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Vegetative Regeneration Delays but Does Not Prevent Regeneration Debt: Thirty Years of Compositional and Structural Change in Adjacent Appalachian Forest Communities

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Abstract

Eastern deciduous forests are undergoing directional compositional shifts, marked by the progressive replacement of *Quercus*-dominated canopies with generalists and shade-tolerant taxa. These shifts are increasingly interpreted within a regeneration debt framework, in which canopy composition persists despite recruitment failure and regeneration mismatch in smaller size classes. We evaluated 30 years (1995–2025) of compositional and structural change in adjacent upland and cove forests on the southern Cumberland Plateau, Tennessee, using a permanent nested circular plot design to determine whether previously observed upland resistance reflects durable resilience or delayed demographic transition. Both habitats exhibited continued *Quercus* decline while remaining compositionally distinct. As documented in prior analyses, reductions in small-diameter stems were more pronounced in the cove forest, but now reveal demographic mismatches between canopy and regeneration layers in both habitats. Upland forests maintained a higher representation of species capable of basal sprouting and clonal growth via root suckering, indicating that vegetative regeneration buffered short-term demographic change. However, recruitment into larger size classes declined in both habitats, demonstrating that buffering facilitated by vegetative regeneration delayed but did not prevent the accumulation of regeneration debt. What appeared as differential resistance through 2014 is more accurately interpreted as temporal offset in regeneration debt accumulation.

Keywords: basal sprouting; clonal growth; oak decline; Cumberland Plateau; persistence; regeneration debt; vegetative regeneration

1. Introduction

Appalachian forests are experiencing directional compositional shifts characterized by widespread replacement of *Quercus* L. (oak) species by generalists such as *Acer rubrum* L. and other shade-tolerant taxa [1]. Across the southern Appalachians, altered disturbance regimes including fire exclusion, introduced pathogens, and elevated deer herbivory have contributed to widespread oak regeneration failure and increased density of more shade-tolerant species [2–6]. In many communities, canopy oaks persist while recruitment layers become increasingly dominated by non-oak taxa, generating demographic mismatches between overstory and regeneration strata [7]. Increasingly, these patterns are interpreted within a regeneration debt framework, in which canopy composition persists despite the sustained combination of recruitment failure and regeneration mismatch, delaying and potentially preventing eventual compositional transition [8,9]. Moreover,

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while shifts in density and frequency reflect substantial changes in species composition, changes in biomass and basal area may be masked by the disproportionate influence of large canopy trees. Canopy trees mask compositional changes because they can continue to persist and accumulate biomass even as their overall population density declines [10–14]. As a result, forests may appear structurally stable while simultaneously accumulating regeneration debt.

The Cumberland Plateau of southern Tennessee provides a natural experiment for examining these dynamics. Xeric upland forests on sandstone-derived soils occur immediately adjacent to mesic cove forests on shale- and limestone-derived substrates, yet maintain distinct species assemblages structured primarily by edaphic differences rather than elevation [15,16]. Both forest types have been exposed to similar anthropogenic pressures, including fire exclusion [3], chestnut blight [17], dogwood anthracnose [18], and increased deer herbivory [6], raising the question of whether shared disturbance drivers promote convergence, divergence, or differential resilience across strong environmental gradients. Research addressing this issue in Southern Appalachian forests indicates non-convergent trajectories of compositional shifts among adjacent upland and cove forests [1].

Sustained compositional and structural change in both upland and cove habitats of the southern Cumberland Plateau has been documented with permanent plots established in 1995. Across successive analyses, both communities showed declining *Quercus* spp. representation and increasing *Acer* spp. L. dominance while remaining compositionally distinct [19,20]. Structural shifts included reductions in small-diameter stems—particularly in the cove forest—and a strong representation of sprouting species in the upland understory [19]. Continued monitoring revealed ongoing oak decline, but suggested greater apparent resistance and slower species turnover in the upland forest compared to the cove forest [20]. Evans et al. [20] proposed that vegetative regeneration (including basal sprouting and clonal growth via root suckering) may have contributed to upland stability by maintaining species representation in regeneration layers despite limited seedling recruitment.

Vegetative regeneration plays a critical but often underappreciated role in eastern hardwood forest dynamics. Many canopy and midstory species possess the capacity for basal sprouting or clonal growth, particularly following disturbance, allowing persistence under conditions unfavorable for sexual recruitment [21–23]. Basal sprouting can maintain local occupancy, stabilize stem density, and accelerate canopy reoccupation following disturbance events [24]. In fire-suppressed systems, vegetative regeneration may allow species to persist beneath increasingly closed canopies or thick litter layers that inhibit seedling establishment [25]. However, vegetative regeneration does not necessarily confer demographic replacement; vegetative stems often represent the persistence of existing genets rather than successful cohort recruitment [26], potentially masking long-term regeneration failure. Thus, forests with a high capacity for vegetative regeneration may exhibit apparent short-term resistance to compositional change while simultaneously accumulating regeneration debt.

