nature sustainability

Article

https://doi.org/10.1038/s41893-023-01203-8

Sensitive tree species remain at risk despite improved air quality benefits to US forests

Received: 3 February 2023

Accepted: 19 July 2023

Published online: 21 August 2023

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Justin G. Coughlin [1] ✉, Christopher M. Clark [2] ✉, Linda H. Pardo [3], Robert D. Sabo [2] & Jeremy D. Ash [4]

Atmospheric nitrogen (N) and sulfur (S) deposition can significantly affect forest biodiversity and production by altering the growth and survival of trees. Three decades of air quality regulations in the United States have led to large reductions in oxides of N (44–81%) and S (50–99%) emissions and associated deposition. Here we evaluated the magnitude and extent of effects over 20 years from atmospheric N and S deposition on the growth and survival of 94 tree species—representing 96.4 billion trees and an average of 88% of forest basal area across the contiguous United States (CONUS). Overall, species' growth and survival rates have responded positively to declining deposition, but we find that decreases of at least 2.5 kg ha^{-1} yr^{-1} N are needed across 19.8% (growth) and 59.5% (survival) of the CONUS to prevent detrimental effects to sensitive species. Reduced forms of N ($NH_x = NH_3 + NH_4^+$) are now the dominant form of N deposition in 45.4% of the CONUS—notably in agricultural regions—and exclusively need to be reduced by ≥5.0 kg ha^{-1} yr^{-1} N in some areas. Further S deposition decreases of ≥1.0 kg ha^{-1} yr^{-1} S are needed in 50.4% (growth) and 56.2% (survival) of the CONUS to protect sensitive species and, notably, evergreen trees. Total basal area is increasing in much of the country (85.2%) because of N fertilizing effects, but these growth increases could result in biodiversity loss. Our findings can be used to evaluate past successes of air quality policies and the future benefits of air pollution reductions to terrestrial ecosystems.

Atmospheric nitrogen (N) and sulfur (S) deposition can be important drivers for terrestrial carbon cycling and plant biodiversity within forests[1,2]. In the United States, deposition levels have been declining due to air quality regulations in the Clean Air Act Amendments of 1990 and associated rules[3–6]. While deposition has decreased, emissions are expected to continue causing detrimental impacts on terrestrial ecosystems[7]. Deposition of oxidized N forms (for example, NO_3^-) has declined due to regulations, but reduced forms of N deposition ($NH_x = NH_4^+ + NH_3$)—which are not directly regulated and have historically been tied to agricultural activity—have begun to increase in some parts of the United States[8,9]. Since 1990, S deposition has declined by 1.0–1.7% annually due to sulfur dioxide emissions reductions[6,10]. Ecosystem impacts from atmospheric N and S deposition can be examined using measures of ecosystem health such as the growth and survival of tree species[11–15]. Nitrogen deposition influences these health indicators, overall biodiversity and terrestrial carbon sinks by contributing to soil acidification, limiting or stimulating nutrient uptake and increasing the growth of opportunistic species[16–21]. While N deposition often enhances growth[22], excessive N in soils can also contribute to tree mortality[23,24]. Atmospheric S deposition negatively impacts ecosystems by increasing soil aluminium mobility and cation leaching, which leads to soil acidification and can ultimately cause increased tree mortality and reduced growth[4,25–27].

[1]Air and Radiation Division, US Environmental Protection Agency Region 5, Chicago, IL, USA. [2]Office of Research and Development, US Environmental Protection Agency, Washington, DC, USA. [3]Northern Research Station, USDA Forest Service, Burlington, VT, USA. [4]Southern Region, USDA Forest Service, Asheville, NC, USA. ✉e-mail: jcoughlin@sonomatech.com; clark.christopher@epa.gov

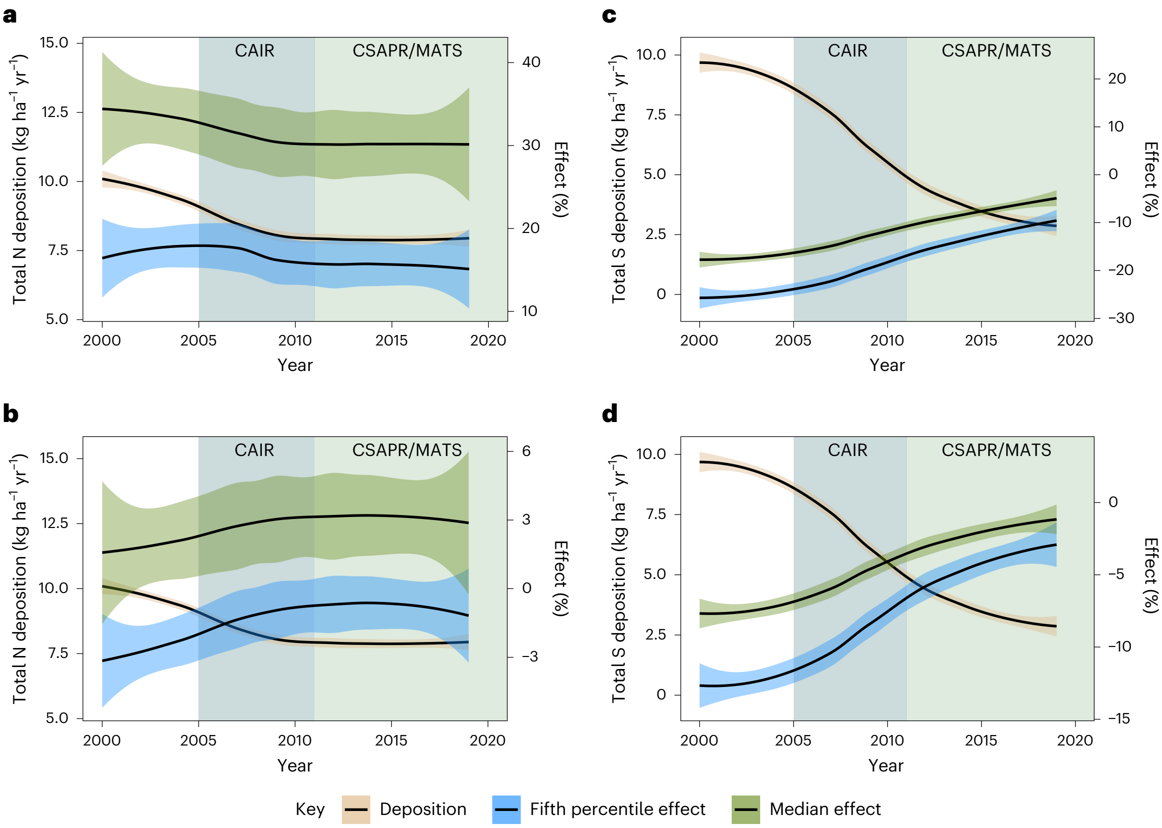

Fig. 1 | Annual trends of average N and S deposition and the fifth percentile effects on species' growth rates and survival probability. a,**b**, Average N deposition experienced by species and its effects on growth (**a**) and survival (**b**). The left axis is deposition (kg ha^{-1} yr^{-1}), and the right axis is effect (percentage increase or decrease) on growth or survival rate. **c**,**d**, Average S deposition experienced by species and its effects on growth (**c**) and survival (**d**). Deposition is first averaged across all FIA plots, by species, then loess-smoothed across species' averages. Effects (growth or survival rates) are the loess-smoothed medians or the g(N,Q5), s(N,Q5), g(S,Q5) or s(S,Q5) effects for all species. Interspecific medians and fifth percentiles were calculated using all FIA plots across the CONUS for each corresponding year. Standard deviations around each loess-smoothed line are shown in the respective shaded areas. In addition, the time frames when the Clean Air Interstate Rule (CAIR) (dark green shading), Cross-State Air Pollution Rule (CSAPR) (light green shading) and Mercury and Air Toxics Standard (MATS) regulations were applicable are shown in the shaded areas. The CAIR was replaced by the CSAPR in 2011.

Critical loads are estimates of pollutant exposure defined as the point below which significant harmful effects are unlikely to occur[14,28–31]. In the past decade, there have been considerable advances in the development of critical loads for terrestrial ecosystem components[12,21,32–36]. Notably, researchers generated dose–response curves for 71 tree species across the contiguous United States (CONUS) relating N and S deposition impacts to aboveground growth rates and decadal survival probability[12]. These relationships relied on Forest Inventory and Analysis (FIA) data[12]—a measurement dataset compiled from a nationally standardized plot system[37]. This research updated previous critical loads for tree species that focused solely on growth or were reflective of large geographic regions[13,21,38,39]. Traditionally, critical load evaluations have been expressed in terms of exceedances (deposition minus the critical load). The use of dose–response relationships has added benefits because magnitudes of effect provide more accurate reflections of impacts to ecosystem services[40].

In this Article, we present a combination of national plot-level (point-based approach) and spatially continuous[41,42] (gridded approach) evaluations of 94 different tree species' responses to atmospheric N and S deposition for the current forest structure and composition. We included 23 more species than the initial analysis[12] to better represent total forest basal area. Effects on trees were assessed using growth- and survival-rate responses from 2000 to 2019, a period over which notable shifts in N and S emissions and deposition occurred. Assessments were aggregated across species (interspecific), within a species' national population (species-level), at geographic locations (plot-level), across phenotypes (for example, deciduous) and by ecosystem services (for example, wood products). We first evaluated the fifth percentile of growth- and survival-rate effects to examine how more sensitive species have responded to changes in atmospheric pollution. Individual species' responses can be positive, neutral (flat) or negative, so the fifth percentile within an FIA plot, or grid cell, can also be positive, neutral or negative. We use this metric because it represents the level of effect occurring to at least 5% of species or trees (sensitive species or trees). The effect could also be worse for some species or trees. Second, we determined the level of deposition that would protect 95% of evaluated trees, or species, across the CONUS and the decreases in deposition that are needed to achieve that level of protection; this approach is similar to the concept of critical loads. Last, we calculated the net change in basal area that is currently occurring across forests to identify the worst impacted areas from a national forest-level perspective.

Sensitive species' response to air pollution over two decades

From 2000 and 2019, we evaluated the effect of N and S deposition at FIA plots by holding all other environmental conditions constant and by using each species' dose–response curve. When averaging across species (interspecific), N deposition had a positive effect on growth, but increases in growth rates became less positive as N deposition declined over the past two decades (Fig. 1a). For example, when the fifth percentile effect within a species (species-level) was averaged, growth rates fell by 1.6% between the 2000–2009 (17.3%) and 2010–2019 (15.6%) periods, an average of 0.1% less growth annually. From 2000 to 2019, N deposition had a positive effect on survival when averaging medians (2.7%) across species (interspecific median), but there was a negative effect (−1.4%) when fifth percentile effects were averaged. Sulfur deposition had a negative effect on growth and survival at the interspecific median and interspecific fifth percentile, with negative effects that lessened (got less negative) as S deposition decreased. It should be noted that S deposition dose–response curves were constrained to always be negative, so decreases are expected, and some species had very low S critical loads[12]. Recent machine-learning estimates found similarly low S deposition critical loads[43]. Regardless, growth and survival rates (interspecific averaged fifth percentile) have increased by 0.9% and 0.6% annually since 2000, respectively, due to reductions in S deposition.

