

RESEARCH ARTICLE

Compounding human stressors cause major regeneration debt in over half of eastern US forests

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Abstract

1. The future of temperate forests in the face of global change and anthropogenic stressors remains uncertain. The regeneration stage, which is a critical bottleneck for many organisms, is a key indicator of forest health, future canopy composition and forest adaptive capacity.
2. In trees, seemingly healthy forests can be at long-term risk due to insufficient juveniles to replace them (regeneration failure), or compositional differences between juveniles and adults (regeneration mismatch). We propose 'regeneration debt' to collectively describe regeneration failure and mismatch in analogy to extinction debt. To demonstrate this concept, we conducted a macroecological analysis of regeneration debt and anthropogenic stressors in eastern US forests.
3. Using U.S. Forest Service-Forest Inventory and Analysis data, we quantified regeneration debt in 18 states from Maine to South Carolina, and evaluated the influence of site, anthropogenic stressors and climate drivers in the most affected regions.
4. We identified three distinct regions, with little debt in the north, moderate debt in the south and severe regeneration debt in the central, mid-Atlantic region. In this region, multiple anthropogenic stressors (invasive plants, deer overabundance and land use) were associated with both low-regeneration abundance and the prevalence of disease-prone and/or suboptimal species.
5. *Synthesis and applications.* Without management intervention, the severe regeneration debt in the mid-Atlantic region will likely lead to long-term declines in forest cover, with cascading negative effects on forest-dependent taxa and ecosystem services. Moreover, the location of the regeneration debt, which is at the northern edge of and involves many of the tree species that are predicted to gain suitable habitat in the Northeastern US, has consequences that extend far beyond its current geographic extent. In fact, this regeneration debt may already be functioning as a barrier to poleward tree migration. Our results demonstrate the value of regeneration debt as an indicator of ecosystem health and forest adaptive capacity.

KEYWORDS

anthropogenic stressors, forest adaptive capacity, forest inventory and analysis, mesophication, regeneration debt, temperate forests, tree migration, tree regeneration

1 | INTRODUCTION

The fate of temperate forests, which sustain roughly 20% of the world's plant biomass and provide essential economic and ecosystem services, will depend on their capacity to adapt to global change (Bonan, 2008; Millar & Stephenson, 2015). Tree regeneration, which includes the germination, growth and survival of seedlings and saplings to reproductive maturity, is a key indicator of forest adaptive capacity (Bradshaw & Waller, 2016; Stevens-Rumann et al., 2017; Zhu, Woodall, & Clark, 2012), particularly given that the regeneration niche tends to be more restrictive and sensitive to climate extremes than adult trees (Anderson-Teixeira et al., 2013; Grubb, 1977). Tree migration, which was the primary mechanism for adapting to past climate change, is largely dependent on successful regeneration of tree species into newly suitable habitat (Clark et al., 1998; Davis & Shaw, 2001). The regeneration layer in temperate forests is therefore an important indicator of their future composition and long-term persistence.

Given long-life spans of trees, regeneration and adult phases are temporally separated. A forest can appear viable based on a healthy adult population, while closer examination suggests that the adult population is unlikely to be replaced due to insufficient juveniles (regeneration failure) or different juvenile species composition (regeneration mismatch). Regeneration mismatch can be adaptive. For example, under climate change where trees will need to shift poleward to track their climate niche, regeneration composition may be more skewed to newly arriving species than adult populations (Woodall et al., 2009; Zhu et al., 2012). Regeneration mismatch is also adaptive in successional forests. Conversely, regeneration failure or mismatch can indicate unhealthy ecosystems. Forests experiencing chronic regenerative failure from, for example, excessive deer browse, may convert to non-forest vegetation (Stromayer & Warren, 1997). Regeneration mismatches involving invasive or suboptimal (e.g. low canopy) plant species may still maintain forest cover, but it will be a very different forest that is indicative of human-caused change (Kain, Battaglia, Royo, & Carson, 2011; Rossell, Gorsira, & Patch, 2005).

We propose the term "regeneration debt" to collectively describe regeneration mismatch and regeneration failure in analogy to the term 'extinction debt' (Tilman, May, Lehman, & Nowak, 1994). The usage of "debt" emphasizes that future changes (i.e. extinctions) are committed to occur due to past events (e.g. habitat loss) even though they have not happened yet (Vellend et al., 2006). Regeneration debt captures this same notion in the context of a mismatch in absolute numbers or species composition between adults and juveniles in long-lived organisms, such that eventual loss of a canopy species is the result of prolonged regeneration failure due to the presence of stressors and/or climate change. As with extinction debt, regeneration debt may be adaptive or indicative of human-caused decline in ecosystem health. It is the causes and circumstances (and human norms), such as management objectives, that interpret regeneration debt as good or bad. Nonetheless, regeneration debt is usually inevitable

where the current regeneration trajectory differs from the adult community. In the near term, regional patterns of consistently low-regeneration density or suboptimal composition can reveal concerns about the long-term viability and adaptive capacity of a given forest biome (Bradshaw & Waller, 2016; Russell et al., 2017).

Although the regeneration niche has been extensively studied, we are aware of few macroecological studies that examine the influence of multiple stressors on regeneration abundance and composition. For example, Russell et al. (2017) documented strong associations between stressors and low-seedling densities covering a large area of the eastern US forest. However, they did not consider regeneration mismatch (composition) and their analysis was not spatially explicit. In contrast, regeneration mismatch has been observed in eastern US oak-hickory forests, with juvenile stages favouring maples (*Acer* spp.) and beech (*Fagus grandifolia*) over oaks (*Quercus* spp.) and hickories (*Carya* spp.; Nowacki & Abrams, 2008). Called mesophication, this has variously been attributed to altered fire regimes, past human disturbances, and deer overabundance (Nowacki & Abrams, 2008), and climate and land use change (McEwan, Dyer, & Pederson, 2011). While mesophication has been documented throughout the eastern oak-hickory forest, the spatial extent has yet to be fully described and regeneration failure has not been examined.

