

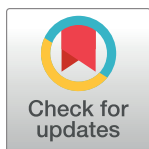
RESEARCH ARTICLE

The hidden value of trees: Quantifying the ecosystem services of tree lineages and their major threats across the contiguous US

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Abstract

Trees provide critical contributions to human well-being. They sequester and store greenhouse gasses, filter air pollutants, provide wood, food, and other products, among other benefits. These benefits are threatened by climate change, fires, pests and pathogens. To quantify the current value of the flow of ecosystem services from U.S. trees, and the threats they face, we combine macroevolutionary and economic valuation approaches using spatially explicit data about tree species and lineages. We find that the value of five key ecosystem services with adequate data generated by US trees is \$114 billion per annum (low: \$85 B; high: \$137 B; 2010 USD). The non-market value of trees from carbon storage and air pollution removal far exceed their commercial value from wood products and food crops. Two lineages—pines and oaks—account for 42% of the value of these services. The majority of species face threats from climate change, many face increasing fire risk, and known pests and pathogens threaten 40% of total woody biomass. The most valuable US tree species and lineages are among those most threatened by known pests and pathogens, with species most valuable for carbon storage most at risk from increasing fire threat. High turnover of tree species across the continent results in a diverse set of species distributed across the tree of life contributing to ecosystem services in the U.S. The high diversity of taxa across U.

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S. forests may be important in buffering ecosystem service losses if and when the most valuable lineages are compromised.

Author summary

Humans benefit from trees in many ways, including the role they play in regulating climate, filtering air pollution and providing food, fiber and fuel. Trees also face increasing risks of damage and mortality from global change forces, threatening the benefits forests and plantations provide. Trees in the contiguous US generate over \$114 billion per year from five key ecosystem services. The “hidden” value of trees—the non-market value from carbon storage and air pollution filtration—far exceeds their commercial value. Most tree species face threats from climate change, many face increasing risk of exposure to major forest fires, and 40% of total woody biomass is threatened by pests and pathogens. The most valuable US tree species and groups—including the pines and the oaks, which also contain the highest numbers of species—are under threat from pests and pathogens. The services generated by trees come from many different lineages across the tree of life as a consequence of the high turnover in the species and lineages across regions. The study highlights the importance of sustaining ecosystem services from the diversity of trees that grow across the US.

Introduction

Trees contribute to human well-being by sequestering and storing greenhouse gasses, filtering air pollutants, providing aesthetic and recreational benefits, provisioning wood, food, and other marketable products, and creating habitat for numerous other species [1–3]. The abundance and composition of US trees is changing due to a complex set of accelerating global change drivers, including increasing invasive pests and pathogens [4,5], greater frequency of major fires [6], and changing climatic regimes [7]. These threats have the potential to undermine the benefits trees provide and the societal value they could provide to future generations. In this study we seek to determine the ecosystem services value of US trees and of individual phylogenetic lineages across the tree of life, identify the services that contribute most to their value and quantify the extent to which these services are threatened by global change. We ask how the non-market value of trees compares to their commercial value, and whether the tree species and lineages that currently provide the greatest benefits are facing substantial global change threats. In doing so, we provide a baseline accounting—as comprehensively as feasible given current data—of the value of US tree ecosystem services, the major threats they face, and their distribution in geographical and macroevolutionary space.

We synthesize existing data sources to estimate the annual net monetary value of five key ecosystem services provided by over 400 tree species across the contiguous US. Our analysis includes two regulating services—climate and air quality regulation—and three provisioning services—managed production of wood products, food crops and Christmas trees. Spatially explicit information by species was available for these five services. We did not include other important ecosystem services generated by trees, such as aesthetics or recreation, because spatially explicit information by species was not available.

Analyses of regulating and provisioning ecosystem services supported by biodiversity typically use ecosystems or landscapes [8] rather than individual species [9] or lineages as the unit

of study, even though conservation efforts frequently target species, particularly rare or endangered species [10] and consider their phylogenetic context [11,12]. To our knowledge, no assessment currently exists of the service value of individual tree species and tree lineages. Filling this gap can increase our basic knowledge of the tree species and lineages on which we depend and contribute to precision management of forests—efforts that focus on the health and growth of individual species or lineages, considering their symbionts, pests and pathogens, environmental preferences and physiological tolerances. In this study, we assess for the first time, to our knowledge, the production of ecosystem services of individual tree species in the contiguous U.S. based on their characteristics and tree inventories that allow them to be mapped accurately across space. The contiguous U.S. refers to the lower 48 states not including Alaska and Hawaii.

No single tree species has the physiological tolerance to occur in all forests across a continent. Over time, different species have evolved that collectively tolerate a wide range of climatic and environmental gradients [13]. The tree of life comprises all of the phylogenetic lineages—groups of species with shared ancestry—that have evolved on Earth. These span larger climatic and environmental gradients than individual member species [14,15]. Due to their shared ancestry, species in a lineage share characteristics unique to that group in terms of genetic potential, form, and traits that influence ecosystem function and contribute to ecosystem services and can also influence susceptibility to certain threats [16–19]. Some ecosystem services, such as edible fruit production, will be concentrated in certain lineages with particular characteristics. Such narrowly distributed services may be at risk if those lineages become threatened. Other ecosystem services, such as carbon storage, will be distributed broadly across the tree of life, given that all trees store carbon. However, if dominant tree species or lineages that provide a large fraction of these services are threatened, then the provisioning of these services is also at risk, at least for a period of time before other species grow to take their place.

As a consequence of the evolved variation among species in physiological tolerances and niches, the turnover—or beta diversity [13,20,21]—of tree species and phylogenetic lineages across major environmental gradients may be important to generating the full value of tree ecosystem services. While we do not explicitly consider the value of tree biodiversity in terms of net biodiversity effects—enhanced productivity [22,23], multifunctionality, resilience [24] and ecosystem services [25] of diverse tree stands compared to expectations from monocultures—we consider how the breadth of tree species and tree lineages across the tree of life that inhabit the range of environments across the contiguous US contribute to current ecosystem services. To do so, we map the value of trees and calculate the economic contributions to these services of every US tree species and lineage.

To gain insight into where trees are most threatened regionally and by what type of threat, we map where trees are most threatened by pests and pathogens [4], climate change [7] and increases in the frequency of major fires [6]. We further calculate the extent to which each tree species is threatened to understand how these threats are differentially distributed among taxa. Vulnerability to these threats varies among species both because of differences in physiology and spatial proximity to threats [26–28]. Environmental change, pests, and disease are anticipated to cause decline in some species and lineages that currently provide high levels of services in certain regions of the U.S. [29–31]. We identify the locations across the U.S. and across the tree of life where service value is likely to be most affected. This analysis identifies potential problems that can be targeted by precision forestry management practices [10]. Our approach goes beyond previous work by allowing us to identify where tree conservation and threat mitigation will be most valuable and which specific lineages within a landscape deserve particular attention.

Results

Between 2010 and 2012, trees in US forests, orchards, and plantations provided nearly \$114 billion (B) per year (low: \$85 B, high: \$137 B; 2010 USD) in net value via two regulating services (climate and air quality regulation) and three provisioning services (wood products, tree crops and Christmas tree production) (Fig 1A). Climate regulation benefits via carbon storage in tree biomass represented 51% of this net annual value, while preventing human health damages due to air pollution filtering by trees, i.e., air quality regulation, represented 37% of the annual net value. The remaining 12% of the net annual value came from provisioning services. Estimates of provisioning services are more precise than the estimates of annual regulating service values. The differences in precision are driven mainly by the differences in the available information about the per unit values—or prices—of these ecosystem services. The provisioning services analyzed here generate commercial products that have a market price. In contrast,