For brevity, we denote the fifth percentile (Q5) effect on growth and survival rates for N deposition across data as g(N,Q5) and s(N,Q5), respectively (nomenclature for S: g(S,Q5) and s(S,Q5)). We indicate whether statistics are across species (interspecific), within species (species-level) or geographic (plot-level) for clarity. As an example, the interspecific s(N,Q5) reflects the fifth percentile effect on survival rates across species, the species-level s(N,Q5) represents the fifth percentile effect within species, and the plot-level s(N,Q5) represents the fifth percentile effect at a given location. An example of these different aggregations is shown in Supplementary Fig. 3. Interspecific N-growth effects (Fig. 1a) initially increase and then stabilize between 2003–2008 where the loess-smoothed g(N,Q5) effect peaks at +19.6% for growth rates in 2006 then slowly decreases afterwards (+15.3% in 2019). The positive growth rate experienced across species reflects the fertilizing effect that moderate levels of atmospheric N deposition can have on tree species, even sensitive ones. As of 2019 however, ten species had g(N,Q5) effects decreases of >2%, demonstrating that sensitive trees were still experiencing reduced growth. The interspecific N-survival effect was negative and between −3.0 and −0.2%, on average, throughout the period of record with average loess-smoothed s(N,Q5) effects of −1.4% (Fig. 1b). For S-influenced growth effects, the loess-smoothed interspecific g(S,Q5) effect went from −26.2% to −9.7% between 2000 and 2019 (Fig. 1c), coinciding with considerable decreases in S deposition. Like N effects, interspecific S-influenced survival effects were slightly less drastic than growth-rate responses but also experienced an increasing trend (Fig. 1d). Between 2000 and 2019, the average interspecific s(S,Q5) effect went from −13.0% to −2.9%. It is worth noting that growth and survival decreases should not be considered equally adverse because small changes in the rate of survival can have large implications across a forest population.

We next compared species-level fifth percentile effects in 2000 and 2019. Since species vary widely in their distribution and their vulnerability to atmospheric deposition[12], species-level effects may be considerably different from national effects. We found sensitive trees for some species (for example, *Celtis occidentalis*, *Populus tremuloides*) experienced large increases (>35%) in growth between 2000 and 2019 (Fig. 2a), meaning these species experience less harm than they did 20 years ago. Conversely, growth rates were reduced by ≥1% for 39 species since 2000 (Fig. 2a). Both of these trends are due to N deposition decreases across the CONUS. In 2019, 18% of species (11) still had g(N,Q5) effects below 0%, although 10 of these species benefited from N deposition decreases (Fig. 2a). In addition, evergreen trees' growth rates tended to respond more negatively to N deposition than did those of deciduous trees (Extended Data Fig. 1); a Kolmogorov–Smirnov (K–S) test on effects within the 95% confidence interval demonstrates that impacts across phenotypes are significantly different ($P < 0.001$) in both 2000 and 2019 (Extended Data Fig. 1). Furthermore, species used for wood products[44] (building materials and unfinished products) have higher growth rates from N deposition in 2019 than non-wood product species (Extended Data Fig. 2). For survival, s(N,Q5) effect shifts between 2000 and 2019 were minimal for most species but generally positive (average of +0.6%) (Fig. 2b). Although many positive trends were observed across this time frame, 33 species still experienced negative s(N,Q5) effects (<0%) in 2019. Deciduous trees experienced slightly more negative survival-rate effects than evergreen trees in both 2000 and 2019 (Extended Data Fig. 1). There was little difference among wood product categories for N-influenced survival rates (Extended Data Fig. 2).

Due to decreasing S deposition since 2000, species-level effects trended positively (environmental conditions became more favourable), but nearly all species still had detrimental growth impacts in 2019. The 20-year species-level increases in g(S,Q5) and s(S,Q5) effects were as high as +46.9% and +32.6%, respectively (Fig. 2c,d). Eight species had g(S,Q5) increases greater than 25%, and there was an overall average increase of 16.5%. Although trends were positive, 98% of species (45) still had negative g(S,Q5) effects in 2019, demonstrating further needs to reduce S deposition (Fig. 2c). In 2000, deciduous and evergreen trees experienced similar growth-rate reductions from S deposition, while larger disparities were apparent in 2019, with evergreen trees being more detrimentally impacted; however, 2000 and 2019 K–S tests were significantly different (Extended Data Fig. 1). In 2019, species used for both building materials and unfinished products[44] tended to experience higher amounts of reduced growth from S deposition than did other ecosystem service species (Extended Data Fig. 2). All species (53) experienced an increase in s(S,Q5) effects (Fig. 2d), with an average s(S,Q5) effect increase of 7.3% over the past two decades. In 2019, 64% of species (34) still had s(S,Q5) effects <−1.0%. A higher percentage of evergreen trees experienced negative survival effects than did deciduous trees in both 2000 and 2019 (Extended Data Fig. 1). Similar to effects from N deposition, survival effects in 2019 were minimally different when evaluating across ecosystem services (Extended Data Fig. 2).

Recent (2017–2019) deposition levels harm sensitive species

Although conditions have improved, spatial patterns reveal that sensitive species continue to experience negative impacts at recent (2017–2019 average) levels of N and S deposition (Fig. 3). While much of the CONUS experiences increased growth due to N deposition (national average of +8%), 17.1% of the CONUS has sensitive species experiencing ≥5% in reduced growth (Fig. 3a). Moreover, 12 species have at least 1% of their trees experiencing ≥5% reduced growth. Geographically, much of the northern Eastern Temperate Forests, northern Midwestern forests and parts of the Rocky Mountains have negative g(N,Q5) effects below −10%, even though N deposition is moderate (<10 kg ha^{-1} yr^{-1} N).

Fig. 2 | Fifth percentile species-level effect from N and S deposition on the growth and survival rates of tree species between 2000 and 2019. a–d, The fifth percentile of species-level effect shifts between 2000 (green shapes) and 2019 (blue shapes) on growth rates due to N deposition (g(N,Q5)) for 60 species (**a**) survival rates due to N deposition (s(N,Q5)) for 43 species (**b**), growth rates due to S deposition (g(S,Q5)) for 46 species (**c**) and survival rates due to S deposition (s(S,Q5)) for 53 species (**d**). Only species that had established dose–response curves for the stressor (N/S deposition) were included. Tree responses were aggregated to the fifth percentile for each species (species-level). The 0% effect threshold is denoted by a dashed red line. Species were ordered by their phenotype and then by their 2000 fifth percentile value. Different wood product uses are also denoted by the shape: B, strictly building materials (filled square); UP, unfinished wood products (filled triangle); UP + B, unfinished wood products and building materials (filled circle); Neither, neither of those types of wood products (upside-down open triangle). Light green shading in the plots denotes evergreen phenotypes; darker green shading denotes deciduous phenotypes.

Areas in the central Appalachian Mountains and Northwestern Forested Mountains also have g(N,Q5) effects below −5% (Fig. 3a). Although N deposition remains high in the Appalachian Mountains, much of the western United States experiences N deposition levels below 2.5 kg ha^{-1} yr^{-1}. Further examination of western US impacts shows that g(N,Q5) effects are driven primarily by *Picea engelmannii*, which

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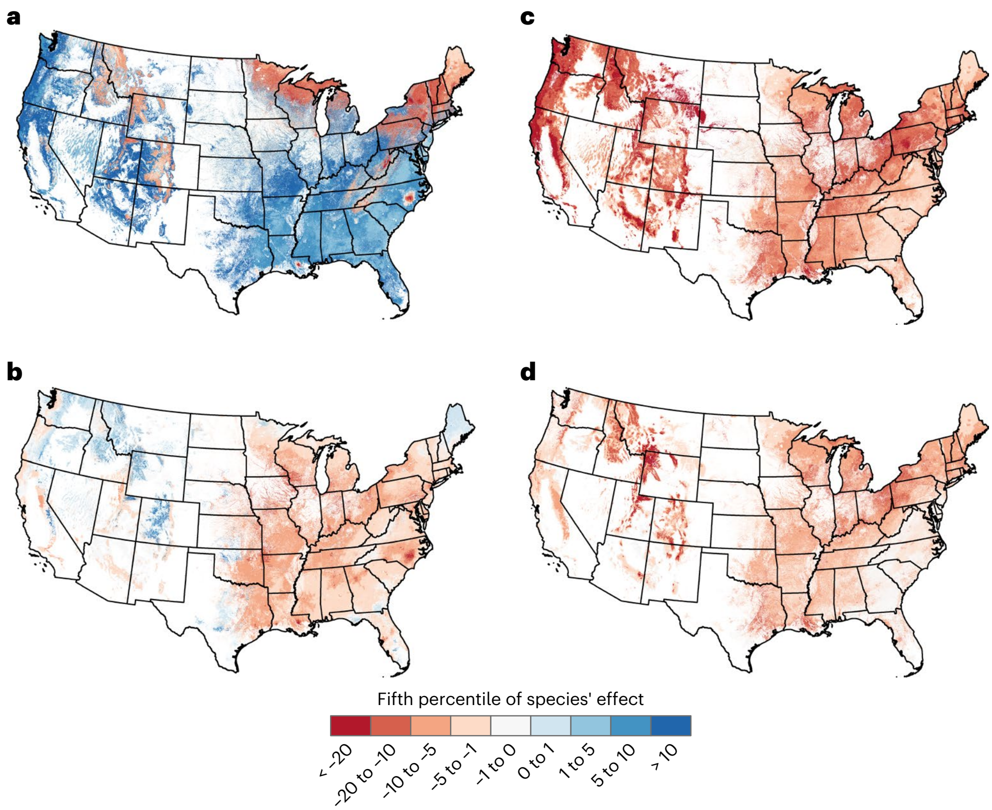

Fig. 3 | Recent three-year average (2017–2019) N and S deposition effects on the fifth percentile of all species nationally. a–d, The g(N,Q5) (**a**), s(N,Q5) (**b**), g(S,Q5) (**c**) and s(S,Q5) (**d**) effects across all species due to recent three-year average (2017–2019) N and S deposition levels. Continuous tree species' effect grids (250 m) were aggregated to the fifth percentile to determine respective effects. Both negative and positive responses are shown. State boundaries generated by the US Census Bureau[62]. Species' surfaces modified from ref. 42.

has a low N deposition critical load for growth and is in areas with low species counts (<7).