Here, we extend this permanent-plot record to 30 years (1995–2025) to evaluate long-term trajectories of composition, structure, and regeneration strategies in adjacent upland and cove forest communities. Specifically, we ask: (1) whether the distinctness of these habitats persists after three decades of shared disturbance; (2) whether upland forests retain the apparent resistance documented through 2014 [20], or exhibit emerging regeneration debt; and (3) whether differences in vegetative regeneration traits correspond to divergent demographic trajectories. We predicted that both habitats would show increasing evidence of regeneration mismatch between canopy and recruitment layers, that regeneration debt signals would be more pronounced in the cove forest, and that upland forests would retain greater proportional representation of vegetatively regenerating species.

2. Materials and Methods

2.1. Study Area

Our study plots were located along the southwestern margin of the Cumberland Plateau in Franklin County, Tennessee, USA, on lands owned by the University of the South. Sampling occurred within and immediately adjacent to Thumping Dick Hollow (also known as Dick's Cove; 35°13′ N, 85°57′ W; see Figure 1 in Evans et al. [20]). Detailed environmental descriptions of this site are provided in Evans et al. [27]. The two forest types examined—cove and upland plateau—occur in close proximity and are separated by an approximate 25 m drop in elevation along the bluffline, allowing for potential exchange of propagules between communities.

Climatic conditions in the region are characterized by mean monthly temperatures ranging from approximately 2 °C in January to 23 °C in July. Precipitation is highest in December (16.76 cm) and lowest in October (9.73 cm), with an average annual total of 170.33 cm. Based on the 1995–2025 Monteagle, Tennessee precipitation records within March–September, 2006, 2007, and 2016 had precipitation below the 10th percentile (<29.3 in) and can be considered as severe growing-season drought years [28]. Upland plateau soils are typically shallow, sandy, acidic, and relatively low in moisture availability and cation exchange capacity. In contrast, soils within the cove contain greater clay content, resulting in higher moisture retention, elevated pH, and increased cation exchange capacity [20].

Historical records from the University of the South indicate that the cove forest has remained unlogged since at least 1858, when the University was established. This area is recognized as old-growth and has been designated a National Natural Landmark by the U.S. National Park Service. The adjacent upland plateau forest represents a mature second-growth mixed-oak system typical of the southern Cumberland Plateau [27]. While University records have not consistently tracked deer densities across the University property, reported densities have been as high as 57 individuals per km^2 [20]. This study revisits a network of randomly established plots set up in 1995 across both cove and upland habitats, as described in Reid et al. [19] and Evans et al. [20]. Within the upland sites, half of the plots (located on the eastern portion) were subjected to a diameter-limit selective harvest (35.5 inches) in 1976, while the remaining plots had not experienced logging for at least six decades. Basal area between the two sides of the upland plots was significantly different in early census periods due to the logging effect, but no longer significantly different by 2014 [20]. While compositional legacy effects from this harvest are possible, the scope of our analysis is unable to clarify these effects, given that our permanent plots were established nearly twenty years after this harvest.

2.2. Sampling Design

We sampled a total of sixteen permanent plots (0.1 ha each), with eight located in the cove (545 m elevation) and eight situated on the adjacent upland plateau (570 m elevation). The mean distance between the adjacent upland and cove plots is 169.78 m (±9.48 SD). In maintaining temporal consistency in sampling design [19], we surveyed woody stems using a nested circular plot design to capture multiple strata of the woody plant community. We measured canopy trees (E: dbh > 20 cm) across the full 0.1 ha plot, assessed midstory individuals ($\geq$1.5 m in height) within a 0.05 ha subplot (12.6 m radius), and their diameters at breast height (dbh, measured at 1.5 m) were categorized into three classes: B (0–2.5 cm), C (2.5–10 cm), and D (10–20 cm). We measured understory individuals using a height class (A: <1.5 m tall), and sampled within a 0.001 ha subplot (5.6 m radius). Data collection occurred in 2005, 2014, and 2025, and these observations were compared with the original 1995 dataset. Additional methodological details are available in Reid et al. [19].

2.3. Vegetative Regeneration Trait Categorization

To assess vegetative regeneration traits across species in our study, we searched relevant academic and applied literature for evidence of these clonal life history traits. Search terms used for basal sprouting included "sprouting" and "basal sprouting", while terms used for clonal growth included "clonal growth", "root suckering" and "root sprouting". Basal sprouting for our purposes does not include induced sprouting from cuts, fire, frost damage, or anything that causes initial stem mortality prior to the production of replacement stems. Evidence of vegetative regeneration traits was first assessed in the academic literature, and if no evidence was available, our second assessment was through the Silvics of North America [29]. In cases of ambiguity, trait designations were resolved through consensus between authors. Species lacking explicit evidence of basal sprouting or clonal growth were classified as "None". Results from our literature review are listed in Appendix A Table A1 and inform vegetative regeneration categorization, where "None" includes species that do not possess the ability for basal sprouting or clonal growth, "Basal Sprouting" includes species that basal sprout, "Clonal Growth" includes species that possess clonal growth habits, and "Both" includes species that are regularly capable of both vegetative regeneration traits.