Several studies have looked for adaptive regeneration debt in trees of eastern US forests as an early indicator of forest response to climate change (Fei et al., 2017; Woodall et al., 2009; Zhu, Woodall, Ghosh, Gelfand, & Clark, 2014; Zhu et al., 2012). For most of the species examined in these studies, widespread adaptive regeneration debt in response to climate change does not appear to be happening (except possibly in some northern species). Whether this lack of observed poleward migration is a lagged response to climate change or the result of other underlying factors has yet to be examined.

Here we conduct the first large-scale assessment of regeneration debt, using eastern US temperate forests as our study system. This study is spatially explicit in the sense that we are looking at how patterns vary across the region rather than using aggregative statistics like species mean latitudes (Woodall et al., 2009), and are examining multiple human stressors (e.g. climate change, deer browsing, land use, invasive species) in combination. We take a community-level rather than species-range approach to identify regions with or without regeneration debt and provide correlational support for which anthropogenic stressors may be causing these patterns.

2 | MATERIALS AND METHODS

2.1 | Data preparation

We compiled seedling, sapling, tree and stand data from the fuzzed, swapped plot locations from the U.S. Forest Service-Forest Inventory and Analysis (USFS-FIA) program (<http://www.fia.fs.fed.us/tools-data/>, accessed November 2017). We selected Phase 2 plots that were inventoried during the most recent evaluation period per state

(range: 2009–2016). Seedlings and saplings were sampled in four 2.07-m radius microplots per plot, and trees were sampled in four 7.31 m radius subplots (US Forest Service, 2017). Seedlings were <2.54 cm diameter at breast height (DBH) and ≥ 15.24 or 30.48 cm tall for conifer and deciduous species, respectively, saplings were ≥ 2.54 cm DBH and <12.7 cm DBH, and trees were ≥ 12.7 cm DBH. We calculated seedling and sapling density (stems/m²) for all plots having at least one recorded forest condition and sampled microplot.

Because similarity analyses are sensitive to scale (Lennon, Koleff, Greenwood, & Gaston, 2001), we only included USFS-FIA plots with four fully sampled and forested subplots and microplots. For each plot, we calculated Sørensen (incidence-based) and Horn (abundance-based) similarity between seedlings or saplings and trees. Calculating multiple similarity metrics can show how robust patterns are, as each metric treats abundance and shared versus unmatched species components of similarity differently (Koleff, Gaston, & Lennon, 2003; Lennon et al., 2001). We compiled all of the data and conducted all analyses in R (R Core Team, 2017). Our code is available for download from Zenodo <https://doi.org/10.5281/zenodo.2576104> (Miller & McGill, 2019).

We compiled additional predictor variables from the USFS-FIA dataset (refer to Table S1 for list of considered predictors and Table S2 for Akaike information criteria (AIC) tables of considered models). We calculated plot-level relative abundance based on the stem density within each life stage (i.e. seedlings, saplings or trees) and relative tree basal area by species or species group (e.g. invasive trees). Species groups included tree genera (e.g. *Quercus*, *Pinus*), low-canopy trees and invasive tree species (see Table S3). Low-canopy trees, such as pawpaw (*Asimina triloba*) and striped maple (*Acer pensylvanicum*), can reach tree diameter size (i.e. >12.7 cm DBH), but rarely reach the height of the canopy. The primary exception is where true-canopy species fail to recruit and these species form a lower-stature canopy, hence the term 'low canopy' (Kain et al., 2011). Both low canopy and invasive species were based on growth habit and nativity listed in the USFS-FIA reference plant dictionary. We considered red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*) together as the maple group during model selection.

We calculated average percent cover of invasive species on the forested area for each USFS-FIA plot sampled for invasive species (Invasive Subplot Status Code = 1 or 2). While USFS-FIA plots with consistent invasive species data are well-distributed across our study area, this metric was only available for a subset of USFS-FIA plots in our study (10,171 out of 29,512 plots) due to USFS-FIA protocol changes that started in 2013. We included stand size code (1 = large, 2 = medium and 3 = small diameter, and 4 = non-stocked), as a continuous (ordered) variable. Given that 11% of plots had ≥ 2 classes, we calculated a weighted average of stand size class using proportion of the plot as the weight. We calculated plot-level canopy cover by averaging canopy cover across subplots having sampled forest conditions, and weighted cover by area of forest sampled within each subplot.

In 2012, USFS-FIA surveyors in the Northern Research Station began assessing deer browse impacts on a scale of 1–5 (US Forest

Service, 2017), but this metric was not available for the entirety of our study region. Thus, we used deer-density estimates from the Quality Deer Management Association (2009 [QDMA]) for years 2001–2005, and digitized by Walters, Woodall, and Russell (2016). The categories of deer density were (a) rare, absent or urban area with unknown population, (b) <5.8 deer/km², (c) 5.8–11.6 deer/km², (d) 11.6–17.4 deer/km² and (e) >17.4 deer/km². It is important to note that the QDMA data are very coarse and data quality may vary across states due to different collection methods (Walters et al., 2016). For our analysis, we excluded category 1, and recoded the others (to run 1–4), which corresponded roughly to categories of sustainable (category 1), moderate (category 2), and unsustainable (3+) deer densities (Russell et al., 2017). We extracted the deer-density estimate for each jittered USFS-FIA plot where data were available.

We used the 2011 National Land Cover Database (NLCD; Homer et al., 2015) to examine the influence of land use on regeneration. We reclassified the 2011 NLCD to human modified (1) and natural land cover (0) at the original 30 m resolution using the raster R package (Hijmans, 2017). We aggregated data to a 300 m cell size and calculated the proportion of each cell in human modified land cover classes (Developed: classes 21–24, Grassland/Herbaceous: class 71, and Planted/Cultivated: classes 81–82), and considered the remaining land covers to be natural.