When evaluating the other three endpoints, there are mostly negative fifth percentile impacts across much of the CONUS (Fig. 3b–d). The N-influenced survival rates varied, with some positive s(N,Q5) effects occurring in the Northwestern Forested Mountains and northern Maine (Fig. 3b). Overall, 66% of forested areas in the CONUS have 5% of species experiencing ≥1% reductions in survival probability due to N deposition. Therefore, if 1% reductions in survival are a threshold to monitor, at least 66% of the CONUS is in exceedance. Much of the Eastern Temperate Forests have negative s(N,Q5) effects (<−1%), with some hotspots present in the Midwest—an area where reduced forms of N are becoming increasingly dominant (>50%) within total N deposition budgets[9]. Previous studies have shown that reduced forms of N can cause more substantial impacts in terrestrial ecosystems, depending on the species[45,46]. For example, there can be strongly varied plant species responses to NH_x because of underlying environmental conditions (for example, soil buffering capacity)[47]. Some of these differing impairment levels are thought to be because NH_x more easily induces soil acidification, causing larger disadvantages to species that are poorly adapted to N (ref. 48). While we cannot distinguish the relative degree of impact from oxidized and reduced forms of N here, more detrimental effects could be occurring in reduced N hotspots.

The S effects are ubiquitously negative across the CONUS (Fig. 3c,d). Of the four endpoints we evaluated, the most detrimental effects were decreased growth rates due to S deposition. There are some areas with very negative interspecific g(S,Q5) effects (<−10%) where S deposition is among the highest in the country (≥4.5 kg ha^{-1} yr^{-1}). In addition, much of the western United States is experiencing similar g(S,Q5) effects, but S deposition is very low (<0.5 kg ha^{-1} yr^{-1}) (ref. 37). Notably for western species, there are some extremely low S critical loads (<0.01 kg ha^{-1} yr^{-1} S)[12]. These low critical loads are uncertain but are some of the best current estimates for many western species. There are fewer negative influences along the southeastern seaboard—g(S,Q5) effects ranging between −1 and 0%—but the rest of the CONUS is more negatively impacted (Fig. 3c). In general, more evergreen trees (28.8%) had ≥10% reduced growth between 2017 and 2019 than did deciduous trees (5.4%). Overall, 42% of the CONUS has sensitive species experiencing large S-influenced growth-rate reductions (≥10%). In addition, s(S,Q5) effects in the west are some of the most negative (<−20%) (Fig. 3d). Of the CONUS forested area, 77.3% has sensitive species experiencing ≥1% reductions in survival probability due to S deposition. When evaluating ecosystem services, S deposition had similar magnitudes of effect on growth and survival. Median effects were much less negative for all four endpoints (Supplementary Fig. 6), where N effects on growth were generally positive (>10%), N effects on survival were area specific (−5% to 0% in much of the east; −5% to >+10% in the west), and S effects were still negative across the CONUS but less so. Of note, the gridded approach may be underestimating median and fifth percentile growth impacts by ~9.5–13.7 times for N effects, which has larger intercepts, and ~1.3 times for S effects, as well as for survival effects (~1.6–3.7 times); uncertainty evaluations are contained in Supplementary Figs. 16–23. Protection of half of the forest is not consistent with the concept of critical loads, however, which is why we focus on 95% protection levels.

There are no well-established thresholds for how large of a negative effect is too large. Direct and interactive effects of wildfire, pests and drought can lead to 100% mortality of all individuals in an area, but such disturbances occur across much smaller areas than the total forested

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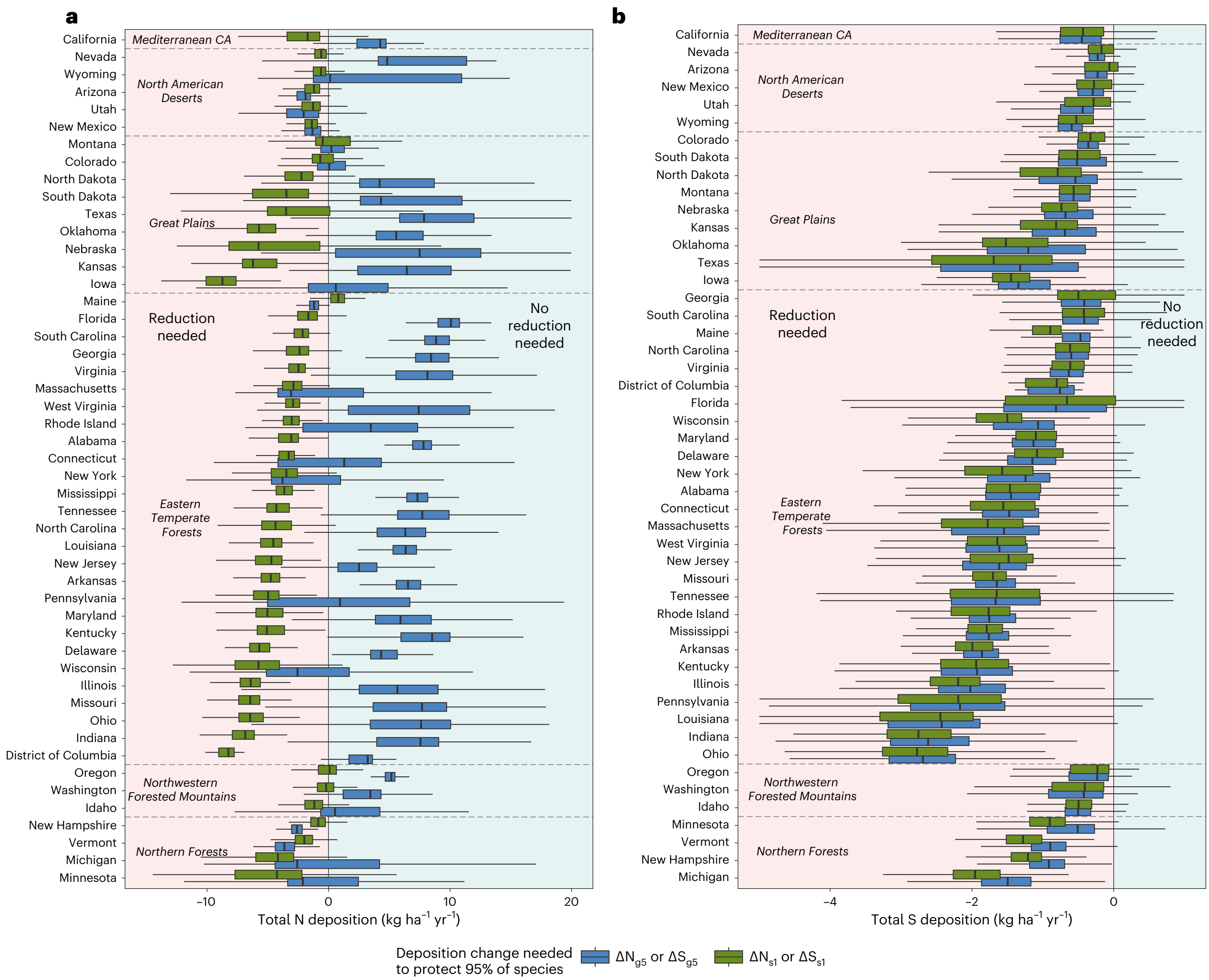


Fig. 4 | Deposition changes needed from 2017–2019 levels to prevent detrimental effects for sensitive species across states. a, Statewide ΔN_{s1} and ΔN_{g5} values. **b**, Statewide ΔS_{s1} and ΔS_{g5} values. Growth and survival rates are shown in blue and green, respectively. Each state's distribution of deposition reductions represents the amount decrease needed to protect 95% of present species (fifth percentile within a grid cell). Box plots where further reductions are needed are shown in the red shaded area, and areas where reductions are not needed are shown in the blue shaded area. The central black lines display the median, the box limits display the quartiles, and the whiskers represent 1.5 times interquartile range. Outliers are not shown. States were ordered by the Ecoregion I level[57] that the state predominately resides in and then by median growth values. The predominant Ecoregion I classification is shown in text. The ranges in the *x* and *y* axes were constrained for data visualization purposes. Geographic visualizations are also shown in Extended Data Fig. 3. Summary statistics for each state are provided in Supplementary Tables 1 and 2.

area across the CONUS (~671 million acres). Since 1960, national-scale wildfire data show that the largest annual acreage burned has totalled ≤10 million acres[49]. These events can be catastrophic at local (10–1,000s of acres) and regional (10,000–100,000s of acres) scales. While cumulative forest-area impacts from wildfires are becoming an increasing concern due to climate change, the effects shown here are much more widespread, with most forested acres in the United States affected by one or more stressors.

Deposition changes needed to avoid harmful impacts

We estimated the amount of N and S deposition change that is needed to prevent growth- and survival-rate decreases at a predetermined threshold. As noted, there currently is no existing N or S deposition impact threshold in the United States, but we may learn from other pollutants. For ozone-related damage, the US Environmental Protection Agency set 6% as the amount of biomass loss that was unacceptable for ecosystem welfare using the median species effect[50]. Here we use 1% and 5% reductions in survival and growth rates, respectively, as thresholds for illustration. While these thresholds may seem low, over the course of 100 years, decadal reductions of 1.4% survival over the baseline could lead to roughly 5% fewer trees after 100 years *ceteris paribus*. Similarly, a 5% reduction in the baseline growth rate would roughly equate to 21% less biomass after 100 years. In other words, small incremental impacts over long periods can have compounding impacts to a forest ecosystem. It should be noted that this demonstration does not account for forest recruitment (the growth of new trees), but we assume the same patterns hold for new individuals as they would for existing ones.

Using this framework, we calculated the N and S deposition levels needed to avoid 5% and 1% reductions in growth and survival rates, respectively, for all species in a plot or grid cell and determined the fifth percentile (Supplementary Fig. 10). This corresponds to the protection of 95% of trees in a plot or 95% of species in a grid cell. We subtracted recent deposition levels (2017–2019 average) to determine how much further N or S deposition needs to decrease to avoid harmful effects and evaluated these across CONUS states (Fig. 4). Henceforth, we denote the N or S deposition change needed to protect 95% of species or trees from a 5% reduction in growth rates as ΔN_{g5} (kg ha^{-1} yr^{-1} N) and ΔS_{g5} (kg ha^{-1} yr^{-1} S), respectively (similar nomenclature for thresholds avoiding a 1% reduction in survival, ΔN_{s1} and ΔS_{s1}).

Nitrogen deposition decreases are needed in about half of the states throughout the CONUS to prevent harmful growth reductions in sensitive areas. States in Northern Forests are particularly sensitive and need larger N declines (>2.5 kg ha^{-1} yr^{-1}) across > 45% of their forested areas to protect 95% of species (Fig. 4a). Overall, N deposition reductions of ≥2.5 kg ha^{-1} yr^{-1} are needed in 9.8% of the CONUS for growth-rate protection (Extended Data Fig. 3). In much of the CONUS (82.4%), N deposition could increase before growth rates reach the 5% reduction threshold. Larger N deposition decreases are needed to prevent detrimental survival effects. Nationally, 56.1% of the CONUS needs N deposition decreases of ≥2.5 kg ha^{-1} yr^{-1} to prevent harmful tree mortality rates (Extended Data Fig. 3). Notably, Midwestern states have some of the lowest ΔN_{s1} values (<−5 kg ha^{-1} yr^{-1}) (Fig. 4a). Overall, all 48 CONUS states require some level of decrease in N deposition to protect 95% of species from ≥1% reductions in survival rates (Fig. 4a). Sulfur deposition declines are needed across all states in the CONUS to prevent deleterious effects to both growth and survival. Many states have median ΔS_{g5} and ΔS_{s1} values that are nearly the same (Fig. 4b). States needing the largest S deposition decreases (for example, lowest ΔS_{g5} value) are areas where S deposition is currently the highest in the country. Nationally, S deposition decreases of ≥1 kg ha^{-1} yr^{-1} are needed across 46.5% and 52.8% of the CONUS to prevent deleterious growth and survival effects, respectively (Extended Data Fig. 3).