2.4. Statistical Analyses

Changes in observed species richness between 1995 and 2025 were assessed using two-sided paired *t*-tests, with analyses conducted separately for each of five size classes within cove and upland habitats. *p*-values for these ten related tests were adjusted for family-wise error using Bonferroni correction. Differences in stem density among habitat–year combinations within each size class were evaluated using linear mixed-effects models with habitat, year, and their interaction as fixed effects and plot identity included as a random effect. Estimated marginal means were compared using Tukey-adjusted post hoc tests, and significant differences were indicated using compact letter displays in Figure 1. Differences in vegetative regeneration category stem allocation between habitats were evaluated separately for 1995 and 2025 using negative binomial generalized linear mixed-effects models with habitat, year, vegetative regeneration category, and their interactions as fixed effects. Plot identity was included as a random effect to account for repeated sampling through time. A negative binomial distribution was used to accommodate overdispersion in stem count data. Plot-level stem counts within each vegetative regeneration category were modeled using a negative binomial GLMM, with the log of total stems per plot included as an offset to estimate proportional allocation of stems. We tested for overdispersion using DHARMa residual diagnostics, and no overdispersion was shown. The summary statistic C was calculated using the direction of change in the average density of stems in each size class in each interval (with an increase in density resulting in a value of 1, no change resulting in a value of 0, and a decrease in density resulting in a value of -1), and summing the change values for the three intervals together. The following equation was used for calculating C: $\mathrm{C} = \mathrm{sign}(\mathrm{D}_{2005} - \mathrm{D}_{1995}) + \mathrm{sign}(\mathrm{D}_{2014} - \mathrm{D}_{2005}) + \mathrm{sign}(\mathrm{D}_{2025} - \mathrm{D}_{2014})$, where D is equal to the density of stems in a given size class. All analyses were conducted in R v4.5.2 [30].

3. Results

In the cove, *Quercus* spp. have had inconsistent or absent densities in the intermediate size classes, and no noticeable increases in density among any size class between 1995–2025 (Appendix A Table A2). In particular, species in the white oak subgenus (*Quercus* sect. *Quercus*) have demonstrated low levels of stem density in the intermediate size classes (*Q. alba* L.: only size class D stems; *Q. montana* Willd: only size class C stems), while species in the red oak subgenus (*Quercus* sect. *Lobatae* Loudon) have never had any stems in the intermediate size classes (*Q. rubra* L., *Q. velutina* L'Hér. ex A.DC.). On the plateau, a number of *Quercus* spp. (*Q. alba*, *Q. coccinea* Münchh., *Q. montana*, and *Q. velutina*) show consistent presence among all size classes, with all but *Q. coccinea* demonstrating relative stability or increasing density in the canopy, while densities in their intermediate-sized stems show noticeable declines (Appendix A Table A2). Additional *Quercus* spp. (*Q. stellata* Wangenh., *Q. rubra*, and *Q. muehlenbergii* Engelm.) show sporadic presence among shorter-sized stems on the plateau. Across both habitats, *Carya* spp. Nutt. exhibit declining densities in all size classes. In the cove, *Acer saccharum* Marshall shows declining densities in smaller size classes (A–C) but increasing densities in larger classes (D–E), with some stem density fluctuations in size A (Appendix A Table A2). On the plateau, *Acer rubrum* increased in size classes A, C, and D, with stability in the canopy and moderate declines among stems in size class B.

3.1. Density and Species Richness Change

We observed a decrease in stem density in all but size class E in both the cove and plateau habitats, with decreases being most pronounced in size classes B and C (Figure 1). There was a decreasing trend in species richness across all size classes in both habitats between 1995 and 2025. Significant decreases in species richness were found in size classes B and C in the cove and in size class B on the plateau (Table 1).

Table 1. Comparison of mean (±standard deviation) number (#) of species and species richness change by size class, 1995–2025. Species richness change was evaluated using Bonferroni-adjusted Welch's *t*-test results. * = $p \leq 0.05$; ** = $p \leq 0.01$.

Habitat	Size Class	Mean # Species 1995	Mean # Species 2025	Richness Change 1995–2025	t	*p*
Cove	A	12 ± 4.2	9.8 ± 1.8	−2.3 ± 3.9	−1.6	1
	B	6.4 ± 3.2	1.3 ± 0.7	−5.1 ± 2.8	−5.2	0.013 *
	C	6 ± 1.5	2.1 ± 1	−3.9 ± 1.5	−7.5	0.001 **
	D	4.6 ± 2.6	1.9 ± 1.1	−2.8 ± 2.2	−3.6	0.093
	E	6.8 ± 1.3	6.5 ± 0.9	−0.3 ± 1.7	−0.4	1
Plateau	A	14.5 ± 2.1	12.4 ± 1.2	−2.1 ± 2.9	−2.1	0.769
	B	11.3 ± 2.8	5.3 ± 1.7	−6 ± 3.6	−4.7	0.021 *
	C	9 ± 2.1	6.6 ± 1.1	−2.4 ± 2.8	−2.4	0.460
	D	6.4 ± 1.2	4.9 ± 1.6	−1.5 ± 2	−2.1	0.716
	E	5.3 ± 1.2	5.1 ± 1	−0.1 ± 1	−0.4	1