To examine the influence of climate change on regeneration, we acquired annual maximum temperature and monthly precipitation data for years spanning 1911–1940, and the most recent 30-year normals (1980–2010; Hart & Bell, 2015; Prism Climate Group, 2017). 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 calculated the yearly average of the summed April–September precipitation. For maximum temperature, we calculated the average maximum temperature for each period. Finally, we calculated the percent change between the early and current periods to represent climate change over the two periods. We used maximum temperature and April–September precipitation as important measures of drought stress that have been associated with regeneration mismatches in our study area (McEwan et al., 2011). While other potentially important metrics of climate change may be useful predictors of regeneration debt, exhaustively examining which climate metrics have the strongest associations with regeneration debt is beyond the scope of this study.

To help with visual interpretation of results, we used the spatstat R package to create smoothed rasters of the point data (Baddeley, Rubak, & Turner, 2015). We chose a 10-km-bandwidth with Gaussian kernel to provide the greatest spatial coverage while not over-simplifying patterns in the data. For the spatial regressions, we used the original plot locations, along with the data collected at the plot locations (e.g. stand size code). We also extracted the percent of human modified land cover and the percent change in maximum temperature and April–September precipitation for each plot in the analysis, although these rasters were not smoothed. As invasive plant data were recorded on a subset of USFS-FIA plots, we extracted the average percent cover of invasive plants from the

kernel-smoothed raster. All spatial data were projected in Albers conical equal area with NAD83 datum.

To quantify regeneration debt, we created an index that combined seedling and sapling densities with compositional similarity indices. While there are no obvious minimum seedling and sapling densities that can ensure sufficient regeneration for future canopy recruitment, seedling densities between 0.1 and 0.25 stems/m² (1,000–2,500 stems/ha) and sapling densities of 0.01–0.1 stems/m² (100–1,000 stems/ha) are frequently cited as insufficient (e.g. Abrams & Johnson, 2012; Bressette, Beck, & Beauchamp, 2012; Russell et al., 2017). We therefore used ≤ 0.25 seedlings/m² and ≤ 0.1 saplings/m² to indicate regeneration failure. We were also unable to find published composition mismatch thresholds. We set a conservative similarity threshold of 0.2, which equates to roughly 1 in 5 or fewer species in common between the regeneration and canopy layers. For composition mismatch, we only used Horn similarity because it is a better assessment of dominant patterns in the regeneration layer. To quantify regeneration debt, seedling density, sapling density, seedling versus canopy similarity and sapling versus canopy similarity were reclassified (based on above thresholds) into binary rasters, with 1 indicating either regeneration failure or composition mismatch and 0 indicating otherwise. Because regeneration density and similarity were not calculated on the exact same set of plots, we created kernel-smoothed rasters for each. We then overlaid and summed the rasters to quantify the degree of regeneration debt for each pixel, with 0 indicating no regeneration debt and the remaining values ranging from 1 (only 1 metric fell below the target threshold) to 4 (all 4 metrics fell below the target threshold). Finally,

we summarized the percentage of area covered by each regeneration debt score.

2.2 | Statistical analysis

To understand drivers of abundance and similarity, candidate models were fit using ordinary least squares and compared using AIC. We square root transformed the seedling and sapling densities and logit transformed similarity metrics to meet OLS assumptions. We tested 10 candidate models for each dependent variable (Table S2), and only considered models where all predictor variables had a variance inflation factor < 2 . We did not include treatment or stand origin type (i.e. natural vs. artificial regeneration) as potential variables because most plots in the spatial regression had no recent observable treatment (94.8% of plots) and were naturally regenerated (94.6% of plots).

Spatial autocorrelation was evident based on variograms, Moran's I and spatial residual plots. We addressed this issue by using conditional autoregressive (CAR) regression, which estimates the response variable as a function of the response values within a specified neighbourhood of points (Dormann et al., 2007). We used AIC to determine the best neighbourhood structure (20 km with row-standardized weights). Due to computational limitations (e.g. required > 32 GB of virtual memory), we restricted our final regression models to the area experiencing the most severe regeneration debt. Predictor variables were scaled to assess their relative degree of influence on the response in each model. Finally, we used regression trees to examine nonlinear

