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ARTICLE

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# Overabundant deer and invasive plants drive widespread regeneration debt in eastern United States national parks

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**Abstract**

Advanced regeneration, in the form of tree seedlings and saplings, is critical for ensuring the long-term viability and resilience of forest ecosystems in the eastern United States. Lack of regeneration and/or compositional mismatch between regeneration and canopy layers, called regeneration debt, can lead to shifts in forest composition, structure, and, in extreme cases, forest loss. In this study, we examined status and trends in regeneration across 39 national parks from Virginia to Maine, spanning 12 years to apply the regeneration debt concept. We further refined the concept by adding new metrics and classifying results into easily interpreted categories adapted from the literature: imminent failure, probable failure, insecure, and secure. We then used model selection to determine the potential drivers most influencing patterns of regeneration debt. Status and trends indicated widespread regeneration debt in eastern national parks, with 27 of 39 parks classified as imminent or probable failure. Deer browse impact was consistently the strongest predictor of regeneration abundance. The most pervasive component of regeneration debt observed across parks was a sapling bottleneck, characterized by critically low sapling density of native canopy species and significant declines in native canopy sapling basal area or density for most parks. Regeneration mismatches also threaten forest resilience in many parks, where native canopy seedlings and saplings were outnumbered by native subcanopy species, particularly species that are less palatable deer browse. The devastating impact of emerald ash borer eliminating ash as a native canopy tree also drove regeneration mismatches in many parks that contain abundant ash regeneration, demonstrating the vulnerability of forests that lack diverse understories to invasive pests and pathogens. These findings underscore the critical importance of an integrated forest management approach that promotes an abundant and diverse regeneration layer. In most cases, this can only be achieved through long-term (i.e., multidecadal) management of white-tailed deer and invasive plants. Small-scale disturbances that increase structural complexity may also promote regeneration where stress from deer and invasive plants is minimal. Without immediate and sustained management intervention, the forest loss we are already observing may become a widespread pattern in eastern national parks and the broader region.

**KEYWORDS**

forest management, long-term trends, National Park Service Inventory and Monitoring, regeneration debt, regeneration failure, tree regeneration

## INTRODUCTION

Forests perform essential ecosystem services, provide critical food and habitat for countless taxa, and generate significant economic benefits to surrounding regions (Hein, 2011; Krieger, 2001; Pearce, 2001). Promoting resilience, which is the ability of an ecosystem to experience disturbance and maintain similar ecosystem functions, structure, and composition (Holling, 1973), is important for ensuring long-term forest viability (Millar et al., 2007). As the impacts of novel or persistent disturbances accumulate and interact, forest resilience diminishes through the loss of individual species and/or size/age cohorts, thereby reducing the system's response variability (Hessburg et al., 2019; Johnstone et al., 2016; Millar et al., 2007; Stevens-Rumann et al., 2017). In the eastern United States, forests currently face many compounding stressors that reduce resilience and threaten to alter the future composition and structure of eastern forests (Miller & McGill, 2019; Webster et al., 2018). Stressors include forest pests and pathogens that functionally eliminate individual species from the canopy, including emerald ash borer (*Agrilus planipennis*), hemlock woolly adelgid (*Adelges tsugae*), and, more recently, beech leaf disease complex (Ewing et al., 2019; Webster et al., 2018). Climate change, altered disturbance regimes, and human-modified land use are also associated with altered forest composition and structure (Itter et al., 2017; Miller & McGill, 2019; Nowacki & Abrams, 2008). Without intervention, the trajectory ultimately leads to novel, often less resilient forest ecosystems and, in more severe cases, forest loss (Webster et al., 2018).

Gap dynamics, where small openings in the canopy caused by the death of a single or a few mature trees allow sufficient light to reach the forest floor, are the primary natural regeneration process in eastern U.S. forests (Lorimer & White, 2003; Runkle, 1982; Saladyga et al., 2020). The composition and abundance of tree seedlings and saplings present when canopy gaps occur, known as advanced regeneration, are the primary drivers of future forest composition and structure (Yamamoto, 2000). The regeneration layer is therefore a primary indicator of forest response to canopy disturbance, and patterns of consistently insufficient regeneration or altered species composition call into question the long-term viability and resilience of forest ecosystems (Bradshaw & Waller, 2016; Russell et al., 2017).

In eastern forests, the regeneration layer is currently experiencing an onslaught of chronic stressors that threaten the composition and structure of the forests' future (Bradshaw & Waller, 2016; Russell et al., 2017). Shifts in climate and/or disturbance regimes are driving regeneration mismatches to alter dominant forest ecosystems, such as the mesophication of oak-dominated forests (Itter et al., 2017; Nowacki & Abrams, 2008). Prolonged white-tailed deer (*Odocoileus virginianus*) overabundance in particular is critically impairing regeneration in eastern forests. At moderate levels, deer overabundance shifts understory composition toward browse-tolerant species, driving species mismatches between the regeneration and canopy layers (McWilliams et al., 2018; Stromayer & Warren, 1997). Many of these browse-tolerant species, like paw paw (*Asimina triloba*), American holly (*Ilex opaca*), and American hornbeam (*Carpinus caroliniana*), are short-stature trees that are unable to grow to current canopy height (Miller & McGill, 2019). In severe cases, chronic deer browse pressure leads to widespread regeneration failure, where tree seedlings are unable to persist for long enough to recruit into the sapling and subsequent canopy layers, ultimately leading to forest canopy loss (Bradshaw & Waller, 2016; McWilliams et al., 2018; Webster et al., 2018). In addition, overabundant deer facilitate the invasion and spread of non-native plants and earthworms (Fisichelli & Miller, 2018) and negatively impact soil (Kardol et al., 2014), suggesting their role as ecosystem engineers that can cause cascades of biotic and abiotic impacts through forest ecosystems (Gorchov et al., 2021; Nuttle et al., 2011). The impacts of chronic excessive browse also accumulate, creating legacy effects that persist for decades (Nuttle et al., 2014; Tanentzap et al., 2012; Webster et al., 2005).

The concept of regeneration debt was developed to collectively describe the patterns of regeneration failure and compositional mismatch that, if prolonged, will lead to a shift in canopy composition and structure and, ultimately, forest loss in extreme cases (Miller & McGill, 2019). However, the regeneration debt concept has been limited in its translation to management action. This is especially challenging in eastern U.S. forests, as deer and invasive plant management is extremely costly and requires a long-term effort to ameliorate (Nagy et al., 2022; Schmit et al., 2020). Knowing when, where, and how best to intervene is critical for land managers to use limited resources most effectively and efficiently.

Here we use data from the National Park Service (NPS) Inventory and Monitoring (I&M) Program from 1515 permanent plots spanning 39 parks and 12 years as a case study to further refine and apply the regeneration debt concept into actionable management recommendations in eastern U.S. parks. Our study examines both status, which is based on the most recent survey of plots, and temporal trends across 12 years (i.e., three surveys) to assess the condition of the regeneration layer and identify signals of regeneration debt impacting the canopy. We then use model selection to determine the likely drivers of these patterns, the results of which inform park management recommendations. The results of this study will feed directly into a regional forest management strategy for eastern national parks. More broadly, our approach and recommendations are applicable to land managers across the eastern United States and beyond who are facing similar forest challenges.

# METHODS

## Field methods and study sites

The I&M Program is implemented through ecoregional "networks" that group parks linked by geography and shared natural resource characteristics (Fancy et al., 2009). Five I&M networks covering 39 parks in the eastern United States share similar forest monitoring protocols (Comiskey, Schmit, Sanders, et al., 2009), allowing for regional analysis of forest condition (e.g., Miller et al., 2021). The parks in this analysis range in size from 29 ha in Wolftrap National Park for the Performing Arts (WOTR) in Virginia to over 22,000 ha in Delaware Water Gap National Recreation Area (DEWA) in New Jersey and Pennsylvania (Figure 1, Table 1). With the exception of Marsh-Billings-Rockefeller National Historical Park (MABI) in Vermont, all parks in this analysis are protected from logging and have been so for many decades to over a century. Additionally, the NPS employs passive management to allow forests to follow natural processes and disturbance regimes and only intervenes when stressors, like overabundant deer or invasive plants, are degrading them and/or interfering with natural processes (National Park Service, 2006). In each of the 39 parks, plot-monitoring locations were established using Generalized Random Tessellation Stratification (GRTS) to generate a spatially balanced, randomized sample across the parks' forests (Stevens & Olsen, 2004). Forests were defined as having at least 25% cover of canopy species and/or habitats, like old fields, that are succeeding to forest. Plots were sampled on a 4-year rotating panel, such that one panel containing one quarter of the network's plots was sampled every year. Each plot was sampled every 4 years, the length of one complete sampling cycle.

While some aspects of plot design and field protocols vary among networks, many measurements are standardized across all five networks. For example, all trees in each plot that are ≥10 cm in dbh are assessed for status (i.e., live or dead), identified to species, and measured for dbh (Comiskey, Schmit, & Tierney, 2009; Perles, Finley, et al., 2014; Schmit et al., 2009; Tierney et al., 2017). Plot sizes vary across networks, with the largest plot size (706 $m^2$) in the Eastern Rivers and Mountains Network (ERMN) and the National Capital Region Network (NCRN) and the smallest plot size (225 $m^2$) in Acadia National Park (ACAD) in Maine. All other parks and networks in this study utilize 400-$m^2$ plots. In microplots nested within plots, live saplings that are ≥1 cm and <10 cm dbh are identified to species and measured for dbh. Microplot size and number vary across networks, with ERMN sampling four 2-m-radius microplots, the Northeast Temperate Network (NETN) sampling three 2-m-radius microplots, and the Mid-Atlantic Network (MIDN), Northeast Coastal and Barrier Network (NCBN), and NCRN all sampling three 3-m-radius microplots. Tree seedlings ≥15 cm tall and <1 cm dbh are tallied in four height classes (McWilliams et al., 2015) either in microplots (ERMN and NETN) or in twelve 1-$m^2$ quadrats (MIDN, NCBN, NCRN). In addition, characteristics of the stand and site are assessed in each plot across all five networks, including slope, aspect, characteristics of the substrate (e.g., percentage rock, bare soil), and a five-point index of deer browse impacts (DBIs). Ideally, we would measure deer density alongside our monitoring to more directly relate deer densities to impacts on regeneration. However, monitoring deer density is beyond our capacity to implement across all the parks in our study. Additionally, deer density typically has a nonlinear, delayed response and is strongly influenced by legacy effects (Tanentzap et al., 2011). For example, where chronic deer overabundance has occurred, lowered deer densities may still cause unsustainable impacts on the few remaining palatable seedlings present (Brose et al., 2008). Browse intensity is another possible metric to monitor deer impacts.