We also evaluated the deposition decrease needed to protect 95% of trees as a function of the form of N being deposited using both the FIA plot and gridded approaches. Reduced N deposition ranges from 0 to 5 kg ha^{-1} yr^{-1} (Fig. 5a) across FIA plots but is increasing across much of the CONUS (Supplementary Fig. 12). Previous research has attributed this trend to modest fertilizer increases causing higher ambient NH_3 concentrations, fine particulate matter ($PM_{2.5}$) formation shifting away from NO_3^--dominated compositions, on-road emissions sources and climate change impacts[51,52]. When comparing deposition magnitudes against ΔN_{s1} and ΔN_{g5} values, there are some areas where even if oxidized N deposition were zero, additional decreases of N deposition would be needed to protect 95% of trees (Fig. 5b,c). For example, 1.2% (growth) and 4.3% (survival) of FIA plots would still need N deposition decreases to protect sensitive trees, even with no oxidized N deposition (Fig. 5b,c). Using the gridded approach, we found that 0.6% (growth) and 6.7% (survival) of the CONUS—notably in the Midwest and North Carolina—specifically need reduced forms of N to decrease by at least 2.5 kg ha^{-1} yr^{-1} N, when oxidized N is zeroed out. Some of the CONUS (growth: 1.8%; survival: 0.5%) also requires larger oxidized N deposition declines (≥2.5 kg ha^{-1} yr^{-1} N) to protect 95% of species, even with no reduced N deposition.

Increased and decreased productivity in total forested area

We now shift to an examination of impacts to total forest basal area (m^2 ha^{-1}). To determine the extent of basal area affected by air pollution, we considered individual species' areal proportion to the total forest. We also evaluated the weighted basal area effect (%) to understand effects in terms of percentage forest area lost or gained. Like results from previous analyses, growth-rate responses to N deposition display a fertilization effect across much of the CONUS (Extended Data Fig. 4a,e). Conversely, N-influenced tree mortality, in terms of basal area, is diverse across the CONUS (Extended Data Fig. 4b,f). While some areas (for example, Eastern Temperate Forests) are undergoing net positive survival effects on total basal area (>10 m^2 ha^{-1}), total basal area decreases (0–10 m^2 ha^{-1}) are interwoven throughout these regions. All of the CONUS has decreases in total basal area because of S deposition impacts to growth and survival rates. As a result, 1.8% (survival) to 11.3% (growth) of the CONUS forested area experiences total basal area losses of ≥5 m^2 ha^{-1} (Extended Data Fig. 4c,d,g,h). There are more-pronounced effects occurring in the western United States, where many S-sensitive species are present. As previously discussed, many of these western species have such low S critical loads that even low S deposition amounts (<0.5 kg ha^{-1} yr^{-1} S) can result in very large apparent reductions in basal area.

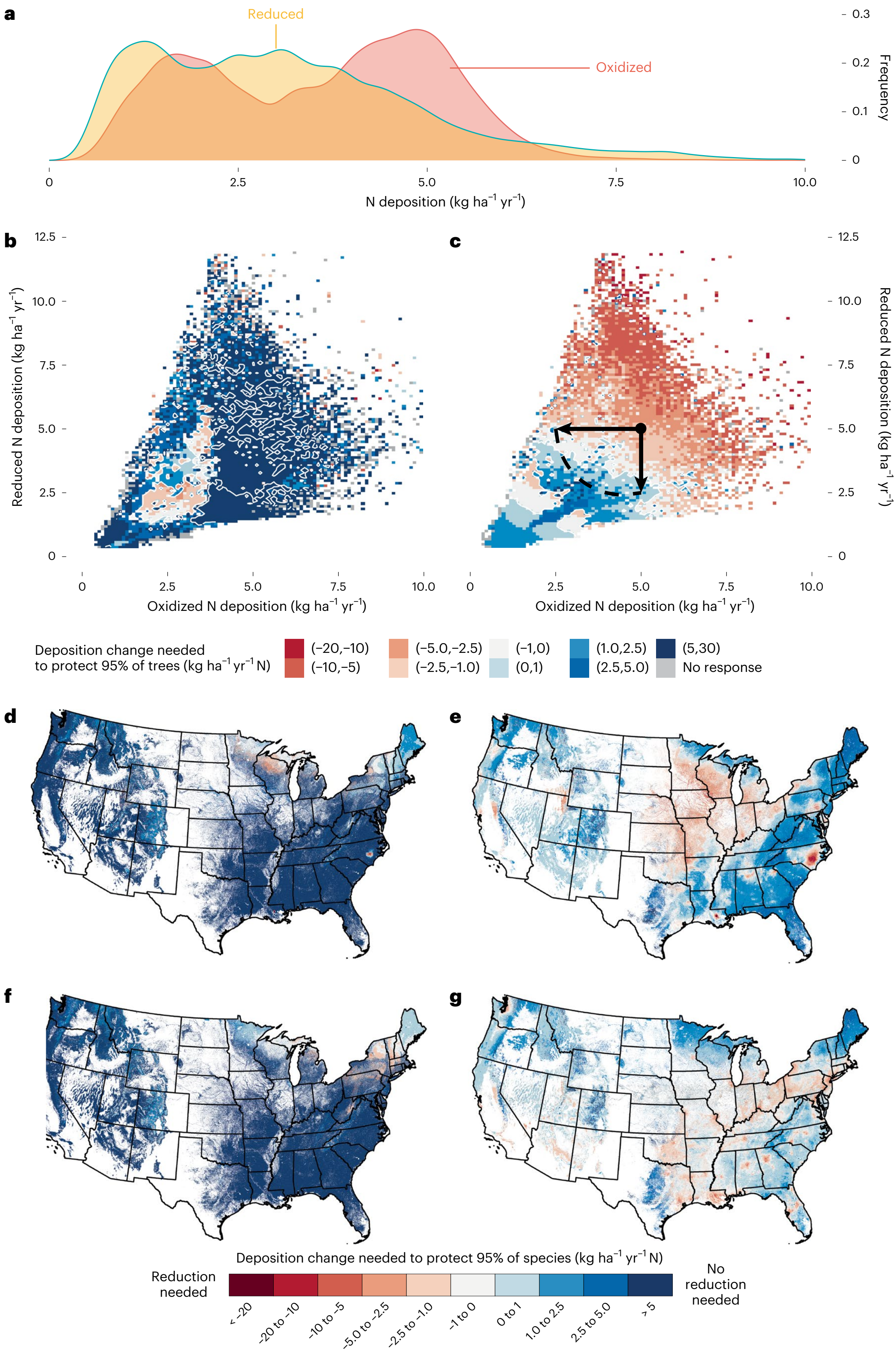
We combined the total basal area effects across all four ecological endpoints to understand how the forests on a national level are faring under recent air pollution conditions (Fig. 6a). There are many western and northern states where 250 m^2 cells have total basal area losses of >35 m^2 ha^{-1}, but there are also other areas, within the same states, experiencing net positive effects (>125 m^2 ha^{-1}) (Fig. 6a). Across the CONUS, 14.8% of areas are experiencing net decreases in total basal area (Fig. 6b). While net positive effects are occurring in many regions, sensitive species are experiencing reduced growth and increased mortality, which could contribute to forest biodiversity loss, although we do not address that here.

Discussion

In the past 20 years, there has been substantial progress in reducing air pollution emissions due to air quality policies. Emissions decreases have led to notable improvements in both ambient air quality and deposition. As a result, tree species' growth and survival rates have tended to trend positively, with some species experiencing large increases in growth rates and survival probability since 2000. Despite these positive effects, there are still many sensitive species and regions experiencing detrimental impacts, notably N effects on survival and S effects on both growth and survival. In addition, while many trees have increased growth with N deposition, 91.2% of the CONUS requires N deposition decreases to ensure decadal survival rates do not fall by more than 1% for 95% of species. Furthermore, deciduous species tend to have more negatively impacted survival rates than evergreen species because of N deposition. N deposition declines are needed in reduced forms of N across 6.7% of the CONUS and notably in agricultural areas of the country. Overall, there are both benefits and harms being experienced due to atmospheric N deposition across the CONUS, while S deposition impacts are negative and vary considerably across the

Fig. 5 | The oxidized and reduced N deposition levels at FIA plots compared with deposition changes needed to protect 95% of trees. a, The distribution of oxidized and reduced forms of N deposition (kg ha^{-1} yr^{-1} N) experienced at FIA plots. **b**,**c**, The scatterplots display the oxidized and reduced N deposition levels at FIA plots with the averaged ΔN_{g5} (**b**) and ΔN_{s1} (**c**) values, at the paired oxidized–reduced deposition, shown in the colour gradation. **d**–**g**, The maps display ΔN_{g5} with oxidized N deposition zeroed out (**d**), ΔN_{s1} with oxidized N deposition zeroed out (**e**), ΔN_{g5} with reduced N deposition zeroed out (**f**) and ΔN_{s1} with reduced N deposition zeroed out (**g**). Grey areas in **b** and **c** reflect plots where no trees had a response for that endpoint. The overlay in **c** illustrates an FIA plot that is receiving 5 kg ha^{-1} yr^{-1} each of oxidized (*x* axis) and reduced (*y* axis) N deposition. This FIA plot needs N deposition to be lowered (colour gradient) by 2.5–5.0 kg ha^{-1} yr^{-1} to meet the ΔN_{s1} threshold. This deposition decrease could occur by lowering oxidized N (left arrow), reduced N (down arrow), or some combination (dashed line) so that the referenced FIA plot no longer experiences harmful growth impacts. The ranges in the *x* and *y* axes in **b** and **c** were constrained for data visualization purposes (FIA plots with reduced N deposition above 12.5 kg ha^{-1} yr^{-1} (n = 156) and with oxidized N deposition above 10.0 kg ha^{-1} yr^{-1} (n = 10) are not shown). State boundaries generated by the US Census Bureau[62]. Species' surfaces modified from ref. 42.