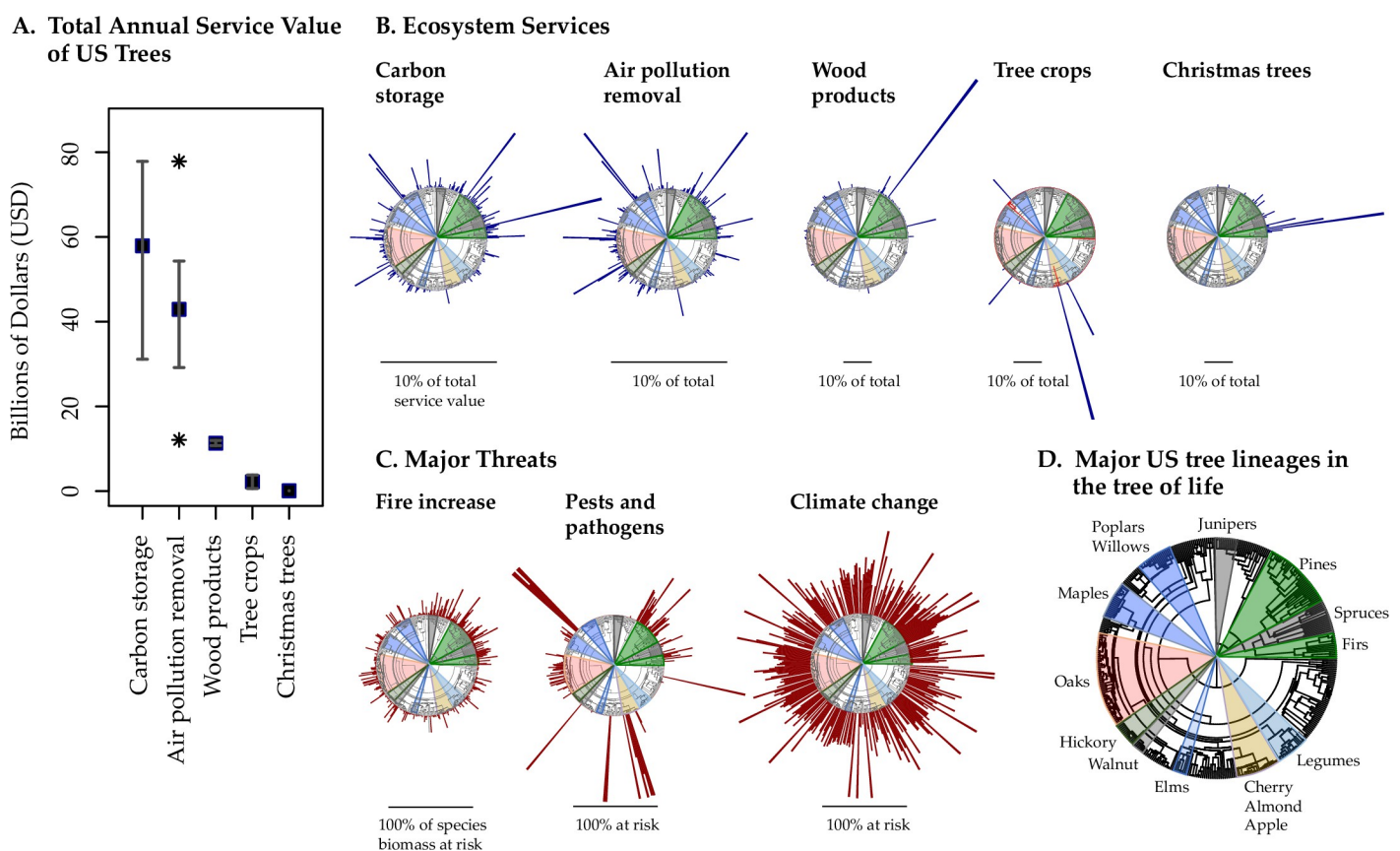


Fig 1. (A) Total net annual ecosystem service values provided by contiguous US trees between 2010 and 2012. The squares give mean estimated value and the error bars show the range in expected values. (B) Ecosystem service annual value (blue bars) and (C) potential threats (brown bars) for tree species across the tree of life. Ecosystem service value bars emanating from each tree of life measure the percentage of total service value generated by each species. Threats bars emanating from each tree of life measure the percentage of each species' current total biomass at risk from the indicated threat. Climate change refers to tree biomass threatened from changes in multiple temperature and precipitation variables. (D) Phylogeny of the US trees, with color wedges indicating the location of particular clades (also shown in (B) and (C) trees of life). Note that ecosystem service values for some tree crop species in B are negative and shown in red pointing inward. See the Methods and Data section for details on error bound calculations in A. The error bound around air quality regulation reflects uncertainty in the air pollution dose–human health damage response function. Asterisks for air quality regulation represent the additional uncertainty created when the uncertainty in the value of a statistical life (VSL) is included in the calculation of human health damages avoided by tree-based filtering of air pollution. Contributions of tree species to carbon annual value (B) (and total ecosystem service value) are significantly more dispersed across different branches of the tree of life than expected at random—with mean phylogenetic distances, MPD = 489 ($P = 0.012$) and MPD = 475 ($P = 0.037$)—while contributions of tree species to crop value are significantly more clustered within certain branches of the tree of life than expected at random (MPD = 189, $P = 0.001$). The threat from increases in frequency of severe fires is significantly overdispersed across the phylogeny (C), (MPD = 505, $P = 0.001$), while pests and pathogen threats are more likely to threaten a close relative that is also threatened than expected at random (MNTD = 52, $P = 0.001$). See S2 Table for details.

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the per unit values of climate and air quality regulating services, given by the social cost of carbon (SCC) and the value of a statistical life (VSL), respectively, are estimated with a range of models with different sets of assumptions and simplifications, all using imperfect data, leading to large error bounds [32–35].

Most valuable tree lineages in US forests, plantations, and orchards

Benefits provided by trees in the US are distributed across the tree of life (Fig 1B), yet two major lineages—the pines (*Pinus*) and the oaks (*Quercus*)—respectively generated \$25.4 B and \$22.3 B in net benefit annually between 2010 and 2012 and are by far the most valuable genera in the contiguous US (Table 1). Both lineages have a high number of species that occupy diverse ecological niches and collectively contribute to their high abundance and biomass across the continent [15]. Pines dominated annual net revenues from wood products at \$7.4 B, due in part to the high volume of wood produced and partly due to their higher than average price. Pines generate more than five times the timber net revenue of any other genus (Table 1). Oaks had the highest annual climate (\$10.7 B) and air quality regulation values (\$11.0 B). All US tree species provide some carbon storage and air quality regulation service value. A species' air quality regulation value depends on its abundance and total leaf area as well as the proximity to human populations affected by pollution [28,36]. Consequently the importance of oaks for regulating service value can be attributed to the high number of species and large populations sizes of many of those species across the US landscape; and in the case of air quality regulation, their abundance near large human population centers.

Within the family Rosaceae, the genus *Prunus*, which includes almonds, peaches, and cherries, contributed nearly \$2.0 B to US agricultural net revenue annually between 2010 and 2012 (*Prunus* species made up 35.1% of all tree crop acreage between 2010–2012), while the apple genus (*Malus*) contributed more than \$0.94 B. Although apple's market value per unit of yield was not very high between 2010 and 2012, it was the third most planted tree crop genus, only behind *Prunus* and *Citrus*. The *Citrus* genus (family Rutaceae), is also an important crop genus in the US (the second most widely planted genus between 2010 and 2012). However, the annual net returns from citrus products were negative between 2010 and 2012 due to abnormally low citrus market prices [37] and the prevalence of citrus greening bacterial disease in Florida and to a lesser extent, Arizona and California [38].

For the set of ecosystem services examined here, the most valuable tree species in the US as of 2010–2012 were loblolly pine (*Pinus taeda*), generating \$12.9 B (low: \$11.0 B; high: \$14.3 B;

Table 1. The most valuable contiguous US tree genera ranked according to aggregate net annual value (2010 USD) generated across five ecosystem services between 2010 and 2012: annual climate regulation value via carbon storage, annual air quality regulation via health damages avoided due to air pollution removal (PM_{2.5} and O₃), and annual net revenue from wood products, tree crops, and Christmas tree production.

Rank	Common Name	Scientific Name	Aggregate	Climate Regulation	Air Quality Regulation	Wood Products	Tree Crops	Christmas Trees
1	Pine	<i>Pinus</i>	\$25,389,289,489	\$10,597,549,418	\$7,402,536,592	\$7,380,913,415		\$8,290,065
2	Oak	<i>Quercus</i>	\$22,327,731,163	\$10,702,056,084	\$11,048,359,855	\$577,315,224		
3	Maple	<i>Acer</i>	\$11,074,529,157	\$5,243,370,527	\$5,534,340,848	\$296,817,782		
4	Douglas-fir	<i>Pseudotsuga</i>	\$8,555,113,301	\$5,908,159,459	\$1,455,004,741	\$1,183,176,063		\$8,773,039
5	Hemlock	<i>Tsuga</i>	\$4,467,535,785	\$3,008,325,009	\$1,225,172,716	\$234,038,059		
6	Cherry/Almond	<i>Prunus</i>	\$4,125,822,231	\$780,954,517	\$1,074,096,913	\$217,688,989	\$2,053,081,812	
7	Spruce	<i>Abies</i>	\$3,839,147,244	\$2,885,232,261	\$818,850,801	\$75,832,332		\$59,231,849
8	Hickories	<i>Carya</i>	\$3,598,686,663	\$1,738,261,008	\$1,752,900,146	\$60,175,136	\$47,350,374	
9	Tulip tree	<i>Liriodendron</i>	\$3,009,207,291	\$1,373,715,800	\$1,499,753,000	\$135,738,491		
10	Ash	<i>Fraxinus</i>	\$2,908,276,099	\$1,384,668,426	\$1,454,588,583	\$69,019,090		

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2010 USD) in net value annually and Douglas-fir (*Pseudotsuga menziesii*). Almond trees generated \$2.5 B annually between 2010 and 2012, the highest annual net return across all crop trees in the US (low: \$1.9 B; high \$3.1 B) (S1A Table). The high almond tree value was due to their abundance (471,259 ha; 20,397 more ha per annum than the next most abundant fruit tree, oranges) and high market price (between 2010 and 2012, the nominal price of a pound of almonds was \$1.99; of all the tree crops, only pistachios had a higher per pound market price during this period).