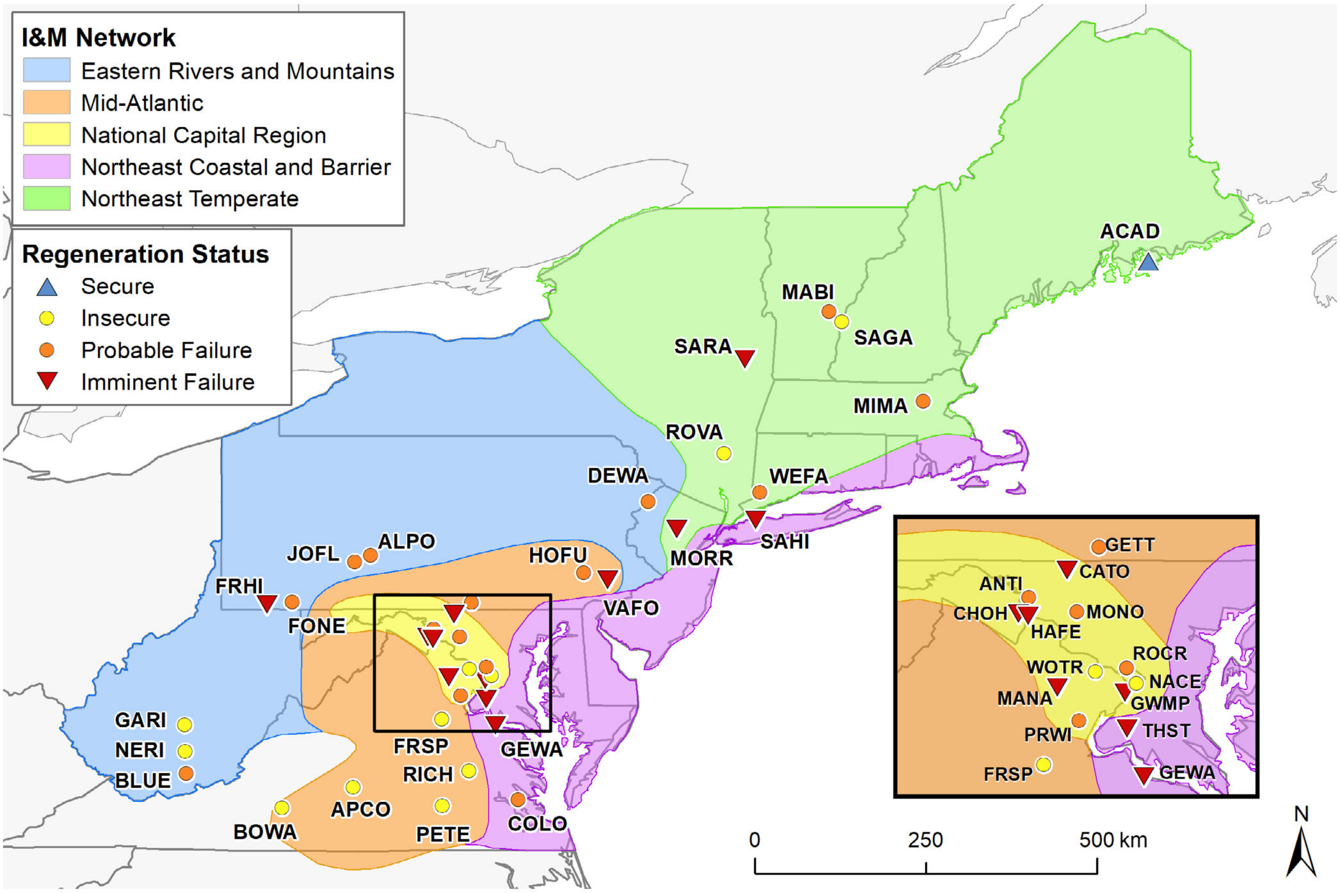


**FIGURE 1** National Park Service monitoring networks and parks included in this study. See Table 1 for park names associated with the four-letter code shown in the map. For definitions of regeneration debt categories and how park regeneration debt was assessed, see the *Methods* section.

However, as browse pressure increases, the amount of browse observed diminishes as palatable seedlings decline. Browse intensity is therefore best used to assess changes in moderate browse pressure. The DBI index we implement assesses the amount of pressure deer are putting on the regeneration layer and is appropriate across the full range of deer impacts (Brose et al., 2008; McWilliams et al., 2015). This index is also widely used to assess impacts of deer on vegetation, including by the Northern Research Station of the U.S. Forest Service Inventory and Analysis Program (McWilliams et al., 2015). Methods for tallying tree seedlings and measuring saplings also follow methods developed for the Northern Research Station of the U.S. Forest Service Forest Inventory and Analysis (McWilliams et al., 2015). Finally, our protocols have gone through extensive peer review. To ensure our methods and sample sizes are appropriate to meet the objectives of our protocols, which include monitoring status and trends in regeneration abundance, composition, and impacts of deer at the park scale, we conducted multiple power analyses (Comiskey, Schmit, Sanders, et al., 2009: Miller & Mitchell, 2014: Perles, Wagner, et al., 2014; Schmit et al., 2009). We also conduct rigorous quality assurance/quality control procedures to ensure crews are collecting high-quality and consistent data and have documented these procedures in quality assurance plans (Miller et al., 2022; Perles et al., 2018).

## Plot-level forest metrics

To assess regeneration debt status and trends, we calculated plot-level metrics of forest structure and regeneration. The basal area of live trees and saplings and the density of live trees, saplings, and seedlings were calculated by origin and functional group: (1) native canopy, which included only canopy-forming tree species native to the United States; (2) native subcanopy, which included species native to the United States and typically subcanopy trees such as paw paw and striped maple (*Acer pensylvanicum*); and (3) exotic, which included tree species not native to the United States. Classifications of native subcanopy and exotic were based on growth habit and nativity listed in the USDA PLANTS database

**TABLE 1** Number of plots sampled in National Park Service (NPS) monitoring networks and parks over three monitoring cycles.

| Network | Park name | Code | Park area (ha) | | No. forest plots |
|---|---|---|---|---|---|
| | | | Total | Forest | |
| NETN | Acadia National Park | ACAD | 14,577 | 8178 | 176 |
| ERMN | Allegheny Portage Railroad National Historic Site | ALPO | 503 | 430 | 22 |
| NCRN | Antietam National Battlefield | ANTI | 759 | 129 | 13 |
| MIDN | Appomattox Court House National Historical Park | APCO | 687 | 442 | 28 |
| ERMN | Bluestone National Scenic River | BLUE | 1236 | 1144 | 40 |
| MIDN | Booker T. Washington National Monument | BOWA | 100 | 62 | 8 |
| NCRN | Catoctin Mountain Park | CATO | 2282 | 2237 | 49 |
| NCRN | Chesapeake and Ohio Canal National Historical Park | CHOH | 5980 | 4261 | 75 |
| NCBN | Colonial National Historical Park | COLO | 2219 | 1471 | 48 |
| ERMN | Delaware Water Gap National Recreation Area | DEWA | 22,839 | 19,313 | 102 |
| ERMN | Fort Necessity National Battlefield | FONE | 373 | 276 | 20 |
| ERMN | Friendship Hill National Historic Site | FRHI | 280 | 224 | 20 |
| MIDN | Fredericksburg & Spotsylvania National Military Park | FRSP | 3056 | 2180 | 104 |
| ERMN | Gauley River National Recreation Area | GARI | 1930 | 1779 | 43 |
| MIDN | Gettysburg National Military Park | GETT | 1743 | 548 | 33 |
| NCBN | George Washington Birthplace National Monument | GEWA | 216 | 87 | 8 |
| NCRN | George Washington Memorial Parkway | GWMP | 1661 | 969 | 20 |
| NCRN | Harpers Ferry National Historical Park | HAFE | 1480 | 1091 | 20 |
| MIDN | Hopewell Furnace National Historic Site | HOFU | 343 | 270 | 16 |
| ERMN | Johnstown Flood National Memorial | JOFL | 72 | 23 | 12 |
| NETN | Marsh-Billings-Rockefeller National Historical Park | MABI | 223 | 196 | 24 |
| NCRN | Manassas National Battlefield Park | MANA | 1727 | 784 | 17 |
| NETN | Minute Man National Historical Park | MIMA | 391 | 234 | 20 |
| NCRN | Monocacy National Battlefield | MONO | 530 | 132 | 15 |
| NETN | Morristown National Historical Park | MORR | 676 | 626 | 28 |
| NCRN | National Capital Parks East | NACE | 3088 | 1942 | 48 |
| ERMN | New River Gorge National Park and Preserve | NERI | 21,528 | 19,615 | 102 |
| MIDN | Petersburg National Battlefield | PETE | 1092 | 923 | 52 |
| NCRN | Prince William Forest Park | PRWI | 5089 | 4899 | 145 |
| MIDN | Richmond National Battlefield Park | RICH | 819 | 585 | 32 |
| NCRN | Rock Creek Park | ROCR | 1061 | 812 | 19 |
| NETN | Roosevelt-Vanderbilt National Historic Sites | ROVA | 446 | 338 | 40 |
| NETN | Saint-Gaudens National Historical Park | SAGA | 80 | 48 | 21 |
| NCBN | Sagamore Hill National Historic Site | SAHI | 29 | 17 | 4 |
| NETN | Saratoga National Historical Park | SARA | 1156 | 687 | 32 |
| NCBN | Thomas Stone National Historic Site | THST | 179 | 123 | 8 |
| MIDN | Valley Forge National Historical Park | VAFO | 1395 | 538 | 28 |
| NETN | Weir Farm National Historical Park | WEFA | 28 | 18 | 10 |
| NCRN | Wolf Trap Park for the Performing Arts | WOTR | 43 | 26 | 6 |

*Note*: Network acronyms represent: Eastern Rivers and Mountains Network (ERMN), Mid-Atlantic Network (MIDN), Northeast Coastal and Barrier Network (NCBN), National Capital Region Network (NCRN), and Northeast Temperate Network (NETN). Park areas are based on the values of total and forested NPS-owned area at the time network sample designs were established. Actual park area may currently be larger than reflected by these values.

(USDA, 2021). Note that ash species (*Fraxinus* spp.) were not considered suitable, future canopy-forming trees due to the devastating impacts of emerald ash borer across much of the region. Thus, they were classified as native subcanopy trees. Appendix S1: Table S1 provides nativity and functional group assignment for all tree species observed. Appendix S1: Table S2 summarizes the number of species per functional group and per stratum (i.e., tree, sapling, seedling) in each park. Additionally, we calculated total live tree basal area and density by dbh classes (e.g., 10–20, 20–30, 30–40 cm) to examine patterns in the smaller-diameter trees that might make up the future forest canopy. We compiled additional covariates to determine the best predictors of regeneration abundance and similarity using model selection. We used the 2016 National Land Cover Database (NLCD; Jin et al., 2019) to classify land cover into human-modified (1) and natural land cover (0) at the initial 30-m resolution, then aggregated the data to a 300-m grid size and summarized the proportion of original cells that were human-modified land use following Miller and McGill (2019). We compiled canopy cover for each plot using the 2016 Tree Canopy Cover data set from NLCD (Dewitz, 2019). For climate change covariates, we acquired annual maximum temperature and monthly precipitation data for years spanning 1911–1940 and the most recent 30-year normals (1990–2020; Hart & Bell, 2015; Prism Climate Group, 2022). We chose the 1911–1940 period to represent a time largely uninfluenced by human-caused climate change (McEwan et al., 2011). For each 30-year period, we summed the yearly average April–September precipitation and calculated the average maximum temperature. We then calculated the percentage change between the early and current 30-year normals to represent climate change over the two periods. We selected these predictors because they have been shown to be important measures of drought stress that are associated with regeneration mismatches in our study area (McEwan et al., 2011). We compiled the ecological province for each plot using Bailey's ecoregions of the conterminous United States (Bailey, 2016). Finally, we specified the DBI index as a categorical rather than continuous variable to account for the often nonlinear response observed with this index. We also combined the two lowest categories of the DBI index (i.e., DBI 2 and 3) as the reference categories in the models because they occur within the acceptable threshold for this metric (Table 2). Note that there were no plots in the DBI = 1 category (i.e., inside a well-maintained deer exclosure with no impacts of deer browse) in our data set.