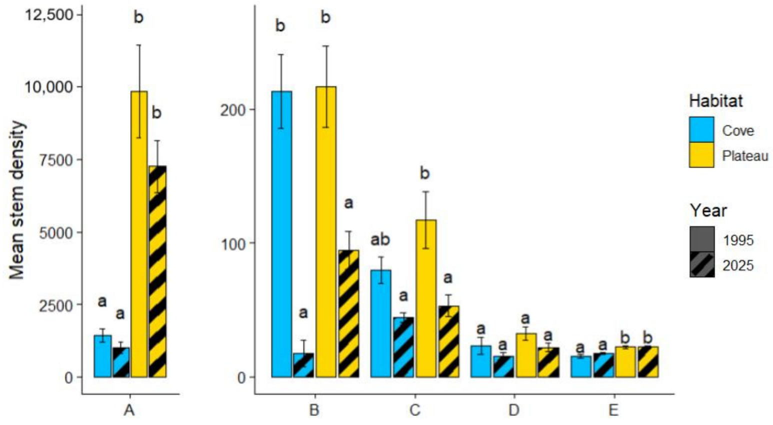

Figure 1. Mean density changes by size class from 1995 to 2025 in the cove and plateau. Error bars represent ±1 standard error of the mean. Different letters indicate significant differences among groups within each size class (Tukey-adjusted post hoc tests, $p < 0.05$).

3.2. Allocation of Stem Density by Vegetative Regeneration Traits

There were highly significant interactions between habitat and vegetative regeneration category in both 1995 ($\chi^2 = 212.71$, df = 3, $p < 0.001$) and in 2025 ($\chi^2 = 162.54$, df = 3, $p < 0.001$). The habitats show marked differences in proportional stem density allocation between habitats, with the cove maintaining high levels of stems with no vegetative regeneration traits, and the plateau maintaining high levels of stems with basal sprouting and both vegetative regeneration traits (Figure 2).

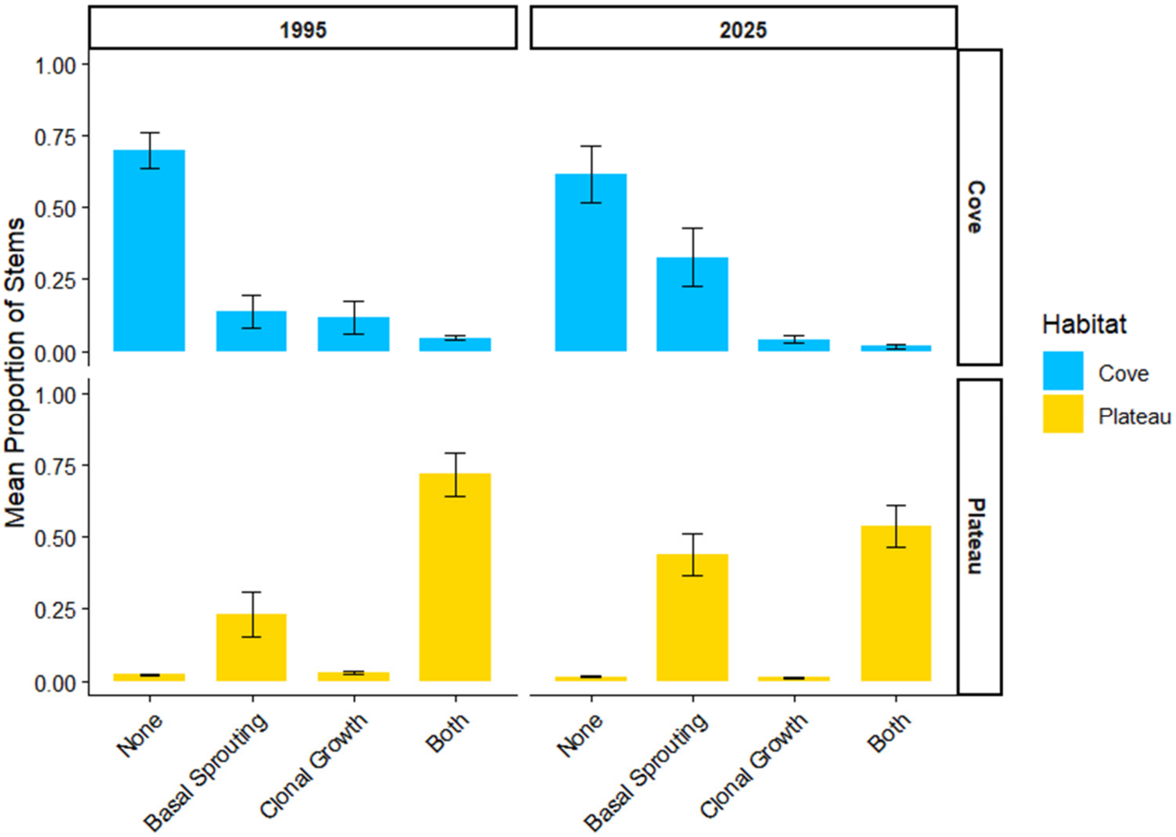

Figure 2. Mean proportional allocation of stem density by vegetative regeneration category in the cove and plateau for 1995 and 2025. Error bars represent ±1 standard error of the mean.

