# The Forest of Unintended Consequences: Anthropogenic Actions Trigger the Rise and Fall of Black Cherry

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*The twentieth century confluence of clear-cutting, deer overabundance, and rising nitrogen deposition favored dominance by the shade-intolerant, unpalatable, and nitrogen-demanding black cherry* (Prunus serotina) *throughout the Allegheny Plateau of the eastern United States. The abundance of this species conferred unique and valuable ecological and economic benefits that shaped regional biodiversity and societies. Sustaining these values is increasingly difficult because black cherry, seemingly inexplicably, has experienced diminished establishment, growth, and survival in the twenty-first century. In the present article, we chronicle the change and assess underlying drivers through a literature review and new analyses. We found negative plant–soil microbial feedback loops and lowered nitrogen deposition are biologically, temporally, and geographically consistent with observed declines. The evidence suggests that black cherry dynamics are the unintended consequence of actions and policies ostensibly unconnected to forests. We suggest that these shifts are a bellwether of impending changes to forests, economies, and ownership patterns regionally and beyond.*

*Keywords: Allegheny hardwoods, conspecific negative density dependence, climate, nitrogen, Clean Air Act.*

**The structure and composition of the eastern** deciduous forests of North America shifted markedly from the postcolonial to the modern era (Thompson et al. 2013, Nowacki and Abrams 2014). Although the drivers of these changes are often intentional and their impacts generally known (e.g., intensive harvests promote early successional species dominance), additional factors that are often unrelated to land management activities can exert unintended and often adverse outcomes on plant communities (for a review, see Tilman and Lehman 2001). For example, ornamental horticulture and international trade inadvertently introduced exotic pests and pathogens that caused collapses in American chestnut (*Castanea dentata*), elm (*Ulmus* spp.), and ash (*Fraxinus* spp.) populations (Gibbs 1978, Anagnostakis 1987, Herms and McCullough 2014). Aside from these notorious cases, there are myriad examples in which anthropogenic actions exert unforeseen effects on plant populations such as acid deposition predisposing sugar maple (*Acer saccharum*) and red spruce (*Picea rubens*) to mortality or reductions in fire frequency constraining oak (*Quercus* spp.) recruitment (Brose et al. 2001, Long et al. 2009, Adams et al. 2012). Collectively, these changes diminish diversity, threaten the provisioning of ecosystem services and, potentially, alter ecosystem functioning.

Throughout the northeastern United States, extensive exploitative clear-cutting radically altered forest composition and structure (Greeley 1925). In the Allegheny Plateau region of the eastern United States (figures 1 and 2), old-growth hemlock–beech–maple forests were cut around the turn of the twentieth century, creating the present-day second-growth stands dominated by early to mid-successional species (Hough and Forbes 1943, Whitney 1990). Turn of the twentieth century harvesting occurred in phases with white pine removed first (ship masts) where it was present, followed by hemlock removal (tanning industry) and ultimately a complete overstory removal (chemical wood cut), with each entry increasing the black cherry proportion (Marquis 1992). Consequently, black cherry (*Prunus serotina*) was among the principal beneficiaries, increasing in relative abundance by an order of magnitude from precolonial levels across the Northeast (Thompson et al. 2013, Nowacki and Abrams 2014) and becoming one of

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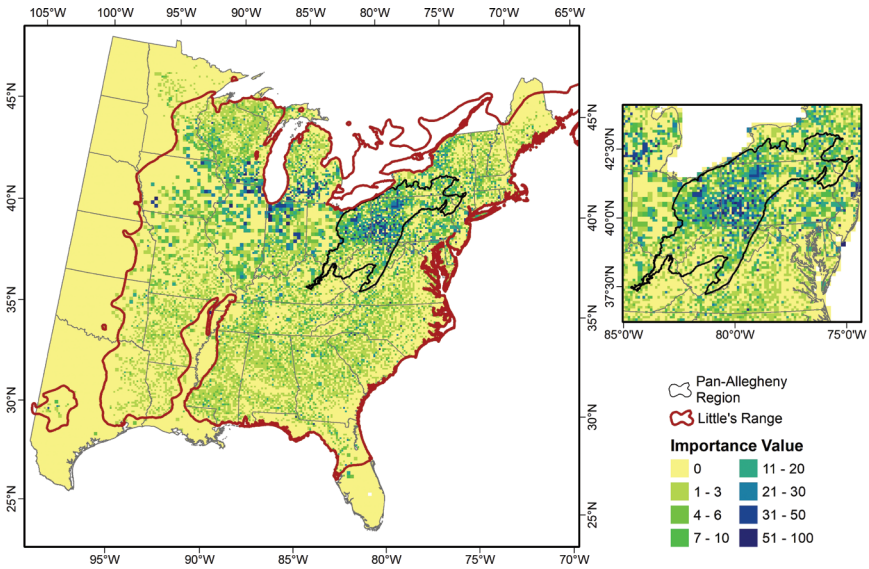


***Figure 1. Map of black cherry (*Prunus serotina*) distribution and abundance (importance value$_{BC}$ = $\frac{50 \times basal\ area_{BC}}{basal\ area_{All\ species}} + \frac{50 \times stem\ density_{BC}}{stem\ density_{all\ species}}$) throughout the eastern United States based on current Forest Inventory and Analysis (FIA) data (www.fs.fed.us/nrs/atlas/tree/762; see also Prasad et al. 2014). Little's range (1971) is outlined in red. The Pan-Allegheny region is outlined in black. For a delineation of the five ecoregions contained within the Pan-Allegheny region, see figure 2.***

the dominant species across the 6.5 million hectares (ha), representing the core of its distribution on the Allegheny Plateau of the eastern United States (figures 1 and 2; Prasad et al. 2014). The regional dominance of black cherry was so pronounced that the Allegheny hardwoods forest type was defined to differentiate it from the broader northern hardwood forest type. Classification as an Allegheny hardwood type requires black cherry, tulip poplar (*Liriodendron tulipifera*), and white ash (*Fraxinus americana)* to jointly represent at least 50% of the total basal area (Eyre 1980); however, in the core of the Allegheny Plateau, inventory data find black cherry alone often represents 31% of the basal area overall, and 52% of the basal area in stands of the Allegheny hardwood forest type (Allegheny National Forest 2019).

The regional success of this shade-intolerant species in the twentieth century is only partly explained by the high-light environment clear-cutting created at the dawn of the century. Competitive dynamics during succession were further inadvertently shaped by two additional anthropogenic drivers in ways that heavily favored black cherry. Namely, game management policies that promoted high white-tailed deer (*Odocoileus virginianus*) densities benefitted black cherry, a low preference browse, over more browse-sensitive species, and anthropogenic increases in nitrogen availability enhanced black cherry survival and more than doubled its relative growth rates (Thomas et al. 2010, Canham and Murphy 2017).