## Status and classification of regeneration debt

Along with the metrics used by Miller and McGill (2019), which consisted of seedling and sapling stem density and Sørensen similarity between regeneration and canopy layers, we compiled six additional metrics from the literature that characterized the abundance and composition of the regeneration layer: average stocking index, proportion of stocked plots, average DBI, and proportion of seedlings and saplings that are native canopy species. The stocking index, developed by the U.S. Forest Service (McWilliams et al., 2015), assigns weights to native canopy tree saplings and seedlings by height class to quantify whether observed regeneration is sufficient to restock the forest canopy. Plots are considered stocked if the stocking index attained a benchmark level, dependent on the observed DBI following McWilliams et al. (2015). The index of DBI, also developed by the U.S. Forest Service

**TABLE 2** Thresholds for rating regeneration metrics used to classify regeneration debt.

| Regeneration metric | Critical | Caution | Acceptable | Related references |
|---|---|---|---|---|
| Sapling density (stems/m$^2$) | <0.1 | 0.1–0.159 | ≥0.16 | Miller & McGill (2019), McWilliams et al. (2015) |
| Seedling density (stems/m$^2$) | <0.25 | 0.25–1.99 | ≥2.00 | Miller & McGill (2019) |
| Percentage of stocked plots | <33% | 33%–66% | ≥67% | |
| Stocking index | <25 | 25–100 | ≥100 | McWilliams et al. (2015) |
| Deer browse impacts | ≥4.00 | 3.01–3.99 | ≤3.00 | Brose et al. (2008); McWilliams et al. (2015) |
| Flat tree diameter distribution | Linear fit for distribution model | … | Log-normal fit for distribution model | |
| Sørensen similarity index | <0.2 | … | ≥0.2 | Miller & McGill (2019) |
| Seedling and sapling composition | <50% native canopy species | 50%–70% native canopy species | >70% native canopy species | Marquis (1994), Leak et al. (2014) |

(Brose et al., 2008), is a qualitative assessment of the impact of browse at each plot based on the amount of observed browse damage and the presence of browse-preferred and nonpreferred woody and herbaceous species. Plots with DBI >3 (moderate) require a stocking index of ≥100 to be considered stocked, while plots with DBI ≤3 require a stocking index of ≥50 to be considered stocked (McWilliams et al., 2015). We evaluated regeneration composition by calculating the proportion of total seedlings and saplings that were native canopy-forming species (Appendix S1: Table S1). Finally, we evaluated the shape of tree diameter distributions to identify parks where prolonged regeneration failure has led to shifts in canopy size class distributions through the loss of small trees. For this assessment, we fit log-normal and linear models to total tree density data binned by 10-cm size classes at the park scale, since the number of trees on individual plots is insufficient for plot-level analysis. We used the Akaike information criterion (AIC) to determine which model better predicted diameter distribution by size class for each park during the most recent sampling cycle (2016–2019; Anderson et al., 1998). If AIC determined a linear fit to be the best model, then fewer trees than expected occurred in smaller size classes, suggesting prolonged recruitment failure of small-diameter trees. Conversely, parks with diameter distributions best fit by log-normal models are expected to contain sufficient small-diameter trees to sustain forest maturation.

The regeneration debt index focused on the status (i.e., most recent survey) of each metric, as requiring long-term data for an index intended to inform management decisions is not always practical. Specifically, we calculated park-level averages or proportions for each of the 10 regeneration debt metrics listed previously using the most recent survey of each plot (2016–2019) and applied thresholds from the literature to rate each metric as critical, caution, and acceptable (Table 2). Critical values indicate a severe issue in the regeneration layer. Caution indicates values that likely are not sufficient to promote a healthy regenerating forest but may allow a forest to respond if conditions improve. Acceptable values indicate a metric is within desired levels to maintain a healthy regenerating forest. Ideally, these thresholds would vary by site condition (e.g., dry, mesic, hydric), successional stage, and/or ecological province. However, neither our data nor the literature is sufficient to provide custom thresholds at this time. As we observe forests recover from overabundant deer and seedlings successfully recruit into sapling and canopy layers, we will revise these thresholds for given forest types as needed. However, we likely need at least another decade of monitoring in the parks currently managing deer before successful recruitment of this nature can be observed across much of the study area. Additionally, our thresholds that distinguish critical from caution are intentionally conservative and reflect the bare minimum of what a forest in the eastern United States that regenerates largely through gap-phase dynamics needs to persist over the long term. These thresholds may therefore be lower than what certain forests actually require. Conservative thresholds also allow for natural variability in regeneration abundance across a forest. Note, however, that 78% of the forest plots in this study are classified as mature or late successional stands and 79% of plots have ≥80% canopy cover (Appendix S2: Table S1), so we would expect forest regeneration to be present in most plots.

After rating each metric, we classified regeneration debt status for each park based on the number of metrics rated critical. For this approach, we reclassified the original 1–4 regeneration debt index (as described by Miller & McGill, 2019) into four categories (Figure 2) adapted from Vickers et al. (2019): imminent failure, probable failure, insecure, and secure. We define imminent failure as forests that are experiencing severe regeneration failure and are at risk of forest loss, as indicated by six or more regeneration debt metrics rated critical. Forests in imminent regeneration failure have very low seedling and sapling abundance, as well as species mismatches between canopy and regeneration layers. These forests are one major disturbance away from forest loss. Forests classified as probable failure had four or five critical regeneration debt metrics. These forests contain insufficient regeneration, often low sapling densities, though seedlings and saplings are generally more abundant than in forests classified as imminent failure. Forests classified as insecure had two or three critical regeneration debt metrics. These forests typically lack sufficient sapling density and contain a low proportion of stocked plots but often have sufficient and increasingly abundant seedling layers that tend to match the canopy composition more closely. Finally, forests with zero or one critical regeneration debt metric were classified as secure. We used these four categories to group parks based on similar regeneration debt indices (Figure 2) to communicate to managers the severity of regeneration debt.

## Park trends in regeneration debt

In addition to assessing regeneration debt status, we examined trends in forest structure and regeneration to add nuance to the park-level status interpretations and to examine directional patterns, such as early signs of decline and/or positive responses to deer management. To estimate trends over time in forest structure and regeneration metrics (Figure 2), we used sampling cycle as a numeric

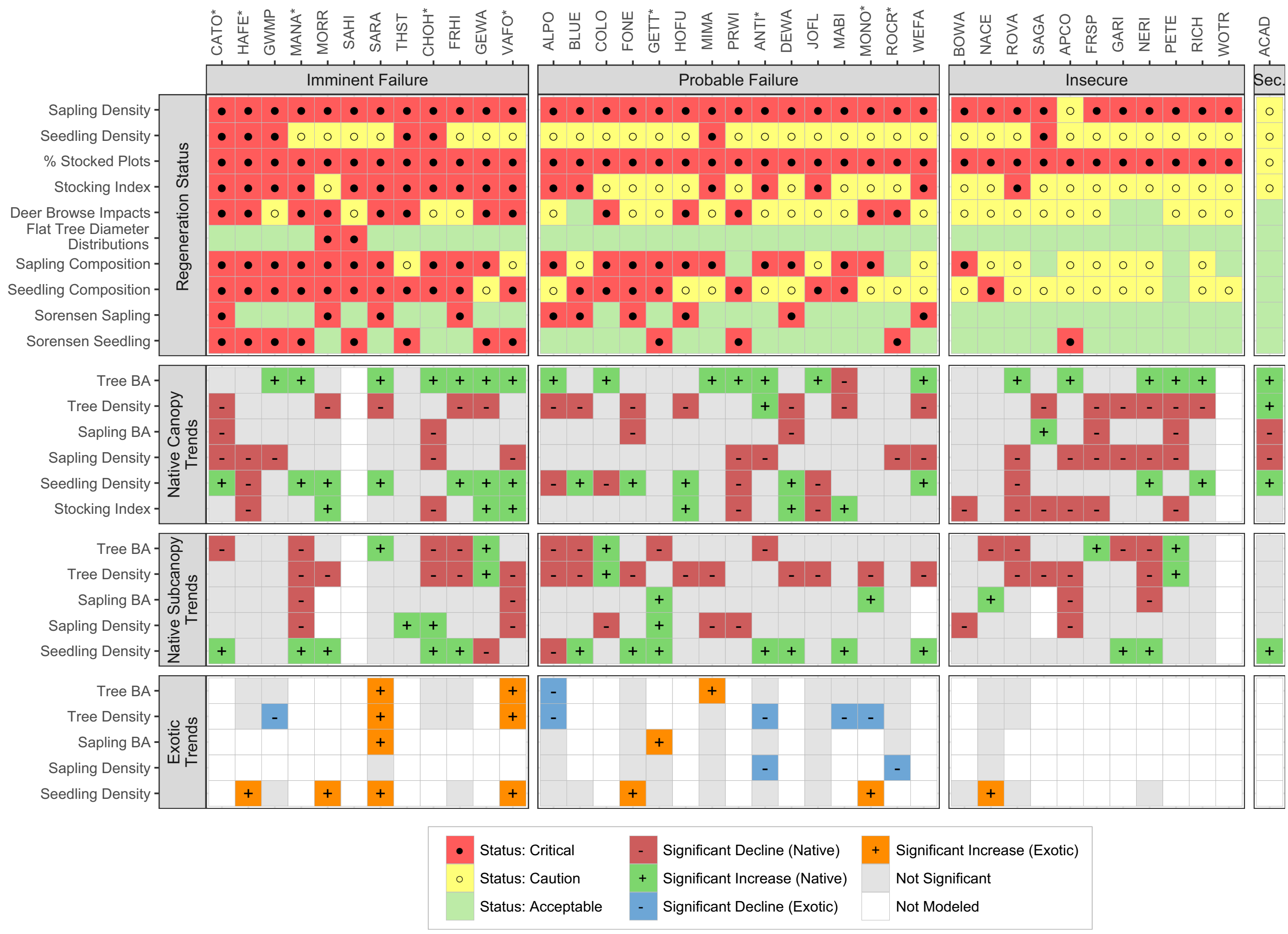


**FIGURE 2** Summary of status and trends for regeneration metrics by park, grouped by regeneration debt category and ordered from highest to lowest number of critical status metrics within regeneration debt category. Each park is represented by a column, and each cell represents a metric (status) or model result (trends) for a given park. Trends not modeled for a given park were due to insufficient data or insufficient plot numbers. The "secure regeneration" debt category is abbreviated "Sec." Status metrics (Facet row 1) are based on the most recent 4 years of data (2016–2019). Criteria for critical, caution, and acceptable status for each metric is shown in Table 2. Trend metrics (Facet rows 2–4) are grouped by species functional groups, with "Native Canopy," including native, canopy-forming species; "Native Subcanopy" (abbreviated "Subcan."), including native species that are typically subcanopy trees; and "Exotic," including non-native tree species. See Appendix S1: Table S1 for assignment of tree species to these functional groups. For definitions of regeneration debt categories and how park regeneration debt was assessed, see the *Methods* section. Parks with an asterisk are actively managing deer. See Appendix S2: Tables S1 and S2 for the values and confidence intervals populating the figure. BA, basal area.

independent variable in our models, with Cycle 1 covering survey years 2008–2011, Cycle 2 covering survey years 2012–2015, and Cycle 3 covering survey years 2016–2019. The majority of plots (97%) included in this analysis were monitored for three cycles (Table 1). The main exception is Colonial National Historical Park (COLO) in Virginia, which only had two complete cycles of data because monitoring in COLO started in 2011. However, because of the algorithm (Stevens & Olsen, 2004) used to determine plot locations, the plots sampled at COLO in cycle 1 were an unbiased, random sample, even though the estimates are likely to be less precise than if a full cycle had been completed.