Variation among species in ecosystem service value

Tree species with high carbon storage value, the most valuable service, are more evenly dispersed across the tree of life than expected at random (NRI = -2.04, $P = 0.02$, S2 Table). Air quality regulation value is distributed at random across the tree of life (NRI = -0.54, ns). At a finer scale looking only at close relatives, nearest evolutionary neighbors tend to have similar air quality regulation values (NTI = 1.61, $P = 0.02$, S2 Table), even though these clusters of similar and closely related species are spread across all lineages.

Unlike the regulating services, tree crops are significantly clustered in the tree of life (NRI = 4.35, $P = 0.001$, S2 Table) and include relatively few lineages, such as trees in the Rose family (almonds, apples, pears, and cherries) (Fig 1B, Table 1). Many lineages provide wood products, but the amounts vary widely among species within those lineages, and the most valuable species are not significantly clustered within any lineage. The overall value of ecosystem services for the benefits evaluated are dispersed more evenly across the tree of life than expected at random (NRI = -1.69, $P = 0.037$), consistent with trends found at global scale [39]. Species that generate individual services—like tree crops, wood products, or Christmas trees—tend to be found in different places in the tree of life, and the overdispersion of the most valuable service (carbon) shows that many different lineages contain abundant species that contribute to carbon storage.

Spatial variation in ecosystem services of trees across the contiguous U.S.

The spatial distribution of ecosystem services produced by US trees between 2010 and 2012 largely reflects forest, plantation, and orchard distribution (Fig 2). Climate and air quality regulation service values are a direct consequence of where forests grow; they cover most of the contiguous US, excluding grassland and desert biomes (Figs 2A and 2B). However, health damages avoided by tree-based air pollution removal values tend to be greatest near large urban areas that are surrounded by forests. Between 2010 and 2012 people living in eastern urban areas, particularly the New York, Boston, Pittsburgh, and Atlanta areas, as well as Seattle and California's Bay Area benefited greatly from air pollution removal by forests between 2010 and 2012 (Fig 2B, S1H and S1I Text, S7 and S8 Tables, S3 Fig). Trees can also filter and absorb pollutants released by forest fires [28,40]. However, our air quality regulation service valuation is only based on the industrial and transportation-related emissions that trees filter and absorb.

The most valuable tree crops are grown on the coasts, in the Southwest, and in warm and arid climates, often where forests do not grow (Fig 2C). Tree crops produce the highest net returns in California but also generate high net values in several Southwest, Southern, and Eastern states. In contrast, timber production is concentrated in a subset of the regions that also produce high climate regulation and air pollution removal values, including the Southeast and the Pacific Northwest, as well as in the Northeast and Upper Midwest (Fig 2D).

Both services and threats are spatially heterogeneous, with different kinds of services and threats concentrated in different parts of the contiguous U.S. (Figs 2 and 3). Climate change threatens species in all parts of the continent (Fig 3A), while pest and pathogen threats are

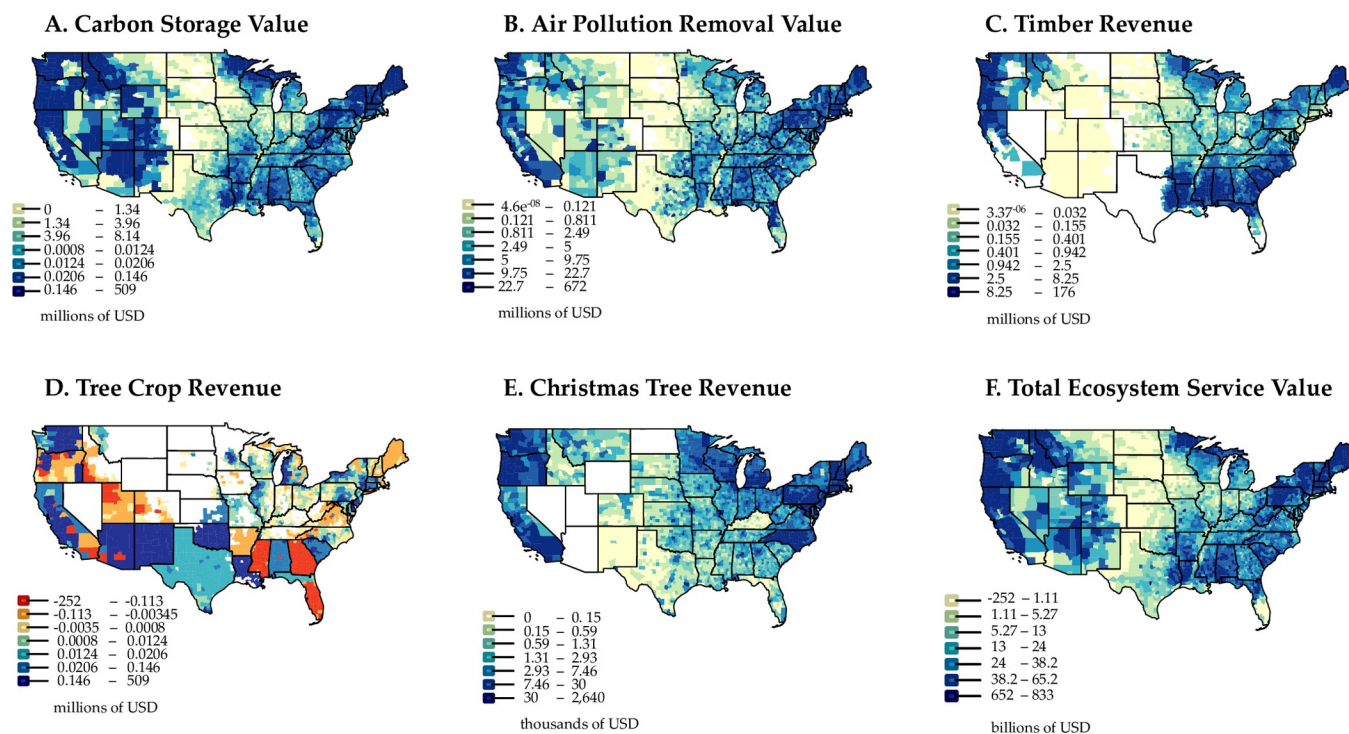


Fig 2. Annual net ecosystem service value generated between 2010 and 2012 (in 2010 USD) (A) climate regulation via carbon storage, (B) air quality regulation via human health damages avoided by tree-based filtering of air pollution (C), wood product net revenue (D) tree crop net revenue, (E) Christmas tree net revenue, (F) and the total value across all five services in contiguous US counties across the U.S. Darker shades of blue indicate higher annual net values. Shades of orange and red represent negative net annual values. Missing data are indicated in white. A-D are reported in millions of USD, E in thousands of USD and F in billions of USD. Annual Tree crops, wood product, and Christmas values account for costs of production while annual provisioning service values (climate and air quality regulation) have no cost of production (these values are incidental). See Methods and Data for details of how values are allocated to counties.

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strongest in counties of the Southwest and Southeast (Fig 3B). Major wildfires are expected to increase especially in California and the Intermountain West (Fig 3C), coincident with where carbon annual storage value is highest (Fig 2A).

