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

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Classification
Biological sciences (Environmental sciences) and Economic sciences

Keywords
US trees, ecosystem service value, global change threats, tree of life

Author contributions

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

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Figures 1 to 4
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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 US trees, and the potential threats they face, we combine macroevolutionary and economic valuation approaches using spatially explicit information about tree species and lineages. The value of ecosystem services generated by US trees in forests, orchards, and plantations across five key services with adequate data is $114 billion per annum (low: $85 B; high: $137 B; 2010 USD). Two lineages--pines and oaks--account for 42% of these services. The non-market 'hidden' value of trees from carbon storage and air pollution removal far exceed their commercial value from wood products and food crops. The most valuable US tree species and lineages are also among those most threatened by known pests and pathogens, and species most valuable for carbon storage are most at risk from increasing fire. Different species in different regions contribute to carbon storage and air pollution removal, which is distinct from tree crops that are often provided by the same species in different regions. A diverse set of species distributed across the tree of life contribute to ecosystem services in the US, which is a consequence of their high spatial turnover across the continent, highlighting the need to sustain the diversity of US trees in the face of global change.

Significance Statement

Trees in the continental US generate over $114 billion in net returns to society annually from five key ecosystem services. Importantly, the "hidden" value of trees—the non-market value from carbon storage and air pollution filtration—far exceeds their commercial value. 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 broad distribution of services across the tree of life is a consequence of the high turnover in the species and lineages across regions that provide these hidden values, highlighting the importance of sustaining ecosystem services from the diversity of trees across the US.

Introduction

Trees contribute to human well-being by sequestering and storing greenhouse gasses, filtering air pollutants, providing wood, food, and other products, providing habitat for numerous other species, along with providing aesthetic and recreational value [1-3]. The abundance and composition of US trees is changing due to a complex set of drivers. As global change factors continue to accelerate [3], increasing invasive pests and pathogens [4,5], greater frequency of major fires [6], and changing climatic regimes [7] increase threats to trees. These threats have the potential to undermine the contributions of trees to humans and the societal value they could provide to future generations. Understanding which tree species and lineages contribute more to ecosystem services and which are under greater threat is critical to managing ecosystems for sustainability. In this study we advance towards this goal by providing a baseline accounting—as comprehensively as feasible—for the value of US tree ecosystem services, 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 continental 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, such as for aesthetics or recreation, where spatially explicit information by species was not available. To calculate net value we accounted for the value of benefits provided minus the direct costs incurred to produce these services.

No single tree species has the physiological tolerance to occur in all forests across a continent. Over time, different species have evolved that collectively can tolerate a wide range of climatic and environmental gradients [8]. Phylogenetic lineages—groups of species with a shared ancestry—span larger climatic and environmental gradients than individual member species [9,10]. Species in a lineage share characteristics unique to that group in terms of genetic potential, form, traits that influence ecosystem function and contribute to ecosystem services due to their shared history. 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 as those lineages become threatened. Other ecosystem services, such as carbon storage, will be distributed broadly across the tree of life (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 at risk.

As a consequence of the evolved variation among species in physiological tolerances and niches, the turnover--or beta diversity (sensu Bryant et al. 2008)--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 overyielding—enhanced productivity [11,12] and ecosystem services [13] 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 continent 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 force, 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 and lineage is threatened to understand how these threats are differentially distributed among taxa. Vulnerability to these threats varies among species and lineages because of differences in physiology and spatial proximity to threats. Environmental change, pests, and disease will cause decline in some species and lineages that currently provide high levels of services in certain regions of the US. We identify the locations in the US 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 specific management practices. However, it is beyond the scope of our study to project and compare alternate scenarios of tree services over the next 100 years.

Analyses of regulating and provisioning ecosystem services supported by biodiversity typically use ecosystems or landscapes [14] rather than individual species e.g., [15] or lineages as the unit of study, even though conservation efforts frequently target species, particularly rare or endangered species [16] and consider their phylogenetic context [17,18]. However, we can allocate the production of ecosystem services to specific tree species because they are large and sessile, allowing them to be mapped accurately across space. 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). Estimates of provisioning services are more precise than the estimates of annual regulating service values (Fig. 1D). 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. Provisioning services are commercial products that have a market price. 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 [19-22].

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, in the case of Loblolly pine, higher than average net return to a unit of roundwood production. 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). The high almond tree value was due to their abundance (471,259 ha per annum, 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).

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). 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 [23]. Given their higher than average net value as the source of wood products, pines dominated annual net revenues from wood products at $7.4 B. Oaks had the highest annual climate ($10.7 B) and air quality regulation values ($11.0 B). Climate and air quality regulation capabilities are fairly similar per unit of biomass across most US tree species. Consequently the importance of oaks for regulating service value can be attributed to their diversity and abundance across the US landscape, and in the case of air quality regulation in particular, their abundance near large 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 2020 and 2012). However, we found the annual net returns from citrus products to be negative between 2010 and 2012 due to abnormally low citrus market prices [24] and the prevalence of citrus greening bacterial disease in Florida and to a lesser extent, Arizona and California [25].