CONUS. Basal area is generally increasing across the country, but this can be misleading in efforts to protect sensitive tree species. One possible consequence over the long term is an overall homogenization of forests across the CONUS, with a smaller number of dominant species becoming more abundant, leading to further loss of biodiversity in forest ecosystems.



https://doi.org/10.1038/s41893-023-01203-8

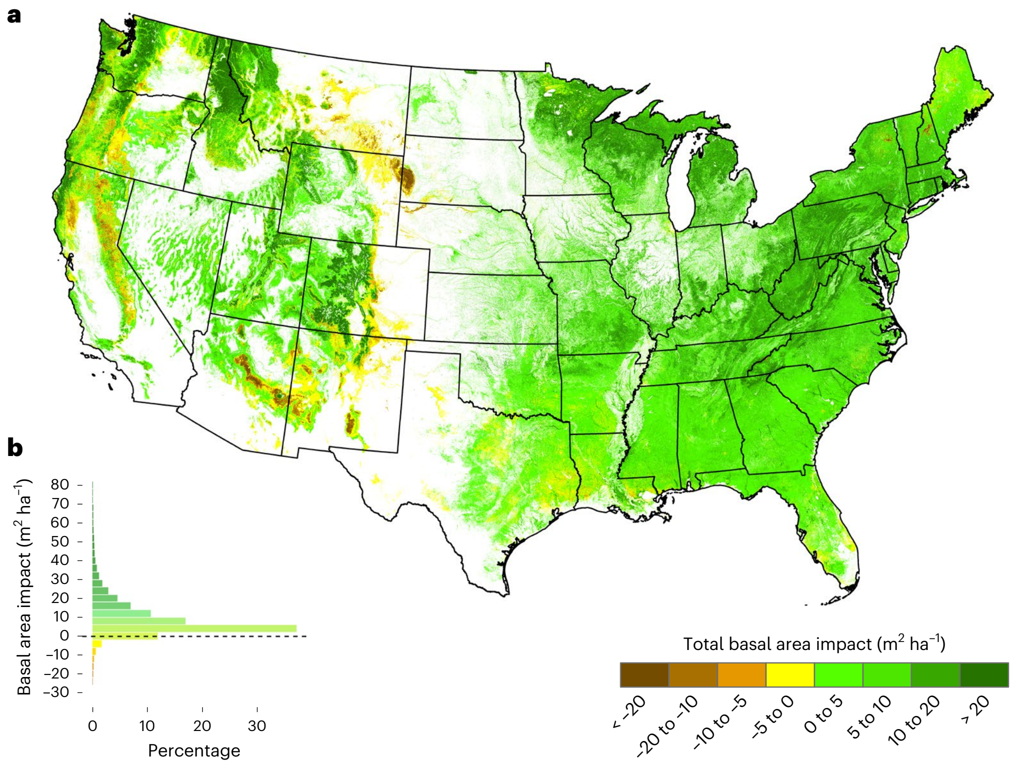


Fig. 6 | The total basal area impacts across the CONUS. a,b, The total basal area impact (m^2 ha^{-1}, net gain or loss) across all of CONUS and all four endpoints due to 2017–2019 average N or S deposition in each 250 m grid cell in a geographic view (**a**) and in a histogram format (**b**) using all 250 m grid cells where percentages are based on the total number of grid cells. State boundaries generated by the US Census Bureau[62]. Species' surfaces modified from ref. 42.

Methods

Deposition data

We obtained N and S deposition data from the National Atmospheric Deposition Program's Total Deposition Science Committee's (TDep's) database[53]. Annual deposition estimates are calculated by TDep using a measurement–model fusion approach that combines measured air concentration and wet deposition data with modelled deposition velocity and dry deposition data[54]. Briefly, TDep combines weekly Clean Air Status and Trends Network air concentration data with dry deposition velocities and then fuses these data with modelled dry deposition estimates from the Environmental Protection Agency's Community Multiscale Air Quality Modeling System. TDep aggregates results to weekly estimates by taking a weekly average deposition velocity and summing dry deposition amounts to calculate annual estimates of dry N and S deposition. In addition, TDep calculates wet deposition estimates by combining weekly precipitation chemistry data from the National Atmospheric Deposition Program's National Trends Network with precipitation estimates from the Parameter-Elevation Regression on Independent Slopes Model (PRISM). TDep combines dry and wet deposition estimates to provide total N and S deposition estimates. We obtained TDep model version 2018.02 grids for total N and S deposition as well as total oxidized and reduced N deposition for years between 2000 and 2019. Grids were analysed in ArcGIS using the Albers projection and the GRS1980 datum. Model version 2018.02 TDep raster surfaces were produced at a 4.1 km grid-cell size on the basis of PRISM data inputs. Nitrogen deposition, with no oxidized N deposition, was calculated using the difference between total N deposition and oxidized N deposition. This was also the method used to determine N deposition with no reduced N deposition, except reduced N deposition was subtracted from the total N deposition. When drawing comparisons against the continuous live-tree basal area grids, we re-sampled TDep raster surfaces to smaller grid-cell sizes (250 m) to prevent edge issues from occurring.

Tree characteristic data

The US Forest Service operates and maintains the FIA programme, which monitors changes in forests across the United States and, in particular, the growth and survival of trees within plots[37]. Growth is measured using the difference between allometric carbon estimates[55] between two time frames, while survival is measured using a binary live or dead determination. A total of 2,214 mainland tree species, excluding subspecies, are included in the FIA database[56]. Here we used forest inventory data for 94 common tree species across 48 states, representing 2.6 million trees across 121,839 plots in the CONUS, which were measured between 2000 and 2016. This area spans ten different Ecoregion I areas[57], representing a large range of climate and forest types[57]. In addition to the individual tree location data from the FIA database, we used continuous estimates of live-tree basal area (species grids) for 2000–2009 as basal area (m^2 ha^{-1}) and as a proxy for species' range in our study[41,42]. These continuous grids represent the amount of live tree species basal area geographically by integrating vegetation phenology from moderate-resolution imaging spectroradiometer imagery and raster data with environmental parameters from the FIA plot database. One advantage of this dataset over the point-based FIA plot data is the increased geographic representation of species across the CONUS. These modelled surfaces use a k-nearest neighbour and canonical correspondence approach with stratification derivations from the 2001 National Land-Cover Database tree canopy layer[42,58]. In addition, tree characteristics data differentiating phenotypes (deciduous, evergreen) were obtained from the TRY database[59]. Ecosystem service (wood products) data for tree species were obtained from the US Forest Service's Air Pollution Effects on Forests: A Guide to Species Ecology, Ecosystem Services, and Responses to Nitrogen and Sulfur Deposition dataset[44]. In our analysis, we included only the following two classifications: (1) unfinished wood products (for example, products such as fence posts, railroad ties and crates) and (2) building materials (for example, products such as plywood and particle board).

Dose–response curves for tree species

For growth and survival dose–response curves, we used the dataset of ref. 12, which used re-measured trees in FIA plots between 2000 and 2016. Ninety-four different tree species, which met a minimum tree sample size of 2,000, had response curves established for both annual N and annual S deposition. In that analysis, roughly 1.5 million trees (~70,000 plots) and 1.3 million trees (~68,000 plots) were used to develop relationships for survival and growth responses, respectively. The ref. 12 analysis included four environmental factors: N deposition, S deposition, mean annual temperature and total annual precipitation. The study did not include other environmental factors such as soil disturbance, pests or fires. The deposition levels in ref. 12 used the previously described TDep N and S deposition surfaces for years that corresponded with the FIA plot re-measurement periods up until 2013, at which point deposition levels were assumed to be constant through 2016. Similarly, the study used temperature and precipitation data from PRISM that also coincided with re-measurement periods[12,60]. Environmental factors were fit to a modified lognormal function, shown in equation (1), that allows for flexibility so that response curves could be monotonically increasing, monotonically decreasing or bell shaped, with varying degrees of steepness for all three major shapes:

$$e^{-0.5\left(\frac{\ln(\mathrm{Ndep}/n_1)}{n_2}\right)^2} \quad (1)$$

In the preceding equation, two terms were statistically estimated: n_1, which governs the location of the peak in the bell-shaped curve, and n_2, which governs how steep the slope is on either side of the peak. Ndep is the average annual N deposition between measurement periods—individually estimated for each plot. In addition to environmental factors, three other factors were included: an intercept, a size term and a competition term. The size and competition terms capture the power-function relationship between growth and size and competing dynamics, respectively. Thus, the growth and survival response curves were developed using the following respective equations:

$$G = a \times \mathrm{size}^z \times e^{a_2\times\mathrm{BAL}+a_3\times\ln(\mathrm{BA})} \times e^{-\frac{1}{2}\left(\frac{\ln\left(\frac{T}{t_1}\right)}{t_2}\right)^2} \times e^{-\frac{1}{2}\left(\frac{\ln\left(\frac{P}{p_1}\right)}{p_2}\right)^2} \times e^{-\frac{1}{2}\left(\frac{\ln\left(\frac{S}{s_1}\right)}{s_2}\right)^2} \times e^{-\frac{1}{2}\left(\frac{\ln\left(\frac{N}{n_1}\right)}{n_2}\right)^2} \quad (2)$$

$$P(s) = \left[a \times (1 - zc_1 \times e^{-zc_2\times\mathrm{size}}) \times e^{-zc_3\times\mathrm{size}^{zc_4}} \times \mathrm{competition} \times e^{-\frac{1}{2}\left(\frac{\ln(T/t_1)}{t_2}\right)^2} \times e^{-\frac{1}{2}\left(\frac{\ln(P/p_1)}{p_2}\right)^2} \times e^{-\frac{1}{2}\left(\frac{\ln(S/s_1)}{s_2}\right)^2} \times e^{-\frac{1}{2}\left(\frac{\ln(N/n_1)}{n_2}\right)^2}\right]^{\mathrm{time}} \quad (3)$$

where in equation (2), a is the intercept, z is the size term, a_2 and a_3 are the competition terms, BA is the plot basal area, BAL is the basal area of trees larger than the tree of interest in a plot, t_1 and t_2 are the temperature terms, p_1 and p_2 are the precipitation terms, s_1 and s_2 are S deposition terms, and n_1 and n_2 are N deposition terms. Similar terms were found for the survival equation (equation (3)) except the equation structure and notation differed for the size term (zc_1, zc_2, zc_3, zc_4). In addition, there were two competition terms for survival equations (equations (4) and (5)):

$$\mathrm{competition} = e^{-\mathrm{br}_1\left(\mathrm{BA}_{\mathrm{ratio}}^{\mathrm{br}_2}\right)\times\left(\mathrm{BA}^{\mathrm{br}_3}\right)} \quad (4)$$

$$\mathrm{competition}_{\mathrm{size-combined}} = e^{-0.5\left(\frac{\ln\left(\frac{\mathrm{BA}}{\mathrm{ba}_1}\right)}{b_2}\right)^2 \times -0.5\left(\frac{\ln\left(\frac{\mathrm{BAL}+1}{(\mathrm{bl}_1+1)}\right)}{\mathrm{bl}_2}\right)^2} \quad (5)$$

where competition terms (br_2, $br_{2_{\mathrm{ratio}}}$, br_3) are fitted parameters. The t (time) term in equation (3) is necessary as the survival responses were based on decadal scales ($t = 10$) rather than annual (growth, $t = 1$). Equation (5) is a combined modified lognormal form. To estimate the parameters for each of the growth and survival models, ref. 12 used simulated annealing (100,000 iterations) in the likelihood package (v. 2.1.1) in R to maximize the likelihood functions. Different combinations of model equations were analysed, five for growth and nine for survival, which were assessed with Akaike information criterion (AIC). In this study, we used the overall best model as determined by AIC. With considerations to the selection of the best model (AIC), ref. 12 established dose–response curves for 60 (N-influenced growth), 43 (N-influenced survival probability), 46 (S-influenced growth) and 53 (S-influenced survival probability) species.