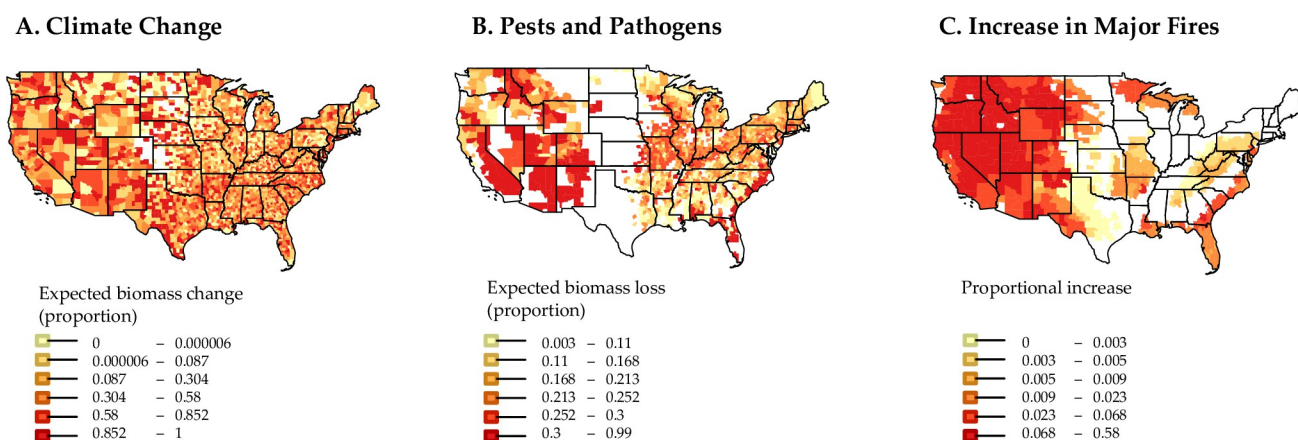


Fig 3. Magnitude of county-level threats across the contiguous US. Darker colors indicate greater threat to the biomass currently located in the county. Missing data are indicated in white. (A) Proportion of current total tree biomass in each county that is expected to be exposed to climatic regimes (determined from multiple precipitation and temperature variables) outside the current range that they can tolerate as of 2050. (B) Proportion of current tree basal area in each county that is expected to be lost to pest and pathogen outbreaks as of 2050. (C) Proportional increase in fire exposure (number of expected major fires per week compared to the 20th century maximum) per county as of 2050. See Methods and Data section for details of how values are allocated to counties.

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Low similarity in the tree species that provide ecosystem service value in different regions

We generally found low similarity in the tree species (Fig 4 and S1 Fig) that provide ecosystem services in different regions. Thus, different tree species tend to account for the same ecosystem service in different ecoregions. Ecoregions represent regional ecological units (Fig 4C) of environmental similarity. Tree crops, which are frequently planted in geographically disparate but climatically similar regions, were an exception. Species similarity values (possible range: 0–1) averaged across pairs of ecoregions, were much higher for tree crops (0.54, SD 0.23) than for carbon storage (0.09, SD 0.13), air quality regulation (0.07, SD 0.13) or wood products (0.04, SD 0.1). Lineage (or phylogenetic) similarities of tree services (S1 Fig) among ecoregions were always higher than species similarities, indicating that different species in the same lineage (e.g., oaks) provide services in different regions. Lineage similarities among regions were again higher for tree crops (0.68, SD 0.16) than for carbon storage (0.56, SD 0.14), air quality regulation (0.55, SD 0.14) or wood products (0.53, SD 0.19). However, Christmas trees, calculated for states only, showed very high lineage similarities among states (0.8, SD 0.24), despite very low species similarities (0.18, SD 0.19), as all of the different tree species that provide this service are from the same major branch in the tree of life.

Pines provided the greatest wood product net revenue in a number of regions, although in some regions Douglas-fir or oak trees provided more of this service. Overall, we found low similarity (high spatial turnover) in the species that provide the ecosystem services we evaluated (Fig 4, S1 Fig) because different species—and to a lesser extent, different lineages—grow

	A. Species similarity			B. Phylogenetic similarity		
	Median	Mean	SD	Median	Mean	SD
Carbon Storage Annual Value	0.02	0.09	0.13	0.54	0.56	0.14
Air Pollution Removal Value	0.01	0.07	0.13	0.54	0.55	0.14
Wood Products Annual Net Revenue	0.00	0.04	0.10	0.50	0.53	0.19
Tree Crop Annual Net Revenue	0.50	0.54	0.23	0.68	0.68	0.17

C. Ecoregions in US Forests



Fig 4. Similarities among species (A) and phylogenetic lineages (B) in the trees that contribute to ecosystems in different ecoregions (C) of contiguous US forests. Shown are the mean, median and standard deviation of pairwise similarities across ecoregions using 1-Bray-Curtis dissimilarities (species similarities) and phylosor (Bryant et al. 2008) similarities (phylogenetic similarities), with values ranging between 0 and 1. Higher values indicate many of the same species or lineages contribute to the ecosystem service in different ecoregions (1 = all of the same species or lineages contribute), while lower values indicate different species or lineages contribute to an ecosystem service in different ecoregions (0 = none of the same species or lineages contribute). Ecoregions are defined by the USDA Forest Service (C). See S1 Fig for details.

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in different regions. Consequently, the current total ecosystem service value of trees in the US results from many different species that occur naturally or are planted across different climates and environments.

Species and lineages most threatened by regional and global change

The important ecosystem services that trees provide are under threat from global change. Climate change, measured as the percentage of the species' biomass expected to be exposed to levels of annual temperature, precipitation, and aridity in 2050 that is outside of the range they can tolerate, fire frequency and intensity, measured by average projected change in fire frequency in the counties that contain the species, and the growing number of invasive pests and pathogens are all projected to impact the health, mix, and spatial distribution of U.S. tree populations. Most tree species in the U.S. are threatened by climate change. Due to increasing aridity, alone, 45% of species are anticipated to have at least 10% of their current biomass encounter climates outside their current climatic envelope. Eighty-eight percent of tree species are projected to have at least 10% of their biomass exposed to climates outside the current climate envelope, impacting nearly 40% of total tree biomass in the contiguous U.S. Known pests and pathogens are threatening 16% of tree species, potentially impacting up to 40% of total tree biomass. Increased fire frequency is expected to impact 40% of species, meaning that these species are expected to encounter at least one additional major fire somewhere across their range (Table 2).

We evaluated the dispersion of these threats across the phylogeny. Threats to tree species were dispersed widely among lineages (S2 Table), except for known pests and pathogens, which clustered within certain lineages (NTI = 2.66, $P = 0.001$, S2 Table), including the oak and pine genera as well as in most of the crop species (Fig 1C). Consequently, tree species that are known to be at risk of damage from pests and pathogens—measured as the fraction of the species' current biomass (tree crop species) or basal area (non-tree crop species) threatened by pests and pathogens—are also significantly more likely to have close relatives also at risk. Tree vulnerability to enemy attacks is tightly linked to phylogenetic identity, given long-term evolutionary processes that drive enemy-host compatibility [17,41,42]. Therefore, phylogenetic lineage is a strong predictor of risk. However, we acknowledge that the pattern may reflect biases in human knowledge as the pests and pathogens that affect the most abundant and most valuable species are the most studied [43]. Risks to less abundant or less valuable tree species, including novel pathogens that could spread to other species, may not be well understood.

In contrast to pests and pathogens, which have high phylogenetic specificity, the vulnerability of tree species and lineages to changes in climate depends most on where species are

Table 2. Summary of the percent of tree biomass and tree species threatened from climate change linked to increasing aridity, multivariate climate change including changes in temperature, precipitation and aridity, known pests and pathogens, and increased fire exposure.

Threat	% of total tree biomass threatened	Threat threshold description	% of tree species threatened
Climate change–aridity	11.3%	Species with more than 10% of their biomass under threat from climate change–aridity	46%
Multivariate climate change	39%	Species with more than 10% of their biomass under threat by multidimensional climate change (temperature, precipitation, aridity)	88%
Pests and pathogens	40%	Species with more than 10% of their biomass under threat by pests and pathogens	16%
Increasing fire frequency	NA*	Species expected to be exposed to one additional major fire on average across their range	40%

*It was not possible to estimate percent of tree biomass threatened with increased fire frequency.

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distributed in relation to predicted climate changes. Tree species forecast to have high exposure to climate threats are widely dispersed—no different from random dispersion—across the tree of life (NRI = -0.30, S2 Table), given that changes in climate are expected across the country. Similarly, the threat due to increases in fire frequency is overdispersed—more evenly spread than random dispersion—across the tree of life (NRI = -4.59, $P < 0.001$, S2 Table), indicating that the spatial distribution of species in regions where fire is increasing matters most in predicting the threat, not their phylogenetic lineage.