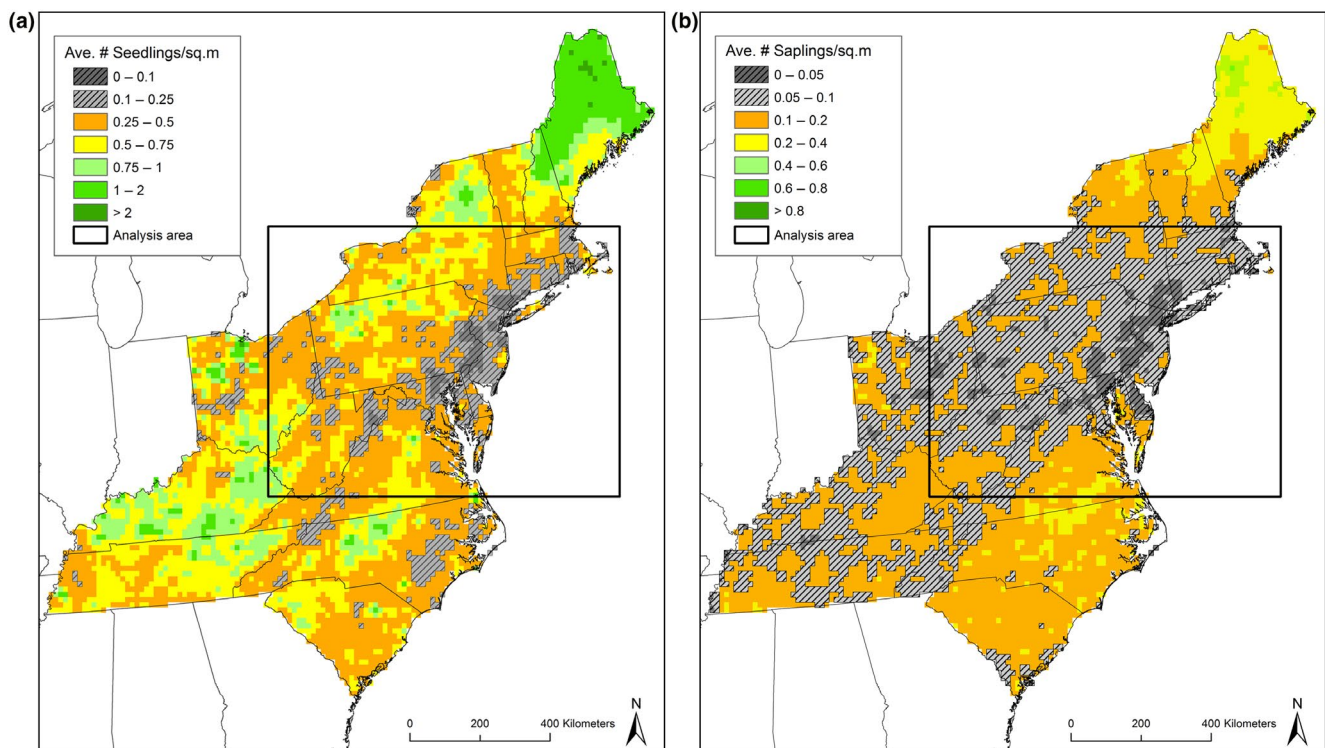


FIGURE 1 Kernel-smoothed (a) seedling stem densities (stems/m²) and (b) sapling stem densities (stems/m²) with area used in CAR regression analysis outlined in black

relationships and interactions among predictors for each of the response variables.

3 | RESULTS

3.1 | Seedling densities

Seedling densities varied considerably across the study area, with very high densities in the northern region and a roughly contiguous area of very low-seedling density spanning northern Virginia through Massachusetts (Figure 1a). Within the mid-Atlantic focal area, seedling density was associated with metrics of climate change, stressors, composition and stand characteristics (Nagelkerke Pseudo- $R^2 = 0.129$, Table 1). Seedling density was negatively associated with percent maximum temperature change and positively associated with percent precipitation change. Stressors influencing seedling density in this region included human modified land cover, average percent cover of invasive plants and deer density. These stressors showed high-spatial overlap with each other and with areas

TABLE 1 CAR regression results with standardized coefficients for seedling and sapling stem densities. Predictors that were not included in the best model for each response variable are indicated by (–). Both April–September precipitation (% Precip. change) and maximum temperature change (% Max. temp. change) metrics calculated change between 1911:1940 and 1980:2010. % Human mod. is the % of human modified land cover within 300 m grid. % Invasive cover is the average percent cover of invasive plant species, and includes all vascular species considered invasive by USFS-FIA. RA is the relative abundance, based on stem density, of tree species within a stratum. Coefficients in italics are significant at $p < 0.05$

Predictor	Seedling density (stems/m ²)		Sapling density (stems/m ²)	
	Coef.	SE	Coef.	SE
Intercept	0.534	0.011	0.255	0.004
% Max. temp. change	–0.055	0.010	–	–
% Precip. change	0.018	0.009	–0.011	0.003
% Human mod.	–0.015	0.004	–0.008	0.002
% Invasive cover	–0.029	0.007	–0.013	0.003
Deer density (QDMA)	–0.023	0.007	–0.007	0.003
% Tree RA: Beech	0.045	0.004	0.007	0.002
% Tree RA: Maple	–	–	–0.005	0.002
% Tree RA: Oak	0.043	0.004	0.011	0.002
% Tree RA: Pine	0.038	0.004	0.020	0.002
% Canopy cover	0.028	0.004	0.040	0.002
Stand size code	0.011	0.004	0.042	0.002
Nagelkerke Pseudo- R^2	0.129		0.162	

of low seedling densities (Figure 2). Based on the stand size code, forests with smaller diameter trees tended to have higher-seedling densities. Seedling density also consistently increased with canopy cover, and was positively associated with tree relative abundance for beech, oak and pine. Areas where relative-tree abundance was high for beech, oak or pine species groups had little spatial overlap with each other (see Figure S1).

3.2 | Sapling densities

Similar to seedling densities, sapling densities were highest in the northern portion of our study, and very low along the Atlantic coast from northern Virginia north through Massachusetts (Figure 1b). However, the area covered by very low-sapling densities was more extensive than seedlings. CAR regression results were similar to the seedling density results and had a Nagelkerke Pseudo- R^2 of 0.162 (Table 1). The main difference between the sapling and seedling density model was that climate change variables were less important for sapling density, with only a minor negative effect of percent precipitation change included in the best model. Human-modified land cover and average percent cover of invasive plants were both negatively associated with sapling density. Deer density also had a negative impact on sapling density, although the effect was small relative to the other predictors.

As with seedling density, forest characteristics and canopy composition were important predictors of sapling density. Smaller diameter forests tended to have higher sapling densities, and sapling density increased with canopy cover. Sapling density was also positively associated with higher beech, oak and pine tree relative abundance and negatively associated with maple tree-relative abundance. Regression trees of seedling and sapling densities had similar results. Relative-tree abundance of beech and pine, low-deer densities, high-canopy cover and small diameter forests were associated with higher seedling and sapling densities (Figures S9 and S10).