Ref. [12] assessed multivariate collinearity for predictor variables as a measure of confidence in the respective response curves. Multivariate collinearity was evaluated using standardized variance inflation factors (VIFs) for N and S as in ref. 12. VIF was calculated using the following:

$$\mathrm{VIF} = \frac{1}{1 - R^2} \quad (6)$$

An ordinary least square regression (R^2) was evaluated where the spatial pattern in N or S deposition was regressed against the spatial pattern in mean temperature, precipitation and S or N deposition, respectively, for each tree species. VIFs explain how much of the explanatory power is conflated by other environmental variables (for example, N or S deposition, precipitation and temperature). Typically, a VIF > 10 is not recommended for use due to the confounding influence from other variables[61]. Here we evaluated an additional principle bivariate correlation: the correlation between N and S deposition, where correlations > 0.7 were determined to yield response curves with low confidence. Overall, 16 species had N/S correlations > 0.7, and two species had VIFs > 10. Here we present all 94 species, including those with high N/S correlations and high VIFs, but we examine how our results varied by removing species that do not meet uncertainty criteria (Supplementary Fig. 15).

Derivation and application of equation for relative responses

To isolate the influence of N and S deposition on growth or survival of trees, we developed a relativized exponential equation that held the temperature, precipitation, size and competition terms constant. In addition, we selected two points of reference for comparison within the relativized equation, where one was the lowest level of deposition observed by a tree of that species in ref. 12 and the other was the deposition at the maximum growth or survival rate. The relativized equations for growth and survival rate used a combined approach where increasing and decreasing legs of a unimodal relationship were treated differently. If the experienced deposition was greater than the maximum of a unimodal response, then the reference point for the exponential equation was the maximum of the curve. If the deposition was lower than the maximum, then the reference point was the minimum deposition observed and thus reflected responses along the rising limb of the response curve. An illustration of these dose–response relationships is shown in Supplementary Fig. 13. This treatment is consistent with the concept of the critical load, where any decrease in growth or survival may be considered a negative effect, regardless of the reference point. The respective relativized equations for growth and survival responses are as follows:

$$\mathit{If}\ D > D_{\max}, R_G = \frac{e^{-0.5\left(\frac{\ln(D/x_1)}{x_2}\right)^2}}{e^{-0.5\left(\frac{\ln(D_{\max}/x_1)}{x_2}\right)^2}} - 1; \mathrm{else}\ R_G = \frac{e^{-0.5\left(\frac{\ln(D/x_1)}{x_2}\right)^2}}{e^{-0.5\left(\frac{\ln(D_{\min}/x_1)}{x_2}\right)^2}} - 1 \quad (7)$$

$$\textit{If } D > D_{\max}, R_S = \frac{e^{-0.5t\left(\frac{\ln(D/x_1)}{x_2}\right)^2}}{e^{-0.5t\left(\frac{\ln(D_{\max}/x_1)}{x_2}\right)^2}} - 1; \text{else } R_S = \frac{e^{-0.5t\left(\frac{\ln(D/x_1)}{x_2}\right)^2}}{e^{-0.5t\left(\frac{\ln(D_{\min}/x_1)}{x_2}\right)^2}} - 1 \quad (8)$$

where D is the observed deposition (N or S deposition), R_G and R_S are a tree's response to the observed deposition for its growth or survival probability, respectively, x_1 is the ascribed critical-load term (n_1 or s_1 from equations (1) and (2)), x_2 is the n_2/s_2 term from equations (1) and (2), respectively, D_{max} is the deposition at the maximum growth or survival rate, D_{min} is the minimum deposition observed by a tree species in the ref. 12 models and t is time in years (1 for growth, 10 for survival).

These relativized equations were utilized for both the FIA plot data (Figs. 1 and 2) and the grids of live-tree range (Fig. 3). For the FIA plot data, trees were spatially joined in ArcGIS to TDep N and S deposition raster surfaces for every year between 2000 and 2019, as well as the most recent three-year average (2017–2019). Equations (4) and (5) were then applied to each tree, within the 94 species, using the R coding language (v. 4.0.3). For the gridded approach[42], the relativized equations were processed in Python (v. 3.1) for the most recent three-year average (2017–2019) N and S deposition. We did not process the species' grids for growth and survival responses for every year and species between 2000 and 2019 due to computational constraints and because 2017–2019 average comparisons between the FIA plot and gridded approaches were in fair agreement (Supplementary Figs. 16–23). Therefore, we present growth and survival responses analyses for (1) the FIA plots and (2) the gridded approach for recent deposition (2017–2019 average). Both datasets were aggregated to various levels, including mean, median and fifth percentile. The fifth percentile was chosen so results would be reflective of impacts to more detrimentally affected species. For both the plot-level and gridded approaches, we flagged any tree where the applied N or S deposition was outside the deposition domain of the ref. 12 response curve for that given species. These trees were not included in the statistics generated. In addition, a K–S test was used to evaluate differences in R_G and R_S between phenotypes. In this analysis, we used the 95% confidence interval of effects to remove the tails of the distributions so comparisons were not skewed. A P value < 0.05 was used as the threshold for determining whether distributions were significantly different.

Derivation and application of deposition-change-needed equation

To determine the amount of deposition needed to prevent 1% and 5% reductions in survival and growth rates, respectively, we derived an inverse equation from equations (5) and (6) (Fig. 5; solving for D given a user-defined value of R). The deposition needed to prevent the respective reductions in response rates was calculated using:

$$D_R = x_1 e^{\sqrt{\frac{-2\ln(1-R_c)x_2^2}{t} + \left[\ln\left(\frac{D_{\max}}{x_1}\right)\right]^2}} \quad (9)$$

In this equation, all parameters are the same as in equations (4) and (5) except for R_c, which is a value chosen by the user for the rate reduction level of interest (for example, 0.05 for 5% rate reduction) and D_R, which is the deposition reduction needed to prevent R_c. Using equation (9), we evaluated a 5% reduction in growth rate and a 1% reduction in survival rate. Moreover, equation (9) was applied to both the plot-level data in FIA plots and the continuous grid. Trees that experienced deposition outside the domain used to generate the dose–response curves were nullified. The CONUS-level surfaces were generated for each tree species using the individual tree species' grids as a geographic mask. The plot-level data and the grids both had the current N and S deposition levels subtracted from them, using:

$$\Delta D = D_R - D_{17-19} \quad (10)$$

where ΔD is the reduction needed (kg ha^{-1} yr^{-1} N or S) to prevent 1% or 5% reductions of survival and growth rates (for example, ΔS_{g5}), respectively, D_R is the term estimated in equation (6) and D_{17-19} is the 2017–2019 three-year average of N or S deposition (kg ha^{-1} yr^{-1} N or S) in the 250 m grid cell or FIA plot location. The fifth percentile deposition level for trees in a plot or species in a grid cell was used to show the deposition reduction needed to protect 95% of trees or tree species. The distribution of those fifth percentiles is presented in Fig. 4 using the predominant Ecoregion I level[57] for that corresponding state (Supplementary Fig. 1). Only trees present within a respective plot or 250 m grid cell were used. The grids were used when examining deposition reductions needed (Fig. 4) to have a wider geographic representation across counties.

Derivation and application of equation for total basal area effect

To determine the total basal area effects in terms of percentage (%) and in a forest areal amount (m^2 ha^{-1}), we used the continuous grids (250 m) of each tree species' effect (R_S *or* R_G) using the 2017–2019 average N or S deposition (Fig. 6 and Extended Data Fig. 4). The total percentage basal area effect was determined using the following equation:

$$\mathrm{BA_P} = \sum_{i=1}^{N} R_i \times \mathrm{PBA}_i \quad (11)$$

where BA_P is the total basal area effect (%) across all species, R_i is the growth or survival-rate response for species i, and PBA_i is the proportion to total basal area for species i (each species was proportional to all 323 species from ref. 42,). The resulting percentage effect rasters removed the need for aggregation (for example, fifth percentile) by converting the endpoint response (for example, N-influenced growth rate) into a percentage basal area effect (Extended Data Fig. 4a–d). The number of species, N, used for the summation varied depending on how many tree species had a response curve for that endpoint in that 250 m grid cell. The resulting raster, BA_P, was then converted into a total basal area impact in areal amounts using the following equation:

$$\mathrm{BA_T} = \mathrm{BA_P} \times \mathrm{BA_A} \quad (12)$$

where BA_T is the total basal area impact (m^2 ha^{-1}) and BA_A is the summed basal area for all species that are present in that 250 m grid cell from the Wilson et. al.[42] dataset. Thus, the total basal area impact provided a total basal area reduction without any sort of aggregation across species (for example, median) and provided insight on forested area effects (Extended Data Fig. 4e–h).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The metadata for datasets generated in this study are available in a data repository (https://doi.org/10.23719/1529199). The repository contains contact information to obtain all of the raw data, processed summary data and raster data. The tree species parameters that were analysed during this study are included in ref. 12 (and its supplementary information files). The continuous grids of tree species that were analysed during this study are included in the ref. 42 dataset. The 2000–2019 air pollution raster surfaces (v. 2018.2) that were used during this study are publicly available from the National Atmospheric Deposition Program[53] (https://nadp.slh.wisc.edu/committees/tdep/). The FIA dataset is available from the US Forest (https://www.fs.usda.gov/research/products/dataandtools/forestinventorydata).

Code availability

Analyses were performed in both Python and R. Relevant scripts and README files are available on a Github repository (https://github.com/Justin-Coughlin/air_pollution_effects_trees).

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Acknowledgements

We thank J. Lynch, J. T. Smith and J. Miller for commenting on earlier versions of this manuscript and the National Atmospheric Deposition Program's Critical Loads of Atmospheric Deposition Committee, which has provided useful insight on this research. We thank K. Horn, J. Phelan and R. Dalton for providing data and/or minor feedback on results. We thank J. James for initial script development assistance and T. Wilson for his helpful advice on the use of the US Forest Service's continuous live-tree basal area dataset. This work was supported with funding from the US Environmental Protection Agency under the Air Climate and Energy National Program within the Office of Research and Development. This research was originally supported by the US Geological Survey's John Wesley Powell Center for Earth System Analysis and Synthesis (forecasting forest response to N deposition: integrating data from individual plant responses to soil chemistry with a continental-scale gradient analysis, 2013). The funders had no role in study design, data collection and analysis, decision to publish or preparation of the manuscript. The views expressed in this manuscript are those of the authors and do not necessarily reflect the views or policies of the US Environmental Protection Agency or the US Forest Service.