Variation among taxa in ecosystem service value

Carbon is stored by all tree species and carbon storage value is concentrated among the most abundant continental US tree species. These high-storing (abundant) species are 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. A species' air quality regulation value depends on its abundance and total leaf area. Air quality regulation benefits further depend on proximity to human populations affected by pollution [2,26]. 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).

Unlike the regulating services, wood product and tree crop producers are concentrated on particular species groups. 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 (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 tend to be greatest 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 by trees between 2010 and 2012 (Fig. 2B, SI Texts 8 – 9, Tables S7 – S8, Figure S2.). Trees can also filter and absorb pollutants released by forest fires. 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).

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

We found low similarity in the composition of forest and plantation tree species (Fig. S1) that provide ecosystem services in different regions. 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 ecodivisions, 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). Ecodivisions represent regional ecological units (Table 1C) of environmental similarity, delineated by the US Forest Service. Lineage similarities of tree services (Fig. S1) among regions were always higher than species similarities, indicating that different species in the same lineage (e.g., oaks) provide services in different regions. Lineage (or phylogenetic) 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), 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. Overall, we find low similarity—in other words, high spatial turnover—in the species that provide the ecosystem services we evaluated (Table 1, Fig. S1) because different species—and to a lesser extent different lineages—grow 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. In contrast, the high diversity of several lineages, whose member species occur in different environments and regions across the US, results in much higher phylogenetic similarity across ecodivisions (Table 1).

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 evaluated the spatial overlap of these threats and tree species and the ecosystem services provided by trees.

We found that threats to tree species were dispersed widely among lineages (Table S1), except for known pests and pathogens, which clustered within certain lineages, including the oak and pine genera as well as in most of the crop species (Fig. 1B, Table S2). Tree species that are known to be at risk of damage from pests and pathogens—measured as the fraction of the species' current production area (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 (Table S1). Tree vulnerability to enemy attacks is tightly linked to phylogenetic identity, given long-term evolutionary processes that drive enemy-host compatibility [27-29]. 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 [30]. Risks to less abundant or less valuable tree species, including novel pathogens that could spread to other species, may not be well understood.

We also studied threats from 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 what they can tolerate—and fire frequency and intensity—measured by average projected change in fire frequency in the counties that contain the species. While pests and pathogens have high phylogenetic specificity, the vulnerability of tree species and lineages to changes in climate depend both on physiological tolerances—which may be similar among close relatives—but also on where species are distributed in relation to predicted climate changes. Therefore, there is wide dispersion across the tree of life of tree species forecasted to have high exposure to climate threats (Table S1).

Associations between services and threats by species

Known pests and pathogens are predicted to disproportionally affect species that generate high annual net climate regulation, air quality regulation, and wood product values (Fig. 4). Some of this positive association is undoubtedly driven by an abundance effect: species with higher abundance generate more economic value, all else equal, and species with higher abundance may 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 [31,32]. 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.

Spatial association of services and threats

Spatial associations between tree services and threats largely parallel species associations (compare Fig. 4B to 4A). The counties with highest carbon annual value from trees coincide with those most impacted by pests and pathogens, increases in fire frequency, and climate change. Likewise, air pollution removal values are highest in counties most threatened by pests and pathogens. However, both services and threats are spatially heterogeneous, with different kinds of services and threats concentrated in different parts of the continental US (Fig. 3). Climate change threatens species in all parts of the continent (Fig. 3A), and is weakly associated with carbon annual value and timber value (Fig. 4B). Pest and pathogen threats to species are strongest in counties of the Southwest and Southeast (Fig. 3B) and negatively associated with timber value in those counties, but positively associated with tree crop values. The threat of major wildfires is expected to increase especially in California and the Intermountain West (Fig.

3C), coincident with where carbon annual storage value is highest, but not with where air pollution removal, timber or tree crop values are highest.

Discussion

This study highlights the importance of sustaining a diverse group of trees for human health and well-being across the US. For the ecosystem services quantified in the paper, climate and air quality regulation, and three commercial provisioning services (wood products, tree crops and Christmas tree production), we found that U.S. continental trees contributed over $114 B annually (2010 USD) in value. The "hidden" values of global climate and local air quality regulation produced by trees across the contiguous US dwarf the values they generate from wood production, crops, and Christmas trees. Both the vast abundance of trees in continental US forests, plantations, and orchards, and their turnover in composition (beta diversity) across the continent contribute to the ecosystem service value of trees.

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 annual service value we calculated, 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 because the species that provide the highest values arise from species across the tree of life (Fig. 1). 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 2). 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 particularly 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 pollution [33] 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 total 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. Addressing these issues is an important but daunting goal for future research

Our analysis likely understates the 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 [26,34]. 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 [2]. Urban trees would also increase our estimate of climate regulation value. For example, Nowak et al. [26] estimate 643 M Mg of carbon are stored in urban areas, which translates to $2.31 B (2010 USD) annually using the annualized SCC (ASCC) of $3.59 Mg of C^{-1}. Second, due to data limitations, we omitted many regulating ecosystem services that trees provide, such as erosion control, flood regulation [35], storm surge regulation [36], urban heat island regulation [37], energy savings due to shade [38], and species habitat provision. Nowak et al [39] 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 the contribution of trees to recreation, ornamental, spiritual, and aesthetic values [40-44]. Including these services in our analysis would greatly increase the value provided by US trees.