4. Discussion

Across three decades of monitoring, adjacent cove and upland forests on the southern Cumberland Plateau have exhibited continued oak decline and regeneration mismatch alongside substantial species richness and stem density declines (particularly in the early midstory), consistent with regional patterns of regeneration debt [9,31,32]. The extended temporal perspective afforded by these permanent plots clarifies that early interpretations of parallel compositional change and apparent differential resistance represent sequential stages within a longer demographic trajectory. Over the thirty-year period, both forest types exhibited declining species richness and density while remaining compositionally distinct across strong edaphic boundaries [19], a finding similarly reported in other upland and cove Appalachian forests [1]. Evans et al. [20] suggested there was greater apparent resistance to species loss in the upland forest relative to the cove, leading to the hypothesis that vegetative regeneration buffered upland forests against compositional transition.

With 30 years of data, we have refined that interpretation. Both habitats now exhibit clear demographic mismatches between canopy composition and recruitment layers, indicating that long-term transition may be underway despite continued canopy persistence.

The trajectory remains more advanced in the cove forest, where reductions in small stems and midstory recruitment were detected early [19], but upland forests now show comparable signals of regeneration limitation. What appeared as differential resistance through 2014 is more accurately interpreted as a temporal offset in regeneration debt accumulation rather than evidence of persistent resilience.

4.1. Vegetative Regeneration as Demographic Buffering

Vegetative regeneration emerges as a key mechanism shaping habitat differences in the rate of demographic change. The upland forest consistently maintained a greater proportional representation of species capable of combined basal sprouting and clonal growth, a pattern first documented during the initial decade of monitoring [19]. The degree of vegetative regeneration differences between the upland and cove forest communities may be more pronounced, given species such as *Sassafras albidum* (Nutt.) Nees demonstrate higher levels of clonally produced stems in upland sites than they do in mesic cove sites [33,34]. Basal sprouting allows individual stems to persist in place despite repeated top-kill, suppression, or partial mortality, repeatedly recruiting into and declining from smaller size classes as conditions vary [35–37]. Clonal growth via root suckering allows genets to persist across space, spreading risk of mortality among microsites and increasing the probability of encountering favorable resource conditions [38]. Together, these modes of vegetative regeneration help individuals buffer demographic variability over time and space and persist beneath closed canopies or thick litter layers that suppress seedling establishment [24,25,39]. Among xeric upland sites, fires historically have been more frequent [40]. This disturbance regime, coupled with nutrient-poor upland soils [41], would have favored species capable of vegetative regeneration. Given the recent history of fire exclusion on the Cumberland Plateau, these legacy traits of vegetative regeneration likely contributed to the apparent upland resistance documented through 2014 [20].

However, vegetative persistence does not necessarily equate to successful demographic replacement [26]. Stems produced by vegetative regeneration frequently represent reiterations of existing genets rather than new recruitment cohorts. As a result, many studies have shown that vegetative persistence may not generate the genetic diversity needed to support long-term population viability [21,42,43]. In the absence of sufficient seedling establishment and sapling recruitment, vegetative regeneration may stabilize short-term stem density while long-term replacement fails. Our extended observations suggest that vegetative regeneration functions primarily as temporal buffering, causing a slowing of the rate of compositional change without preventing eventual transition. In this sense, upland forests appear to have accumulated regeneration debt later than cove forests, but are not insulated from long-term restructuring.

4.2. Implications for Long-Term Forest Trajectories

Taken together, the 10-, 19-, and 30-year analyses reveal a conceptual shift from apparent differential resistance to emerging regeneration debt in both habitats. This progression highlights the necessity of long-term monitoring for distinguishing transient stability from lasting resilience. Forests dominated by long-lived canopy trees and species capable of vegetative persistence may exhibit extended periods of structural continuity even as recruitment bottlenecks accumulate beneath the canopy.

If current disturbance regimes such as fire exclusion and sustained deer herbivory persist [6,27], continued oak recruitment failure suggests that eventual canopy turnover will favor generalists such as *Acer rubrum* and other shade-tolerant taxa in both habitats, strengthening the regeneration debt signal [44]. Among genera, long-term trajectories can be variable, seeing as *Acer rubrum* appears to be increasing or maintaining densities on the upland plateau, whereas its cove counterpart, *Acer saccharum*, is aligned with signals of regeneration debt [45]. Furthermore, *Quercus* spp. declines have varying degrees of regeneration failure depending on species, with many oaks in the red oak (*Quercus* sect. *Lobatae*) subgenus showing greater levels of decline than white oaks (*Quercus* sect. *Quercus*; [46]). While vegetative regeneration may slow these compositional transitions, our results indicate that buffering capacity is finite.

Shifts in canopy species composition among both cove and upland forests can be accelerated by harvest treatments [1]. In particular, clear-cutting disrupts soil microclimate, fragments root systems, and disturbs long-established ectomycorrhizal networks associated with oak-hickory communities, favoring taxa associated with arbuscular mycorrhizal networks such as *Liriodendron* L. and *Robinia* L. [47–49]. In addition to fine-scale edaphic conditions that structure forest community assemblages, effective site-specific management approaches must consider the regeneration mismatch between canopy and understory individuals, as well as the potential for heterospecific seed dispersal between adjacent forest communities [1].

More broadly, these findings reframe vegetative regeneration not simply as a resilience mechanism, but as a demographic buffer capable of delaying the visible consequences of recruitment failure. Recognizing both the stabilizing and masking effects of vegetative regeneration is essential for predicting long-term forest trajectories under sustained environmental change and for designing management interventions aimed at sustaining oak-dominated systems. Further research would benefit from increasing the geographic scope for assessing the role vegetative regeneration plays in both natural and experimental forest regeneration dynamics.

5. Conclusions

Both upland and cove habitats continued to demonstrate signs of *Quercus* spp. decline and broad patterns of regeneration debt, while remaining compositionally distinct. As a characteristic difference between habitats, vegetative regeneration potentially acted as a temporal buffer in compositional and structural change on the upland plateau, but did not prevent the accumulation of regeneration debt within a changing community. Vegetative regeneration life histories should be taken into consideration when planning management interventions that address regeneration debt. These findings underscore that forest stability cannot be inferred from canopy or vegetative regeneration persistence alone, and that the legacy of suppressed disturbance may unfold over timescales longer than commonly assumed.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Vegetative regeneration trait classifications for study species, with supporting citations. Next to each species, the typical life form has been included (Shrub [S] or Tree [T]). We define shrubs as consistently producing multi-stemmed architectures from a common root base with no apparent primary stem, while trees produce a primary stem from a common root base, and if other stems are present, they are secondary to the dominant stem. Sorted in accordance with Appendix A Table A2. * Information found for *Aesculus glabra* var. *arguta*. B.L.Rob. ♦ Information found for *Rhododendron maximum* L.

Habitat	Species	Basal Sprouting	Clonal Growth	Citations
Cove	*Acer saccharum* [T]	N	N	Ward and Williams [50]
	Cercis canadensis [T]	Y	N	Copenheaver and Keyser [51]
	Magnolia acuminata [T]	N	N	Burns and Honkala [29]
	Prunus serotina [T]	Y	Y	Closset-Kopp et al. [35]
	Carya spp. [T]	N	N	Dietze and Clark [24]
	Liriodendron tulipifera [T]	N	N	Dietze and Clark [24]
	Nyssa sylvatica [T]	N	Y	Copenheaver and Keyser [51]; Abrams [52]
	Fraxinus biltmoreana [T]	N	N	Tanis and McCullough [53]
	Oxydendrum arboreum [T]	Y	N	Keyser and Zarnoch [54]; Evans et al. [20]
	Tilia americana [T]	Y	N	Evans and Morris [36]
	Cornus florida [T]	N	Y	Dietze and Clark [24]
	Acer rubrum [T]	Y	N	Ward and Williams [50]
	Asimina triloba [T]	N	Y	Hosaka et al. [55]
	Quercus alba [T]	Y	N	Ward and Williams [50]; Tryon and Powell [56]
	Robinia pseudoacacia [T]	N	Y	Chang et al. [57]; Zhang et al. [58]
	Sassafras albidum [T]	Y	Y	Michel et al. [39]
	Ulmus alata [T]	N	N	Copenheaver and Keyser [51]
	Aesclus glabra [T]	N	Y *	Augspurger [59]; Lim [60]
	Quercus montana [T]	Y	N	Oldfield et al. [37]
	Ulmus rubra [T]	N	Y	Copenheaver and Keyser [51]; Davis et al. [61]
	Lindera benzoin [S]	Y	N	Godt and Hamrick [62]
	Quercus rubra [T]	Y	N	Heggenstaller et al. [63]
	Quercus velutina [T]	Y	N	Liming and Johnstone [64]; Ward and Williams [50]
	Celtis occidentalis [T]	N	N	Sample et al. [65]
	Ailanthus altissima [T]	Y	Y	Martin and Canham [66]; Pile Knapp et al. [67]
	Juglans spp. [T]	N	N	Copenheaver and Keyser [51]
	Ligustrum sinense [S]	Y	Y	Enloe et al. [68]
	Vaccinium spp. [S]	Y	Y	Duval [69]
	Viburnum acerifolium [S]	Y	Y	Overlease [70]; Pickett and Kempf [71]
	Castanea dentata [T]	Y	N	Dietze and Clark [24]; Copenheaver and Keyser [51]
	Ilex montana [S]	Y	N	Wharton [72]
	Ilex opaca [T]	N	N	Burns and Honkala [29]
	Juniperus virginiana [T]	N	N	Martin and Young [73]
	Morus rubra [T]	N	N	Dietze and Clark [24]
	Frangula caroliniana [T]	N	N	Wharton [72]
	Amelanchier spp. [T]	Y	Y	Stushnoff [74]; Paschke et al. [75]
	Viburnum rufidulum [S]	Y	N	Andruk et al. [76]
Plateau	*Acer rubrum* [T]	Y	N	Ward and Williams [50]
	Nyssa sylvatica [T]	N	Y	Copenheaver and Keyser [51]; Abrams [52]
	Oxydendron arboreum [T]	Y	N	Keyser and Zarnoch [54]; Evans et al. [20]