All statistical analyses were conducted in R version 4.1.2 (R Core Team, 2021), and all code and data used in this study are available for download (see *Data availability statement*). For each park, we fit linear mixed-effects models, with plot as a random intercept, to estimate trends in forest metrics using the lme4 package (Bates et al., 2015). We modeled parks individually rather than running a regional hierarchical model for each metric. This assures that trends within a given park, particularly parks with smaller sample sizes or differing levels of heterogeneity, are statistically independent of trends in other parks. Model diagnostics (e.g., residual plots) consistently indicated violations of normality and constant variance assumptions.

Simulation studies have found that while estimates of coefficients (e.g., slope) are robust to violations of non-normal error, conventional significance testing is not (Givens & Hoeting, 2012; Maas & Hox, 2004). We therefore used nonparametric case bootstrapping to generate empirical 95% CIs of model coefficients based on 1000 replicate samples of the data with replacement, such that each sample was the same size as the original data set for each model. Case bootstrapping works by randomly selecting plots (i.e., cases), including the data from those plots in the order they were sampled, to generate a sampling distribution of the data set that maintains the underlying random structure (Givens & Hoeting, 2012). Trends were considered significant if the bootstrap-derived 95% CIs for the slope did not contain 0. While case bootstrapping relaxes underlying assumptions of the error distribution, it also requires a sufficient number of plots to implement because the sampling distribution is entirely derived by resampling the existing data. We therefore were unable to assess trends for Sagamore Hill National Historic Site (SAHI) in New York and WOTR in Virginia because those parks contained too few plots (i.e., <6 plots) to create a usable sampling distribution. Within each park, only regeneration and forest structure metrics with >10% nonzero values were modeled.

## Predictors of regeneration debt

To determine the best predictors of regeneration abundance and similarity, we fit six candidate models to each of the regeneration responses and used AIC to determine the best model. We were primarily interested in evaluating metrics used to assign regeneration debt status. We therefore only modeled the most recent survey of each plot (i.e., Cycle 3) and considered a range of predictors we hypothesized could influence regeneration abundance and similarity (Table 3). The six candidate models evaluated different hypotheses about the drivers of regeneration abundance and similarity. Specifically, the models focused on stressors, climate and geographic variables, forest structure, a combination of the previous models, or a combination with interactions (Table 4). In addition, we fit a null model (i.e., intercept-only) for comparisons. To meet model assumptions, we log-transformed seedling density, sapling density, and stocking index response variables. The similarity responses did not require transformations. We checked for collinearity among variables in the candidate models using variance inflation factors and, as a result, dropped live tree basal area from forest structure candidate models because it was highly correlated with tree density. Predictors were scaled to assess their relative importance on the response variable in each model. Models were fit using linear mixed-effects models with the lme4 R package, with park as a random intercept (Bates et al., 2015).

# RESULTS

## Status of regeneration debt by park

Data from the most recent sampling cycle indicate that most parks' forests are experiencing regeneration debt with levels of regeneration that are insufficient to sustain future forests (Figure 2). Sapling density is critically low across nearly all parks, with only one of 39 parks containing sapling densities ranked as caution and one park with acceptable sapling density. Seedling density ranked as caution for most parks, with critically low seedling density in seven parks. In a third of parks, no plots are sufficiently stocked (Figure 3), and all parks except ACAD contain a critically low percentage of stocked plots. Mean stocking index is critically low in 44% of parks and ranked as caution in all other parks (Figures 2 and 3). Mean DBI ranks as critical for a third of the parks, caution for over half the parks, and acceptable in only four parks. A linear model best fits tree diameter distributions for Morristown National Historical Park (MORR) in New Jersey and SAHI, suggesting that prolonged recruitment failure has resulted in fewer trees than expected in smaller size classes (Figure 2).

Species mismatch is also contributing to regeneration debt in many parks. In approximately half of the parks, native canopy-forming tree species comprise less than 50% of the total saplings and seedlings (Figures 2, 4 and 5). For example, in George Washington Birthplace National Monument (GEWA) in Virginia, native subcanopy species, such as American holly (*I. opaca*) and paw paw, constitute 86% of sapling and 53% of seedling density, respectively. Paw paw constitutes over 67% of saplings in Harpers Ferry National Historical Park (HAFE) and Chesapeake and Ohio Canal National Historical Park (CHOH) and 80% and 50% of the total seedling layer in the parks, respectively. Ash species make up more than half the total seedlings in four parks, namely, Johnstown Flood National Memorial (JOFL) and Friendship Hill National Historic Site (FRHI) in Pennsylvania, Catoctin Mountain Park (CATO) in Maryland, and Manassas National Battlefield Park (MANA) in Virginia. Additionally, a quarter of all saplings in Gettysburg National Military Park (GETT) in Pennsylvania are ash species. Exotic tree species are rare (<2% of total regeneration) in most parks (Figures 4 and 5) but account for >10% of seedlings and/or saplings in seven parks. Exotic saplings and seedlings are most abundant in SAHI, accounting for 20% of seedlings and 43% of saplings. Similarity indices comparing canopy and regeneration

**TABLE 3** Information on response and predictor variables considered for model selection.

| Metric | Data source | Abbreviation | Mean | Range | Units |
|---|---|---|---|---|---|
| Response variables | | | | | |
| Seedling density: Native canopy | NPS I&M | Seed_Dens_NatCan | 0.17 | (0, 13.3) | stems/$m^2$ |
| Sapling density: Native canopy | NPS I&M | Sap_Dens_NatCan | 0.07 | (0, 2.4) | stems/$m^2$ |
| Stocking index | NPS I&M | stock_final | 33.9 | (0, 980.2) | N/A |
| Seedling versus tree similarity: Sørensen | NPS I&M | Sor_Seed | 0.28 | (0, 1) | N/A |
| Sapling versus tree similarity: Sørensen | NPS I&M | Sor_Sap | 0.29 | (0, 1) | N/A |
| Continuous predictors | | | | | |
| Density of live trees | NPS I&M | tree_dens | 496 | (0, 2400) | stems/ha |
| Invasive plant percentage cover | NPS I&M | inv_cover | 10.6 | (0, 112.5) | % |
| Quadratic mean diameter at breast height | NPS I&M | QMD | 29.4 | (0, 66.7) | cm |
| Percentage April–September precipitation change (1911:1940 vs. 1990:2020) | PRISM (2022) | precip | 0.027 | (−0.042, 0.099) | % |
| Percentage maximum temperature change (1911:1940 vs. 1990:2020) | PRISM (2022) | tmax | −0.002 | (−0.057, 0.049) | % |
| Percentage human modified land cover | Dewitz (2019) | hmod300m | 0.120 | (0, 1) | % |
| Percentage canopy cover | Dewitz (2019) | cancov | 82.6 | (0, 1) | % |

| Discrete predictors | Data source | Abbreviation | Levels |
|---|---|---|---|
| Deer browse impacts | NPS I&M | DBI | Low/medium (725); high (541); very high (230) |
| Physiographic class | NPS I&M | physio | Dry (226); dry-mesic (331); mesic (876); hydric (63) |
| Structural stage | NPS I&M | str_stage | Late successional (658); mature (508); pole (136); mosaic (194) |
| Ecological province | Bailey (2016) | prov | Adirondack-New England Mixed Forest-Coniferous Forest-Alpine Meadow (45); Central Appalachian Broadleaf Forest-Coniferous Forest-Meadow (361); Eastern Broadleaf Forest (Oceanic) (343); Laurentian Mixed Forest (176); Outer Coastal Plain Mixed Forest (131); Eastern Broadleaf Forest (Oceanic) (4); Southeastern Mixed Forest (436) |

*Note*: Discrete predictor levels have no. plots per level in parentheses. For the National Park Service Inventory and Monitoring Program (NPS I&M) data source, see *Data availability statement*. Remaining data sets are in the reference section.
Abbreviation: QMD, quadratic mean diameter.

layers fall below the critical threshold in 12 parks for seedling similarity index and in 10 parks for sapling similarity index (Figure 2). The only park with critically low canopy similarity for both sapling and seedlings is CATO.

Using our proposed regeneration debt categories, we found that one third of parks fell in the imminent failure category, experiencing regeneration failure so severe that future disturbances will likely yield forest loss (Figures 1 and 2). In some cases, for example MORR, forest loss is already under way, as seen by the low numbers of small-diameter trees and significant losses in native canopy tree density. Another third of parks were categorized as probable failure. These parks contain insufficient regeneration, specifically inadequate or declining sapling density, though seedlings and saplings are generally more abundant than in forests ranked as imminent failure. Compositional mismatches between canopy and regeneration layers are common in parks classified as probable failure.

**TABLE 4** Candidate models tested using model selection.

| Model name | Predictors |
|---|---|
| Null | 1 + (1\|Park) |
| Stressors | DBI + inv_cover + hmod300m + (1\|Park) |
| Climate change and site conditions | tmax + precip + prov + physio + (1\|Park) |
| Structure | tree_dens + QMD + cancov + str_stage + (1\|Park) |
| Combination | DBI + inv_cover + tree_dens + cancov + physio + (1\|Park) |
| Combination with interactions | DBI × inv.cover + physio + tree_dens + cancov + (1\|Park) |

*Note*: For full predictor names and details, refer to Table 3.
Abbreviations: DBI, deer browse impacts; QMD, quadratic mean diameter.