Associations between services and threats by species

Known pests and pathogens are predicted to disproportionately affect species that generate high annual net climate regulation, air quality regulation, and wood product values (Fig 5A). Some of this positive association is undoubtedly driven by an abundance effect. Species with higher abundance generate more economic value, all else equal. More abundant species may also attract a higher prevalence of insects and pathogens and enable faster spread, exacerbated by the fact that some of the most abundant species are closely related and hence more susceptible to the same threats [41,44]. Pests and pathogens of more abundant species may also be better documented. The only other statistically significant positive associations between species-level economic value and species-level threats are 1) wood product value and degree of risk due to climate change and 2) carbon storage value and the risk of increasing frequency of major fires. These associations are less easily explained by species abundances and are likely linked to a spatial confluence of high value species and these particular threats.

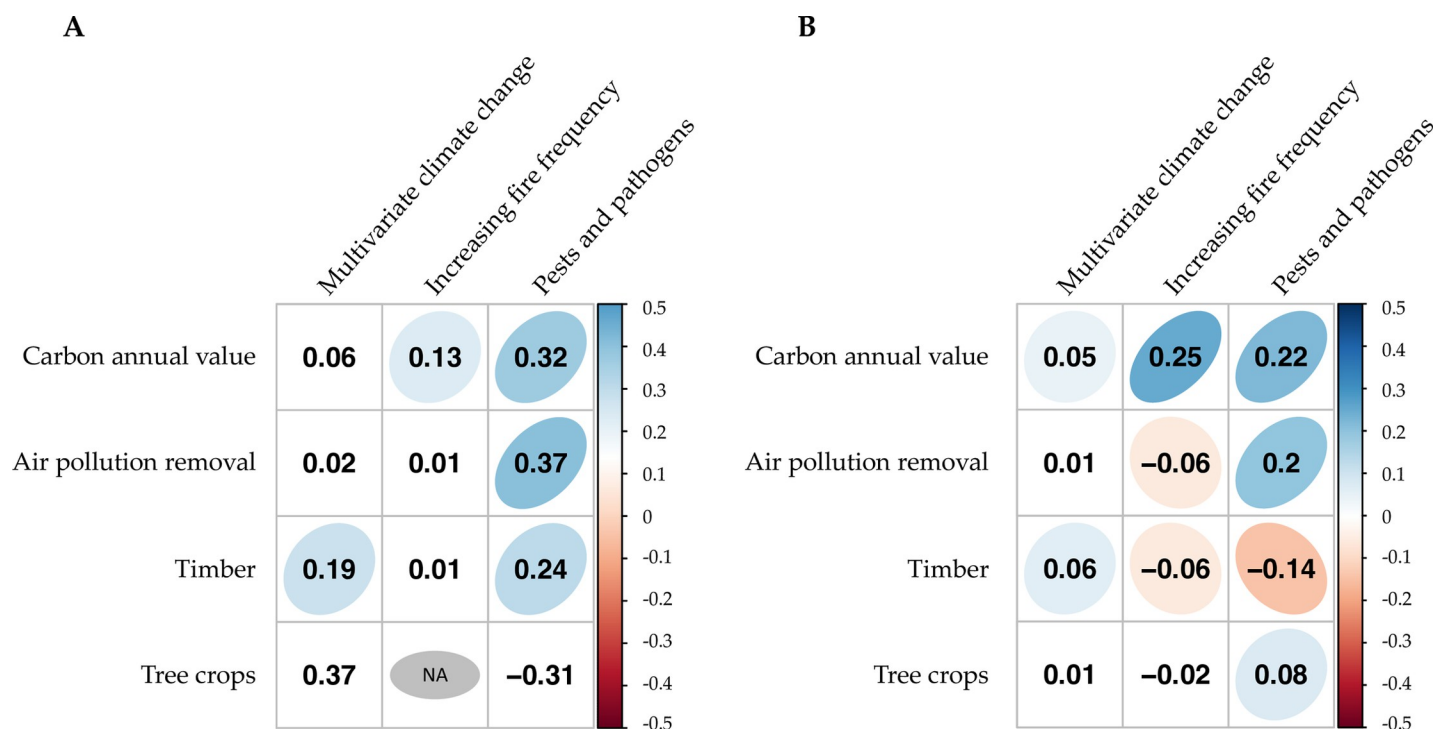


Fig 5. Associations between annual net ecosystem service values of tree species in the US and their predicted threats and drivers of change based on Spearman's rank-order correlations. A) Species-level correlation coefficients (ρ) between annual net ecosystem service value and predicted threats. B) Spatial correlations between annual net ecosystem service value and predicted threats by US counties. Colors (blue) indicate significant positive associations, indicating more valuable tree species are under more threat. Darker colors indicate stronger correlations. Service values refer to those generated between 2010 and 2012. Modeled expectations for changes in frequencies of major fire are not available in some regions precluding accurate estimation of their potential threat to some tree crop species in A; correlation is not shown.

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Spatial association of services and threats

Spatial associations between tree services and threats largely parallel species associations (compare Fig 5B to 5A). The counties with highest carbon annual value from trees coincide with those most impacted by increases in fire frequency, pests and pathogens, and climate change. Likewise, air pollution removal values are highest in counties most threatened by pests and pathogens. Pest and pathogen threats—strongest in counties of the Southwest and Southeast—are negatively associated with timber value, but positively associated with tree crop values.

The only major disagreement between species- and spatial-level tree service and threat correlations is found in the wood product–pest and pathogen nexus. While the most valuable wood product (timber) species are disproportionately affected by pests and pathogens, many of the counties that produce more timber value are less affected by pest and pathogen threats than counties that produce less timber. Given that species vary in abundance and counties vary in diversity, we do not necessarily expect species and spatial correlations to correspond. We further note that the associations are determined by non-parametric spearman-rank correlations which depend on the rank order rather than the magnitude of values. The discrepancy could also be linked to spatial variability in the spread of pests and pathogens and where timber is produced. Some of the major pests and pathogens that impact important timber species in the western and central US have not yet invaded or do not currently impact areas with high wood product production in the northeastern and southeastern US. For example, mountain pine beetle (*Dendroctonus ponderosae*), a species of pine bark beetle that carries pathogenic fungi, yeast and bacteria, has caused considerable damage in British Columbia and the western U.S. to pines that are valuable timber species [45,46]. However, it is currently not present in the northeastern or southeastern U.S., both regions that have high timber production [47]. Similarly, the oak wilt fungus (*Bretziella fagacearum*), which is killing widely distributed and valuable oak species in the central U.S., has not yet invaded the eastern U.S. [29,48], including regions where timber production is high.

Discussion

This study shows that the “hidden” value of trees—the non-market value from carbon storage and air pollution filtration—far exceeds their commercial value. The most valuable U.S. tree species and groups—including the pines and the oaks, which also contain the highest numbers of species—account for 42% of the value of these services and are under greater threat from pests and pathogens than other lineages. Overall, nearly 90% of species face substantial threats from climate change, many face increasing fire risk, and 40% of total woody biomass is threatened by pests and pathogens (Table 2). For the ecosystem services quantified in the current study—climate and air quality regulation, and three commercial provisioning services (wood products, tree crops and Christmas tree production)—trees in the contiguous U.S. contributed over \$114 B annually (2010 USD) in value. The broad distribution of services across the tree of life is a consequence of the high turnover in composition (beta diversity) across the continent, highlighting the importance of sustaining a diverse group of trees for human health and well-being across the U.S.

Regulating ecosystem services in different regions of the country are provisioned by different tree species, such that each region gets their climate and air quality regulation services from a different set of species. No single species is responsible for a large portion of the calculated annual service value, and individual tree species differ markedly in their ecosystem service value. Consistency of these services across regions depends on the maintenance of tree diversity across the country as the species that provide the highest values arise from species across the tree of life (Fig 1B). In contrast to individual species, two genera, the pines and oaks,

contribute disproportionately to the five ecosystem services we assess, generating nearly \$47.7 billion each year (Table 1). These two highly valuable lineages are also the most diverse, with a large number of individual species occupying diverse niches that span the continent.

These important genera are at risk from lineage-specific pests and pathogens that have specialized for specific branches of the tree of life. Other global change threats, including climate change and fire, impact lineages all across the tree of life. Wildfires are a dangerous threat, particularly in the western regions, as they (at least temporarily) destroy tree service supply while at the same time creating local and regional air pollution [49] that will be less effectively mitigated by trees. As forest ecosystems are impacted by global change, the mix of tree species that provide critical ecosystem services will be altered. The consequences of these changes are unknown and could lead to losses in ecosystem benefits and human well-being but could also plausibly lead to an increase in some services. Anticipating the consequences of these changes remains a critical challenge.