Table A1. *Cont.*

Habitat	Species	Basal Sprouting	Clonal Growth	Citations
	Sassafras albidum [T]	Y	Y	Michel et al. [39]
	Carya spp. [T]	N	N	Dietze and Clark [24]
	Quercus alba [T]	Y	N	Tryon and Powell [56]; Ward and Williams [50]
	Quercus coccinea [T]	Y	N	Tryon and Powell [56]; Ward and Williams [50]
	Quercus montana [T]	Y	N	Oldfield et al. [37]
	Quercus velutina [T]	Y	N	Liming and Johnstone [64]; Ward and Williams [50]
	Robinia pseudoacacia [T]	N	Y	Chang et al. [57]; Zhang et al. [58]
	Pinus strobus [T]	N	N	Burns and Honkala [29]
	Acer saccharum [T]	N	N	Ward and Williams [50]
	Cornus florida [T]	N	Y	Dietze and Clark [24]
	Amelanchier spp. [T]	Y	Y	Stushnoff [74]; Paschke et al. [75]
	Liquidambar styraciflua [T]	Y	Y	Loehle [77], Sutherland et al. [78]
	Prunus serotina [T]	Y	Y	Closset-Kopp et al. [35]
	Kalmia latifolia [S]	Y	Y	Faison et al. [79]
	Diospyros virginiana [T]	N	Y	Burns and Honkala [29]; Ross et al. [80]
	Juniperus virginiana [T]	N	N	Martin and Young [73]
	Quercus stellata [T]	Y	N	Tryon and Powell [56]; Copenheaver and Keyser [51]
	Fraxinus biltmoreana [T]	N	N	Tanis and McCullough [53]
	Ilex decidua [S]	Y	N	Wharton [72]
	Vaccinium spp. [S]	Y	Y	Duval [69]
	Viburnum acerifolium [S]	Y	Y	Overlease [70]; Pickett and Kempf [71]
	Rhododendron spp. ♦ [S]	Y	Y	Elliott and Vose [81]
	Liriodendron tulipifera [T]	N	N	Dietze and Clark [24]
	Magnolia acuminata [T]	N	N	Burns and Honkala [29]
	Quercus rubra [T]	Y	N	Heggenstaller et al. [63]
	Quercus muehlenbergii [T]	Y	N	Tryon and Powell [56]; Short et al. [82]
	Frangula caroliniana [T]	N	N	Wharton [72]
	Rhus copallinum [T]	Y	Y	Evans et al. [20]
	Vaccinium arboreum [T]	N	Y	Ellair [83]; Logan et al. [84]

Table A2. Mean change in density and trends in mean density patterns for species between 1995 and 2025. The ∅ value indicates that no stems were present for that species and size class in any census period (whereas 0 indicates presence, but no change). Table is sorted by cove and plateau, then number of size classes represented (5–1), class (increase–decline, with species loss coming last in each class), then alphabetically. *C* is measured by the direction of change from the average density of stems in each size class in each interval. If the average of *C* across size classes >1, it is in the Increase class, <−1 it is in the Decrease class, and between or equal to −1 and 1, it is in the Stable/Fluctuating (S/F) class. ♦ = species loss; species that is no longer present in any size class in 2025. * = species gain; species that was not initially present in any size class in 1995.

Habitat	Species	Mean Δ Density (1995 vs. 2025)					*C*					Class
		A	B	C	D	E	A	B	C	D	E	
Cove	*Acer saccharum*	−301	−179	−8	6	3	1	−3	−1	3	3	S/F
	Cercis canadensis	64	−4	−8	−2	0	1	−3	−3	−1	1	S/F
	Magnolia acuminata	−1	−1	−1	0	0	−1	−1	−2	−1	2	S/F
	Prunus serotina	−28	−1	−1	−2	1	−1	−2	−1	−3	2	S/F
	Carya spp.	−16	−2	−2	−2	−1	1	−1	−1	−3	−3	Decline
	Liriodendron tulipifera	78	−5	−2	−1	2	−1	−3	−1	−3	2	Decline
	Nyssa sylvatica	−145	−2	−2	−2	0	−3	−1	−3	−1	0	Decline
	Fraxinus biltmoreana	−159	−6	−1	∅	0	−1	−2	0	∅	1	S/F