3.3 | Seedling versus tree similarity

The patterns of similarity between seedlings and trees consistently showed an area of high similarity in the northern region of our study (Figure 3). Similarity was lowest in the mid-Atlantic states, particularly around the metropolitan area spanning central New Jersey south through Washington, DC. The pattern of dissimilarity was stronger for Horn than Sørensen.

CAR regressions were similar across the two similarity metrics, with predictors related to composition consistently more important than climate change and stressors (Table 2). The Horn models explained more variance than the Sørensen models (Nagelkerke Pseudo- R^2 values of 0.257 and 0.121 respectively). Both similarities were negatively correlated with relative abundance of beech and low-canopy species in the seedling layer; and positively associated with relative abundance of maple, oak and pine. Percent maximum temperature change was positively associated with Horn similarity. Deer density only had a significant negative effect on Sørensen similarity.

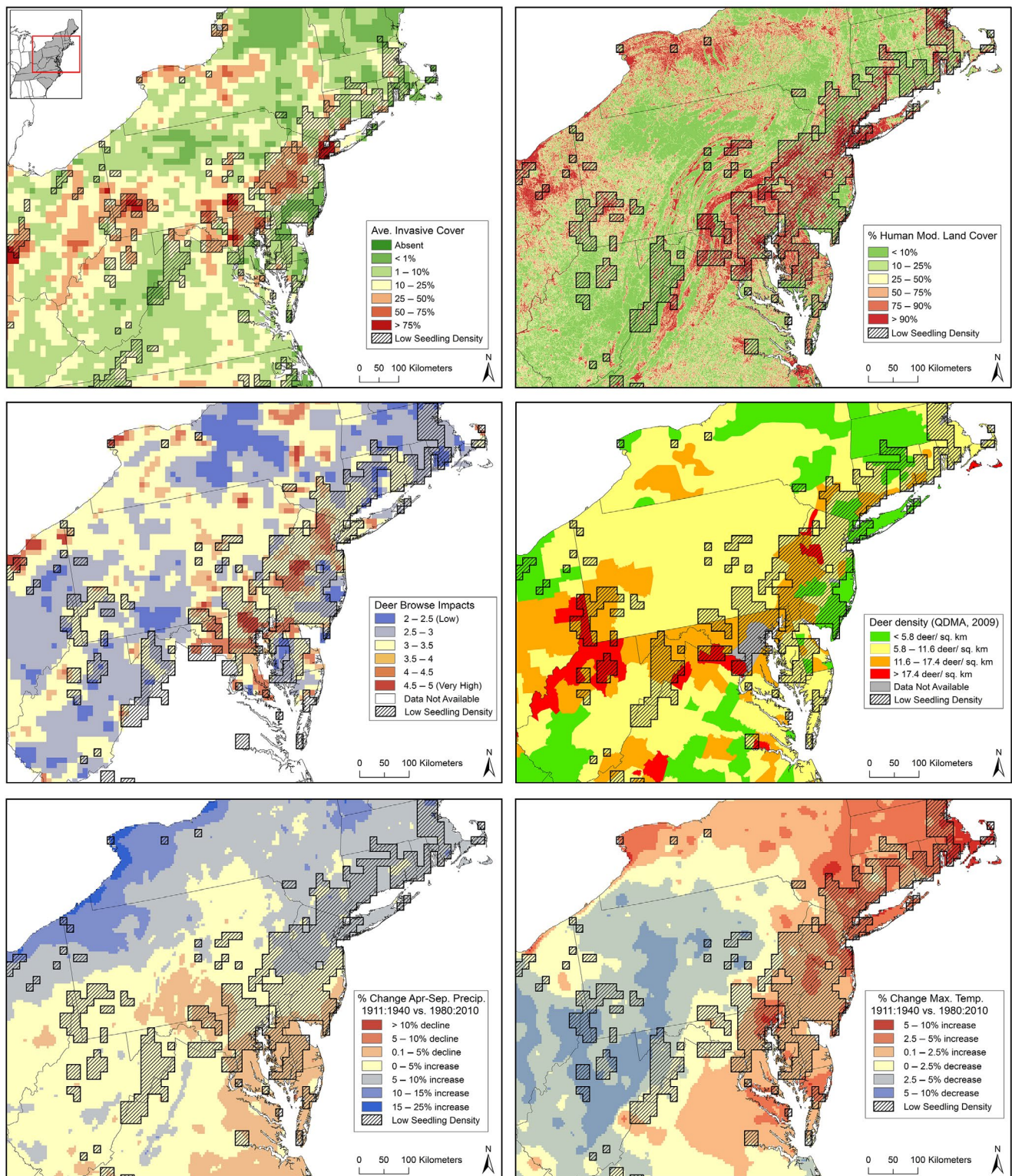


FIGURE 2 Stressors most associated with regeneration abundance in the CAR regression models, with areas of exceptionally low seedling densities (<0.25 seedlings/ m^2 , covering roughly 21% of the modelled area) overlaid on maps. Deer browse impacts were not included in the CAR regression. Refer to Figures S3–S8 for full predictor maps

In contrast to relative abundance of seedlings, relative-tree abundance of oak and pine were both negatively associated with Sørensen and Horn similarity. These results suggest that where oak

and pine are abundant as seedlings, they tend to also be abundant in the canopy. However, forests that are dominated by oak and pine in the canopy tend to differ compositionally in the seedling layer.