Although Allegheny hardwood forests are the artifact of exploitative clear-cuts, browsing, and nitrogen deposition, the vast and nearly contiguous block of forest cover provides a range of unique, diverse, and valuable ecological and economic services. Forests in the region have low incidence and prevalence of exotic invaders (Iannone et al. 2015) and provide important breeding habitat for forest interior birds (Robertson and Rosenberg 2003). Black cherry produces the most predictable and energy-dense soft mast available to birds and mammals in northeastern forests and its foliage hosts an abundant, distinct, and diverse lepidopteran larvae community (Ryan et al. 2004, Tallamy and Shropshire 2009, Rose et al. 2014). Until recently, black cherry was the highest value timber species regionally, with average prices as much as 78% greater than the second most valuable species (Ray 2018), making these forests among the most profitable forests, on a per-board-foot basis, nationally (USDA Forest Service 2019b). This value forms the backbone of a multimillion dollar forest products industry that, in just a portion of the overall region (26 counties in northwest Pennsylvania and southwest New York: 62,094 square kilometers [km$^2$]), contributes an estimated $34 million to local economies (USDA Forest Service 2016).

Unlike the twentieth century when these ecological services developed reliably, sustaining the values and services of Allegheny hardwood forests is increasingly challenged in the twenty-first century because black cherry, the archetypal species of this forest type, is currently in decline. On the Allegheny Plateau, Forest Inventory and Analysis (FIA) data indicates black cherry mortality rates (the percentage of trees per ha per year; diameter at breast height [dbh] ≥ 12.7 centimeters [cm]) that were, on average, initially lower than that of all other species combined, increased throughout the Pan-Allegheny region by 35% over the past 15 years, with a 73% increase in the northern unglaciated Allegheny Plateau ecoregion specifically (figure 3). In contrast, the mortality rates of all other species remained relatively consistent over that time period (figure 3). Similarly, black cherry tree growth, as measured by basal area increment (in square centimeters per year per tree), has fallen by an average of 29% across all diameter classes, whereas that of all other species has declined only modestly (approximately 6%; supplemental material S1). Therefore, from a relative perspective, black cherry is waning compared with other species.

Black cherry crown health measured in 102 plots of the US Forest Service Forest Health Monitoring Program distributed across the Allegheny National Forest indicate that crown

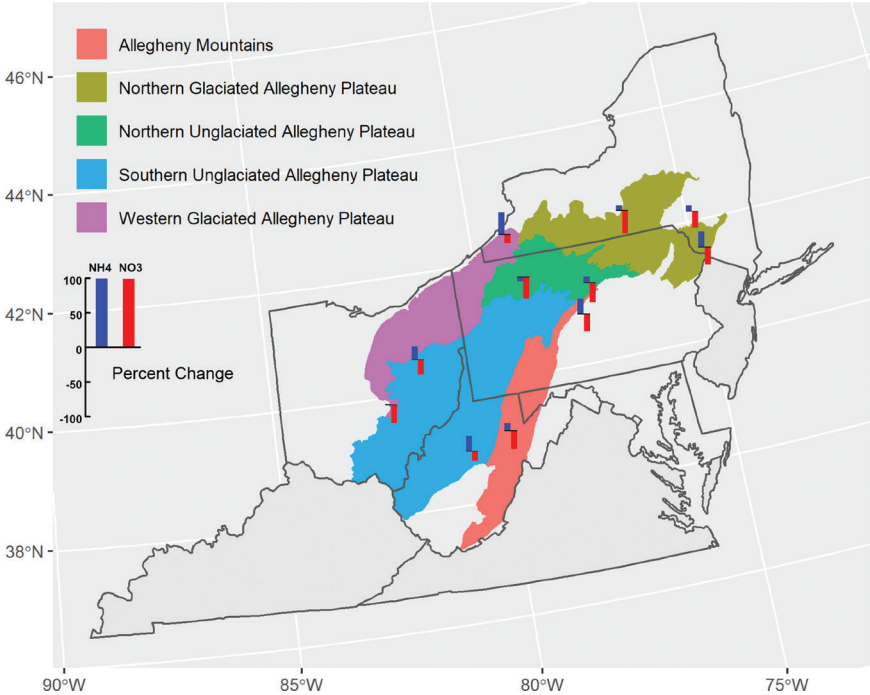


***Figure 2. Map depicting the five ecological sections within the broader Allegheny Plateau (i.e., the Pan-Allegheny region) region that form the commercial core of black cherry (*Prunus serotina*) and the Allegheny hardwood forest type. The bar graphs depict the percentage change in average wet nitrogen deposition (ammonium [$NH_4^+$] and nitrate [$NH_3^-$]) annual rates in the 28-year period preceding (1972–1990) and following (1990–2018) the Clean Air Act Amendments. Source: The deposition data were retrieved from the National Atmospheric Deposition Data/National Trends Network (http://nadp.slh.wisc.edu/NADP). See supplemental material S3 for specific site locations.***

density (the amount of light blocked by leaves and branches) and the live crown ratio have both decreased substantially in recent (2014–2016) surveys compared with earlier (1998–2006) surveys (Long et al. 2017). Historic versus current seed production surveys reveal mast crops have become more erratic and infrequent (Long and Ristau 2020). Reduced seed production has resulted in a concomitant decline in seedling densities. Indeed, FIA records reveal a 60% decline in established seedling densities (height ≥ 30 cm, dbh less than 2.5 cm) across the entire Allegheny Plateau region and near 76% declines in the northern unglaciated Allegheny Plateau since 2000 (figure 4; see also USDA Forest Service 2019a). The declining seedling establishment numbers have caused black cherry to drop in relative abundance from approximately 25% in 2004 to a mere 4% in 2019.

The observed declines in black cherry regeneration cannot simply be attributed to successional dynamics that predict increasingly shade tolerant species dominance over time. Although succession may play a role, three lines of evidence suggest something more pernicious underlies the contemporary declines. First, widespread reports from the twentieth century describe black cherry as "ubiquitous" in the regeneration layer (Collins and Pickett 1982) in undisturbed forests, including the low-light conditions of old growth stands (Maguire and Forman 1983, Collins 1990, Smith and Vankat 1991, Horsley et al. 2003). Second, this recently observed pattern of a sharp decline in black cherry densities in a region overwhelmingly dominated by mid-successional forests (less than 100 years; Pan et al. 2011) is inconsistent with the generally steady and gradual species replacement patterns that occur during succession (e.g., Xi et al. 2019). Third and most remarkably, even when natural or anthropogenic stand replacing disturbances reinitiate succession, the once copious regeneration of this iconic species (e.g., Husch 1954, Fredericksen et al. 1998, Vickers and Fox 2015) is no longer observed (e.g., Krueger et al. 2009, Royo et al. 2016). In fact, in a region in which even-aged silviculture is widely practiced by public and private industrial land managers as a tool to sustain the high-value timber and additional ecosystem services provided by early successional forests, surveys of regenerating stands reveal the magnitude of the change. For example, research from the 1960s and 1980s demonstrated that black cherry was abundant and successfully recruited into the sapling (more than 1.52m) size classes forming a major (more than 31%) fraction of the regenerating tree community (supplemental material S2). In contrast, contemporary studies show that few stems recruit into the larger size classes and form only a miniscule portion (approximately 3%) of the regenerating tree community (supplemental material S2). Overall, the declines in black cherry health and regeneration are so pronounced that regional stakeholders have identified the challenges as a priority threat to the sustainability of the Allegheny hardwood forests in the region, coequal with losses in other tree species resulting from pests and pathogens (Stout et al. 2019).

Initially, managers across the region believed these changes were temporary anomalies. Only over the past ~15 years have all stakeholders fully grasped their scope and extent. Therefore, the science to determine the underlying causal factors is ongoing and definitive answers remain elusive. Below, we outline a set of hypothesized causal mechanisms for the observed black cherry health and regeneration declines and use a combination of synthesis of existing work and new analyses to examine the support for these hypotheses. We focus on five factors known or assumed to influence forest health broadly and black cherry dynamics specifically: climate variability, deer browsing, senescence, negative plant–soil microbe feedback loops (i.e., pathogens), and

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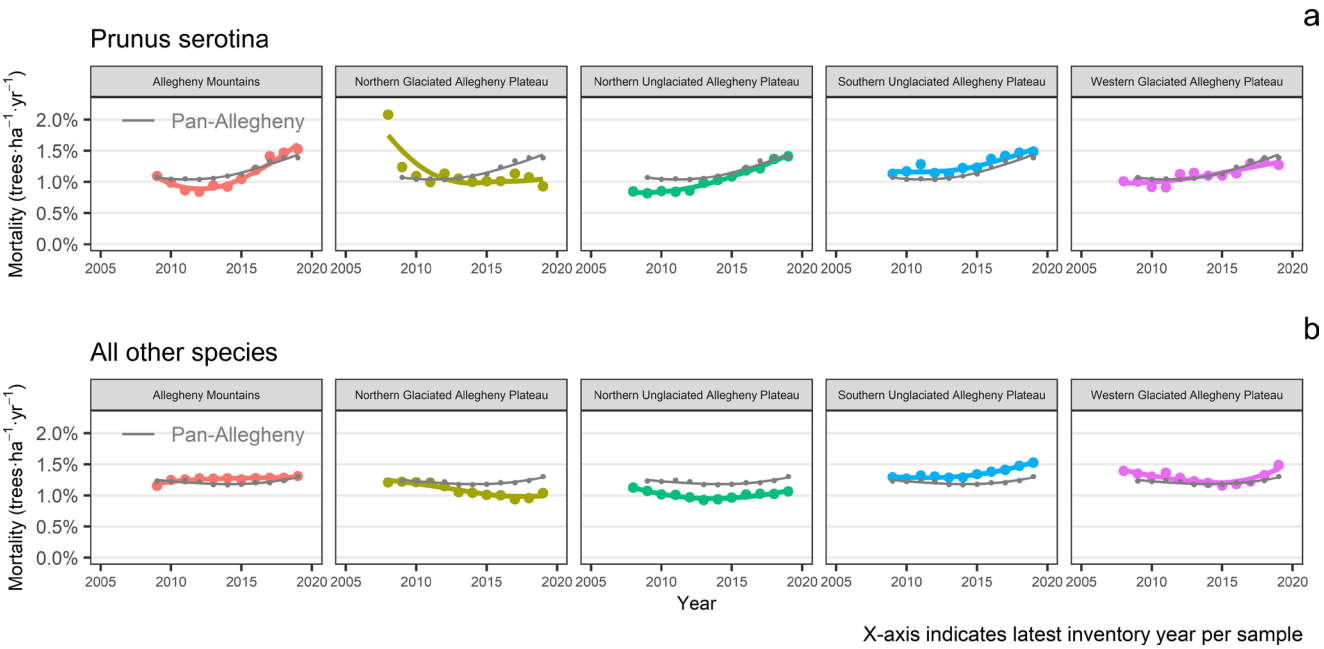


***Figure 3. Annual mortality rates (percentage of trees per hectare per year; dbh ≥ 12.7 cm) for (a) black cherry (*Prunus serotina*; top panels) and (b) all other species (bottom panels) from 2004 to 2019 as calculated from USDA Forest Inventory and Analyses plots (USDA Forest Service 2019a, Stanke et al. 2020). The points represent annualized estimates from FIA inventories, and the solid line represents a nonparametric smoothed trend line. The grey line represents the average response (i.e., Pan-Allegheny) across all five ecological sections within the Allegheny Plateau. The colored lines for the individual sections are identical to those in figure 2. For a complete list of all included species, see supplemental material S5.***

reduced nitrogen availability. Although other punctuated and often spatially heterogeneous components of declines can and do exist (e.g., pest outbreaks, drought), our focus is on factors that are well established, chronic, and geographically widespread.

## Climate

Plant recruitment, growth, and survival rates are generally temperature and precipitation dependent with species distributions matched to and constrained by their climatic envelope or niche (Tilman and Lehman 2001). For many plant taxa, the current pace of climate change may increasingly decouple the optimal environmental conditions from the species' current distribution potentially decreasing tree survival and recruitment and causing notable shifts in species ranges (e.g., Ibáñez et al. 2007, Loarie et al. 2009). Given that tree species ranges are defined by the presence and abundance of mature, long-lived individuals, range shifts may exhibit considerable temporal lags. However, demographic parameters such as tree mortality and seedling recruitment and survival may serve as early barometers of climate-driven changes (Vanderwel et al. 2013). Therefore, one might posit that marked deviations from the long-term (i.e., twentieth century) average climatic conditions and a shifting climate envelope may detrimentally affect black cherry overstory health and seedling recruitment.

Multiple lines of evidence, however, suggest climatic departures from long-term trends are not the primary factor underlying recent changes in black cherry demographic parameters. First, declines in black cherry health and reproduction are strongest within the northern unglaciated Allegheny Plateau, near the geographic core of the species' range, rather than at its range boundaries, where climate-driven impacts may be most detectable (e.g., Hanberry and Hansen 2015). Moreover, the geographic core of the species is only predicted to shift modestly northeastward by about 35–53 kilometers under various climate scenarios (Peters et al. 2019). Notably, vegetation monitoring data from the last 10–28 years do not reveal substantial shifts in black cherry seedling or sapling distributions (Zhu et al. 2012, Woodall et al. 2018). If anything, the data suggest a minor range expansion, particularly at the southern edge (Hanberry and Hansen 2015).

We tested for any such hypothetical climate-driven changes by compiling data from 93 weather stations within the Pan-Allegheny region and a focused look within the 13 stations located within the northern unglaciated Allegheny Plateau (supplemental material S3) with continuous records since 1950 (www.ncdc.noaa.gov). Those data were used to test for deterministic changes in July temperatures and growing season (May–September) precipitation over the 70-year period from 1950 to 2019. We focused on these two

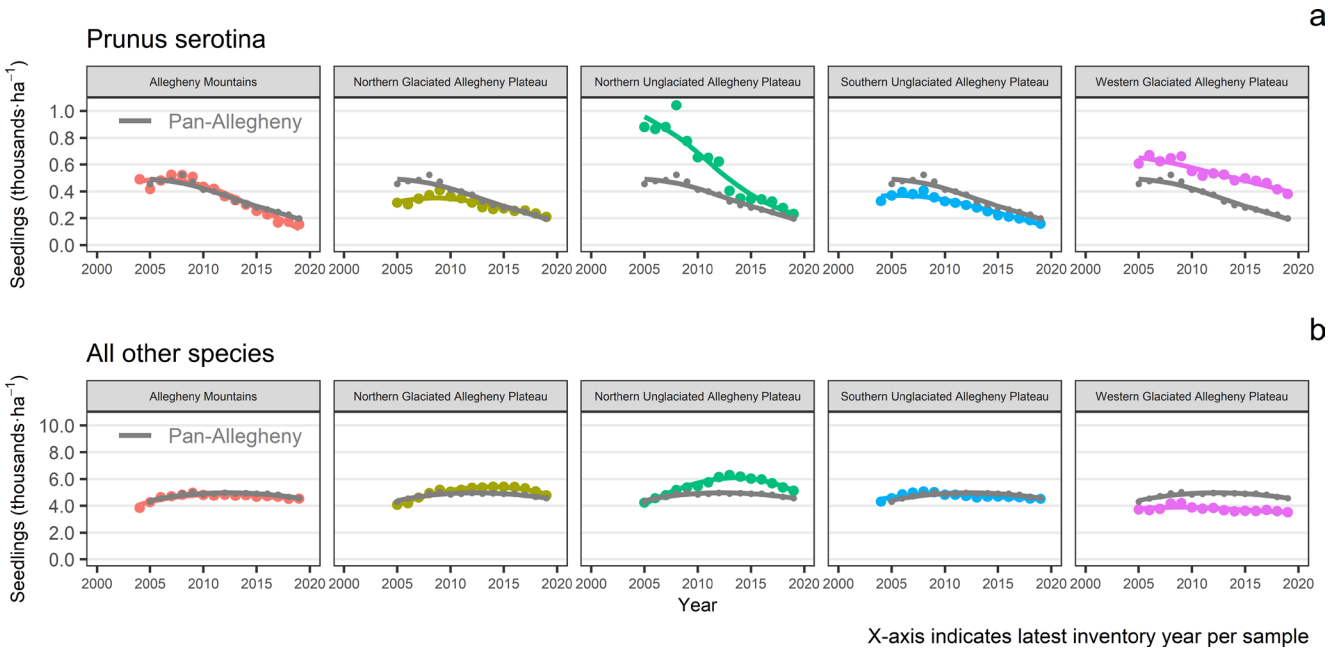


***Figure 4. Seedling densities (height ≥ 30 cm, dbh < 2.5 cm) for (a) black cherry (*Prunus serotina*; top panels) and (b) all other species (bottom panels) from 2004 to 2019 as calculated from USDA Forest Inventory and Analyses plots (USDA Forest Service 2019a, Stanke et al. 2020). The points represent annualized estimates from FIA inventories, and the solid line represents a nonparametric smoothed trend line. The grey line represents the average response (i.e., Pan-Allegheny) across all five ecological sections within the Allegheny Plateau. The color lines for the individual sections are identical to those in figure 2. Note the scale differences between the top and bottom panels. For a complete list of all included species, see supplemental material S5.***

variables as niche-based habitat suitability models find both variables are the predominant climatic factors shaping black cherry habitat suitability (Prasad et al. 2014). In addition, we tested for increases in minimum temperatures during the spring months of March through May, to assess whether warmer, earlier growing seasons may have occurred that might facilitate expansion of pathogens.

We performed a regression analysis on the average July temperature and the year from 1950 to 2019 for the 93 sites in the Pan-Allegheny region but found no evidence for any change in average temperatures over the past 70 years ($r^2$ = .005, $F$ = 0.58, $p$ = .31). However, restricting the same analysis to the 13 stations within the core northern unglaciated Allegheny Plateau range revealed a significant increase in July minimum temperatures over the past 70 years ($r^2$ = .19, $F$ = 16.26, $p$ < .001) of 0.255 degrees Celsius (°C; 0.46° Fahrenheit [F]) per decade, on average (figure 5a). In addition, the average minimum temperature from March through May for the core 13 sites increased significantly over time ($r^2$ = .17, $F$ = 13.9, $p$ < .001) at an average rate of 0.16°C (0.29°F) per decade (figure 5b). The average cumulative precipitation received from May through September increased significantly since 1950 for the entire Pan-Allegheny region ($r^2$ = .11, $F$ = 8.1, $p$ = .006) at an average rate of 1.35 cm (0.53 inches) per decade and in the core northern unglaciated Allegheny Plateau ($r^2$ = .12, $F$ = 9.4, $p$ = .003) the increase was at a slightly higher rate of 1.81 cm (0.71 inches) per decade (figure 5c). Therefore, the climate throughout the Pan-Allegheny region has become progressively warmer and wetter in the past 70 years, especially so in the northern unglaciated Allegheny Plateau. However, given the broad geographical and climatic range occupied by black cherry, it seems unlikely that these slight changes in climate have been the primary driver of observed declines; nevertheless, changing climatic conditions may interact with other factors (e.g., fungal pathogens; see below).

## White-tailed deer browsing

Overbrowsing is often cited as a major contributing factor to tree regeneration failures in forests worldwide (Rooney and Waller 2003, Côté et al. 2004). Given that chronically high deer populations persisted throughout the Allegheny Plateau in the twentieth century (Royo and Stout 2019), it is possible variation in browse pressure may account for observed changes in black cherry regeneration dynamics. Specifically, higher browse pressure may directly limit black cherry establishment and growth through tissue consumption or, alternatively, lower browse pressure may indirectly limit cherry establishment and growth by intensifying interspecific competition (Horsley et al. 2003).

Support for a direct adverse browsing effect on recruitment is weakened by the fact black cherry is often considered

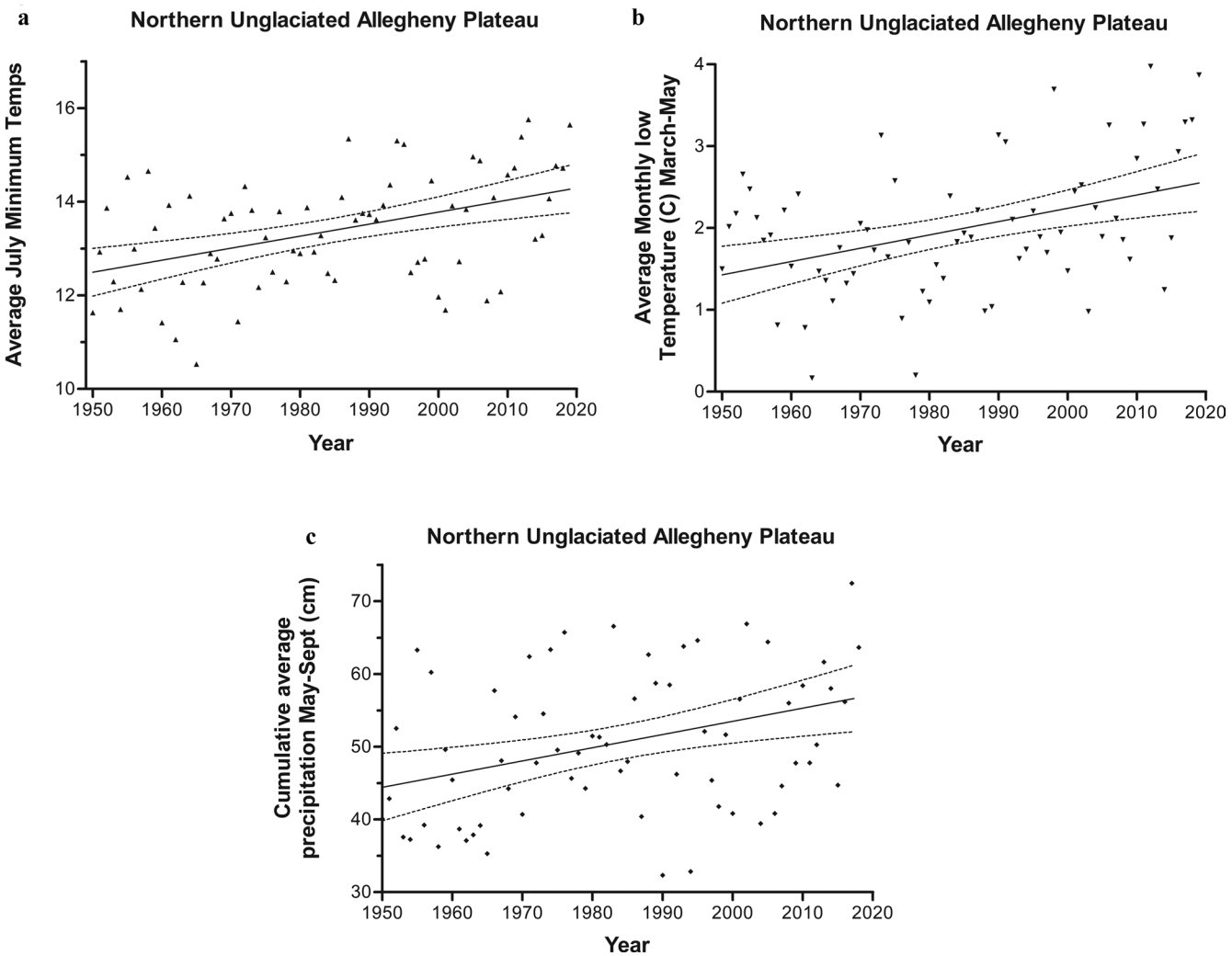


***Figure 5. Seventy year change (1950–2019) in climatic variables on the northern unglaciated Allegheny Plateau show (a) increased average July temperature ($r^2$ = .19, $F_{1,68}$ = 16.26, p < .001), (b) increased March–May average minimum ($r^2$ = .17, $F_{1,68}$ = 13.9, p < .001), and (c) greater average cumulative precipitation from May to September ($r^2$ = .12, $F_{1,67}$ = 9.4, p = .003).***

a low to moderately preferred browse species, relative to most other co-occurring tree species (Healy 1971, Latham et al. 2005). Low foliage, stems and fruit are unpalatable because of the presence of cyanogenic glycosides prunasin and amygdalin, which are toxic (Bischoff and Smith 2011). These palatability differences relative to co-occurring species clarify how black cherry densities can be reduced when browse pressure is high but still increase in relative abundance (e.g., Marquis 1974, Horsley et al. 2003; see also supplemental material S2). More importantly, the argument that browsing severely limits black cherry regeneration in the twenty-first century is unreasonable, given that the deer densities within the core of the Pan-Allegheny region, where seedling numbers have declined the most, have declined by as much as 45% over the past two decades relative to the late twentieth century (Royo and Stout 2019). This suggests that the diminished browse pressure and concomitant increase of browse-sensitive species (Royo et al. 2010) may intensify competition, thereby limiting black cherry establishment and survival. Indeed, a controlled browsing experiment conducted in the 1980s found lower deer densities (3.9–7.8 deer per km$^2$) promoted recruitment of co-occurring hardwood species thereby reducing the absolute and relative abundance of black cherry (Horsley et al. 2003). Nevertheless, even when low deer abundance favored denser and more speciose competitive neighborhoods, black cherry establishment and growth remained high and the species ultimately represented a third of the basal area, firmly establishing these forests as Allegheny hardwoods (see also supplemental material S2).

Contemporary studies at both low and moderately high deer densities (4.46–13.4 deer per km$^2$) have shown a deeply altered dynamic. Cherry seedling banks have declined by as much as 76% within the northern unglaciated Allegheny Plateau (figure 4), and relative growth rates have dropped by as much as 50% (see Gottschalk 1985, Krueger et al. 2009),

thereby diminishing black cherry relative abundance to a mere 3%–14.6% (e.g., Royo et al. 2016; supplemental material S2). Therefore, although deer browsing was a major determinant of tree recruitment success regionally over the past century (Royo and Stout 2019) and might still limit black cherry in portions of the species' range in which white-tailed deer densities remain very high (McWilliams et al. 2018), we suspect other factors are more directly tied to the observed black cherry declines of the twenty-first century in the core of its range.

### Senescence

Evolutionary theory predicts that senescence, a decline in fecundity and increased mortality risk with age, should be a near universal phenomenon (Kirkwood 1977). Although empirical examinations of tree fecundity schedules with age are rare (Harper and White 1974), demographic analyses indicate a majority of trees species (81%) exhibit no to negligible senescence (Silvertown et al. 2001, Baudisch et al. 2013). As was noted above, the vast proportion of trees in the Allegheny hardwood type originated from a short, intense period of exploitative harvesting late in the nineteenth century and early twentieth century. Therefore, trees making up the canopy of these stands now are largely mature. Black cherry is an early successional species that exhibits growth declines and increased mortality beginning at age 80 and an estimated mean lifespan of 100 years, with some individuals achieving upward of 250 years (Hough and Forbes 1943). Therefore, it is reasonable to hypothesize that senescence is responsible for the decreased survival and fecundity.

Analyses of tree mortality using repeatedly measured plots throughout the eastern United States find stand age is not a strong predictor of mortality for hardwood species, including black cherry (Dietze and Moorcroft 2011, Morin et al. 2015). These results are unsurprising because forests throughout the region are relatively young with a majority clustered in the 40–80 year age class and because of the inherent variability in ages of individual trees within stands, particularly in multiple-age stands (Pan et al. 2011). However, even on the Allegheny Plateau, where average stand ages for black cherry are greater, we find little support for the senescence hypothesis. A recent study comparing canopy health and seed production in 70 versus more than 110-year-old forest stands showed that tree health, as assessed by the percentage of standing dead, live crown ratio, dieback, and density metrics, was better in the older stands than in younger stands (Long and Ristau 2020). Moreover, comparisons of seed production in stands measured in the 1970s and remeasured in the 2010s revealed that although the periodicity in bumper crops years became more temporally and spatially idiosyncratic in the twenty-first century, older black cherry dominated stands (more than 110 years old) produced as much or more seed than younger (less than 80 year old) stands (Bjorkbom 1979, Long and Ristau 2020). This follows the results from Martin and Canham (2010) showing that seed production is limited in smaller size classes but nearly constant across size after trees reach 34 cm dbh. Relatedly, Royo and Ristau (2013) extensively surveyed seed banks in 39 stands spanning a 46–106 year stand age gradient. Despite black cherry seed's ability to remain viable for multiple years in the soil (i.e., seed bank), they found viable black cherry in only three of the 39 stands (65, 67, and 91 years old) and even there, only at low abundance (167 seeds per ha). To the degree seed banks correlate with seed production, these findings are in stark contrast to work in the 1970s by Bjorkbom (1979) who found the black cherry seed bank averaged 642 seeds per ha. Overall, the data indicate some factor other than age-related senescence is causing the deterioration.

### Negative plant–soil microbial community feedback loops

An alternative explanation views tree species as active participants changing their environment through chemical, physical, and biological interactions. Mature forest trees shape their associated forest soil microbial communities and, in some cases, amass microbial antagonists that ultimately hinder plant recruitment (Mills and Bever 1998). These negative plant–soil microbial community feedback loops can lead to conspecific negative density or distance dependence (CNDD) and limit tree recruitment in tropical and temperate forests (Hyatt et al. 2003). Therefore, it is reasonable to hypothesize that the high relative abundance of black cherry in the Allegheny hardwood forests may cause high associated microbial antagonist (e.g., pathogenic fungi) densities that limit black cherry establishment, growth, and survival.

Robust support exists for this hypothesis. For example, infection risk on and mortality to black cherry seedlings by the foliar ascomycete pathogen *Blumeriella jaapii* (cherry leaf spot) positively correlates with seedling density in nurseries (Stanosz 1992). More notably, Packer and Clay (2000, 2003) first documented negative plant–soil microbe feedback loops with temperate forests in the black cherry–*Pythium* spp. (root rot) system. This work, along with subsequent corroboration, demonstrates strong negative plant–soil microbial feedback loops on black cherry elsewhere in its native range (e.g., Reinhart et al. 2005). Indeed, assessments of the pervasiveness and strength of CNDD in North American temperate trees find arbuscular mycorrhizal (AM) species, including black cherry, suffer disproportionately from CNDD effects with black cherry exhibiting the strongest or near strongest negative feedback loops of all tested species (55 species, Bennett et al. 2017; 151 species, Johnson et al. 2012). Multiple studies have shown that these plant–soil microbial interactions cause high black cherry seedling mortality close to mature conspecifics, thereby shifting seedling distributions away from mature trees (e.g., Packer and Clay 2003, Martin and Canham 2010).

Over time, these antagonistic microbial effects are hypothesized to intensify as host tree populations mature

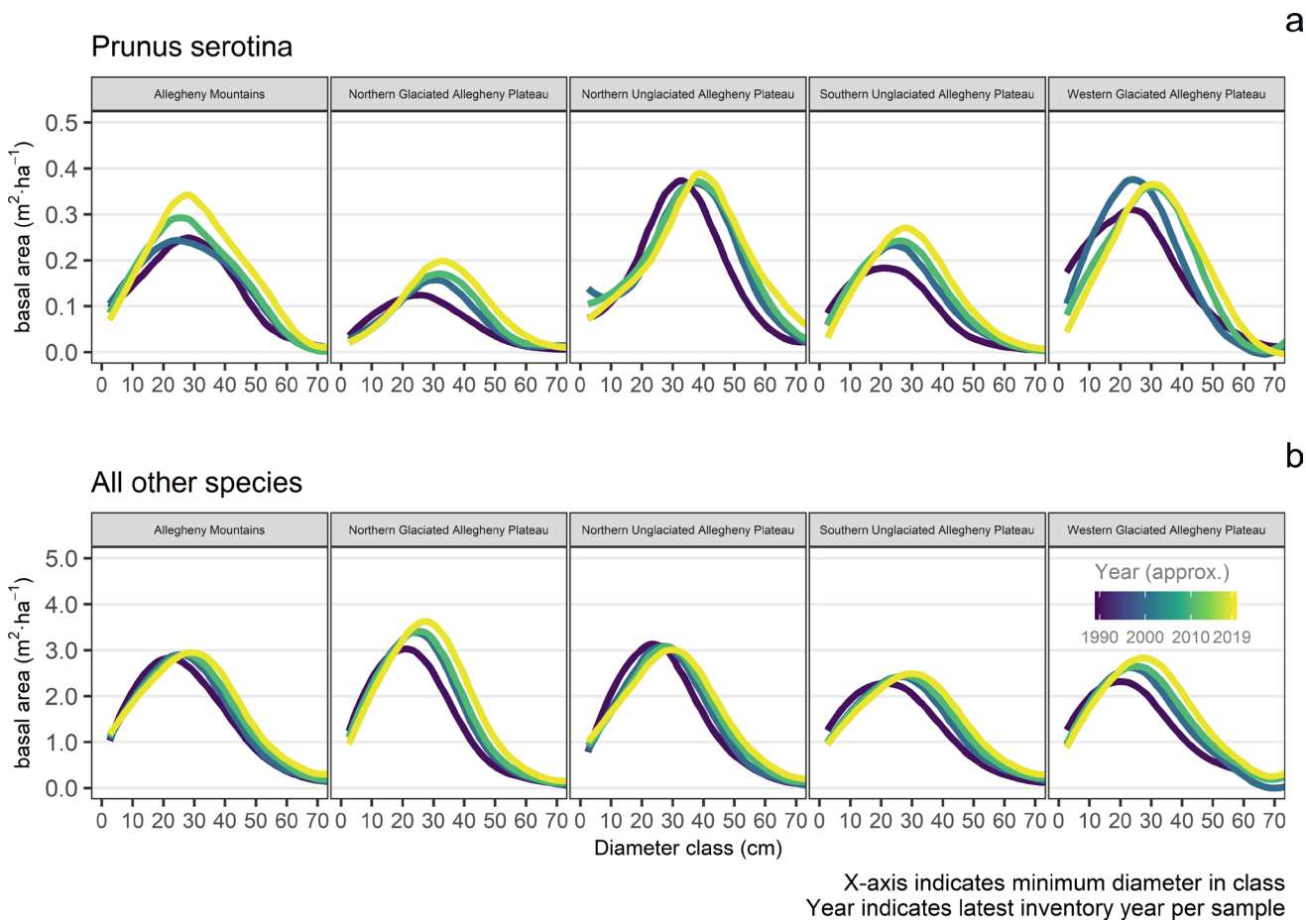


***Figure 6. Basal area (in square meters per hectare) diameter distributions for (a) black cherry (*Prunus serotina*; top panels) and (b) all other species (bottom panels) in each of the five ecoregions contained within the Pan-Allegheny region in four time periods spanning 1990–2019 as calculated from USDA Forest Inventory and Analyses plots (USDA Forest Service 2019a, Stanke et al. 2020).***

and their root systems expand, thereby extending the zone of potential pathogen influence (Packer and Clay 2004). An examination of the overstory tree community from 1990 to the present shows that the black cherry population structure of individuals at least 2.54 cm throughout the Pan-Allegheny region is shifting toward fewer but decidedly larger trees. Regionally, declines in tree density are primarily driven by losses in smaller diameter stems with a concomitant increase of 34% in the quadratic mean diameter and a 26% increase in basal area (supplemental material S4, figure 6). Among the five ecoregions, the northern unglaciated Allegheny Plateau has the highest basal area of black cherry (3.0 square meters [$m^2$] per ha in 2019), but it experienced the steepest (76%) decline in seedling densities over time (figures 4 and 6). In contrast, black cherry basal area in the northern glaciated Allegheny Plateau ecoregion is the lowest of all five ecoregions (1.4 $m^2$ per ha in 2019) and, in the present study, cherry seedling densities have remained consistently low over time (figure 4). Although further examination of the variation in pathogen loads and their effects across a host tree density gradient would help support or refute the negative plant–soil microbial feedback hypothesis, the accruing mature tree versus declining seedling population dynamics documented in the present article are consistent with Packer and Clay's (2004) prediction that antagonistic microbial effects may intensify as host trees grow larger.

## Altered nitrogen deposition patterns

The temperate forests of North America, long considered N limited, experienced marked increases in nitrogen availability through atmospheric deposition in the post-industrial era (Aber et al. 1989). This increased nitrogen availability was accompanied by positive growth and recruitment of several tree species and particularly benefited AM associates, such as black cherry, at the expense of ectomycorrhizal species (Averill et al. 2018). In fact, among the common species of the eastern deciduous forests, black cherry saplings and mature trees exhibit a strong monotonic growth increase in response to nitrogen deposition second only to *L. tulipifera* (see also Thomas et al. 2010, Canham and Murphy 2017).

Biologically, this positive response is expected because N, particularly as nitrate, is fundamental for black cherry germination and growth (Auchmoody 1979, 1982). This suggests the high nitrate deposition rates in the twentieth century benefited black cherry relative to other species.

In the three decades following the 1990 Clean Air Act Amendments (CAAA), nitrogen and sulfur deposition rates declined precipitously and particularly so throughout the northeastern United States, where total nitrogen (predominantly nitrate) and total sulfur deposition rates dropped by an estimated −1.4% and −1.7%, respectively, per year, with the majority of the drop in nitrogen occurring after 1990 (Nopmongcol et al. 2019). Within the Pan-Allegheny region, nitrate deposition declined 47% on average (range = 25%–64%) when comparing 18-year period before 1990 with the 18 years after 1990 (figure 2). In contrast, ammonium has increased an average of 25% (range 12% decline to 62% increase) during the same interval (figure 2). These deposition reductions are particularly pronounced on the Allegheny Plateau because this region experienced among the highest nitrate deposition rates in the east with deposition rates in the late 1970s through the 1980s averaging 22 kilograms (kg) of nitrogen per ha per year and dropping to 4.5 kg of nitrogen per ha per year by 2018 (National Atmospheric Deposition Program 2019). Concurrent with these falling deposition rates, regional FIA surveys reveal that black cherry radial growth (stems ≥ 12.7 cm dbh) has declined at least since 2000, whereas growth rates of all other species remained stable (supplemental material S1). To better understand whether shifting atmospheric deposition rates underlie the waning growth rates more rigorous study, ideally with long-term, high resolution, individual tree growth records, needs to be conducted.

The varying nitrogen deposition patterns over the past century also triggered other changes in soils that affect black cherry health. For example, long-term research in cherry-dominated stands in the Allegheny mountain section of the Allegheny Region found chronic nitrogen fertilization reduced base cation availability and was associated with premature leaf fall in black cherry and declines in canopy area index (Gilliam et al. 2019, May et al. 2005). These results contradict findings from the northern unglaciated Allegheny Plateau ecoregion, where atmospheric nitrogen deposition similarly diminished calcium and magnesium in the late-twentieth century (Bailey et al. 2005), a period that preceded any observable declines in black cherry. Nevertheless, we cannot rule out cation driven effects as changes in soils and plant communities are predicted to lag behind the changing nitrogen inputs (i.e., hysteresis *sensu* Gilliam et al. 2019; see also Long et al. 2011). Similar hysteretic outcomes may arise as nitrogen deposition reductions and shifting nitrate to ammonium ratios slowly alter forest microbial and tree communities toward ectomycorrhizal associates and ammonium preferring species at the expense of AM associates and nitrate demanding species (e.g., black cherry) that grow increasingly disadvantaged (Gilliam et al. 2019, Lilleskov et al. 2018).

In summary, the highly dynamic nitrogen deposition history may have had the further unintended consequence of reversing the prior and proximate fertilization effects that benefitted black cherry throughout the twentieth century. We hypothesize that the current reductions in nitrogen (particularly as nitrate) deposition, potentially coupled with associated soil chemical and microbial legacies, may underlie observed reductions in black cherry canopy health, seedling growth and survival. The potential effects of reductions in and changing composition of atmospheric deposition (Li et al. 2016) to forest dynamics and function is only recently being recognized (Groffman et al. 2018, Schmitz et al. 2019). The impacts may accrue over the long-term, exhibit lags, and be difficult to distinguish from co-occurring effects (Gilliam et al. 2019).

### Interacting ecosystem drivers

Among all the hypotheses explored, declining nitrogen and negative density dependence are both consistent with and spatially and temporally coincident with the declines in black cherry over the past quarter century. However, it is important to note these two hypotheses are not necessarily mutually exclusive and may act additively or synergistically. For example, as was noted above, negative plant–soil microbial feedback loops on black cherry from *Pythium* spp. may intensify as host trees grow larger, but the observed recruitment failures in the Pan-Allegheny region are a phenomenon only widely reported by land managers beginning this century. If pathogens are a causal factor, then a separate predisposing factor may explain the sudden and marked increase in disease incidence and severity. Nutrient dynamics are known to alter plant disease tolerance or risk both directly and indirectly through their effects on seedling growth, biomass, or mycorrhizal associations (for a review, see Walters and Bingham 2007). Stanosz and Auchmoody (1989), for example, concluded leaf spot (*Blumeriella jaapii*) infection severity to black cherry seedlings was greatly intensified near the soil surface (at least 50% leaf area chlorotic or necrotic: 55.8% versus 2.5% of leaves sampled in the less than 30 cm stratum versus the more than 30 cm stratum, respectively). Therefore, the reduced seedling growth rates noted in recent years, potentially because of decreasing nitrate availability, may prevent individuals from quickly attaining a size beyond which disease risk declines. Reduced deposition of other nutrients may also play a role in mediating disease risk. For example, sulfur and sulfur containing compounds are long-established fungicidal agents (e.g., copper sulfate was marketed as the first oomycete fungicide in 1885; Russell 2005). Therefore, it is possible that post-CAAA declines in sulfate deposition may increase disease risk in forest communities in the same manner as reductions in sulfur deposition across Europe have been linked to rising disease incidence and severity in crops (e.g., Walters and Bingham 2007). Relatedly, the increasingly warmer

and wetter climate of the northern unglaciated Allegheny Plateau may increase pathogenicity by modifying environments favoring infection (Pugnaire et al. 2019). Although the manner, prevalence, and magnitude of co-occurring and potentially interacting factors remain unknown overall, we suggest that it deserves more attention and should be the focus of future studies.

## Economic and cultural importance of black cherry

Black cherry declines may be a bellwether of coming changes to local economies and forest ownership patterns. As a dominant species in the region's forests, black cherry has had economic and social importance as well. Kane, Pennsylvania, in the United States, has called itself the "Black Cherry Capital of the World" for decades, suggesting a high level of cultural identification with the species. This community is nearly surrounded by the Allegheny National Forest and home to the sawmill associated with Collins–Kane Hardwoods, the largest private landowner in the state. Federal and state-level agencies recognized this economic and cultural importance and increased research budgets beginning in the 1960s to develop appropriate silvicultural and management strategies to sustain the Allegheny hardwood forest type (Stout and Brose 2014). The research pointed to variants of even-age silviculture sometimes including expensive investments in managing competing vegetation or fencing to exclude deer. Over time, this research was synthesized into a systematic approach to conducting vegetation inventories, summarizing the data, and proposing science-based silvicultural treatments. This approach has grown into a series of training sessions and a decision support system that is taken and used by thousands of forest managers across the Pan-Allegheny region.

By the 1980s and 1990s, demand for high-quality timber and veneer products from trees from this region rose. European and Asian import demand was high, as was domestic demand. Stumpage prices for black cherry were sometimes an order of magnitude higher than those for other hardwood species (Jacobson 2005), and the return to both public and private landowners shaped forest practices. Jim Grace, Pennsylvania State Forester from 1993 to 2007, described the impact of cherry prices and the overall high demand for high quality hardwood products on management of state forests as follows: "From 1995 to 2007 (when the recession occurred) stumpage prices of many of the prominent hardwood species (hard and soft maple, red and white oak, ash) were up by 100% to 150%. During the same period black cherry prices rose by an unprecedented 500 to 1000%. Even though harvest levels remained constant, annual timber sales revenue for the entire state forest system rose from $20 million to $40 million annually. In many cases black cherry accounted for more than 50% of the revenue even though it occurred on less than one third of the state forest.

"In 1995, legislation was passed which set aside 10% of the revenue from timber sales to be dedicated for forest regeneration practices. The additional timber sale revenues allowed the Pennsylvania Bureau of Forestry to add additional staff, infrastructure, and equipment and to fully incorporate ecosystem management. An average of over $3 million a year was spent on deer fencing, removal of competing vegetation, and some supplemental planting to ensure adequate regeneration following harvest. These practices were carried out on all the state forest timber sales, not just those areas with black cherry and their benefits in terms of stocking and diversity of emerging forest growth in harvested stands were significant" (Jim Grace, Pennsylvania Bureau of Forestry, Camp Hill, Pennsylvania, United States, Personal communication, 10 February 2020). Similarly, on the Allegheny National Forest, the high stumpage prices allowed ample reinvestments for infrastructure and forest regeneration activities (Andrea Hille, Ecosystems Staff Officer, Allegheny National Forest, Warren, Pennsylvania, United States, personal communication, 6 March 2020).

It may be because of the economic opportunities associated with black cherry that the mean ownership tract size in this region of the state is substantially higher than that in parts of the state dominated by other species (James C. Finley, Pennsylvania State University, State College, Pennsylvania, United States, personal communication, 6 March 2020), creating the kind of continuous forest cover that creates important wildlife habitat and forest recreation settings. Stumpage prices don't correlate with the ecology of a forest's species, of course, and cherry prices have recently been slower than those of some other species to recover from the 2007 recession in part because international demand is low (Luppold et al. 2014). Therefore, landowners may not be able to afford practices that might stabilize black cherry as a continuing element of regional forests if such practices can be identified by research.

## Research and management considerations

Given black cherry responds strongly to fluctuating nitrogen dynamics and negative plant–soil feedback loops, it is possible observed regional changes to black cherry may signal looming changes to population dynamics of other tree species and overall species composition across the eastern deciduous forests. The hypothesized roles of nutrient availability and pathogen dynamics deserve further investigation in black cherry and other species. In fact, research that includes species with varying sensitivities to these specific abiotic and biotic factors (e.g., Bennett et al. 2017, Canham and Murphy 2017) offers a priori testable predictions that may shed light on the relative importance of factors altering forest dynamics and composition. For instance, if nitrogen and pathogens co-limit recruitment, growth, or survival, then manipulations that increase nitrogen availability and lower pathogen loads (e.g., selective fungicide applications) should benefit species such as black cherry that are colimited by nitrogen and negative feedback loops (e.g., *L. tulipifera*, *Sassafras albidum*). In contrast, these manipulations should adversely affect species that respond negatively to higher nitrogen with the magnitude of the effect dependent

on whether the species experiences negative feedback loops (e.g., *Thuja occidentalis*, *Robinia pseudoacacia*) or not (e.g., *Fagus grandifolia*, *Populus tremuloides*). Relatedly, forest health resurveys may offer insight into these dynamics. For example, yellow poplar (*L. tulipifera*) observed 5-year mortality rates are among the highest of all tracked species (6.83%) and its mortality rate, along with that of black cherry (8.07), is predicted to continue to increase on the basis of currently poor crown conditions (Morin et al. 2015).

Understanding the drivers that led to the rise and subsequent fall of black cherry as a dominant species in the core of its native range may also help inform black cherry management in Europe, where it is a widespread invasive species (Starfinger et al. 2003). As in the native range, increased forest harvesting and ungulate herbivory hastened black cherry proliferation (Vanhellemont et al. 2010), particularly during the latter half of the twentieth century when nitrate deposition levels were high across Europe (Engardt et al. 2017). As the species becomes increasingly naturalized and stands mature, it remains an open question whether the currently weak microbial negative feedback loops on the species that exist in Europe will intensify (Reinhart et al. 2010) and whether the declining nitrogen deposition will lessen its rate of spread and continued dominance.

The declines in black cherry health and regeneration identified are no longer thought to be temporary anomalies. Instead, they may signal coming changes to ecological dynamics and economies across the Alleghenies and beyond. Although a definitive understanding of the drivers of these unintended changes remains elusive, our review of the existing evidence suggests that altered nitrogen deposition dynamics and strengthened negative soil microbial feedback loops (CNDD), particularly given a warmer and wetter climate, represent promising avenues for future research. In contrast, although many other factors including succession, senescence and deer browsing may have an influence in localized instances, we do not suspect these factors underly the regional decline. Continued efforts at multiple scales may reveal additional unintended consequences on forest communities and further challenge the capacity and appetite of managers to grapple with them.

Our work is focused on changes in an iconic species in the heart of its range. The historic importance of black cherry led to a community of practice that engaged scientists and managers (Stout and Brose 2014, Hanson et al. 2020). Because of the collaborative work of this community, we had detailed historic data to confirm that change is occurring and inform early efforts to understand its causes. Our observations, however, are not important because of this individual species but rather because the story of change in mixed species forests in the coming century is likely to reflect the response of many individual tree species to changing environmental conditions, biotic stressors, and their interactions. We offer this narrative of changes in black cherry and the forests of the Allegheny Plateau as an early chapter of that story.

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## Supplemental material

Supplemental data are available at *BIOSCI* online.

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