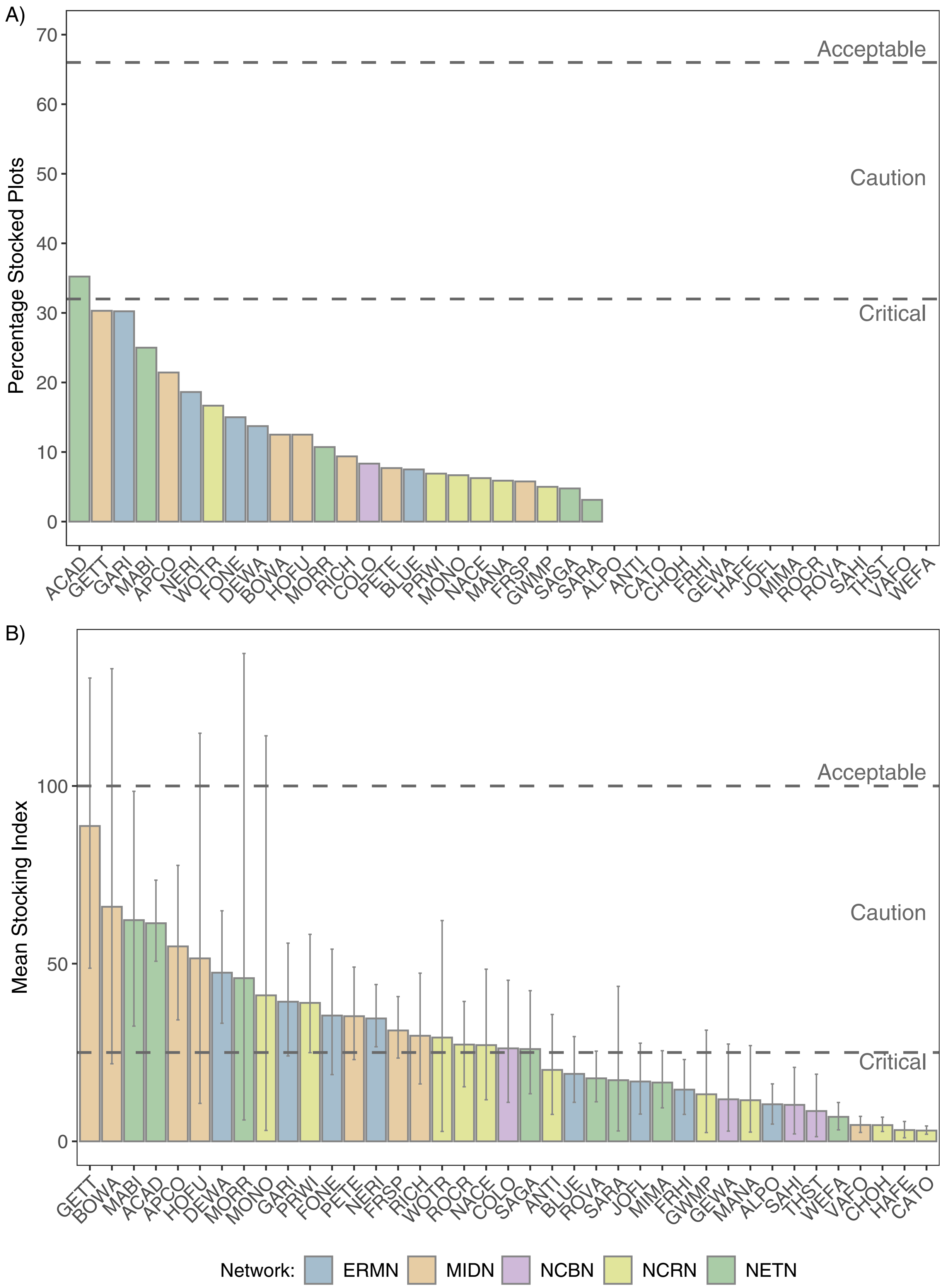


**FIGURE 3** Percentage of sufficiently stocked plots (A) and average stocking index with bootstrapped 95% CI (B) by park in the most recent 4-year period (2016:2019), sorted from high to low values. Parks without bars had no sufficiently stocked plots. The dashed line indicates the thresholds used to determine regeneration status (Table 2).

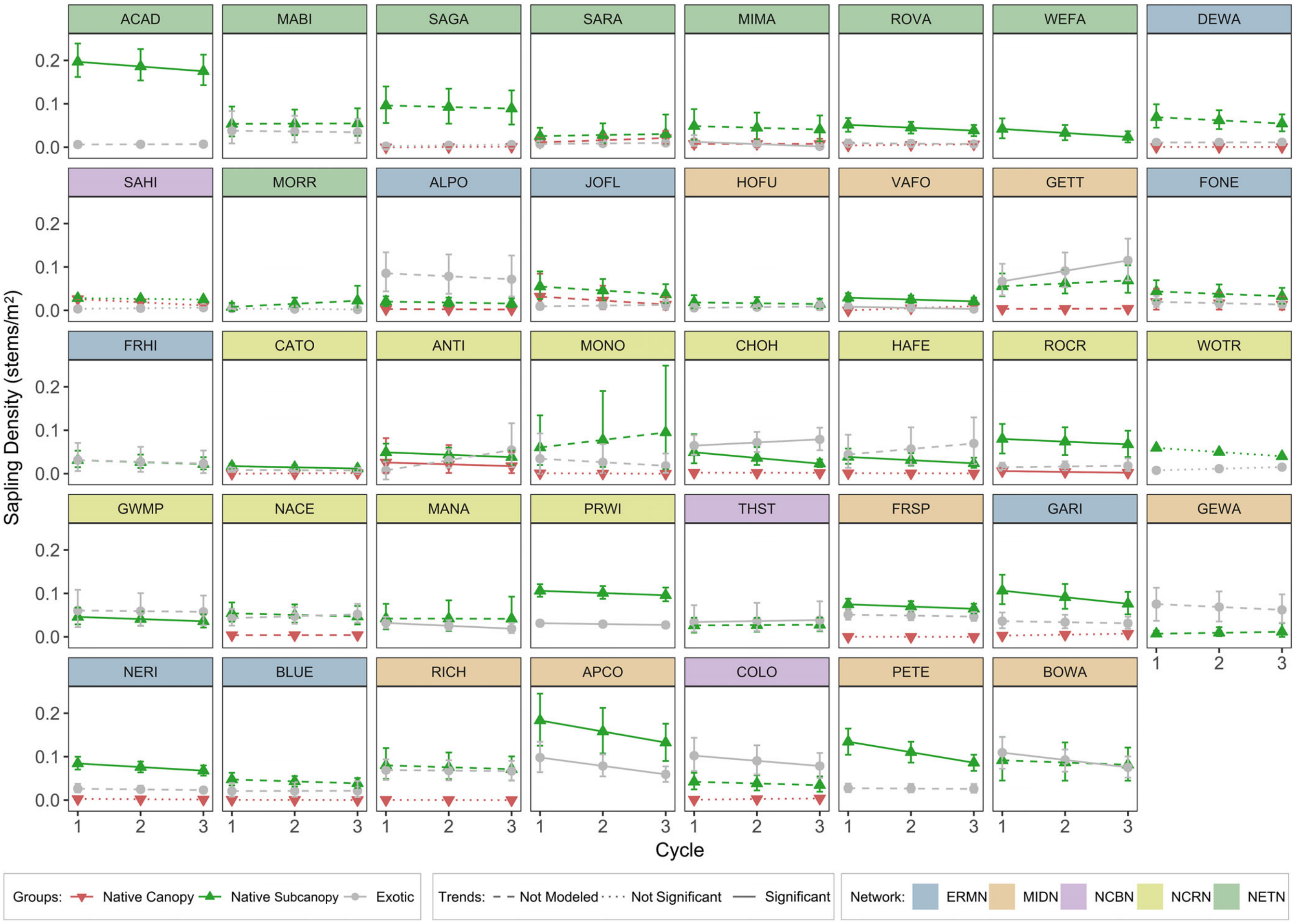


**FIGURE 4** Modeled trends in sapling density (stems/m$^2$) by species nativity and functional group in 39 parks across three sampling cycles. Sampling years include Cycle 1 = 2008:2011, Cycle 2 = 2012:2015, and Cycle 3 = 2016:2019. Parks are sorted from high to low latitude.

Approximately 30% of parks were classified as insecure for regeneration debt. These parks lack sufficient sapling density and contain a low proportion of stocked plots but often have sufficient and increasingly abundant seedling layers that tend to match the canopy composition more closely. Overall, these parks also experience lower DBIs. Finally, ACAD was the only park classified as secure for regeneration debt, since its forests contain sufficiently abundant and compositionally appropriate seedlings and saplings, with no critically ranked status metrics.

## Trends in regeneration debt by park

Trends in tree basal area and density (Figure 2) indicate that park forests are maturing. Native canopy tree basal area was stable or increasing in all parks except for Marsh-Billing-Rockefeller National Historical Park (MABI) in Vermont, the only national park in the study actively harvesting trees. Native canopy tree density was stable or decreasing for all but two parks, as is typical of middle-aged eastern deciduous forests (Thompson et al., 2013). Increasing native canopy tree density was observed in Antietam National Battlefield (ANTI) in Maryland, due to increases in eastern red cedar (*Juniperus virginiana*), as well as in ACAD. The increase in ACAD tree density was largely driven by recruitment of red spruce (*Picea rubens*) into the canopy following recovery from the 1947 stand-replacing fire that covered 30% of Mount Desert Island, ACAD's largest unit, and 20% of the forest plots we monitor in ACAD (Wheeler et al., 2015). Red spruce recovery from acid deposition, a phenomenon that has been observed throughout the northeastern United States, may also be contributing to the increase in red spruce density (Kosiba et al., 2018). While the density of native canopy saplings declined in ACAD, the subsequent increase in native tree density indicates that saplings are successfully recruiting into the canopy. Native canopy-forming seedling density also significantly increased; stocking index was stable for ACAD, and ACAD was second only to Bluestone National Scenic River

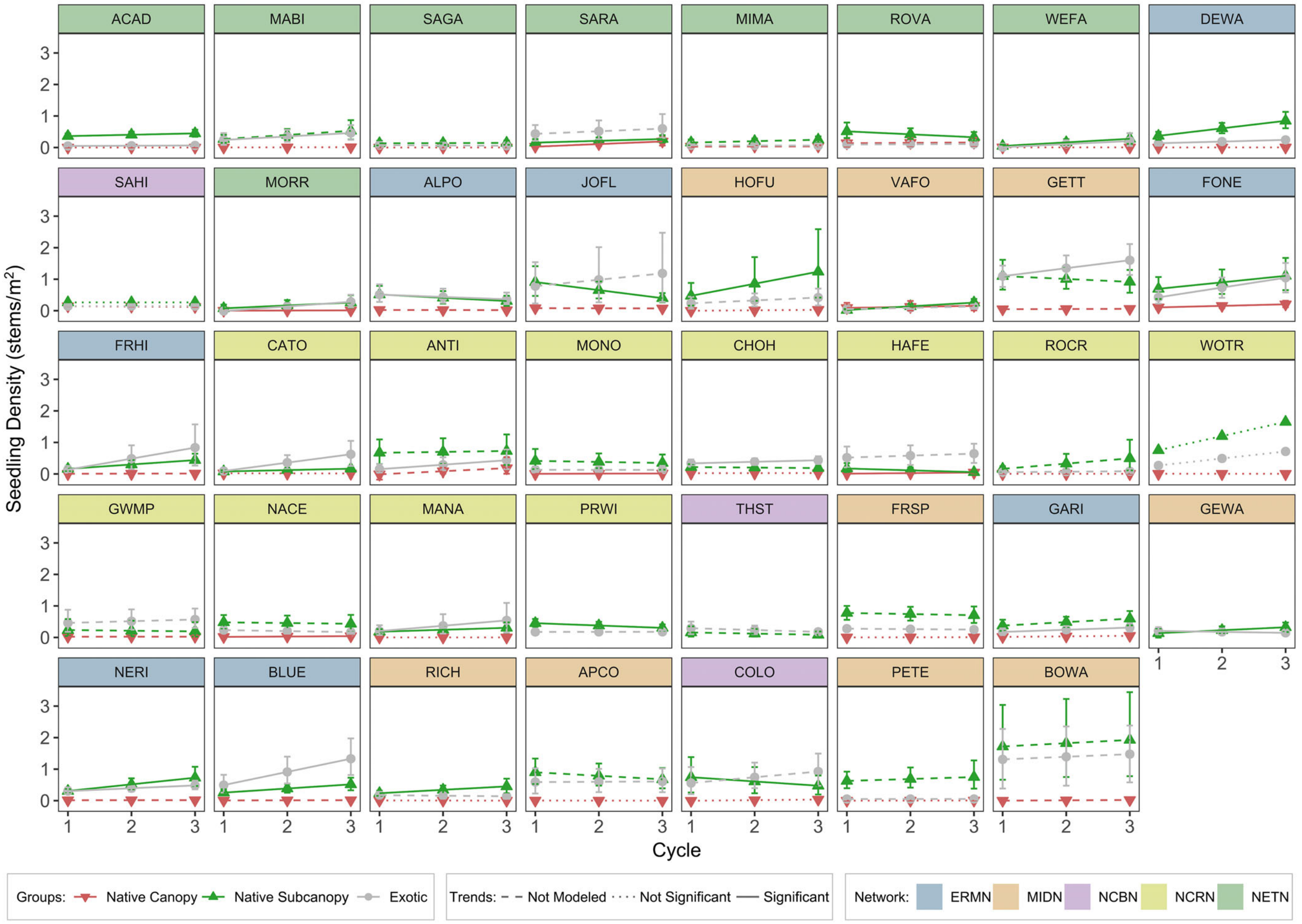


**FIGURE 5** Modeled trends in seedling density (stems/m$^2$) by species nativity and functional group in 39 parks across three sampling cycles. Sampling years include Cycle 1 = 2008:2011, Cycle 2 = 2012:2015, and Cycle 3 = 2016:2019. Parks are sorted from high to low latitude.