Our estimate of the annual value of ecosystem services provided by trees depends on the stock of trees at the time of evaluation (2010–2012), and as such represents a static snapshot of the value of trees. A full dynamic analysis of the value of trees would attempt to estimate the present value of the flow of ecosystem services through time incorporating the potential future trajectories for distribution of trees and the potential future trajectories for prices for services. Such an analysis should incorporate potential future threats from pests and pathogens, fire, climate change, and other risks. How forest composition would change in response to such threats requires analysis of what species might be well-adapted to future conditions, and what species might expand should a pest or pathogen reduce the abundance of a currently common tree species. Further, we treat climate change, pests, and fires as independent threats, due to the complexity of the modeling of their relationships and the availability of data. Addressing these issues is an important but challenging goal for future research.

The current analysis likely understates the value provided by U.S. trees for several reasons. First, most urban ecosystems are not considered in this analysis. The USFS Forest Inventory Analysis (FIA) databases used in this analysis only include natural forests and tree stands managed for productive use, of which few are in urban areas [50,51]. No nationwide spatial database of urban trees exists. Inclusion of urban trees in the analysis would significantly increase the value of health damages avoided due to tree-based air pollution removal, given that air quality improvement benefits are greatest in the most population dense areas [28]. Urban trees would also increase our estimate of climate regulation value. For example, Nowak et al. [50] estimate 643 M Mg of carbon are stored in urban areas, which translates to \$2.31 B (2010 USD) annually using our climate regulation valuation approach (see the Methods and Data section). Second, due to data limitations, we omitted many regulating ecosystem services that trees provide, such as erosion control, flood regulation [52], storm surge regulation [53], urban heat island regulation [54], energy savings due to shade [55], and species habitat provision. Nowak et al. [56] estimate that trees and forests in urban areas in the continental U.S. annually reduce electricity use by 38.8 M MWh and heating use by 246 M MMBtus, translating to \$7.8 B in energy savings annually. We also leave out the contribution of trees to recreation, ornamental, spiritual, and aesthetic values [57–61]. Including these services in our analysis would greatly increase the value provided by U.S. trees.

A complete accounting of the value provided by U.S. trees would also require estimates of the damages trees cause and the cost of their maintenance. While we do account for some of the costs of providing and maintaining wood product, tree crop, and Christmas tree products, there may be additional hidden costs we do not capture, such as the full cost of water used for almond tree production in California. Tree-related damages include pollen and sap-related irritations, injuries to people and property caused by falling trees and limbs, and their role in

generating fires [62–65]. Further, while trees remove some of the air pollution humans would otherwise inhale, trees can exacerbate the damage caused by air pollution. For example, in certain urban street grids, trees block airflow, trapping pollution that would otherwise dissipate [66]. Additionally, trees are a source of the volatile organic compounds (VOCs) isoprene and monoterpenes, which contribute to tropospheric ozone and secondary particle formation [67]. However, trees simultaneously decrease VOCs potentially leading to a slight net reduction [68]. We were unable to include all service and disservice values, a task no study to date has systematically tackled.

The estimated annual values of the climate and air quality regulation have large uncertainty due largely to uncertainty in the social cost of carbon and the value of a statistical life (i.e., the value that people assign to small reductions in the risk of premature death due to improvements in environmental quality). Further imprecision is introduced to the air quality regulation value because of uncertainty in the air pollution dose–mortality response function, although the uncertainty in VSL alone explains approximately 90% of the range in air pollution removal value (S7 Table). The estimated annual values of the provisioning services are more precise because they are calculated from the market price for the per unit value of tree crops, wood products, and Christmas trees, as well as reliable production volume data.

The hidden value of regulating services is the most important source of value generated by trees. Regulating services are currently provisioned from a diverse collection of evolutionary lineages across the continent. The same services are provided by different species in each region—suggesting that regulating services lost due to local or regional extinction of particular species could (eventually) be provided by other species. However, replacement or evolutionary adaptation by tree populations will take time [69–71] during which regulating services may be reduced. In areas where substitute provider species do not emerge or lag times are extensive—which is likely given the long generation times and slow evolutionary rates of many trees—policy intervention will be necessary to preserve the climate and air quality regulation services. Regulating services are not sold on markets and are often not appreciated by the public; therefore, market forces cannot be expected to fill gaps in future regulating services without additional policy instruments [72]. Mechanisms—such as carbon payments, if designed properly—may help enhance regulating services [73].

In contrast to regulating services, provisioning services are generated primarily from a small number of crop trees that cluster within a small portion of the tree of life ($\text{NRI} = 4.35$, $P = 0.001$, S2 Table). Threats to these relatively few tree species and lineages with high provisioning service value are likely to be managed by landowners given the financial rewards to threat mitigation can be captured in existing markets. For example, there are commercial incentives to invest in protection against pests and pathogens that target commercially valuable species like grafting one species onto rootstock of a closely related species that is more resistant to pathogens or abiotic stress [74]. Further, changing environmental conditions may create incentives for these species to be grown in new locations [75,76].

Left unchecked, threats posed by lineage-specific pests and pathogens that target forest trees are of particular concern because major losses of dominant species and lineages that currently have high ecosystem service value would undermine forest capacity to provision these benefits. Currently, the most valuable and diverse tree species and lineages, the pines and the oaks, are under increasing threats from pests and pathogens, such as pine beetle [77,78] and oak wilt [29]. These threats appear to be increasing partially as a consequence of climate change [30, 48], and multiple threats can interact, exacerbating outcomes [79]. The results presented here highlight the importance of targeted management efforts to slow the spread of these diseases and agents of forest decline. Despite successes in developing resistant strains of crop trees and containing pathogen threats, the number of disease and insect threats that

currently put trees at risk is alarming [29, 80, 81], threatening over 40% of U.S. forest biomass [82]. Chestnut blight and Dutch elm disease are two powerful examples of how once-dominant tree species that provided many services were decimated by disease [4].

The high diversity of taxa across U.S. forests may be important in buffering ecosystem functions service losses if and when the most valuable lineages are compromised. If major losses of tree taxa are incurred as a consequence of rising threats, other species will need to fill those voids to maintain ecosystem services. Sustaining the value that trees currently contribute to human well-being depends on sustaining the many tree species and lineages that collectively occupy the diversity of ecological niches across the continent. To do so requires intentional management of forests and trees in the face of myriad and simultaneous global change threats. Our study provides information and an approach that can contribute to precision forestry practices and ecosystem management—an approach that is applicable to other regions globally.

Materials and methods

Ecosystem services

We measured the net value of five tree-related ecosystem services by accounting for the value of benefits provided, minus the direct costs incurred to produce these services when applicable. Climate regulation and air pollution removal have no direct costs. The sources of direct costs for wood products production are in [S3 Table](#) and [83]; for tree crops and Christmas tree production, the sources are in [S4 Table](#). These five services all had publicly available data, national coverage, and well-vetted valuation methods. These five services included two regulating services (climate regulation and air pollution removal) and three provisioning services (wood products, tree crops, and Christmas trees). We did not analyze services such as recreation, wildlife habitat, coastal protection, and aesthetic benefits derived from trees because these services either lacked a nationwide database or a suitable methodology linking benefits to specific tree species.

Annual value of climate regulation via carbon storage. Forest carbon stocks (live aboveground and belowground carbon) of trees by species by county were estimated using data and methods from the U.S. Forest Service (USFS) Forest Inventory and Analysis (FIA) [84]. Total standing live aboveground carbon stocks was estimated following the method of Woodall et al. [85]. The live belowground carbon stocks were modeled as a function of the aboveground live tree carbon stocks following [84] (see [S1 Text D](#)).

The FIA data does not include carbon stored in fruit and nut orchards or Christmas tree farms. We calculated estimates for live aboveground carbon for fruit and nut orchards and Christmas tree farms by species by county. Christmas tree farms have short harvest rotations; fruit and nut orchards have longer rotations. We set carbon storage values for these production systems equal to the mean carbon stored in an orchard or farm's biomass halfway through its rotation (see [S5 Table](#), [S1E Text](#)). We use county level data on orchard acreage to get carbon stored by fruit and nut trees by county [86]. Only state level acreage is reported for Christmas tree farms. We allocated Christmas tree farm acreage to counties based on county-level population (U.S. Census Bureau 2016; see [S1F Text](#), [S6 Table](#)). Overall results for carbon storage are insensitive to county allocation for Christmas tree farms because the latter make up 0.0004% of total calculated carbon storage.