Table A2. *Cont.*

Habitat	Species	Mean Δ Density (1995 vs. 2025)					*C*					Class
		A	B	C	D	E	A	B	C	D	E	
	Oxydendrum arboreum	−3	∅	0	−1	0	−1	∅	−1	−1	1	S/F
	Tilia americana	∅	−1	−1	−1	0	∅	−2	−1	−1	−1	Decline
	Cornus florida	−8	−1	−11	−2	∅	−1	−1	−2	−3	∅	Decline ♦
	Acer rubrum	−9	−1	0	∅	∅	−1	−2	0	∅	∅	S/F
	Asimina triloba	14	1	1	∅	∅	1	0	2	∅	∅	S/F
	Quercus alba	9	∅	∅	−2	0	−1	∅	∅	−2	1	S/F
	Robinia pseudoacacia	1	0	∅	∅	0	1	0	∅	∅	−1	S/F
	Sassafras albidum	−10	−1	0	∅	∅	1	−1	1	∅	∅	S/F
	Ulmus alata	3	0	1	∅	∅	1	−1	2	∅	∅	S/F
	Aesclus glabra	0	−1	0	∅	∅	1	0	−1	∅	∅	S/F ♦
	Quercus montana	−8	∅	−1	∅	0	−3	∅	−1	∅	−1	Decline
	Ulmus rubra	−1	−1	−1	∅	∅	−1	−2	−2	∅	∅	Decline ♦
	Lindera benzoin	125	7	∅	∅	∅	−1	0	∅	∅	∅	S/F
	Quercus rubra	−1	∅	∅	∅	−2	1	∅	∅	∅	−3	S/F
	Quercus velutina	0	∅	∅	∅	0	0	∅	∅	∅	−1	S/F
	Celtis occidentalis	20	∅	∅	∅	∅	2	∅	∅	∅	∅	Increase
	Ailanthus altissima	1	∅	∅	∅	∅	1	∅	∅	∅	∅	S/F *
	Juglans spp.	∅	∅	∅	∅	0	∅	∅	∅	∅	0	S/F
	Ligustrum sinense	1	∅	∅	∅	∅	1	∅	∅	∅	∅	S/F *
	Vaccinium spp.	−4	∅	∅	∅	∅	−1	∅	∅	∅	∅	S/F
	Viburnum acerifolium	−16	∅	∅	∅	∅	−1	∅	∅	∅	∅	S/F
	Castanea dentata	∅	0	∅	∅	∅	∅	−1	∅	∅	∅	S/F ♦
	Ilex montana	−1	∅	∅	∅	∅	−1	∅	∅	∅	∅	S/F ♦
	Ilex opaca	−1	∅	∅	∅	∅	−1	∅	∅	∅	∅	S/F ♦
	Juniperus virginiana	−1	∅	∅	∅	∅	−1	∅	∅	∅	∅	S/F ♦
	Morus rubra	−1	∅	∅	∅	∅	−1	∅	∅	∅	∅	S/F ♦
	Frangula caroliniana	∅	0	∅	∅	∅	∅	−1	∅	∅	∅	S/F ♦
	Amelanchier spp.	−11	∅	∅	∅	∅	−2	∅	∅	∅	∅	Decline ♦
	Viburnum rufidulum	∅	−1	∅	∅	∅	∅	−2	∅	∅	∅	Decline ♦
Plateau	*Acer rubrum*	450	−7	8	1	0	1	−1	3	1	0	S/F
	Nyssa sylvatica	−114	−23	−11	1	0	−1	−3	−3	1	0	S/F
	Oxydendron arboreum	−8	−3	−3	−3	0	−1	−1	1	−2	1	S/F
	Sassafras albidum	−955	−1	−22	1	0	−3	1	−3	1	0	S/F
	Carya spp.	−99	−10	−8	−1	−1	−1	−3	−3	−1	−1	Decline
	Quercus alba	−65	−7	−12	−2	1	−1	−3	−3	−2	3	Decline
	Quercus coccinea	199	−4	−2	−2	−3	1	−3	−2	−3	−3	Decline
	Quercus montana	243	−3	−6	−4	2	−1	−3	−3	−3	3	Decline
	Quercus velutina	3	−3	−1	0	0	−1	−2	−3	−1	1	Decline
	Robinia pseudoacacia	−49	−4	−4	−1	0	−3	−1	−3	−3	−1	Decline
	Pinus strobus	11	0	0	0	∅	2	1	1	1	∅	Increase
	Acer saccharum	−1	−2	1	0	∅	0	−3	1	1	∅	S/F
	Cornus florida	−6	−4	−3	−1	∅	−2	−3	−2	−2	∅	Decline
	Amelanchier spp.	26	−1	−1	∅	∅	3	−1	−2	∅	∅	S/F
	Liquidambar styraciflua	3	0	0	∅	∅	2	0	1	∅	∅	S/F *
	Prunus serotina	−16	−1	0	∅	∅	−1	−3	1	∅	∅	S/F
	Kalmia latifolia	−86	−7	−2	∅	∅	−1	−3	−1	∅	∅	Decline
	Diospyros virginiana	−8	−1	0	∅	∅	−3	−1	−1	∅	∅	Decline ♦
	Juniperus virginiana	−1	∅	0	∅	∅	0	∅	−1	∅	∅	S/F
	Quercus stellata	1	∅	0	∅	∅	1	∅	−1	∅	∅	S/F
	Fraxinus biltmoreana	−1	0	∅	∅	∅	−1	−1	∅	∅	∅	S/F ♦
	Ilex decidua	−1	0	∅	∅	∅	−1	−1	∅	∅	∅	S/F ♦
	Vaccinium spp.	−2054	−42	∅	∅	∅	−3	−1	∅	∅	∅	Decline
	Viburnum acerifolium	−28	−1	∅	∅	∅	−2	−1	∅	∅	∅	Decline
	Rhododendron spp.	−14	∅	∅	∅	∅	−1	∅	∅	∅	∅	S/F
	Liriodendron tulipifera	−8	∅	∅	∅	∅	−1	∅	∅	∅	∅	S/F
	Magnolia acuminata	3	∅	∅	∅	∅	1	∅	∅	∅	∅	S/F
	Quercus rubra	∅	0	∅	∅	∅	∅	1	∅	∅	∅	S/F
	Quercus muehlenbergii	−1	∅	∅	∅	∅	0	∅	∅	∅	∅	S/F ♦
	Frangula caroliniana	0	∅	∅	∅	∅	0	∅	∅	∅	∅	S/F ♦
	Rhus copallinum	−1	∅	∅	∅	∅	−1	∅	∅	∅	∅	S/F ♦
	Vaccinium arboreum	0	∅	∅	∅	∅	0	∅	∅	∅	∅	S/F *,♦

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