(BLUE) in West Virginia in having the lowest average DBI of the 39 parks in this study. These patterns suggest forest dynamics that are largely unrelated to deer impacts and are more likely related to recovery from disturbance and/or stressors. No other park with significant declines in native canopy-forming saplings showed this subsequent increase in live tree density. Increases in native subcanopy trees were evident in Petersburg National Battlefield (PETE) in Virginia, GEWA, and COLO, primarily driven by increases in American holly, sourwood (*Oxydendrum arboreum*), and American hornbeam.

Basal area and density of native canopy saplings were stable or declined significantly over time in all parks, with 10% of parks showing declines in both native canopy sapling basal area and density (Figures 2 and 4). The only park with increasing native canopy saplings was Saint-Gaudens National Historical Park (SAGA) in New Hampshire, where basal area is increasing due to the growth of existing stems of shade-tolerant American beech (*Fagus grandifolia*) and eastern hemlock (*Tsuga canadensis*). Sapling basal area and/or density of native subcanopy species increased in five parks, primarily due to increases in paw paw, ash species, American holly, and eastern redbud (*Cercis canadensis*).

Seedling density of native canopy species increased in 38% of parks, with significant declines seen in 15% of parks and no significant trends in the remaining parks (Figures 2 and 5). Native subcanopy seedling density also increased in 38% of parks, though not the same suite of parks with increasing native canopy seedling density. Native subcanopy seedling density decreased in only two parks. Stocking index increased in six parks and declined in 10 parks (Figure 2).

Exotic trees, saplings, and seedlings were too rare to model trends in 59%, 77%, and 54% of the parks, respectively (Figure 2). Exotic trees increased in basal area in three parks, two of which also showed increasing trends in exotic tree density, primarily due to increases in tree of heaven (*Ailanthus altissima*) and Norway maple (*Acer platanoides*). Declines in exotic tree density were observed in five parks, and exotic tree basal area declined in only one park, Allegheny Portage Railroad National Historic Site (ALPO) in Pennsylvania, where crabapple (*Malus* spp.) and hawthorn (*Crataegus* spp.) trees were being outcompeted in closed-canopy forests. Increases in exotic sapling basal area were observed in two parks, while exotic sapling density declined at two different parks (Figures 2 and 4). Exotic seedling density increased in 18% of parks (Figures 2 and 5). Saratoga National Historical Park (SARA) in New York showed increasing trends of exotic trees, saplings, and seedlings due to increases in common buckthorn (*Rhamnus cathartica*).

## Predictors of regeneration debt

The combination model was consistently the best model for metrics of regeneration abundance, namely, seedling density, sapling density, and stocking index, and the combination model performed better than the null, intercept-only models in all three cases (Table 4, Appendix S2: Table S2). DBI was a strong negative predictor of seedling density (Table 5, Figure 6). Physiographic class was also an important predictor of seedling density, with dry and dry-mesic sites tending to have the highest density, followed by mesic and hydric classes (Table 5, Figure 6). Tree density was the most important continuous predictor of seedling density, followed by invasive plant percentage cover. Seedling density was negatively associated with both live tree density and invasive plant percentage cover. While seedling densities tended toward 0 for all DBI levels at the highest ranges of tree densities, most tree densities in the data set were well below the extremes and showed strong separation between DBI levels (Figure 7). With a coefficient of 0.01 and standard error of 0.04, canopy cover had a negligible influence on seedling density.

As with seedling densities, DBI and physiographic class were important predictors of sapling density (Table 5, Figure 6). The greatest difference in DBI for sapling density was between low/medium and high/very high levels (Figure 6). Similar to seedlings, dry and dry-mesic physiographic classes averaged higher sapling densities than mesic and hydric sites (Table 5). In contrast, invasive plant percentage cover was the most important continuous predictor and was negatively associated with sapling density (Table 5, Figure 6). Tree density only had a minor positive influence on sapling density based on its scaled coefficient (Table 5, Figure 7). While sapling densities tended toward 0 for all DBI levels at the highest ranges of tree densities, most tree densities in the data set were well below the extremes and show strong separation between low/medium and high/very high DBI levels (Figure 7). Finally, canopy cover was not an influential predictor in the model (Table 5).

The relationships of DBI and physiographic class with stocking index mirrored that of seedlings (Table 5, Figure 6), with strong separation among all DBI levels and hydric sites having overall lower stocking index values than dry and dry-mesic sites. In the case of the stocking index, invasive cover was more influential than tree density, and both were negatively associated with the response (Table 5). Again, canopy cover only had a minor negative influence on stocking index. While the stocking index tended toward 0 for all DBI levels at the highest ranges of tree densities, most tree densities in the data set were well below the extremes and show strong separation between low/medium and high/very high DBI levels (Figure 7).

The best model for seedling versus canopy similarity was the stressor model (Table 4, Appendix S2: Table S2). DBI and invasive plant percentage cover were the most important predictors, and both were negatively associated with seedling similarity (Table 5). The influence of percentage human-modified land cover on seedling similarity was negligible. The forest structure model was the best model for sapling versus canopy similarity (Table 5, Appendix S2: Table S2). Quadratic mean diameter (QMD) was the most important continuous predictor and was negatively associated with sapling similarity. The pole stage tended to have the highest similarity, followed by the late successional stage. Mature and mosaic stands tended to have lower sapling similarity (Table 5). Tree density and canopy cover were both weakly positively associated with sapling similarity.

Based on marginal $R^2$ values from the best models, which are a measure of variance explained by the fixed effects in the models, the models describing seedling density and stocking index better fit the data than did the models describing sapling density and similarity. That said, all models were better than the null model, which only included the intercept and random effects (Appendix S2: Table S2).

# DISCUSSION

## Regeneration debt summary

Based on 12 years of forest monitoring across the 39 parks distributed from Maine to Virginia in our study, we observed widespread regeneration debt in eastern U.S. national parks, in both regeneration abundance and composition. In fact, 70% of the parks in this study were classified as either imminent failure or probable failure for regeneration debt. The most important predictors of regeneration debt were overabundant deer (i.e., DBI) and invasive plant percentage cover, with physiographic class and live tree density exhibiting a secondary influence.

**TABLE 5** Standardized coefficients and SE from best models for each response variable modeled.

| Model | Predictors | Coefficient | SE |
|---|---|---|---|
| Seedling density: Native canopy | Intercept | −1.03 | 0.14 |
| | DBI (high) | −0.46 | 0.09 |
| | DBI (very high) | −1.10 | 0.12 |
| | inv_cover | −0.10 | 0.04 |
| | physio (dry-mesic) | −0.07 | 0.12 |
| | physio (hydric) | −0.76 | 0.21 |
| | physio (mesic) | −0.53 | 0.11 |
| | tree_dens | −0.21 | 0.05 |
| | cancov | 0.01 | 0.04 |
| | Marginal $R^2$/conditional $R^2$: 0.104/0.202 | | |
| Sapling density: Native canopy | Intercept | −2.86 | 0.10 |
| | DBI (high) | −0.24 | 0.06 |
| | DBI (very high) | −0.30 | 0.08 |
| | inv_cover | −0.18 | 0.03 |
| | physio (dry-mesic) | −0.18 | 0.08 |
| | physio (hydric) | −0.46 | 0.13 |
| | physio (mesic) | −0.29 | 0.07 |
| | tree_dens | 0.09 | 0.03 |
| | cancov | 0.00 | 0.03 |
| | Marginal $R^2$/conditional $R^2$: 0.097/0.221 | | |
| Stocking index | Intercept | 2.66 | 0.18 |
| | DBI (high) | −0.68 | 0.12 |
| | DBI (very high) | −1.48 | 0.16 |
| | inv_cover | −0.31 | 0.06 |
| | physio (dry-mesic) | 0.08 | 0.16 |
| | physio (hydric) | −1.05 | 0.27 |
| | physio (mesic) | −0.53 | 0.15 |
| | tree_dens | −0.24 | 0.06 |
| | cancov | −0.08 | 0.05 |
| | Marginal $R^2$/conditional $R^2$: 0.126/0.217 | | |
| Seedling versus tree similarity | Intercept | 0.30 | 0.01 |
| | DBI (high) | −0.03 | 0.01 |
| | DBI (very high) | −0.12 | 0.02 |
| | inv_cover | −0.02 | 0.01 |
| | hmod300m | 0.00 | 0.01 |
| | Marginal $R^2$/conditional $R^2$: 0.052/0.112 | | |
| Sapling versus tree similarity | Intercept | 0.30 | 0.02 |
| | str_stage (mature) | −0.04 | 0.01 |
| | str_stage (mosaic) | −0.03 | 0.02 |
| | str_stage (pole) | 0.02 | 0.02 |
| | QMD | −0.05 | 0.01 |
| | tree_dens | 0.02 | 0.01 |
| | cancov | 0.01 | 0.01 |
| | Marginal $R^2$/conditional $R^2$: 0.080/0.181 | | |

(Continues)

**TABLE 5** (Continued)

*Note*: The density and stocking index responses were log-transformed. Similarity responses were not transformed and used Sørensen similarity. Refer to Table 3 for full predictor names and details.
Abbreviations: DBI, deer browse impacts; QMD, quadratic mean diameter.

It is important to note that these regeneration debt categories are based on park-wide averages. Some parks have multiple management units that are geographically dispersed and contain forests in varying ecological condition. The severity of regeneration debt varies among management units in some parks, such as RICH and NACE, such that unit-specific conditions should be considered when implementing management to improve forest regeneration. For example, the park-wide regeneration status in PRWI is strongly influenced by abundant regeneration in one section of the park that recently experienced an unplanned wildfire. Regeneration in unburned sections of the park is much lower, more closely resembling forests in the imminent failure category. Additionally, a 4-ha deer exclosure established in 2007 in MORR includes one forest plot that randomly landed in the exclosure, and the increases in seedling density and the stocking index are primarily due to understory responses in this exclosure. Outside of the exclosure, conditions in MORR are much more critical. In fact, as suggested by the flat tree diameter distribution, sapling recruitment into the canopy has failed for so long that MORR forests lack trees in smaller size classes (i.e., DBH < 20 cm).