To measure the monetary value of carbon storage for a single year we computed an annualized value for the social cost of carbon (ASCC) ([S1G Text](#)). The ASCC is derived from the social cost of carbon (SCC), which is an estimate of the present value of damages from releasing one ton of carbon into the atmosphere. SCC represents the value of carbon storage in

perpetuity. We converted SCC to an annualized value (ASCC) that represents the value of carbon storage for a single year. We used a range of SCC values to calculate a range of ASCC values. SCC estimates include \$38.57 Mg⁻¹ of C in 2010 \$ assuming a 5% discount rate, \$119.58 Mg⁻¹ of C in 2010 \$ assuming a 3% discount rate, and \$192.87 Mg⁻¹ of C in 2010 \$ assuming a 2.5% discount rate [87]. These values translate to ASCCs of \$1.93 Mg⁻¹ of C in 2010 \$ for a 5% discount rate, \$3.59 Mg⁻¹ of C in 2010 \$ for a 3% discount rate, and \$4.82 Mg⁻¹ of C in 2010 \$ for a 2.5% discount rate.

Annual value of air quality regulation via avoided health damages due to tree-based air pollution removal. Removing air pollutants from the atmosphere provides benefits to human health, crop and timber yields, visibility, materials, and recreational opportunities [88,89]. Here, we calculated the value of the reduction in human mortality from removal of fine particulate matter (PM_{2.5}) and ozone (O₃) from the atmosphere by trees. Reductions in human mortality are the largest of the benefits generated by improving air quality [90].

The benefits from pollution reductions by trees were determined using estimates of the amount of pollution removed by tree species by county by pollutant [28,50], the 2011 National Emissions Inventory [91], and the AP3 integrated assessment model [92–94]. Nowak et al. [28,50] provide estimates of each pollutant removed by species by county by year. We then converted measures of annual pollutant removed by a species in a county to annual average improvements in ambient air quality, measured in µg/m³/year, by dividing the µg/year removed in a county by the volume of air space in the county (land area $\times$ vertical height in meters, see S1H Text).

The AP3 model links emissions of common air pollutants by county in the U.S. to the ambient concentrations PM_{2.5} and O₃ in each county. Using the National Emissions Inventory, AP3, and U.S. EPA's value of statistical life (VSL) estimate of \$7,570,229 (2015 USD), we computed county-level exposures, mortality risk, and monetary damages associated with the baseline level of 2011 emissions [94]. We calculated the average annual damage caused by a pollutant in a county in 2011 (in \$ 2010) by dividing the monetary damage predicted by AP3 for that pollutant in 2011 in the county by the ambient concentration of the pollutant in the county in 2011.

We found the expected annual value of PM_{2.5} removal by a tree species in a county by multiplying the average damage caused by PM_{2.5} in the county (measured in \$/µg/m³) by the amount of the PM_{2.5} removed by the species in the county over the course of a year (also measured in µg/m³). We repeat this process to estimate the annual value generated by a species in a county that removes O₃ from the atmosphere. In Fig 1A shows the expected value of air pollution removal across all species, counties, and the two pollutants.

We used a Monte Carlo analysis to characterize the statistical uncertainty associated with our estimates. Specifically, we constructed two normal distributions, with means and variances that corresponded to the estimated distributions associated with U.S.-EPA's VSL [95] and the concentration-response parameters for PM_{2.5} [96] and for O₃ [97]. We made 1,000 draws from these distributions, calculating benefits of pollution removal by species by county for each draw—thus constructing species and county specific empirical distributions of our benefit estimates. We calculate two sets of 5th and 95th percentile national-level estimates across both pollutants. One set of estimates only uses the uncertainty in the concentration-response function (the mean VSL is always used when constructing this 5th and 95th percentile). The other set of estimates uses uncertainty in both concentration-response function and VSL (S1 H and S1I Texts, S7 and S8 Tables, S3 Fig).

Annual value of wood product production. 2012 roundwood production data (including fuelwood, pulp, and sawlogs) were used at the county level [98]. Some of the roundwood production data in the dataset are attributed to individual species. The remaining production data are reported at the species group level in the dataset. We attributed species group output in a

county to individual species output in that county according to each species' proportion of net volume in the county's total sawlog production from the 2007 to 2012 USFS FIA surveys. We calculated the annual monetary value of a species' roundwood production in a county by multiplying its annual roundwood production in cubic feet by the annualized net value of a cubic foot of harvested roundwood. The annualized harvested roundwood net values assume that all stands are managed as even-age rotation forests. The rotation period or harvest age for each species in a state is given by the FIA. Additional assumptions used when calculating annualized harvested roundwood values include using biomass growth functions parameterized with FIA data [99–101], observed 1998–2014 mean stumpage prices continuing indefinitely (in 2010 USD; S4 Table), and stand establishment costs in 2010 USD [83]. We calculated the expected annualized net value of wood roundwood production across all species and counties. We generated 5th and 95th percentile values of roundwood production at the species and county level using 5th and 95th percentile biomass growth functions for each species in each county. In all cases, we used a 5 percent per annum discount rate (S3 Table, S1 Text A).

Annual value of tree crop production. We calculated annualized net revenues for 21 fruit and nut tree species (S4 Table). We used information on the typical rotation length and the typical number of years between establishment and the production of marketable fruits or nuts to calculate the proportion of years the species produces fruits or nuts. Using state-level data on fruit and nut farm-gate prices for the years 2010 to 2012, state-level data on yields per acre for the years 2010 to 2012 (adjusted by the proportion of years the species produces fruits or nuts), and county-level tree crop acreage data for the years 2010 to 2012 [86], we calculated annual revenue in the years 2010, 2011, and 2012 at the species and county level. Then we used enterprise budget sheets to calculate several estimates of annualized per acre production cost for each species in each county. The expected annualized net revenue for a species in a county across the 2010 to 2012 period is equal to the 2010 to 2012 average annual revenue from that species in that county minus the mean county-level annualized production cost estimate for that species (see S1B Text) and is calculated for all species across all counties. Low and high estimates of annualized net revenue at the species and county level were also generated by using species and county-specific low and high estimates of annualized production cost (S4 Table and S1B Text).

Annual value of Christmas tree production. The number of Christmas trees sold and average price paid (2010 USD) in 2009 by species in each state were determined from USDA data (data were not available for the years 2010 to 2012; see S1C Text) [102]. We then used the sales and price data to estimate annual Christmas tree revenue by species and state. We used enterprise budget sheets to produce several estimates of annualized production cost for each species in each state. Finally, we allocated state and species-level annualized net return (in 2010 USD) from Christmas trees production to the county level using 2010 county-level population [103].

We calculated the expected annualized net value of Christmas tree production across all species and counties. In the mean value estimate we used the mean annualized production cost for each species in each state. Because annualized production costs are uncertain we also generated a low and high annualized net value of Christmas tree production for each species in each state with a low and high estimate of annualized production cost for each species in each state (S1C Text).

Species and lineage similarity in service provisioning across regions and states and dispersion of services across the tree of life

To understand the extent to which individual services are provisioned by similar or different lineages in different geographic regions, we computed matrices of similarity for tree species across USFS ecoregions—which represent ecologically and climatically similar regions

(Fig 4A and S2 Fig). For species we calculated similarity as $1-D$, where D was a matrix of Bray-Curtis dissimilarities to determine the relative proportion of similar species in any two samples. We also examined tree species in the context of their phylogenetic history. Each lineage—or branch—in the tree of life evolved from a common ancestor accumulating novel genes and characteristics over time reflecting the evolutionary diversification process. Consequently, species are organized hierarchically nested within lineages of larger and larger size. For lineages, we calculated matrices of phylogenetic similarity using the PhyloSor [20] method, which calculates the proportion of shared branch length on the tree of life between two samples. For each service, we weighted each species by its service value in each ecoregion. Christmas tree services were only calculated for states, because data were only available at the state level, not the county level, resulting in insufficiently resolved spatial information to aggregate them at the ecoregion level.

The dispersion of ecosystem services across the tree of life was analyzed by calculating the standardized effect sizes of the mean phylogenetic distance (SES MPD), reported as the Net Relatedness Index (NRI) ($-1 \times$ observed z value of MPD) and mean nearest taxon distance (SES MNTD), reported as the Nearest Taxon Index (NTI) ($-1 \times$ observed z value of MNTD) [104] with the 'phylogeny pool' null model—to draw species with equal probability from the tree of life—using the picante package in R [105]. The approach allows inference of whether services are more clustered or evenly spread across the phylogeny and whether close relatives share more or less similar service values than expected by chance (S2 Table and S1J Text). The phylogeny (S1 Data) was based on [14] and pruned to include the species in the study. Species not in [14] were assigned to the appropriate genus based on APG III and IV.