Author contributions

J.G.C., C.M.C. and R.D.S. designed the research. J.G.C. analysed the data. J.G.C., C.M.C., R.D.S., L.H.P. and J.D.A. wrote the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

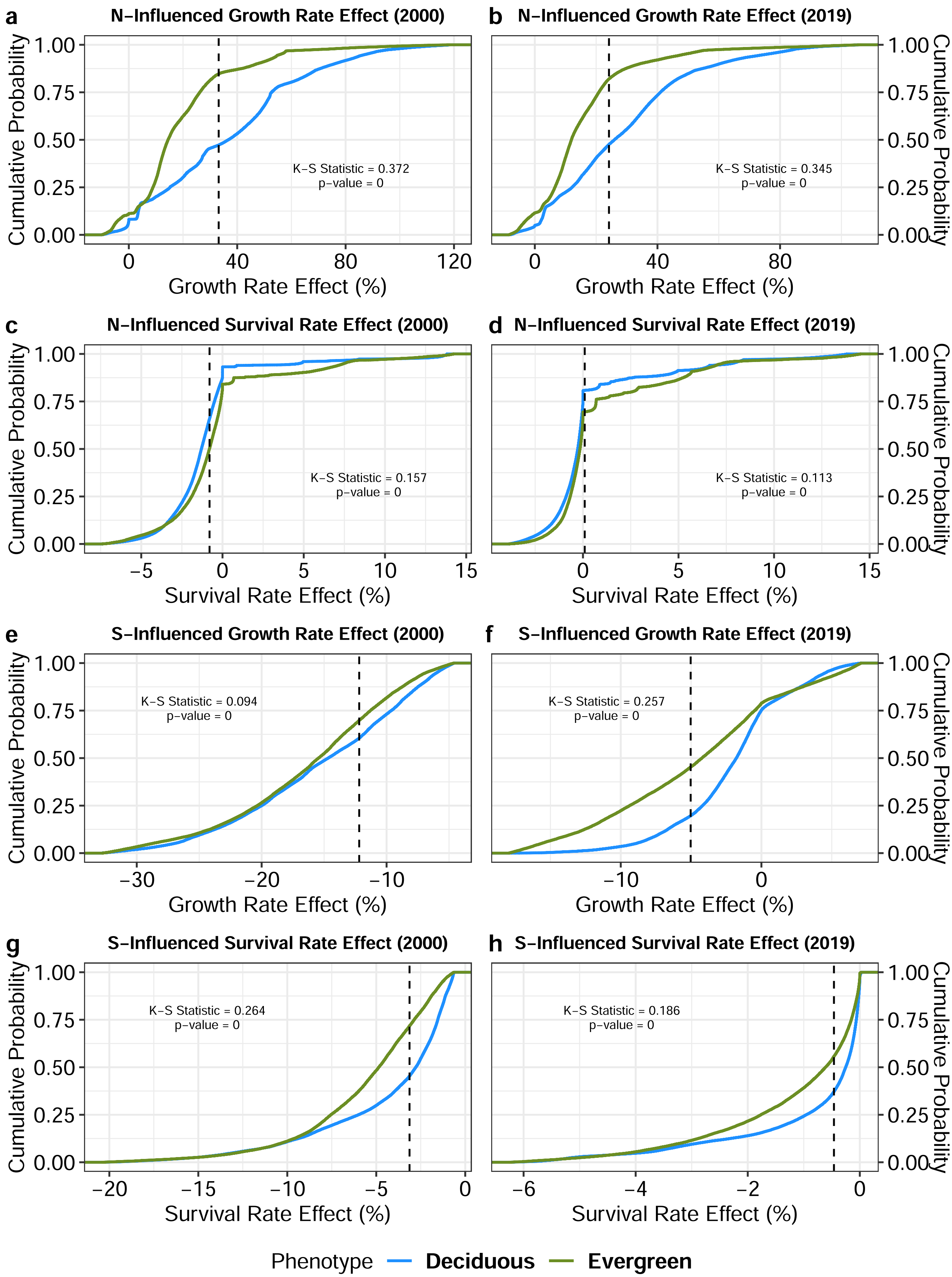
Extended data is available for this paper at https://doi.org/10.1038/s41893-023-01203-8.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41893-023-01203-8.

Correspondence and requests for materials should be addressed to Justin G. Coughlin or Christopher M. Clark.

Peer review information *Nature Sustainability* thanks Samuel Simkin, Carly Stevens and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

https://doi.org/10.1038/s41893-023-01203-8

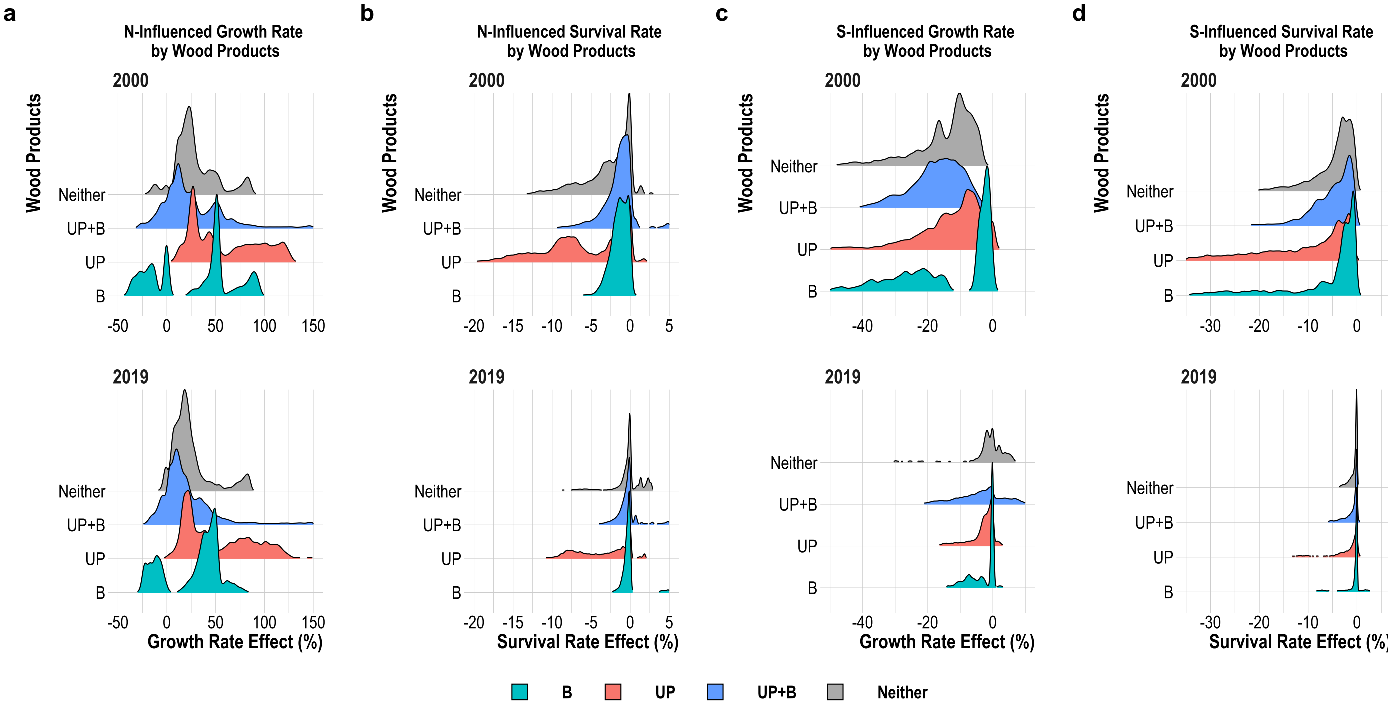


Extended Data Fig. 1 | See next page for caption.

https://doi.org/10.1038/s41893-023-01203-8

Extended Data Fig. 1 | Kolmogorov-Smirnov (K-S) test plots comparing endpoint effects across phenotypes in 2000 and 2019. Cumulative density function (CDF) plots showing the effect for N-influenced growth rates in 2000 (**a**), N-influenced growth rates in 2019 (**b**), N-influenced survival rates in 2000 (**c**), N-influenced survival rates in 2019 (**d**), S-influenced growth rates in 2000 (**e**), S-influenced growth rates in 2019 (**f**), S-influenced survival rates in 2000 (**g**), and S-influenced survival rates in 2019 (**h**). Deciduous (blue) and evergreen (green) trees are differentiated. A two-sided K-S test was used on data within the 95% confidence interval of the sample size. The K-S statistic and corresponding p-value are also shown.

 https://doi.org/10.1038/s41893-023-01203-8



Extended Data Fig. 2 | Histograms of 2000 and 2019 endpoint effects by wood products. Ridgeline histogram plots of N-influenced growth rates (**a**), N-influenced survival rates (**b**), S-influenced growth rates (**c**), and S-influenced survival rates (**d**). The upper panels display distributions of effects from deposition in 2000 and lower panels are effects from deposition in 2019. Different wood product uses are shown where B is strictly building materials, UP is unfinished wood products, UP+B is unfinished wood products and building materials, and Neither is neither of those types of wood products[44].