One of the most pervasive components of regeneration debt observed across parks was the sapling bottleneck in which seedlings are prevented from maturing to saplings despite abundant propagules from canopy trees. Sapling density, especially for native canopy species, is critically low in nearly all parks, with significant declines observed in native canopy sapling basal area and/or density for most parks. Although insufficient light on the canopy floor in closed canopy stands can exacerbate the sapling bottleneck (Chou et al., 2018), our study found high to very high deer browse and invasive plant percentage cover to be more important predictors of sapling density than live tree density or canopy cover. Bradshaw and Waller (2016) corroborated this pattern of high-intensity deer browse and preferential browse on more palatable species as the dominant forces that control regeneration patterns across large regions of the eastern United States. In closed-canopy mature forests with minimal deer and invasive plant impacts, we therefore expect to see suppressed saplings in the understory, instead of the

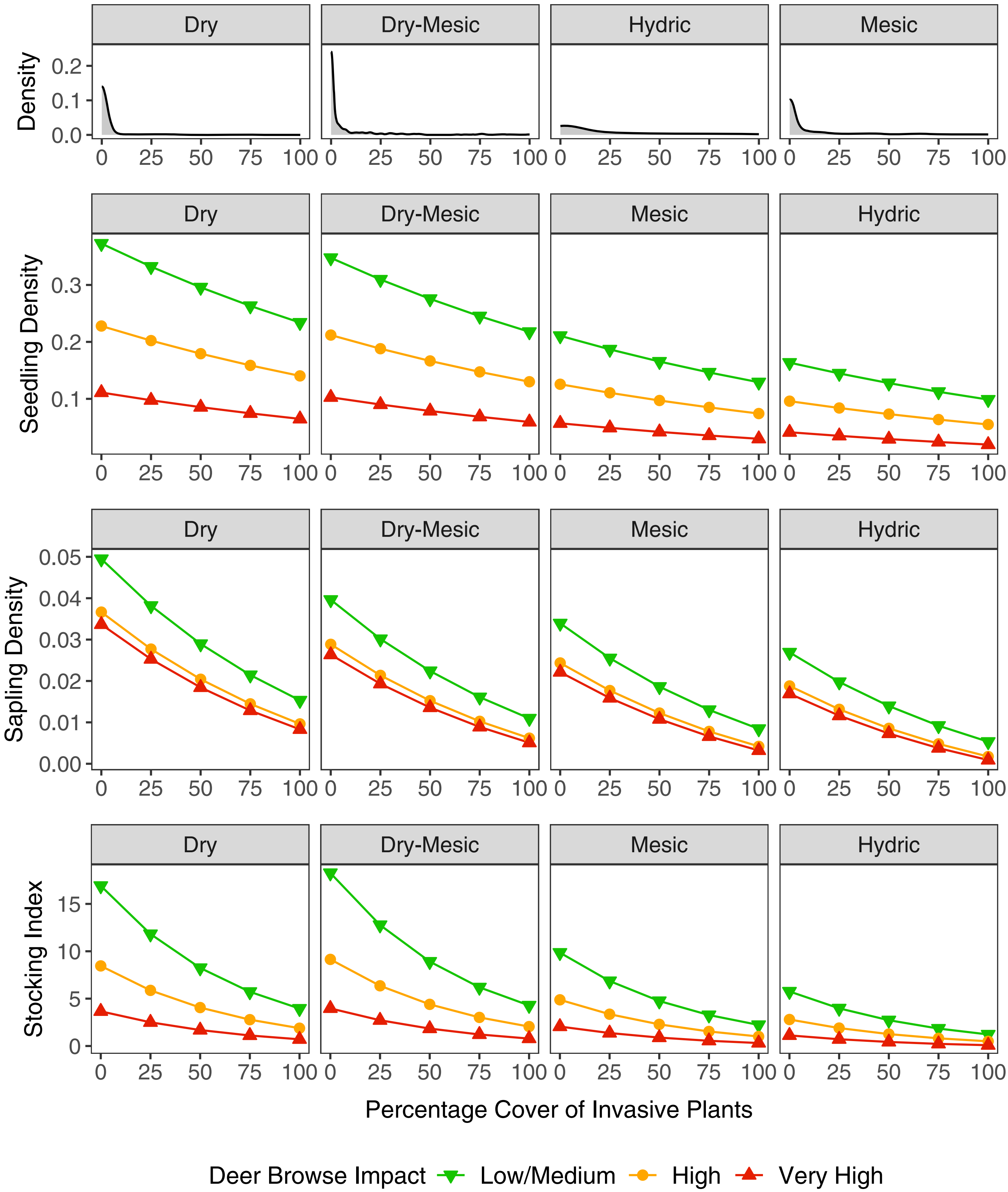


**FIGURE 6** Predicted seedling density, sapling density, and stocking index by a range of deer browse impact (DBI) classes, invasive plant percentage cover, and physiographic classes. The top density panel shows the density distribution of invasive plant percentage cover across the data set. Predictor variables not shown here specified as median values in data set. Seedling and sapling densities units are stems/$m^2$, and stocking index is in the original units.

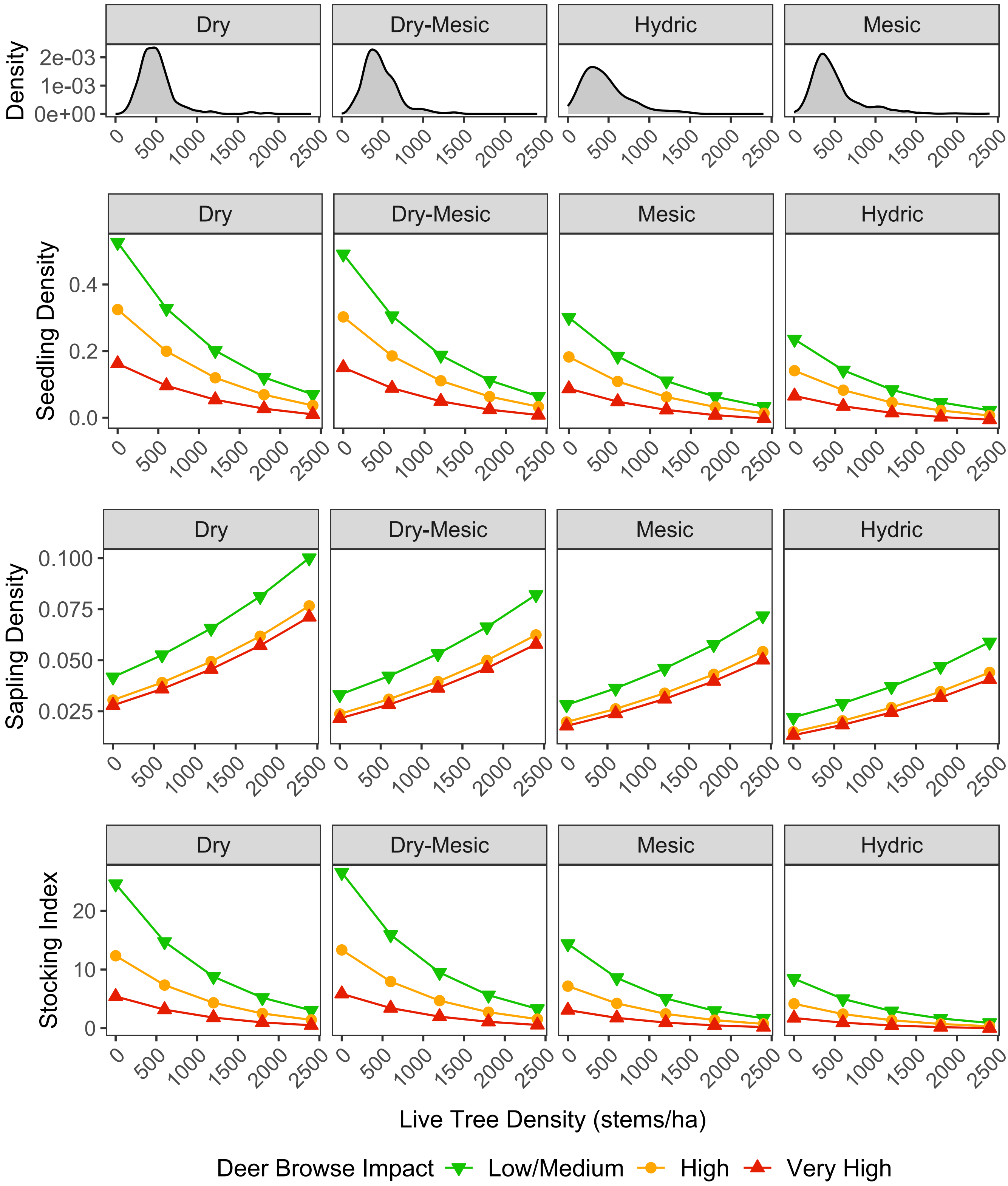


**FIGURE 7** Predicted seedling density, sapling density, and stocking index by a range of deer browse impact (DBI) classes, live tree density, and physiographic classes. The top density panel shows the density distribution of live tree density across the data set. Predictor variables not shown here specified as median values in data set. Seedling and sapling densities units are stems/m$^2$, and stocking index is in the original units.

widespread absence or very low sapling density that is common in many eastern parks. Moreover, some of the most impacted parks (i.e., those rated imminent or probable failure) experienced significant increases in seedling density over time, but these trends are not reflected in saplings.

Regeneration mismatches suggest future shifts in species composition and challenge forest resilience. In approximately half of the parks, native canopy tree species, such as oaks (*Quercus* spp.), hickories (*Carya* spp.), maples (*Acer* spp.), and pines (*Pinus* spp.), comprise less than 50% of total saplings and seedlings. In these forests, native subcanopy tree species, particularly ash, paw paw, and American holly, comprise most of the seedling and sapling layers. Browse-resistant subcanopy native species such as paw paw, striped maple, and American holly are known to increase in areas with high deer densities and can greatly alter forest structure by further suppressing the regeneration of canopy species (Kain et al., 2011; Nyland et al., 2006; Slater & Anderson, 2014).

Forest pests and pathogens also contribute to regeneration mismatches and demonstrate the vulnerability of forests that lack a diverse understory. Regeneration mismatches in many parks were driven by abundant ash regeneration, since emerald ash borer has killed off many of the canopy ash trees in eastern parks and will prevent most current ash saplings and seedlings from reaching the canopy. The devastating impact of eliminating ash as a native canopy tree is most starkly illustrated in GETT, which has actively managed deer since 1996. Consistent deer management over two decades at GETT had resulted in large increases in seedling and sapling densities (Niewinski et al., 2006), such that GETT has the highest mean stocking index of any park in the study and second highest proportion of stocked plots (Figure 3). However, ash species comprise more than half of the total seedlings and one quarter of all saplings in GETT, shifting the park's otherwise secure regeneration status into probable failure. The differences in regeneration status in GETT when ash is not considered a canopy tree are illustrated in Figure 8. With ash as a canopy species, only the Sørensen seedling metric was rated critical. In contrast, when ash is treated as a subcanopy species, five status metrics are rated critical. As beech bark disease complex and the emerging beech leaf disease complex continue to spread through this region (Morin et al., 2007; Reed et al., 2022), we may similarly see exacerbated regeneration debt in parks such as PRWI, Rock Creek Park (ROCR), and SAGA, where American beech is the dominant regeneration component. Moreover, beech thickets formed in response to beech bark disease can suppress regeneration of other native canopy species (Giencke et al., 2014).

Given the model selection results, which consistently found dry and dry-mesic sites to have higher regeneration abundance than mesic and hydric sites, adjusting our thresholds by physiographic class may ultimately improve our classification of regeneration debt. However, before we can adjust thresholds by physiographic class or other site conditions, we first need to separate the impacts of deer and invasive plants on regeneration abundance, which, as we have demonstrated, are widespread problems in our parks. We will revisit these thresholds as forests recover from overabundant deer and invasive plant cover and regeneration successfully recruits into sapling and canopy layers. However, we likely need at least another decade of monitoring in the parks currently managing deer before successful recruitment of this nature can be observed across much of the study area (Nagy et al., 2022; Tanentzap et al., 2011). Additionally, our thresholds that distinguish critical from caution are intentionally conservative and reflect the bare minimum of what a forest in the eastern United States that regenerates largely through gap-phase dynamics needs to persist in the long term. These thresholds may therefore be lower than what certain forests actually require.