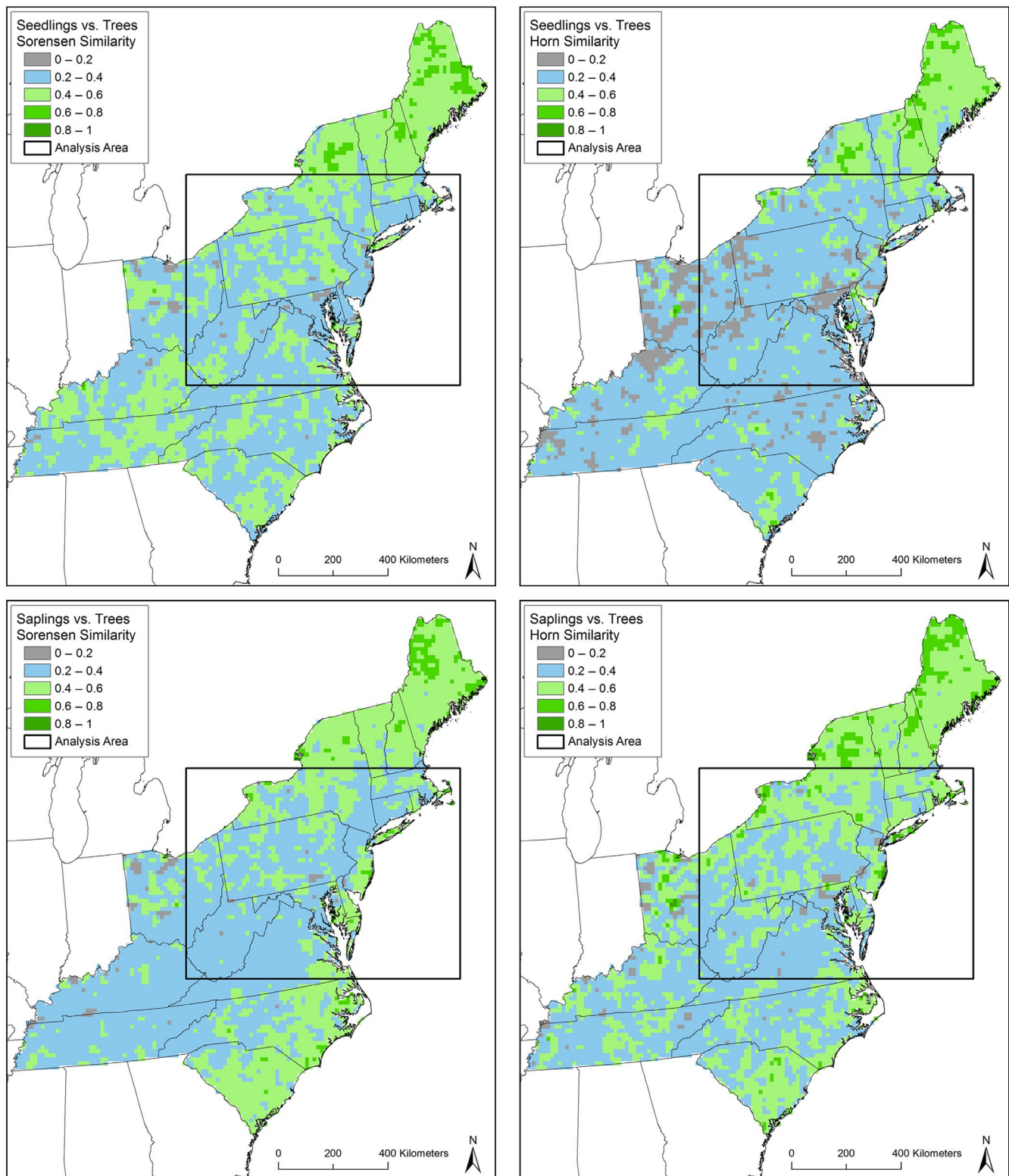


FIGURE 3 Kernel-smoothed Sørensen (left) and Horn (right) similarity for seedlings versus tree (top) and saplings versus tree (bottom)

The opposite pattern was true for beech. Relative-tree abundance of beech was strongly positively associated with similarity, indicating that beech forests tend to have beech-dominated seedling layers. However, high-relative abundance of beech seedlings contributes to decreased similarity, suggesting that where beech seedlings are

abundant, they are often in forests composed of other species in the canopy.

Average percent cover of all invasive plants was not an important predictor in the similarity models. However, relative abundance of invasive tree seedlings had a negative effect on Sørensen similarity.

TABLE 2 CAR regression results with standardized coefficients for seedling versus tree and sapling versus tree similarity metrics. Predictors that were not included in the best model for a given response variable are indicated by (-). Coefficients in italics are significant at $p < 0.05$. See Table 1 caption for additional details

Predictor	Seedling versus tree similarity				Sapling versus tree similarity			
	Sørensen		Horn		Sørensen		Horn	
	Coef.	SE	Coef.	SE	Coef.	SE	Coef.	SE
Intercept	-0.678	0.020	-1.127	0.020	-0.714	0.017	-0.663	0.021
% Max. temp. change	-	-	0.096	0.020	0.073	0.017	0.088	0.021
Deer density (QDMA)	-0.056	0.019	-	-	-	-	-	-
% Regen. RA: beech	-0.126	0.021	-0.191	0.023	-	-	-0.188	0.024
% Regen. RA: Invasive	-0.059	0.015	-	-	-0.067	0.015	-0.069	0.018
% Regen. RA: low canopy	-0.252	0.017	-0.359	0.019	-0.256	0.016	-0.419	0.020
% Regen. RA: maple	0.146	0.016	0.289	0.018	0.135	0.016	0.331	0.021
% Regen. RA: oak	0.151	0.018	0.269	0.020	0.084	0.016	0.153	0.020
% Regen. RA: pine	0.050	0.017	0.246	0.019	0.151	0.016	0.404	0.022
% Tree RA: beech	0.194	0.019	0.523	0.021	0.079	0.016	0.300	0.023
% Tree RA: hickory	-	-	-	-	-0.083	0.015	-0.093	0.019
% Tree RA: oak	-0.042	0.018	-0.098	0.020	-0.140	0.016	-0.388	0.021
% Tree RA: pine	-0.183	0.018	-0.284	0.020	-	-	-0.308	0.023
Stand size code	-	-	-	-	0.186	0.016	0.166	0.020
% canopy cover	-	-	-	-	0.092	0.016	0.085	0.020
Nagelkerke Pseudo- R^2	0.121		0.257		0.155		0.276	

Given that invasive tree seedlings occur at fairly abundances in the analysis area (see Figure S2), it is not surprising invasive tree seedlings were not important predictors in the Horn model. Results of regression trees were similar to the CAR regression, with relative seedling abundance of low canopy species being a strong predictor of low similarity, and relative seedling abundance of oak, maple and pine associated with higher similarity. Similarly, forests with high relative abundance of beech trees tended to have high similarity with the seedling layer (Figures S11 and S12).

3.4 | Sapling versus tree similarity

The patterns of similarity between saplings and trees showed an area of high similarity in the northern region with a stretch of low similarity in the metropolitan areas of the mid-Atlantic states (Figure 3). In contrast to seedling similarity, similarity for saplings versus trees was relatively high along the Atlantic coastline and increased in the southern portion of the study. Like seedling similarity, the Horn model explained more variance than Sørensen, with Nagelkerke Pseudo- R^2 values of 0.276 and 0.155, respectively. For both metrics, greater similarity was associated with forests with smaller diameter trees, higher-canopy cover and increasing maximum temperature (Table 2). Similarity was consistently negatively

associated with relative sapling abundance of invasive and low-canopy species; and positively associated with relative sapling abundance of maple, oak, and pine. Relative-tree abundances of oak and hickory were negatively associated with both similarity metrics, but pine was only negatively associated with Horn similarity. Like seedling similarity, relative-tree abundance of beech was positively associated with similarity, while the relative abundance of beech saplings was negatively correlated with Horn similarity. Regression trees provided similar results, with relative sapling abundance of low-canopy species being a strong predictor of low similarity, and relative sapling abundance of oak, maple and pine associated with higher similarity. In addition, forests with beech in the canopy tend to have high similarity with the sapling layer (Figures S13 and S14). These results suggest that where maple, oak and pine are the dominant saplings, they tend to also be abundant in the canopy. However, forests that are dominated by oak, hickory and pine in the canopy tend to differ compositionally from the sapling layer.

3.5 | Indices of regeneration debt

Our index of regeneration debt, which combines the results from seedling and sapling densities and similarities, was lowest in the northern and far southern regions of this study area and

most severe for the mid-Atlantic region from Washington, DC up through southeastern Pennsylvania and New Jersey (Figure 4). At the full scale of this analysis, 50.5% of the area was experiencing at least one form of regeneration failure (e.g. sapling density $<0.1/\text{m}^2$) or canopy mismatch, with 15.4% of the area is experiencing two or more problems with regeneration (see Table S4). Results were more extreme for the mid-Atlantic region (covered by the CAR regressions), where 74.6% of the analysis area experienced at least one form of regeneration failure or canopy mismatch, and 26.2% experienced two or more such problems.

4 | DISCUSSION

Our study documents the patterns of regeneration debt that fall into roughly three regions: a northern region with little regeneration debt, a southern region which is small due to the borders of our study but appears to have low to moderate regeneration debt, and a mid-Atlantic region showing severe regeneration debt with both regeneration failure and mismatch. Metrics of climate change were associated with regeneration patterns. However, human modified land cover, deer overabundance and invasive plants were more strongly and consistently negatively correlated with regeneration abundance and similarity, and no one factor was dominant. Moreover, while all regions in our study are experiencing these stressors to varying degrees, the mid-Atlantic area is experiencing the greatest levels of anthropogenic stressors (see Figures S3–S8).

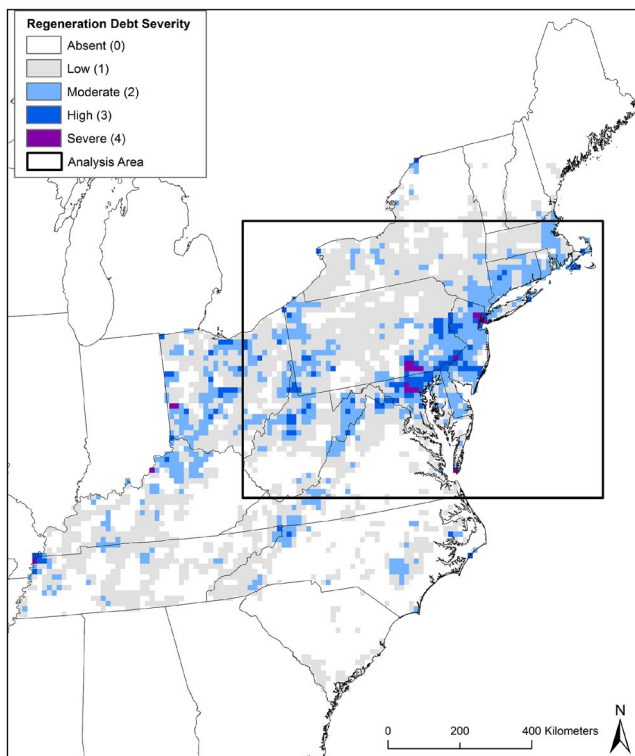


FIGURE 4 Regeneration debt scores for study region, with area used in CAR regression analysis outlined in black

These results are consistent with previous results, but considerably advance our understanding of regional patterns and drivers of regeneration debt. In particular, the mid-Atlantic region with the most severe regeneration debt makes up a large portion of the eastern oak-hickory forest range. This suggests that at least in this eastern portion of the range the mesophication problem is deeper than regeneration mismatch (maple replacing oak-hickory) because it also coincides with extreme regeneration failure. Similarly, our findings may provide the underlying explanation for the lack of observed regeneration mismatch from poleward migration of southern tree species in response to climate change (Fei et al., 2017; Woodall et al., 2009; Zhu et al., 2012, 2014). In other words, regeneration of existing adults is so successful in the northern portions, that adaptive poleward migration of new species is potentially hindered. While in the mid-Atlantic region, regeneration debt may be so high that migration through this region is severely inhibited.

