 2015-mean value of a trait for trees that survived to 2019- and the 2015-mean value of a trait for all trees in a plot, including those that subsequently died. A selection differential >0 indicates selection for higher values of a trait, and a selection differential <0 indicates selection for lower values of a trait. A selection differential of zero indicates no directional selection on that trait. Selection differentials are in the units of the original trait values; for example, if diameter is measured in centimeters and the selection differential for diameter is 5, it means that survivors had higher initial diameter than the population mean by 5 cm.

To quantify differences in stand composition, we compared genotype evenness of stands at high and low competition intensity over time. We used total basal area as a measure of genotype abundance; plot-level genotype evenness therefore represented the among-genotype similarity in contribution to plot basal area. We calculated Pielou's evenness index for each plot using the vegan package in R (57). An evenness index value equal to 1 would indicate that, within that plot, all genotypes had the same total basal area. Lower evenness values indicate dominance of plot basal area by some genotypes and reduced contribution to plot basal area by others.

Data Availability. The dataset associated with the current study is available in the Dryad data repository (DOI: 10.5061/dryad.x95x69phb) (58).

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