## Management recommendations

With the exception of BLUE, all parks classified as imminent or probable failure had critical or caution levels of DBIs. Overabundant deer populations and their resulting impacts on regeneration are not a new phenomenon in many of our parks, with studies calling for deer reduction dating back to the 1990s (e.g., Porter, 1991). In addition, results of the model selection strongly suggested DBIs to be a major predictor of regeneration debt. Deer management is therefore recommended, if not already under way, for all parks classified as imminent or probable failure, except for BLUE. Previous studies showed that reversing regeneration debt requires sustained commitment to deer management for over a decade (Niewinski et al., 2006; Schmit et al., 2020). Once deer management is initiated, recovery of adequate regeneration may be delayed until sufficient seed crops are produced (Long et al., 2007) and deer browse intensity is low enough and sustained for long enough that seedlings can escape deer herbivory and recruit into saplings (Pendergast IV et al., 2016; Royo et al., 2010). In fact, deer exclosure studies suggest that full forest recovery from chronic deer overabundance can take as long as 40–70 years (Anderson & Katz, 1993; Tanentzap et al., 2011). While five out of the nine parks in our study with active deer management programs (i.e., starred parks in Figure 2) show increasing trends in seedling density and/or stocking index (although not all significant), most of these parks are categorized as imminent failure due largely to a lack of saplings and to DBIs that remain unsustainable. Even in parks that have been managing deer for over a decade, including CATO in Maryland and Valley Forge National Historical Park (VAFO) in Pennsylvania, the positive response in small (<1 m tall) seedlings has yet to carry

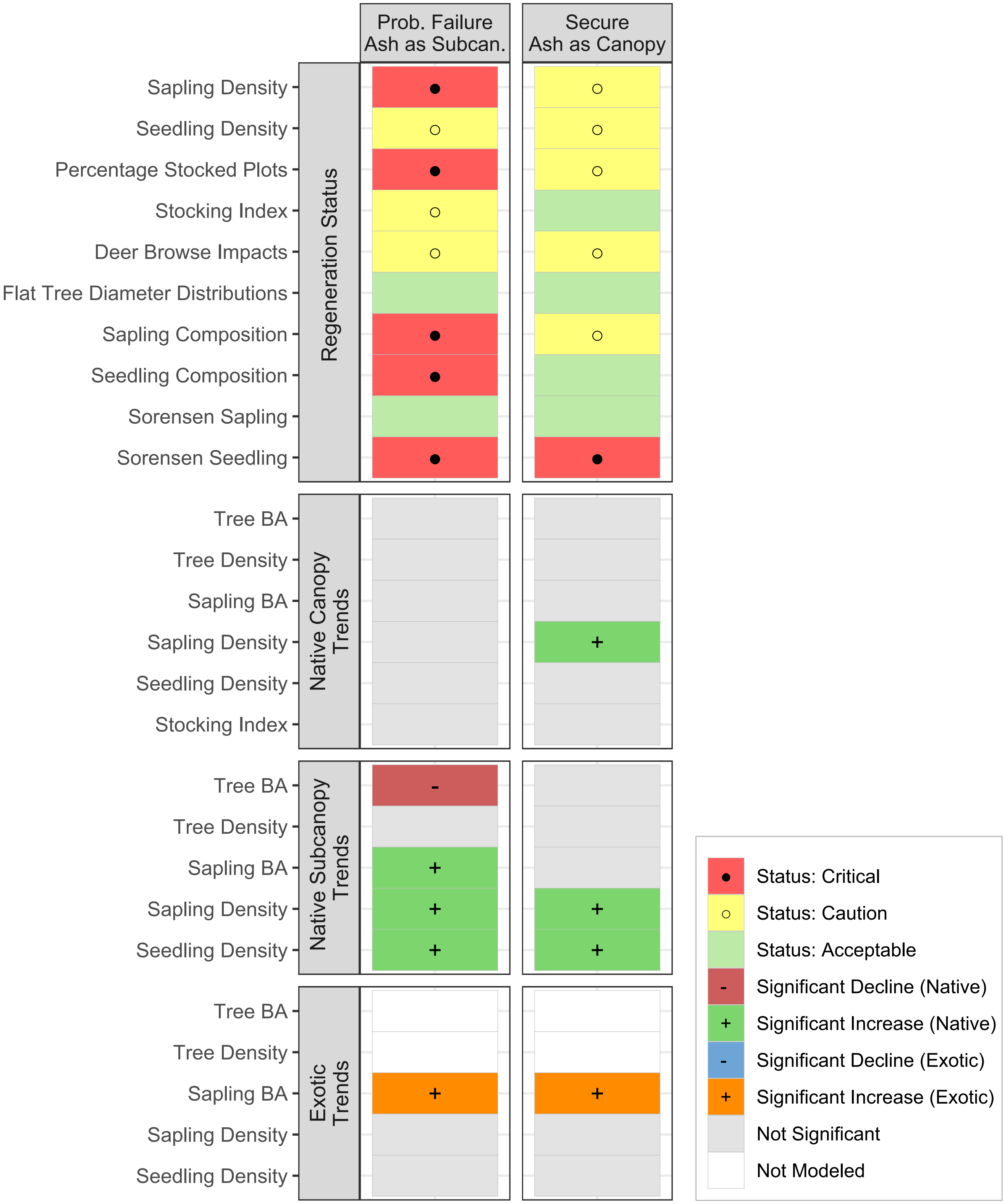


**FIGURE 8** Differences in regeneration metric status in Gettysburg National Military Park when ash is treated a native subcanopy or a canopy tree. BA, basal area; Prob., probable; Subcan. subcanopy.

through to larger seedlings and saplings. This may be partially due to target deer densities that are too high (e.g., VAFO's initial density target was 11.5–13.5 deer per square kilometer) and/or to the fact that it takes over 15 years of continual management to achieve a sufficient regeneration response (Nagy et al., 2022). In fact, we see a positive response only in the sapling layer in GETT, which has been actively managing deer since 1996. Unfortunately, many of the gains from deer management in GETT are expected to be lost to emerald ash borer, underscoring the importance of a compositionally diverse regeneration layer.

Many of the parks experiencing the most severe impacts of chronic deer browse also have the highest and increasing invasive plant loads (Fisichelli & Miller, 2018; Miller et al., 2021). In fact, this study consistently found invasive plant cover to be an important and negatively associated predictor of regeneration abundance, particularly for sapling density and the stocking index. Where overabundant deer and invasive shrubs overlap, canopy gaps often result in conversion to invasive shrub thickets that suppress tree regeneration. In MORR, for example, gaps formed from ash dieback and windthrow events have converted to invasive shrub thickets (Miller et al., 2021). Silvicultural practices that create canopy gaps intended to increase forest resilience by promoting diverse and abundant regeneration must therefore be applied with extreme caution in forests with high deer densities and abundant invasive plants (Webster et al., 2018). Similarly, treating invasives in canopy gaps created by storm events or by pests and pathogens should be management priorities to avoid forest loss in disturbed stands. Promoting resilience through canopy gaps is therefore only recommended for parks, or stands within parks, that have low deer and invasive abundance or the capacity to intensively manage invasives in gaps. Parks like BLUE and PRWI, which have low invasive cover (Miller et al., 2021), are classified as insecure regeneration debt, and are dominated by oak–hickory forest, may be best suited for increasing resilience through thinning subcanopy trees (e.g., maples) to increase light to the forest floor (Iverson et al., 2008). However, potential stands in these parks should be surveyed and treated for invasive plants prior to any thinning. Parks experiencing compositional mismatches and that are dominated by oak–hickory forest types may also benefit from prescribed burning (Perles et al., 2021). However, oak and hickory regeneration must be present prior to burning, and deer browse pressure must be minimized for prescribed fire to be most effective, suggesting that this treatment would be most appropriate in parks classified as insecure (Perles et al., 2021).

In park forests dominated by species vulnerable to pests or pathogens, such as beech-, ash-, or hemlock-dominated forest stands, planting alternative native canopy species and protecting plantings from browse may be an important management tool to maintain forest cover as dominant canopy species die. In addition, beech thickets formed by canopy response to beech bark disease may need to be thinned to promote a more diverse regeneration layer, as is being implemented in MABI (Giencke et al., 2014).

Our findings underscore the critical importance of an integrated approach to forest management that addresses the multiple stressors currently impacting eastern forests, including the widespread regeneration debt documented here, along with threats posed by invasive plants and vulnerabilities of low-diversity forests to pests and pathogens (McShea, 2012; Ward et al., 2017; Webster et al., 2005). Protected forests such as those in eastern national parks require increased and sustained investment in natural resource management to secure sufficient regeneration and thereby ensure the persistence of these forests for future generations. These efforts are most important for parks classified as imminent and probable failure for regeneration debt, as these parks are likely to lose forest cover without intervention.

The presence of widespread regeneration debt across the study area has implications for forest managers across the region facing similar regeneration debt and excessive DBIs (e.g., see Blossey et al., 2019; Jenkins & Howard, 2021; Kilheffer et al., 2019). The regeneration debt index can help managers determine when intervention is necessary (i.e., classified as imminent or probable failure) and evaluate forest response to management over time, as we have shown with parks undergoing deer management.

## Importance of management intervention

Forests in the eastern United States managed by the NPS have both social and conservation value (Haefele et al., 2016). These forests provide scenic viewsheds and recreation opportunities for millions of visitors every year, contributing significant economic benefits to the surrounding communities (Thomas et al., 2015). Since eastern park forests house greater tree diversity (Miller et al., 2018) and structural complexity (Miller et al., 2016) than unprotected forests in the surrounding ecoregions, forests in eastern national parks play a unique role in providing protected habitat for countless organisms and essential ecosystem services. Even in highly urbanized settings, eastern national parks and other protected forests support higher-integrity bird communities than the surrounding unprotected lands (Goodwin & Shriver, 2014; Timmers et al., 2022). Given the importance of eastern park forests, the patterns we documented in this study are even more concerning and require immediate and sustained action to prevent further loss and degradation of forest resources in eastern national parks. Without intervention, the likely outcome, which we are already observing in some parks, is widespread forest loss that will have cascading effects on forest-dependent taxa, ecosystem services, and visitor experiences in eastern national parks.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data sets utilized for this research are as follows: NPS I&M data sets (Miller et al., 2023) are available as tabular_data.zip in the NPS DataStore forest regeneration debt project at https://irma.nps.gov/DataStore/Reference/Profile/2296905; land cover and tree canopy cover data (Dewitz, 2019) are available in a U.S. Geological Survey data release at https://doi.org/10.5066/P96HHBIE; annual maximum temperature and monthly precipitation data for years spanning 1911–1940 and the most recent 30-year normals (Prism Climate Group, 2022) were downloaded from https://prism.oregonstate.edu/. Raster data sets derived from land cover, tree canopy cover, and prism data are available as raster_data.zip at https://irma.nps.gov/DataStore/Reference/Profile/2296905. R code is available as R_Code.zip via the NPS DataStore in the forest regeneration debt project at https://irma.nps.gov/DataStore/Reference/Profile/2296905.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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