Threats to US trees

Climate change. We assessed the threat posed by climate change by 2050 as the proportion of the biomass of each species that is projected to be exposed to climatic conditions that are outside of their current range geographic distribution. Rasters for North America's current and projected climate were obtained from the AdaptWest Project [106]. County level threat for each climate variable was calculated as the sum of the biomass of species under threat divided by the total biomass in that county (S1L Text).

We chose to separately quantify climatic envelopes using mean annual temperature, total annual precipitation and aridity. Temperature and precipitation have been shown to directly impact the growth, spatial distribution, and management of trees [107–109]. Annual mean temperature and total precipitation are highly correlated with interannual measures (e.g. winter precipitation, winter-summer temperature differential, etc.) of these variables so that as a tree species moves out of its annual climatic envelope so too would the species experience movement away from the associated interannual envelope.

To capture the interaction of temperature and precipitation we assess an index of aridity obtained from the AdaptWest Project calculated as the maximum temperature of the warmest month divided by the mean summer precipitation. Drought stress has been shown to negatively impact the provision of forest services throughout the contiguous US [110]. Warmer temperatures can amplify the stress incurred by drought conditions leading to reduced tree growth and higher tree mortality particularly in the Western US [7,31].

For species that extend their ranges into Mexico where climatic conditions may be more arid, Global Biodiversity Information Facility (GBIF) data for all of North America was used to compute their climatic envelope instead of using the FIA data, ensuring that tolerances to aridity were not underestimated. To reduce the effect of outliers, we used the 1% and 99% quantiles of each climatic variable to define the envelope.

Pests and pathogens. To quantify the threat from pests and pathogens for forest species, we compiled the proportion of basal area of each species projected to be lost in each county due to disease outbreaks, as estimated by the US Forest Service [81]. Data referenced by common names were converted to scientific names. We estimated the threat for each species by taking the average projected proportional basal area loss in each county weighted by the proportion of the total biomass of the species in each county. Threats at the county level were calculated as the average predicted basal area loss of all species in the county weighted by the proportion of the biomass of each species in the county (S1K Text).

To quantify the threat from pests and pathogens for tree crop species, we used data from the USDA's Animal and Plant Health Inspection Service [111]. This website identifies each pest and pathogen that affects each fruit and nut tree species in each state. The fraction of each fruit and nut tree species biomass threatened by each pest and pathogen across the contiguous US is given by the amount of the species biomass in states threatened by the pest or pathogen divided by the total species biomass. We also calculated the fraction of fruit and nut tree species biomass threatened by one or more pest and pathogens across the contiguous US in similar fashion.

Forest fires. Forest fire threat was quantified as the projected change in the number of large fires per week per county from the historical late 20th century climate forcing to the mid-21st century forcing scenario as described [112]. We used the spatial raster from [112] to compute the fire threat for each county by taking the mean of the pixels that fell within the county. We then estimated the fire threat for each species as the average projected change in fire frequency in the counties the species occurs in, weighed by the species biomass in that county. Our species-level fire threat estimate is also in units of fires per week and negative values denote a decrease in the threat of major fires whereas positive values indicate an increase in the threat of major fires (see S1M Text).

Associations between ecosystem services and threats

To test for associations between the ecosystem services value of individual tree species and the degree of threat each faces, we calculated Spearman rank-order correlations between services and threats aggregated by species. Similarly, to test for spatial associations between the ecosystem service value of forests or plantations within each county and the degree of threat facing trees in that county, we calculated Spearman rank-order correlations between threats and services aggregated at the county level.

Supporting information

S1 Fig. A-D) Species similarities (1-Bray-Curtis pairwise dissimilarities) between ecodivisions in the tree species provisioning annual climate regulation value, (B) annual air quality regulation value, (C) annual wood product net revenue, and (D) annual tree crop net revenue. E-H) Lineage or "phylogenetic" similarities for the same ecosystem services using Phylosor [20] in the picante package in R [105], which gives the pairwise fraction of shared branch-lengths on the tree of life between two ecodivisions. For species and lineage similarities, green = high similarity in composition (0.66–1), yellow = intermediate similarity in composition (0.33–0.66); orange = low similarity in composition (0–0.33).

(PDF)

S2 Fig. USDA Forest Service map showing the ecosystem divisions (ecodivisions) for the contiguous U.S.

(PDF)

S3 Fig. Annual county-level air quality regulation value per square mile (2010 USD) between 2010 and 2012 and location of continental US urban areas (light blue).

(PDF)

S1 Table. A) The most valuable continental US tree species ranked according to 2010 to 2012 annual ecosystem service value production (USD 2010), showing the highest value species for all services combined and individually for annual climate regulation value via carbon storage, annual air quality regulation via health damages avoided due to air pollution removal ($PM_{2.5}$ and O_3), and annual net revenue from wood products, tree crops, and Christmas tree production. B) The top twenty tree species forecasted to encounter threats from known pests and pathogens, multivariate climate change and increased fire exposure. The extent of threat to each species is given as the % biomass threatened—by pests and pathogens or by climate change forecasted by 2050 for mean annual temperature, total annual precipitation and aridity—or as the % increase in the number of weeks each species is exposed to fire by 2050.

(PDF)

S2 Table. Dispersion of ecosystem services across the tree of life. High mean phylogenetic distance (SES MPD; column “MPD obs Z”) and high mean nearest taxon distance (MNTD; column “MNTD obs Z”) (weighted by dollar value) indicate that services are dispersed widely across the tree of life (SES MPD) and that close relatives tend to have different ecosystem service values (SES MNTD), respectively. Negative values indicate that the services tend to be clustered within lineages (SES MPD) and that close relatives tend to provision services similarly (SES MNTD). Observed MPD and MNTD values (mpd.obs and mntd.obs) are shown relative to the mean (MPD rand mean and MNTD rand mea) and standard deviation (MPD rand SD and MNTD rand SD) of simulated values, based on 999 randomizations (runs) of species across the phylogeny. Standardized effect sizes—SES MPD and SES MNTD—are shown as z scores (MPD obs Z and MNTD obs Z); P values (MPD obs P and MNTD obs P) indicate whether services or threats are significantly clustered or overdispersed compared to random expectation. Significantly clustered ecosystem services are bolded. Significantly overdispersed services are italicized.

(PDF)

S3 Table. Sources of stumpage prices used to calculate the annual net value of wood production in the continental US.

(PDF)

S4 Table. Low and high estimated annualized A) orchard (tree crop) production costs (USD 2011 per acre) by state and B) Christmas tree production costs per tree species and state (USD 2010). Data sources are listed below each table.

(PDF)

S5 Table. Annual Mg of C sequestered by the biomass of an active orchard acre by tree crop species. Data sources are shown.

(PDF)

S6 Table. Amount of carbon stored in a 5-year old stand of trees in species groups that are often used as Christmas Trees.

(PDF)

S7 Table. Estimated mean and 5th and 95th percentile annual value of avoided health damages across the continental US due to tree-based removal of $PM_{2.5}$ and O_3 between 2010

and 2012 (Billions of 2010 USD).
(PDF)

S8 Table. Ordinary least squares estimate of a county's annual air quality regulation value per square mile regresses on the county's standardized distance to nearest large urban area (s) and the county's standardized carbon storage as of 2010–2012 per square mile (as a proxy for tree biomass abundance). Column (I) gives results of a model with standardized distance to the nearest *large* urban area, column (II) gives results with standardized average distance to nearest *five large* urban areas, column (III) gives results with standardized distance to the nearest urban area (regardless of size), and column (IV) gives results with standardized average distance to nearest *five* urban areas (regardless of size).
(PDF)

S1 Text. Further details of the methods and calculations are given in text sections A–N: A. Annual net value of wood product production. B. Annual net value of tree crop (fruits and nuts) production value. C. Annual net value of Christmas tree production. D. Annual value of climate regulation via carbon storage in US forests. E. Annual value of climate regulation via carbon storage in orchards. F. Annual value of climate regulation via carbon storage on Christmas tree farms. G. Annualized Social Cost of Carbon. H. Annual value of air quality regulation via avoided health damages from tree-based removal of air pollutants. I. Explaining annual air quality regulation values across the US. J. Phylogenetic dispersion of ecosystem services. K. Threats from tree pests and pathogens. L. Threats from climate change. M. Threats from change in frequency of major fires. N. References
(PDF)

S1 Data. Phylogeny in newick format.
(TXT)

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