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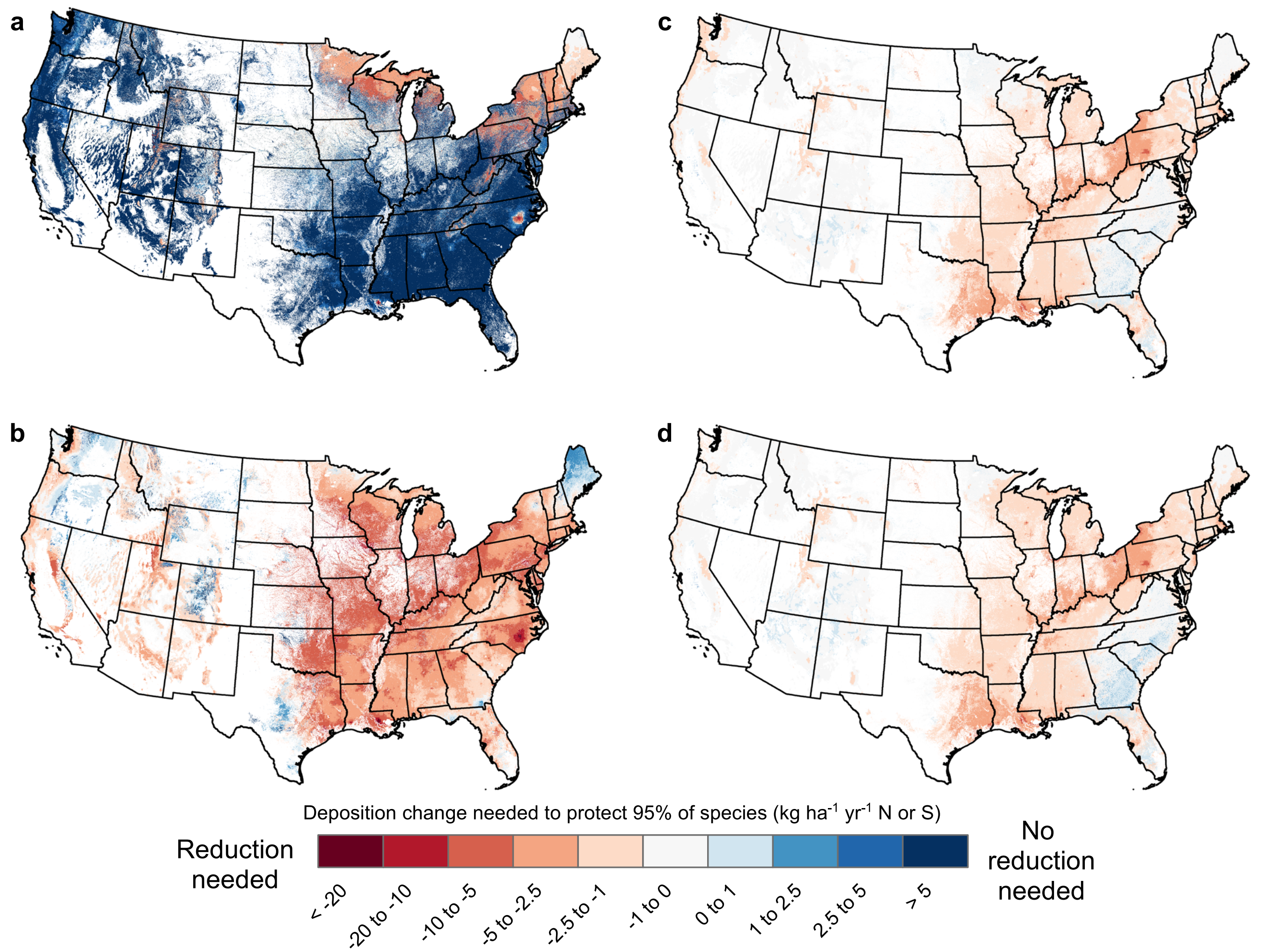
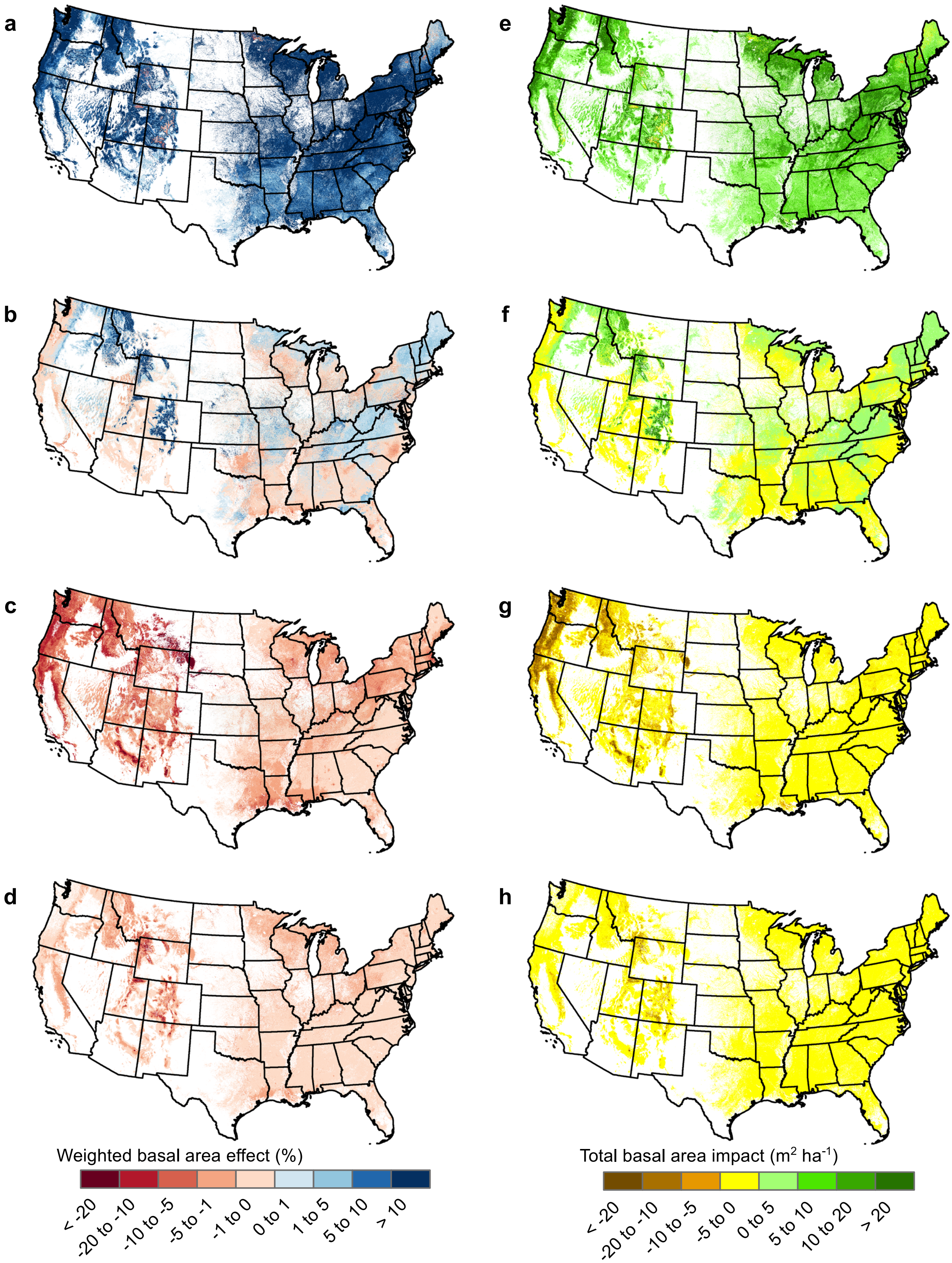


Extended Data Fig. 3 | ΔD_{g5} and ΔD_{s1} values across the CONUS for N and S deposition. Maps of ΔN_{g5} (**a**), ΔN_{s1} (**b**), ΔS_{g5} (**c**) and ΔS_{s1} (**d**) values (kg ha^{-1} yr^{-1} N or S) across the CONUS compared to 2017–2019 average N and S deposition. State boundaries generated by the US Census Bureau[62]. Species' surfaces modified from ref. 42.

https://doi.org/10.1038/s41893-023-01203-8



Extended Data Fig. 4 | See next page for caption.

 https://doi.org/10.1038/s41893-023-01203-8

Extended Data Fig. 4 | The weighted basal area effects (a-d) and the total basal area impact (e-h due to 2017–2019 average N and S deposition. The basal area weighted effect (%, BA_P) due to 2017–2019 average N or S deposition in each 250-m grid cell for N-influenced growth (**a**), N-influenced survival (**b**), S-influenced growth (**c**), and S-influenced survival rates (**d**). The total basal area impact using BA_T (m^2 ha^{-1}) during the same time period are also shown for N-influenced growth (**e**), N-influenced survival (**f**), S-influenced growth (**g**), and S-influenced survival rates (**h**). State boundaries generated by the US Census Bureau[62]. Species' surfaces modified from ref. 42.

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Corresponding author(s): Justin G. Coughlin

Last updated by author(s): Jul 13, 2023

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used for data collection.
Data analysis	R, v. 4.1.1 Python, v. 3.1 ArcGIS Pro, v. 3.0.3 Package names are provided in all relevant README files on the Github code repository and the figshare+ data repository. Python packages: os, timeit, arcpy, arcpy.SpatialAnalyst, numpy R packages: RColorBrewer, ggplot2, dplyr, magrittr, data.table, tidyr, purrr, reshape2, openxlsx, tictoc, tidyverse, lubridate, stringr Python and R code are available at: https://github.com/Justin-Coughlin/air_pollution_effects_trees

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- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
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The datasets generated and analyzed during the current study are available in a data repository (DOI: 10.23719/1529199) and via request for materials through correspondence with CMC. The data repository includes all of the metadata while the raw csv files, aggregated summary files, raw vector-based data, and aggregated raster data are available on OneDrive by contacting CMC. The tree species parameters that were analyzed during this study are included in the Horn et al. (2018) article (and its supplementary information files). The continuous raster surfaces of tree species that were analyzed during this study are included in the Wilson et al. (2013) dataset. The 2000-2019 air pollution raster surfaces (v. 2018.2) that were used during this study are publicly available from the National Atmospheric Deposition Program here: https://nadp.slh.wisc.edu/committees/tdep/.

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	N/A
Population characteristics	N/A
Recruitment	N/A
Ethics oversight	N/A

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	This study evaluates the effects of twenty years of air pollution decreases on two ecological factors (growth rates and survival probability of tree species) across the contiguous United States. Using a constant forest cohort, the study uses dose-response curves for 94 different tree species to quantify the magnitude of effects to the ecological factors in a spatiotemporal manner. Effects were evaluated using both a vectorized (i.e., point-based) and rasterized (i.e., continuous) approach. The study focuses on fifth percentile effects to understand how sensitive species are affected in an effort to understand protection levels for 95% of the forested area. Additionally, forest area effects (m^2 ha^-1) were quantified for 2017-2019 air pollution levels to determine the forest area lost or gained due to recent deposition levels.
Research sample	This study utilizes existing datasets from Horn et al. (2018) for 94 different tree species in the United States. While 71 tree species were reported on in the Horn et al. (2018) dataset, the authors reported on parameterizations for additional species within the Supplementary Information. The 94 species included in this study can be found at the following reference: Horn, K.J., Thomas, R.Q., Clark, C.M., Pardo, L.H., Fenn, M.E., Lawrence, G.B., Perakis, S.S., Smithwick, E.A., Baldwin, D., Braun, S. and Nordin, A., 2018. Growth and survival relationships of 71 tree species with nitrogen and sulfur deposition across the conterminous US. PloS one, 13(10), p.e0205296.
Sampling strategy	Sample sizes were predetermined within this study based on the Horn et al. (2018) cutoff thresholds used for the development of their dose-response curves.
Data collection	No data were collected in this study. Data used in the study are collected by the United States Forest Service Forest Inventory and Analysis Program and by the National Atmospheric Deposition Program.
Timing and spatial scale	This study evaluates air pollution and effects to trees between 2000-2019 across the entire contiguous United States.

Data exclusions	No data were excluded from this study.
Reproducibility	Data and code availability have been provided within the manuscript to allow for reproducibility.
Randomization	Randomization is not included within this study due to the datasets that were used. The Forest Inventory and Analysis dataset is a systematically designed national plot system to provide a coherent and representative dataset of forest characteristics and representativeness across the United States. The objective of this study is to provide a clear picture of the responses of forests to air pollution and how that has been changing over the last twenty years. Because of this, randomization would be counterproductive to the intent of the study.
Blinding	Blinding is not relevant to this study because we use existing datasets.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

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Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging