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

Jeannine Cavender-Bares[1,2*], Erik Nelson[3], Jose Eduardo Meireles[1,4], Jesse R Lasky[5], Daniela A. Miteva[6], David Nowak[7], William D. Pearse[8], Matthew Helmus[9], Amy E. Zanne[10], William Fagan[11,12], Christopher Mihiar[13], Nicholas Z. Muller[14], Nathan Kraft[15], Stephen Polasky[1,2,16]

[1]Department of Ecology, Evolution and Behavior, University of Minnesota, Saint Paul MN 55108
[2]Institute on Environment, University of Minnesota, Saint Paul, MN 55108
[3] Department of Economics, Bowdoin College, Brunswick, ME, 04011-8497, enelson2@bowdoin.edu
[4] School of Biology & Ecology, University of Maine, Orono, ME 04469, jose.meireles@maine.edu
[5]Department of Biology, Pennsylvania State University, University Park, PA, 16802, jrl35@psu.edu
[6]Department of Agricultural, Environmental and Development Economics, The Ohio State University, Columbus, OH 43210, miteva.2@osu.edu
[7]US Forest Service, Northern Research Station, 5 Moon Library, SUNY-ESF, Syracuse, NY 13210, david.nowak@usda.gov
[8]Department of Biology & Ecology Center, Utah State University, Logan, UT, will.pearse@gmail.com
[9]Center for Biodiversity, Department of Biology, Temple University, 1925 N. 12th Street, Philadelphia, PA 19122, mrhelmus@gmail.com
[10]Departmental of Biological Sciences, George Washington University, Washington, DC, aezanne@gmail.com
[11]Department of Biology, University of Maryland, College Park, Maryland, bfagan@umd.edu
[12]SESYNC, University of Maryland, Annapolis, MD,
[13]Department of Applied Economics, Oregon State University, Corvallis, OR, 97330, mihiarc@oregonstate.edu
[14]Department of Engineering and Public Policy, Carnegie Mellon University, Pittsburgh, PA, 15213, nzm@andrew.cmu.edu
[15]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, nkraft@ucla.edu
[16]Department of Applied Economics, University of Minnesota, Saint Paul, MN 55108, polasky@umn.edu

*Corresponding author, Email: cavender@umn.edu

ORCIDs

Jeannine Cavender-Bares: 0000-0003-3375-9630
William F Fagan: 0000-0003-2433-9052
Matthew R. Helmus: 0000-0003-3977-0507
Nathan Kraft: 0000-0001-8867-7806
Jesse Lasky: 0000-0001-7688-5296
Daniela Miteva: 0000-0002-9123-646X
Erik Nelson: 0000-0002-7291-5192
David Nowak: 0000-0002-2043-0062
William D Pearse: 0000-0002-6241-3164
Stephen Polasky: 0000-0003-4934-2434
Amy E Zanne: 0000-0001-6379-9452

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Author contributions

All authors contributed intellectually to the manuscript. JCB, EN, SP, JEM, JL, and WF wrote the manuscript with help from all authors. JCB, EK, JEM, JL, DN, NM, DM, CM and AZ assembled and analyzed data with help from WP and MH.

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Abstract

Trees provide critical contributions to human well-being. They sequester and store greenhouse gasses, filter air pollutants, and provide wood, food, and other products, among other benefits. However, global change threatens these benefits. To quantify the monetary value of US trees and the threats they face, we combine macroevolutionary and economic valuation approaches using spatially explicit information about species and lineages. We show that the value of ecosystem services generated by trees in forests, orchards, and plantations in the US – $114 billion annually (low: $85 B; high: $137 B; 2010 USD) across five key services for which we had adequate data. The high value of trees is a consequence of both their abundance and diversity. The carbon storage and air pollution removal values of US trees far exceed their commercial value from wood product and food crops. Yet the most valuable US tree species and lineages are also among those most threatened by known pests and pathogens, climate change and increasing fire risk. While US tree crops are often provided by the same lineages in different regions, the high ecosystem service value of carbon and air pollution removal depends on different lineages in different regions. The composition of tree species that provide critical ecosystem services are likely to shift with global change, highlighting the importance of maintaining forest abundance and diversity.

Significance Statement

Trees in forests and plantations of the continental US generate over $114 billion in net returns to society annually from five key ecosystem services. This value is greater than the aggregate

annual income generated by all US farmers. Importantly, the “hidden” value of trees—the value not accounted for by markets—far exceeds their commercial value. While the most valuable US tree species and groups—including the pines and the oaks—are under the greatest threat from pests and pathogens. However, the broad distribution of services across the tree of life also highlights the importance of tree diversity in sustaining US ecosystem services from trees.

Introduction

Accelerating losses of biodiversity and shifts in species composition due to regional and global change highlight the need to understand the societal value that biodiversity currently provides and could provide future generations as landscapes and climate continue to change (1). A greater level of biodiversity is valuable to humans for two reasons. First, a greater amount of evolved variation means a thicker portfolio of diverse species that can contribute to a richer set of complementary ecosystem services, including greater diversity of consumable products, a greater range of cultural services, and greater opportunities for future discovery of use (2-4). Second, more diverse ecosystems tend to be more productive and stable (5-7) and are better able to resist pest damage (8). More productive and stable ecosystems mean better regulation of the climate and water systems on which our economies depend (9).

Analyses of regulating and provisioning ecosystem services provided and supported by biodiversity typically use ecosystems or landscapes (10) rather than individual species (e.g., 11) as the unit of study, even though conservation efforts frequently target species. Trees are wellsuited for analysis of ecosystem services at the species-level because they are sessile and large enough to be accurately mapped across space. Furthermore, their evolutionary and biogeographic history has given rise to functional attributes and distributions that are distinctive enough to link individual tree species with the services they provide (12). However, trees and their associated services are increasingly under threat from well-documented pests and pathogens (13), climate change (14), fire (15), invasive species (16), and land-use change (17). Of the 60,000 known tree species globally (18), one out of every six is known to be threatened by one or more of these perturbations (19, 20). Vulnerability to these threats varies among species and lineages because of evolved differences in physiology and spatial proximity to threats. Therefore, a spatially and evolutionarily explicit assessment of the service value that trees provide—and how vulnerable these services are to regional and global threats—is vital if we are to craft effective approaches to conserving the values that trees provide.

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 continental US, where spatially explicit information is available, between 2010-2012. To calculate net value we accounted for all direct costs incurred for trees to produce these services. 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. This synthesis allows us to identify the tree lineages in the US that currently generate the greatest ecosystem service value. In addition, we identify the species and lineages on the “tree tree of life” that are most threatened by climate change, fire, and pests and pathogens across their current geographic distributions. Quantifying the multiple threats to the ecosystem service values provided by tree species and lineages in a spatial context provides several important layers of information for conservation decision makers. In particular, our analysis indicates which species, lineages and ecosystem services are most threatened by regional and global change. In highlighting the monetary benefits provided by trees, including their hidden value, and the extent to which these benefits are threatened, we provide decisionmakers with the value of trees in a common currency that can be compared to other economically driven decisions. Our approach goes beyond previous work by allowing us to identify not only where tree conservation and threat mitigation will be most valuable, but also 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). These benefits are provided by species that are distributed across the tree of life (Fig. 1). 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 (Fig. 1D), which are much more precise than the estimates of annual regulating service values (Fig. 1D). The differences in precision are driven mainly by the differences in how the per unit values—or prices—of these ecosystem services are revealed or calculated. The per unit value society places on provisioning services are typically communicated precisely via markets. In contrast, 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 models that rely on a set of assumptions and simplifications and imperfect data, leading to large error bounds (21-24).

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

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; 2010 USD) in net value annually, followed by Douglas fir (*Pseudotsuga menziesii*) with \$8.5 B (low: \$5.8 B; high: 10.6 B; 2010 USD), red maple (*Acer rubrum*) with \$6.0 B (low: \$4.6 B; high: \$7.0 B; 2010 USD), white oak (*Quercus alba*) with \$4.3 B (low: \$3.3 B; high: \$5.1 B; 2010 USD) and sugar maple (*Acer saccharum*) with \$4.0 B (low: \$3.0 B; high \$4.7 B; 2010 USD). Loblolly pine and Douglas fir were highly valuable in terms of both regulating and provisioning services, as a consequence of their abundance and high demand in the wood product market. 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) (Table 1).

Of the major tree lineages in the US, the pines (*Pinus*) and the oaks (*Quercus*), which respectively generated \$25.4 B and \$22.3 B in net benefit annually between 2010 and 2012, are by far the most valuable genera on the continental US (Table 2). Together, these two lineages contributed over \$21.3 B annually to climate regulation. Pines dominated annual net revenues from wood products at \$7.4 B, while oaks had the highest annual climate (\$10.7 B) and air quality regulation values (\$11.0 B). Within the rose 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, while the apple genus (*Malus*) contributed more than \$0.94 B. The *Citrus* genus (family Rutaceae), is also an important crop genus in the US. However, we found the annual net returns from citrus products to be negative between 2010 and 2012 due to low citrus market prices (25) and the prevalence of citrus greening in Florida and to a lesser extent, Arizona and California (26). Greening is a bacterium that destroys the commercial value of affected citrus groves.

The high regulating service values of oaks and pines are a consequence of their high, often incidental, abundance in US forests. In contrast, the high wood product value of pines and the high crop value of *Prunus* and *Malus* reflect human choices and management decisions.

High variation among species and lineages in ecosystem service value

Even though carbon is stored by all tree species, this ecosystem service in the US as of 2010-2012 was concentrated among the most abundant continental US tree species. These highstoring species are evenly dispersed across the tree of life (Fig. 1A, Table S1). Like the climate regulation service, all continental US tree species provided some air quality regulation service value between 2010 and 2012. A species' air quality regulation value depended on their abundance, leaf area, and proximity to human populations affected by pollution (27, 28). While air quality regulation service value is distributed at random across the tree of life (mean phylogenetic distances between valuable trees are not different than expectation, Table S1), close relatives do tend to have similar values (mean nearest taxon distances between valuable trees are less than expected, Table S1).

Over time, wood product and tree crop producers have concentrated on the lineages and species groups that generate the greatest net economic return. Tree crops are significantly clustered in the tree of life (SI Table S1) and include relatively few lineages, such as trees in the Rose family (almonds, apples, pears, and cherries) (Fig. 1A, Table S1). Many lineages provide wood products, but the amounts vary widely among species, and the most valuable species are not significantly clustered within any lineage. However, conifers include the majority of valuable timber species, and the pine genus (*Pinus*) generates more than five times the timber net revenue than the most valuable angiosperm genus (oaks, *Quercus*) (Table 2).

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

The spatial distribution of ecosystem services produced by US trees between 2010 and 2012 largely reflects forest, plantation, and orchard distribution during this period (Fig. 2). Climate and air quality regulation service values are a direct consequence of where forests grow; they cover most of the continental US, excluding grassland and desert biomes (Figs. 2A, 2B). However, health damages avoided by tree-based air pollution removal values are greatest, all else equal, near large urban areas that are surrounded by forests. We find that between 2010 and 2012 people living in eastern urban areas, particularly the New York, Boston, Pittsburgh, and Atlanta areas, benefited greatly from air pollution removal by trees. Seattle and California's Bay Area were the two western urban areas that particularly benefited from air pollution removal between 2010 and 2012 (Fig. 2B, SI Texts 8 – 9, Tables S7 – S8, Figure S2.).

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). Christmas trees are produced primarily where people live; in other words, on the West Coast, in the Northeast and in the Upper Midwest (Fig. 2E).

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

In forested areas and plantations across the US, we found low similarity in the composition of tree species (Fig. S1) that provide ecosystem services in different regions of the continental US.

Tree crops, which are frequently planted in geographically disparate but climatically similar regions, were an exception. Species similarity values—which can range from 0, where no species are shared across regions to 1, where all the species are shared—averaged across pairs of ecodivisions or states, respectively, were much higher for tree crops (0.54, SD 0.23 and 0.49, SD 0.25) than for carbon storage (0.09, SD 0.13 and 0.15, SD 0.18), air quality regulation (0.07, SD 0.13 and 0.13, SD 0.18) or wood products (0.04, SD 0.1 and 0.08, SD 0.16). Lineage similarities (Fig. S1)—i.e., similarities in the branches of the tree of life providing services in different regions—were higher than for species, given that different species in the same lineage—e.g., closely related species of oaks or pines—can occur in different regions. Nevertheless, lineage similarities were again higher for tree crops (0.68, SD 0.16 and 0.72, SD 0.18) than for carbon storage (0.56, SD 0.14 and 0.59, SD 0.16), air quality regulation (0.55, SD 0.14 and 0.59, SD 0.17) or wood products (0.53, SD 0.19 and 0.60, 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), because 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. All in all, we find low similarity—in other words, high spatial turnover—in the species that provide the five ecosystem services we evaluated (Fig. S1) because different species—and to a lesser extent different lineages—grow in different regions. Consequently, the total ecosystem service value of trees in the US results from many different species and lineages that occur naturally or are planted across different climates and environments. Tree diversity across the US thus contributes to their overall continental abundance and value, reducing human vulnerability to ecosystem service deficits and contributing critically to their well-being.

Species and lineages most threatened by regional and global change

Climate change, increasing fire frequency and intensity, and the growing number of invasive pests and pathogens are critical threats that will affect the health, mix, and spatial distribution of continental US tree populations. We evaluate the spatial overlap of these threats and tree species and the ecosystem services provided by trees.

We find that threats to tree species are dispersed widely among lineages (Table S1), except for known pests and pathogens, which cluster within certain branches of the tree tree of life, including the oak and pine genera (Fig. 1B, Table S2). Tree species that are known to be at risk of damage from pests and pathogens – measured as the species' current basal area expected to be lost to disease outbreaks – are also significantly more likely to have close relatives also at risk (Table S1). Tree vulnerability to enemy attacks is tightly linked to species and lineage identity, given long-term evolutionary processes that drive enemy-host compatibility (29-31). However, 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 (32). 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 the taxonomic specificity of pests and pathogens, the vulnerability of tree species and lineages to changes in climate – measured as the percentage of the species' biomass expected to be exposed to summer aridity levels higher than they can tolerate as of 2050 – and fire frequency and intensity – measured by average projected change in fire frequency in the counties that contain the species – are a function of where species are distributed across the continent. Therefore, there is wide dispersion across the tree of life of tree species forecasted to have high exposure to those threats (Table S1).

The correlations between species' climate regulation, air quality regulation, and wood product net annual values and the percentage of the species' biomass at risk from a threat are positive across all three threat categories (Fig. 4). In particular, we find that known pests and pathogens are predicted to disproportionally affect the biomass of species that generate high annual net climate regulation, air quality regulation, and wood product values. We note that pest and pathogen risk were not calculated for crop trees because data are not available.

Spatial distribution of threats

We find the threats are spatially heterogeneous, with different kinds of threats concentrated in different parts of the continental US (Fig. 3). The climate change threat to species is forecasted to be greatest in the Central Plains, the Pacific Northwest, and southern Florida (Fig. 3A). Pest and pathogen threats to species are strongest in the Southeast and Southwest (Fig. 3B). The major wild fire threat to species are expected to increase in California, the Intermountain West, and, to a lesser extent, the North Central states and the Southeast (Fig. 3C).

Comparing ecosystem services and threats spatially, we find only weak associations (SI Fig. S3). US counties most threatened by increases in major wildfires and pest and pathogens tend to have lower service values, although countries threated by climate change (expected exposure to intolerable summer aridity levels as of 2050) have higher services values (SI Fig. S3-A). When we examine intensity of service value in a county—measured as the service value per km of county area—areas with higher service value intensity tend to be weakly associated with lower threats (SI Fig. S3-B).

Similar to what we find at the county-level spatial analysis, we find threats to valuable services are also distributed unevenly at the regional level. For example, the Pacific Northwest has some of the most profitable annual wood product production and highest annual carbon storage in our analysis, but is also facing dramatically drier summers. Researchers have noted this potential threat before, identifying the growth sensitivity of champion tree *Pseudotsuga menziesii* to summer drought and the likelihood of increasing aridity (34). The coastal plain of the Southeast is home to forests with substantial wood product value but simultaneous threats from pests and pathogens and major fires. The Upper Midwest hosts forests with high levels of stored carbon, air pollution removal, and wood product value that are simultaneously threatened by warmer summers and more frequent major fires. Likewise, the continental US' most valuable regions for tree crop production, particularly California, and Florida, are under threat from increasing fire frequency.

Discussion

This study highlights the importance of tree abundance and diversity for human well-being. Both the vast abundance of trees in continental US forests, plantations, and orchards, and their diversity across the continent explain the high monetary value of trees for select ecosystem services – over $114 B annually (2010 USD) between 2010 and 2012 from climate and air quality regulation, and three commercial provisioning services. To put this number into context, the annual net cash farm income to the *entire* US agricultural sector was approximately $129 B in 2012 (2010 USD) (35).

While tree abundance in the US is obviously an important factor in the benefits they provide to humans, the diversity of trees in the US is just as critical to their high value. Individual tree species differ markedly in their ecosystem service value. Further, the species that provide the highest values are distributed across the tree of life, rather than in a single lineage. In other words, there is no single species or lineage that is responsible for most of the annual service value we calculated. Moreover, ecosystem services in different regions of the country are provisioned by different tree species and lineages, such that each region gets their climate and air quality regulation services from different species. Consistency of services across regions thus depends on the maintenance of tree diversity across the country.

Continental US trees' production of global climate and local air quality regulation values dwarf the values they generate from wood product, crop, and Christmas tree production. Pines and oaks are the most valuable tree genera in the US across the 5 ecosystem services we study, generating nearly $47.7 billion each year between 2010 and 2012. These high-valued genera are also the most at risk to known pests and pathogens. Other global change threats, including climate change and fire impact lineages all across the tree tree of life. As forest ecosystems are impacted by global change, the mix of tree species that provide critical ecosystem services will be altered, both in evolutionary and physical space, with anticipated losses in diversity and likely consequences for total ecosystem benefits and human well-being.

Our net valuation approach understates the social and monetary value provided by continental US 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 (27, 36). No nationwide spatial database of urban trees exists. Inclusion of urban trees in our 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). The inclusion of urban trees in our analysis would also increase the climate regulation value provided by continental US trees. For example, Nowak et al. (27) estimate 1.36 B MT of carbon are stored in urban areas, which translates to $5.8 B (2010 USD) annually. Second, due to data limitations, we omitted many regulating ecosystem services that trees provide, such as erosion control, flood regulation (37), storm surge regulation (38), urban heat island regulation (39), species habitat provision, and energy savings due to shade (40). Nowak et al (41) estimate that trees and forests in urban areas in the continental US 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 most cultural services that trees provide in the US, including many of their ornamental, spiritual, and aesthetic values (2, 4, 42, 43). Including these services in our analysis would greatly increase the value provided by US trees. Of course, a complete accounting of the value provided by continental US trees would require estimates of the damages they cause and the cost of their maintenance. Tree-related damages include pollen and sap-related irritations, injuries to human health and property caused by falling trees and their limbs, and their role in generating fires and smoke (44-47). Further, while trees remove some of the pollution we would otherwise inhale (see above), trees can, in certain circumstances, exacerbate the damage caused by air pollution. For example, trees are a source of the volatile organic compounds isoprene and monoterpenes, which contribute to tropospheric ozone and secondary particle formation (48). Further, in certain urban street grids, trees block airflow, trapping pollution that would otherwise dissipate (49). However, the total value of these disservices is dwarfed by the value of the omitted “goods” provided by trees. Thus, we consider $114 B a low estimate of the annual net value provided to society by continental US trees (50, 51).

The estimated annual values of the climate and air quality regulation values provided by trees have large uncertainty because there is large uncertainty about the values of SCC and VSL. 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 (Table S7). In contrast, the estimated annual values of the provisioning services are relatively precise for several reasons. First, a precise estimate of the per unit value of tree crops, wood products, and Christmas trees are communicated by market prices. Further, decades of management and experience with the trees that provide these services has reduced year to year and spatial variation in production costs. Third, market prices for tree crops, wood products, and Christmas trees are negatively correlated with production levels such that if commodity production is high one year then the price tends to drop that year and vice versa. Consequently, revenues in commodity markets tend to be relatively stable year to year.

The hidden value of trees, which are related to the non-marketed regulating services, is the most important source of value generated by trees. Regulating services are provisioned from a diverse portfolio of evolutionary lineages. 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 will (eventually) be provided by other species. However, replacement could take time during which regulating services may be reduced (52). In the areas where substitute provider species do not emerge or lag times are extensive, 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 (53). Given that regulating services are a consequence of tree abundance and diversity, mechanisms – such as carbon payments, if designed properly – may help enhance regulating services generally (54). Conversely, threats to trees with high provisioning service value are much more likely to be managed by landowners given the financial rewards to intervention these actors can capture in existing markets. For example, modern agriculture has become adept at transplanting commercially valuable species into new regions when environmental conditions in the initial regions have become too extreme (55).

Of all the threats considered, those posed by pests and pathogens are of particular concern, given that they target specific species, unlike the other threats we examined. Pest and pathogens could remove dominant species that currently have the highest abundance and ecosystem service value, undermining the diversity and resilience of forests and their capacity to provision ecosystem services. Currently, our most valuable and diverse tree species and lineages, including the pines and the oaks, are also those most threatened by known pests and pathogens. Major losses within these lineages would compromise a large fraction of ecosystem services from US forests. Provisioning services, particularly crops, can be attributed to relatively small number of species clustered in a small portion of the tree of life. While they encounter the same threats, humans are adept at moving crop species to favorable locations and tend to invest in protection against pests and pathogens that target commercially valuable species. Despite successes in developing resistant strains of crop trees and containing pathogen threats, we are unlikely to keep up with the number of disease and insect threats that currently threaten trees (56, 57). Chestnut blight and Dutch elm disease are two powerful examples of how once-dominant tree species that provided many services were decimated by disease (13). The monetary value that trees contribute to human well-being each year, which rivals important sectors of the US economy, depends on the maintenance of abundant populations of trees and a high diversity of species. These factors, in turn, require intentional management of forests and trees in the face of myriad and simultaneous global change threats.

Methods and Data

Ecosystem Services

We measured the value of five tree-related ecosystem services. 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 lacked either a nationwide database or a proven 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) program (58, 59). We estimated total standing live aboveground carbon stocks following Woodall et al. 2010. The live belowground carbon stocks were modeled as a function of the aboveground live tree carbon stocks following Woodall et al. 2012 (see SI Text 4.)

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 Table S5, SI Text 5). We use county level data on orchard acreage to get carbon stored by fruit and nut trees by county (60). Only state level acreage is reported for Christmas tree farms. We allocated Christmas tree farm acreage to counties based on county-level population (US Census Bureau 2016; see SI Text 6, Table S6). Overall results for carbon storage are insensitive to county allocation for Christmas tree farms because Christmas tree farms make up 0.0004% of total calculated carbon storage.

We converted the measure of carbon stocks to a monetary value by multiplying the carbon stock by the annualized social cost of carbon (ASCC) (SI Text 7). 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 (85) 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. 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 \$.

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 (61, 62). Here, we valued the reduction in human mortality from removal of fine particulate matter ($PM_{2.5}$) and ozone (O_3) from the atmosphere by trees. Reductions in human mortality are the largest of the benefits generated by improving air quality (63). The benefits from pollution reductions by trees were determined using estimates of the amount of pollution removed by tree species by county by pollutant (27, 28), the 2011 National Emissions Inventory (64), and the AP3 integrated assessment model (65-68). The AP3 model links emissions of common air pollutants by county in the US to the ambient concentrations $PM_{2.5}$ and O_3 in each county. Using the National Emissions Inventory, AP3, and USEPA'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 emissions (see 67). Finally, we calculated the average annual damage caused by a pollutant in a county (in \$ 2010) by dividing the monetary damage predicted by AP3 for that pollutant by the ambient concentration of the pollutant in the county in 2011.

When trees remove pollutants from the air some of the human mortality-related damage is avoided. Work by Nowak and colleagues (27, 28) provided estimates of each pollutant removed by species by county by day. We then converted measures of pollutant removed per day by a species in a county to annual average improvements in ambient air quality, measured in $\mu g/m^3$/year, by dividing the µg/day removed in a county by the volume of air space in the county (land area *x* vertical height in meters, see SI Text 8).

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 $\$/\mu g/m^3$) by the amount of the $PM_{2.5}$ removed by the species in the county over the course of a year (also measured in $\mu g/m^3$). We repeat this process to estimate the annual value generated by a species in a county that removes O_3 from the atmosphere. In Fig. 1 we exhibit 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 US-EPA's (69) and the concentration-response parameters for $PM_{2.5}$ (70) and for O_3 (71). 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. In Fig.1 we show two sets of 5th and 95th percentile national-level estimates across both pollutants. One set of estimates only uses the uncertainty in the dose-response function (the mean VSL is always used when constructing this 5th and 95th percentile). The other set of estimates uses uncertainty in both parameters (SI Texts 8 – 9, Tables S7 – S8, Figure S2).

Annual value of wood product production

We used 2012 roundwood production data (including fuelwood, pulp, and sawlogs) at the county level (72). 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 annualized monetary value for roundwood production for a species in a county by multiplying the annual roundwood production in cubic feet by the annualized net present value of a cubic foot of harvested roundwood. The annualized net present value of a cubic foot of harvested roundwood is calculated using biomass growth functions parameterized with FIA data (73-75), observed 1998-2014 mean stumpage prices (in 2010 USD; SI Table S4), and stand establishment costs (in 2010 USD (76). The expected annualized net value of wood roundwood production across all species and counties is shown in Fig. 1. We also 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 (Table S3, SI Text 1).

Annual value of tree crop production

We calculated annualized net revenues for 21 fruit and nut tree species (see SI for the list of tree species). 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 (60), we calculated annual revenue in the years 2010, 2011, and 2012 at the species and county level (2010 USD)(60). 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 SI Text 2). In Fig. 1 we exhibit the expected annualized net value of tree crop production across all species and counties. We also generated a low and high estimate of annualized net revenue at the species and county level by using species and county-specific low and high estimates of annualized production cost (Table S4 and SI Text 2).

Annual value of Christmas tree production

We used data from the USDA to determine the number of Christmas trees sold and average price paid (2010 USD) in 2009 by species in each state (data were not available for the years 2010 to 2012; see SI Text 3) (77). 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 $) from Christmas trees production to the county level using 2010 county-level population (78).

In Fig. 1 we exhibit the expected annualized net value of Christmas tree production across all species and counites. In the mean value estimate we used 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 (SI Text 3).

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 phylogenetic similarity for tree species and lineages across USFS ecodivisions—which represent ecologically and climatically similar regions—and US states. 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; for lineages, we used the PhyloSor (79) 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 ecodivision and each state. 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 ecodivision 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) and mean nearest taxon distance (SES MNTD) (80) with the 'phylogeny pool' null model—to draw species with equal probability from the “tree tree of life"—using the picante package in R (81). The approach allows inference of whether services are more clustered or evenly spread across the phylogeny (SES MPD) and whether close relatives share more or less similar service values (SES MNTD) than expected by chance (Table S1 and SI Text 10).

Threats to continental US trees

Climate change

We quantified threats posed by climate change by year 2050 with the proportion of the biomass of each species projected to be exposed to summer aridity levels (summer heat moisture index) higher than their current climatic envelope indicates they can tolerate based on their geographic distribution in the US. For species that extend their ranges into Mexico where climatic conditions may be more arid, Global Bioidiversity 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 account for outliers, the upper limit of each species' climatic envelope was calculated as the 97.5% quantile of their current summer aridity envelope. Current and projected summer aridity rasters for North America were obtained from the AdaptWest Project (82). County level threat was calculated as the sum of the biomass of species under threat divided by the total biomass in that county (SI Text 12).

Pests and pathogens

To quantify the threat from pests and pathogens, 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 United States Forest Service (83). Data referenced by common names were converted to scientific names. We estimated threat for each species by taking the average projected proportional basal area loss in each county *i* for species *k* weighted by the proportion of the total biomass of species *k* allocated in county *i*. 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 (SI Text 11).

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 in (84). We used the spatial raster from Barbero et al. (84) 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 SI Text 13).

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Figure legends

Figure 1.

(A) Ecosystem service annual value (blue bars) and (B) potential threats (brown bars) for species across the tree 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 represent the proportion of each species' current total biomass at risk from the indicated threat. (C) Phylogeny of the US trees, with color wedges indicating the location of particular clades (also shown in (A) and (B) trees of life). (D) Total net annual ecosystem service values provided by continental US trees between 2010 and 2012. The squares give mean estimated value and the error bars show the range in expected values. See the Methods and Data section for details on error bound calculations. 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.

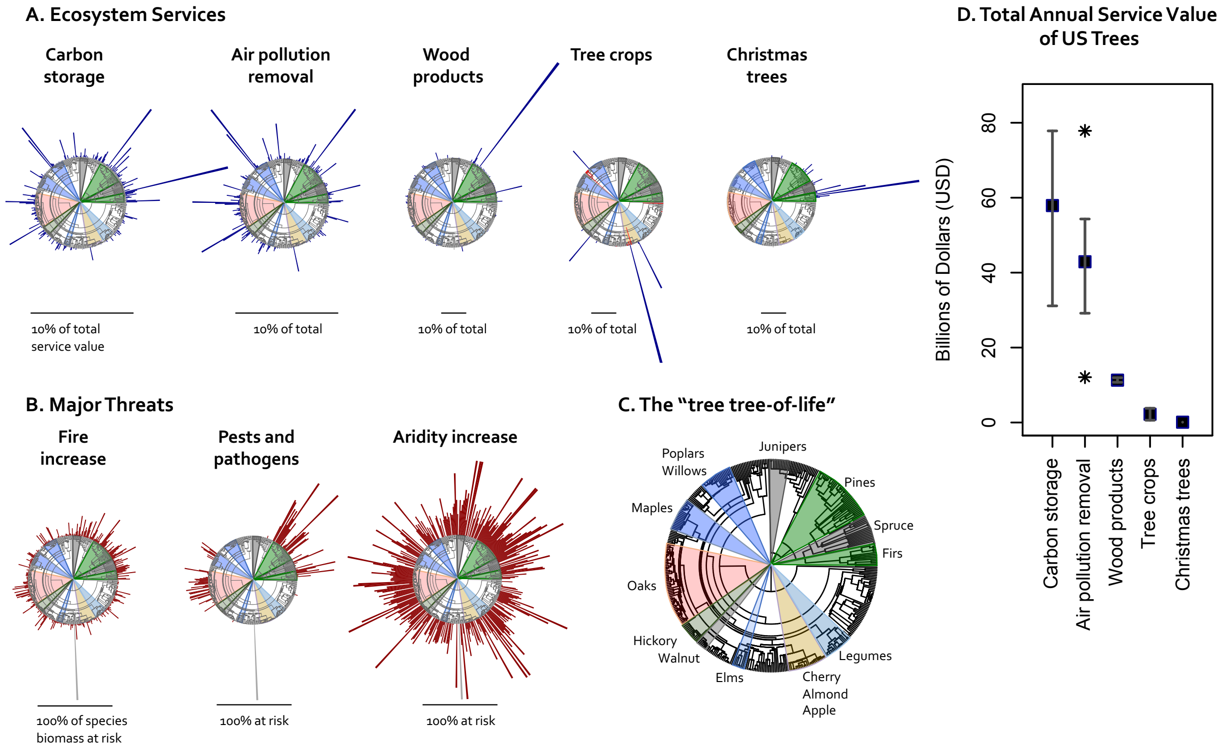
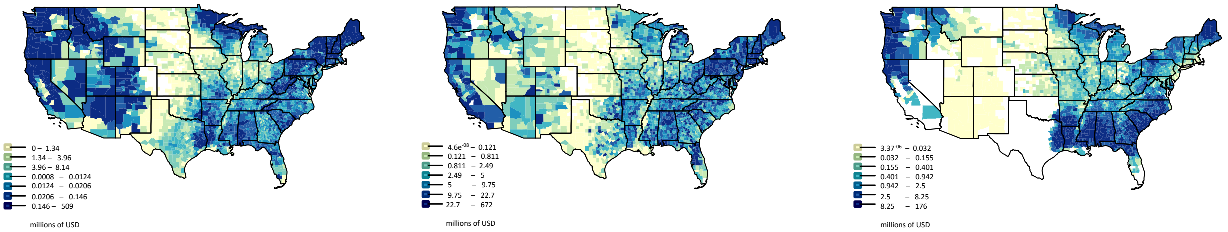


Figure 2.

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 continental 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.

A. Carbon Storage Value B. Air Pollution Removal Value C. Timber Revenue



D. Tree Crop Revenue E. Christmas Tree Revenue F. Total Ecosystem Service Value

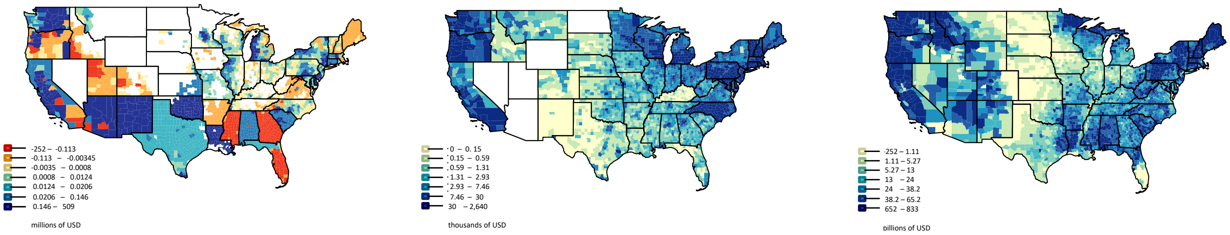


Figure 3. Magnitude of county-level threats across the continental US. Darker colors indicate greater threat to the biomass currently located in the county. Missing data are indicated in white. (A) Proportion of current total tree biomass in each county that is expected to be exposed to summer aridity levels higher than 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.

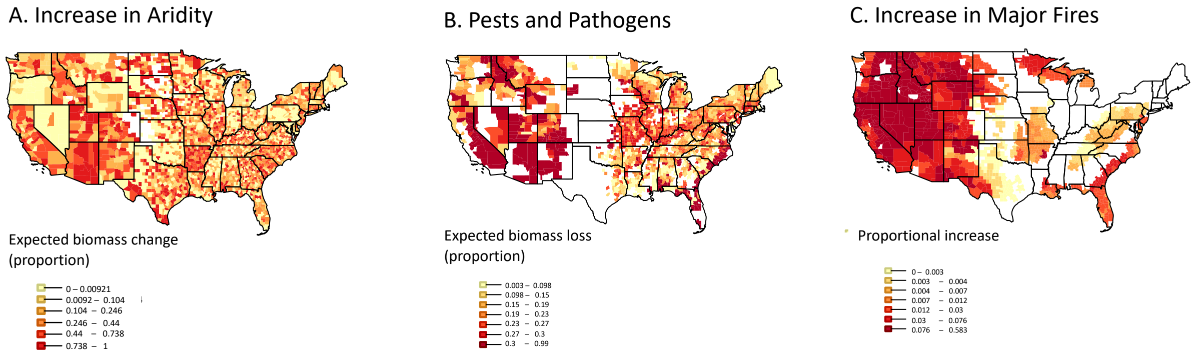


Figure 4.

Associations between annual net ecosystem service values of tree species in the US and their predicted threats and drivers of change. The correlation matrix shows the r value of species-level correlations between annual net ecosystem service value generated between 2010 and 2012 and predicted threats. Colors (blue) indicate significant positive associations, indicating more valuable tree species are under more threat. Darker colors indicate stronger correlations.

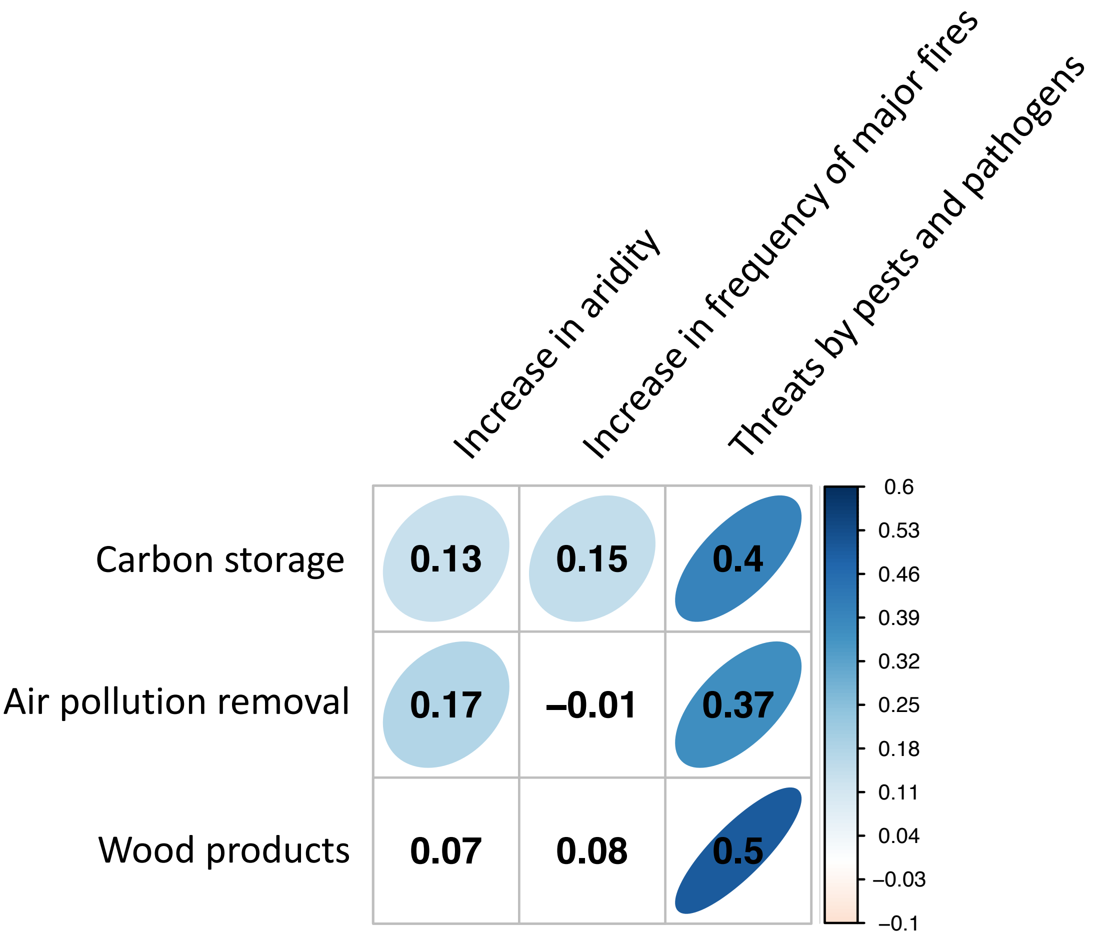
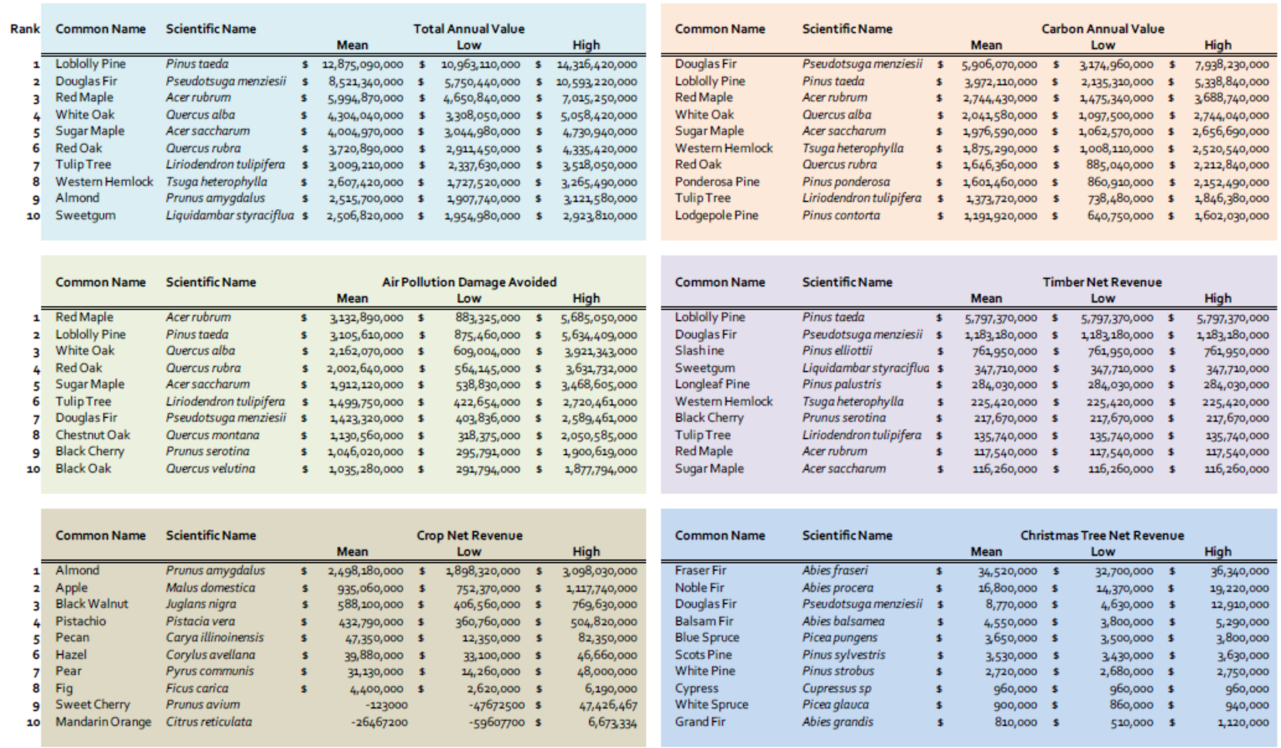


Table 1. The most valuable continental US tree species ranked according to 2010 to 2012 annual ecosystem service value production (USD 2010), showing the highest value species for all services combined and individually for annual climate regulation value via carbon storage, annual air quality regulation 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.



Rank	Common Name	Scientific Name	Total Annual Value		
			Mean	Low	High
1	Loblolly Pine	*Pinus taeda*	$ 12,875,090,000	$ 10,963,110,000	$ 14,316,420,000
2	Douglas Fir	*Pseudotsuga menziesii*	$ 8,521,340,000	$ 5,750,440,000	$ 10,593,220,000
3	Red Maple	*Acer rubrum*	$ 5,994,870,000	$ 4,650,840,000	$ 7,015,250,000
4	White Oak	*Quercus alba*	$ 4,304,040,000	$ 3,308,050,000	$ 5,058,420,000
5	Sugar Maple	*Acer saccharum*	$ 4,004,970,000	$ 3,044,980,000	$ 4,730,940,000
6	Red Oak	*Quercus rubra*	$ 3,720,890,000	$ 2,911,450,000	$ 4,335,420,000
7	Tulip Tree	*Liriodendron tulipifera*	$ 3,009,210,000	$ 2,337,630,000	$ 3,518,050,000
8	Western Hemlock	*Tsuga heterophylla*	$ 2,607,420,000	$ 1,727,520,000	$ 3,265,490,000
9	Almond	*Prunus amygdalus*	$ 2,515,700,000	$ 1,907,740,000	$ 3,121,580,000
10	Sweetgum	*Liquidambar styraciflua*	$ 2,506,820,000	$ 1,954,980,000	$ 2,923,810,000

Common Name	Scientific Name	Carbon Annual Value		
		Mean	Low	High
Douglas Fir	*Pseudotsuga menziesii*	$ 5,906,070,000	$ 3,174,960,000	$ 7,938,230,000
Loblolly Pine	*Pinus taeda*	$ 3,972,110,000	$ 2,135,310,000	$ 5,338,840,000
Red Maple	*Acer rubrum*	$ 2,744,430,000	$ 1,475,340,000	$ 3,688,740,000
White Oak	*Quercus alba*	$ 2,041,580,000	$ 1,097,500,000	$ 2,744,040,000
Sugar Maple	*Acer saccharum*	$ 1,976,590,000	$ 1,062,570,000	$ 2,656,690,000
Western Hemlock	*Tsuga heterophylla*	$ 1,875,290,000	$ 1,008,110,000	$ 2,520,540,000
Red Oak	*Quercus rubra*	$ 1,646,360,000	$ 885,040,000	$ 2,212,840,000
Ponderosa Pine	*Pinus ponderosa*	$ 1,601,460,000	$ 860,910,000	$ 2,152,490,000
Tulip Tree	*Liriodendron tulipifera*	$ 1,373,720,000	$ 738,480,000	$ 1,846,380,000
Lodgepole Pine	*Pinus contorta*	$ 1,191,920,000	$ 640,750,000	$ 1,602,030,000

Rank	Common Name	Scientific Name	Air Pollution Damage Avoided		
			Mean	Low	High
1	Red Maple	*Acer rubrum*	$ 3,132,890,000	$ 883,325,000	$ 5,685,050,000
2	Loblolly Pine	*Pinus taeda*	$ 3,105,610,000	$ 875,460,000	$ 5,634,409,000
3	White Oak	*Quercus alba*	$ 2,162,070,000	$ 609,004,000	$ 3,921,343,000
4	Red Oak	*Quercus rubra*	$ 2,002,640,000	$ 564,145,000	$ 3,631,732,000
5	Sugar Maple	*Acer saccharum*	$ 1,912,120,000	$ 538,830,000	$ 3,468,605,000
6	Tulip Tree	*Liriodendron tulipifera*	$ 1,499,750,000	$ 422,654,000	$ 2,720,461,000
7	Douglas Fir	*Pseudotsuga menziesii*	$ 1,423,320,000	$ 403,836,000	$ 2,589,461,000
8	Chestnut Oak	*Quercus montana*	$ 1,130,560,000	$ 318,375,000	$ 2,050,585,000
9	Black Cherry	*Prunus serotina*	$ 1,046,020,000	$ 295,791,000	$ 1,900,619,000
10	Black Oak	*Quercus velutina*	$ 1,035,280,000	$ 291,794,000	$ 1,877,794,000

Common Name	Scientific Name	Timber Net Revenue		
		Mean	Low	High
Loblolly Pine	*Pinus taeda*	$ 5,797,370,000	$ 5,797,370,000	$ 5,797,370,000
Douglas Fir	*Pseudotsuga menziesii*	$ 1,183,180,000	$ 1,183,180,000	$ 1,183,180,000
Slashine	*Pinus elliottii*	$ 761,950,000	$ 761,950,000	$ 761,950,000
Sweetgum	*Liquidambar styraciflua*	$ 347,710,000	$ 347,710,000	$ 347,710,000
Longleaf Pine	*Pinus palustris*	$ 284,030,000	$ 284,030,000	$ 284,030,000
Western Hemlock	*Tsuga heterophylla*	$ 225,420,000	$ 225,420,000	$ 225,420,000
Black Cherry	*Prunus serotina*	$ 217,670,000	$ 217,670,000	$ 217,670,000
Tulip Tree	*Liriodendron tulipifera*	$ 135,740,000	$ 135,740,000	$ 135,740,000
Red Maple	*Acer rubrum*	$ 117,540,000	$ 117,540,000	$ 117,540,000
Sugar Maple	*Acer saccharum*	$ 116,260,000	$ 116,260,000	$ 116,260,000

Rank	Common Name	Scientific Name	Crop Net Revenue		
			Mean	Low	High
1	Almond	*Prunus amygdalus*	$ 2,498,180,000	$ 1,898,320,000	$ 3,098,030,000
2	Apple	*Malus domestica*	$ 935,060,000	$ 752,370,000	$ 1,117,740,000
3	Black Walnut	*Juglans nigra*	$ 588,100,000	$ 406,560,000	$ 769,630,000
4	Pistachio	*Pistacia vera*	$ 432,790,000	$ 360,760,000	$ 504,820,000
5	Pecan	*Carya illinoinensis*	$ 47,350,000	$ 12,350,000	$ 82,350,000
6	Hazel	*Corylus avellana*	$ 39,880,000	$ 33,100,000	$ 46,660,000
7	Pear	*Pyrus communis*	$ 31,130,000	$ 14,260,000	$ 48,000,000
8	Fig	*Ficus carica*	$ 4,400,000	$ 2,620,000	$ 6,190,000
9	Sweet Cherry	*Prunus avium*	-123000	-47672500	$ 47,426,467
10	Mandarin Orange	*Citrus reticulata*	-26467200	-59607700	$ 6,673,334

Common Name	Scientific Name	Christmas Tree Net Revenue		
		Mean	Low	High
Fraser Fir	*Abies fraseri*	$ 34,520,000	$ 32,700,000	$ 36,340,000
Noble Fir	*Abies procera*	$ 16,800,000	$ 14,370,000	$ 19,220,000
Douglas Fir	*Pseudotsuga menziesii*	$ 8,770,000	$ 4,630,000	$ 12,910,000
Balsam Fir	*Abies balsamea*	$ 4,550,000	$ 3,800,000	$ 5,290,000
Blue Spruce	*Picea pungens*	$ 3,650,000	$ 3,500,000	$ 3,800,000
Scots Pine	*Pinus sylvestris*	$ 3,530,000	$ 3,430,000	$ 3,630,000
White Pine	*Pinus strobus*	$ 2,720,000	$ 2,680,000	$ 2,750,000
Cypress	*Cupressus sp*	$ 960,000	$ 960,000	$ 960,000
White Spruce	*Picea glauca*	$ 900,000	$ 860,000	$ 940,000
Grand Fir	*Abies grandis*	$ 810,000	$ 510,000	$ 1,120,000

Table 2. The most valuable continental 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 O_3), 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	*Pinus*	$25,389,289,489	$10,597,549,418	$7,402,536,592	$7,380,913,415		$8,290,065
2	Oak	*Quercus*	$22,327,731,163	$10,702,056,084	$11,048,359,855	$577,315,224		
3	Maple	*Acer*	$11,074,529,157	$5,243,370,527	$5,534,340,848	$296,817,782		
4	Douglas Fir	*Pseudotsuga*	$8,555,113,301	$5,908,159,459	$1,455,004,741	$1,183,176,063		$8,773,039
5	Hemlock	*Tsuga*	$4,467,535,785	$3,008,325,009	$1,225,172,716	$234,038,059		
6	Cherry/Almond	*Prunus*	$4,125,822,231	$780,954,517	$1,074,096,913	$217,688,989	$2,053,081,812	
7	Spruce	*Abies*	$3,839,147,244	$2,885,232,261	$818,850,801	$75,832,332		$59,231,849
8	Hickories	*Carya*	$3,598,686,663	$1,738,261,008	$1,752,900,146	$60,175,136	$47,350,374	
9	Tulip tree	*Liriodendron*	$3,009,207,291	$1,373,715,800	$1,499,753,000	$135,738,491		
10	Ash	*Fraxinus*	$2,908,276,099	$1,384,668,426	$1,454,588,583	$69,019,090		