Indeed the spatial position of the mid-Atlantic regeneration debt is pivotal. On the human-side this roughly matches the so called Boston-Washington corridor, or the Northeast Megalopolis, which is the largest area of urbanization in the US containing 17% of the US population in 2% of its area (Vicino, Hanlon, & Short, 2007). Simultaneously, this region is a zone of major transition from south-east warm-adapted species (e.g. oak, hickory and southern pines) to more northerly cold-adapted species (e.g. northern hardwoods and conifers). Many southern species have their northern geographic range boundaries just to the south of or within this zone of regeneration debt (see Figure S15), and thus would need to migrate through this region to successfully track their climate niche (Iverson, Prasad, Matthews, & Peters, 2008). A previous study (Miller & McGill, 2018) showed that the spatial configuration of this area (in particular low connectivity of forest habitats) is poorly suited to tree migration. We further suggest that even if corridors were established, other human impact factors (e.g. invasive species and deer browsing) could prevent tree migration through this area due to an inability to regenerate.

Over and above potential failures in climate-driven migration, the extreme regeneration debt we identified in the mid-Atlantic region raises serious concerns about the fate of these forests in the 50–100 year time frame. These forests are extremely vulnerable to disturbances like wind-throw and ice storms, as there is insufficient advanced regeneration to replace the canopy. Although we know of no studies establishing specific thresholds for seedling or sapling density below which a forest cannot persist, the extremely low numbers in this region, especially in comparison to the regions to the north and south, suggest possible forest loss. While silvicultural practices may help promote regeneration, their application in areas with high-deer densities and/or already invaded habitats requires extreme caution, as canopy removal can exacerbate invasive species problems and concentrate deer herbivory, leading to regeneration failure and loss in canopy cover (Webster et al., 2018). Moreover, in this region of regeneration debt, the few juveniles present are composed of different species than the canopies, with invasive or suboptimal species often dominating. For example, several low

canopy, browse-resistant species (e.g. striped maple and pawpaw) have shown increases in areas with high deer densities, which can further suppress regeneration of canopy species and greatly alter forest structure (Kain et al., 2011; Rossell et al., 2005). Beech regeneration, which is similarly browse-resistant (Webster et al., 2018), also consistently contributed to regeneration mismatch, with beech regeneration frequently abundant in areas where it is only a minor canopy component. Increases in beech regeneration have been documented throughout forests in the eastern US (Bose, Weiskittel, & Wagner, 2017; Kain et al., 2011), although the large spatial extent of beech-dominated regeneration that we identify here has not before been documented. Given beech's vulnerability to beech bark disease, which is predicted to cover most of our study area by 2025 (Morin, Liebhold, Tobin, Gottschalk, & Luzader, 2007), beech-driven regeneration mismatch is a significant concern for these forests.

While our focus was on the influence of multiple co-occurring human stressors on regeneration debt, their impacts on other forest taxa and ecosystem functions, and their spatial configuration, warrant further attention, particularly in transitional areas between major forest types like our study area covered. Better availability of stressor data, such as temporal trends in deer density and invasive plants, should improve macroecological assessments of regeneration debt and stressor impacts to forest systems. More detailed regeneration data, such as size class distributions, would further improve assessments of regeneration debt. While the USFS-FIA program has recently added methods for seedling data by size classes, these data (and deer browse impacts) are currently being collected by the Northern Research Station only, which did not include the five southern states in our study (McWilliams et al., 2015). Determining better thresholds of regeneration abundance required to maintain forest cover in different forest types, or alternative measures (e.g. Vickers et al., 2019), would also be valuable for assessing the severity of regeneration debt and inferring forest adaptive capacity.

Given that stressors like invasive species, exotic pests/pathogens and deer overabundance frequently overlap, and often coincide with areas of high human densities, controlling these stressors requires a more holistic approach that tackles multiple stressors simultaneously. No doubt, this will be challenging, costly and likely beyond the current capacities of state and local government agencies (Bierbaum et al., 2013; Simberloff et al., 2013). However, without intervention, the regeneration debt in the mid-Atlantic region of the US could lead to widespread loss in forest cover that will have cascading effects on forest-dependent taxa and ecosystem services. In addition, the spatial position of the mid-Atlantic regeneration debt has implications far beyond the current geographic extent of our study, given its potential as a migration barrier.

While we only focused on one region of the US, the interacting stressors of ungulate overabundance, invasive species and human land use have been documented worldwide (Bradshaw & Waller, 2016; Coomes, Allen, Forsyth, & Lee, 2003; Côté, Rooney, Tremblay, Dussault, & Waller, 2004; Didion, Kupferschmid, Wolf, & Bugmann, 2011; Motta, 2003). Identifying forested areas that are similarly

impacted in other parts of the world and mitigating those impacts are important conservation priorities, particularly if impacted areas are positioned near species-range edges and/or perpendicular to the direction of expected migration. We encourage managers to consider regeneration debt as an important indicator of forest condition and adaptive capacity.

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AUTHORS' CONTRIBUTIONS

K.M.M. and B.J.M. conceived the study. K.M.M. performed the analyses and drafted the manuscript. B.J.M. framed the manuscript and contributed to revisions. All the authors gave final approval for publication.

DATA ACCESSIBILITY

R code used in this study available via Zenodo <https://doi.org/10.5281/zenodo.2576104> (Miller & McGill, 2019).

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SUPPORTING INFORMATION

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