A complete accounting of the value provided by continental US trees would also require estimates of the damages trees cause and the cost of their maintenance. 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 [45-48]. Further, while trees remove some of the pollution we would otherwise inhale (see above), 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 [49]. Additionally, trees are a source of the volatile organic compounds (VOCs) isoprene and monoterpenes, which contribute to tropospheric ozone and secondary particle formation [50]. However, trees simultaneously decrease VOCs potentially leading to a slight net reduction [51]. 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 (Table S7). The estimated annual values of the provisioning services are more precise because we have a market price for the per unit value of tree crops, wood products, and Christmas trees, along with good data on production volumes.

The hidden value of trees, which are related to the non-market 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 [52-55] 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 [56]. Mechanisms—such as carbon payments, if designed properly—may help enhance regulating services [57].

In contrast to regulating services, provisioning services, particularly crops, can be attributed to a relatively small number of species clustered in a small portion of the tree of life. 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, there are commercial incentives to invest in protection against pests and pathogens that target commercially valuable species, and management practices have frequently involved transplanting them into new regions when environmental conditions in the initial regions have become too extreme [58,59].

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, our 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 [60,61] and oak wilt [62]. These threats appear to be increasing partially as a consequence of climate change [63,64]. 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 [62,65,66], threatening over 40% of US forest biomass [67]. 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]. 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.

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 [68,69]. 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 [70]. 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.

To measure the monetary value of carbon storage for a single year, in order to make it comparable to the annual value of other services, we computed an annualized value for the 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 \$ 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 [71,72]. 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 [73]. The benefits from pollution reductions by trees were determined using estimates of the amount of pollution removed by tree species by county by pollutant [2,26], the 2011 National Emissions Inventory [74], and the AP3 integrated assessment model [75-78]. 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 [77]. 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 [2,26] provided estimates of each pollutant removed by species by county by year. 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 [79] and the concentration-response parameters for $PM_{2.5}$ [80] and for O_3 [81]. 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 [82]. 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 value of a cubic foot of harvested roundwood. The annualized harvested roundwood 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 [83-85], observed 1998-2014 mean stumpage prices continuing indefinitely (in 2010 USD; SI Table S4), and stand establishment costs in 2010 USD[86]. 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 [70], we calculated annual revenue in the years 2010, 2011, and 2012 at the species and county level (2010 USD)[70]. 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) [87]. 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 [88].

In Fig. 1 we exhibit 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 (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 similarity for tree species 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

We also examine 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 charactericts 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 [89] 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) [90] with the 'phylogeny pool' null model—to draw species with equal probability from the tree of life—using the picante package in R [91]. 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 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 [92]. 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 (SI Text 12).

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 [93-95]. 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 continental US [96]. Warmer temperatures can amplify the stress incurred by drought conditions leading to reduced tree growth and higher tree mortality particularly in the Western US [7,97].

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 United States Forest Service [98]. 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 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).

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 website (https://www.aphis.usda.gov/aphis/resources/pests-diseases/hungry-pests/The-Threat). This website identifies each pest and pathogen p that affects each fruit and nut tree species k in each state s. Let I_{pks} = 1 if state s contains pest and pathogen p and p is known to affect fruit and nut tree species k. I_{pks} = 0 otherwise. The percentage of fruit and nut tree species k's biomass threatened by pest and pathogen p across the continental US is given by $\sum_{s=1}^{S} I_{pks} B_{ks} / \sum_{s=1}^{S} B_{ks}$ where B_{ks} is the average annual biomass of species k found in state s over the years 2010 to 2012 (see SI Text X for details on the calculation of B_{ks}). Let I_{ks} = 1 if state s contains one or more pests and pathogens known to affect fruit and nut tree species k. I_{ks} = 0 otherwise. The percentage of fruit and nut tree species k's biomass threatened by one or more pest and pathogens across the continental US is given by $\sum_{s=1}^{S} I_{ks} B_{ks} / \sum_{s=1}^{S} B_{ks}$.

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 [99]. We used the spatial raster from Barbero et al. [99] 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).

Acknowledgements

This work was supported by the National Socio-Environmental Synthesis Center (SESYNC) under funding received from the National Science Foundation DBI-1052875. Mary Shelley (SESYNC), Ian Muñoz (SESYNC), Belinda Befort (University of Minnesota), Chris Woodall (USFS), John Lyle Anderson (Bowdoin College), and Dylan Dilla (Bowdoin College) contributed to data retrieval, data compilation, scripting, data analysis and/or data synthesis.

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Figure legends

Figure 1.

(A) Ecosystem service annual value (blue bars) and (B) 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 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). Note that ecosystem service values for some tree crop species in B are negative and shown in red pointing inward. Contributions of tree species to carbon annual value 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, (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 Table S1 for details. (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.

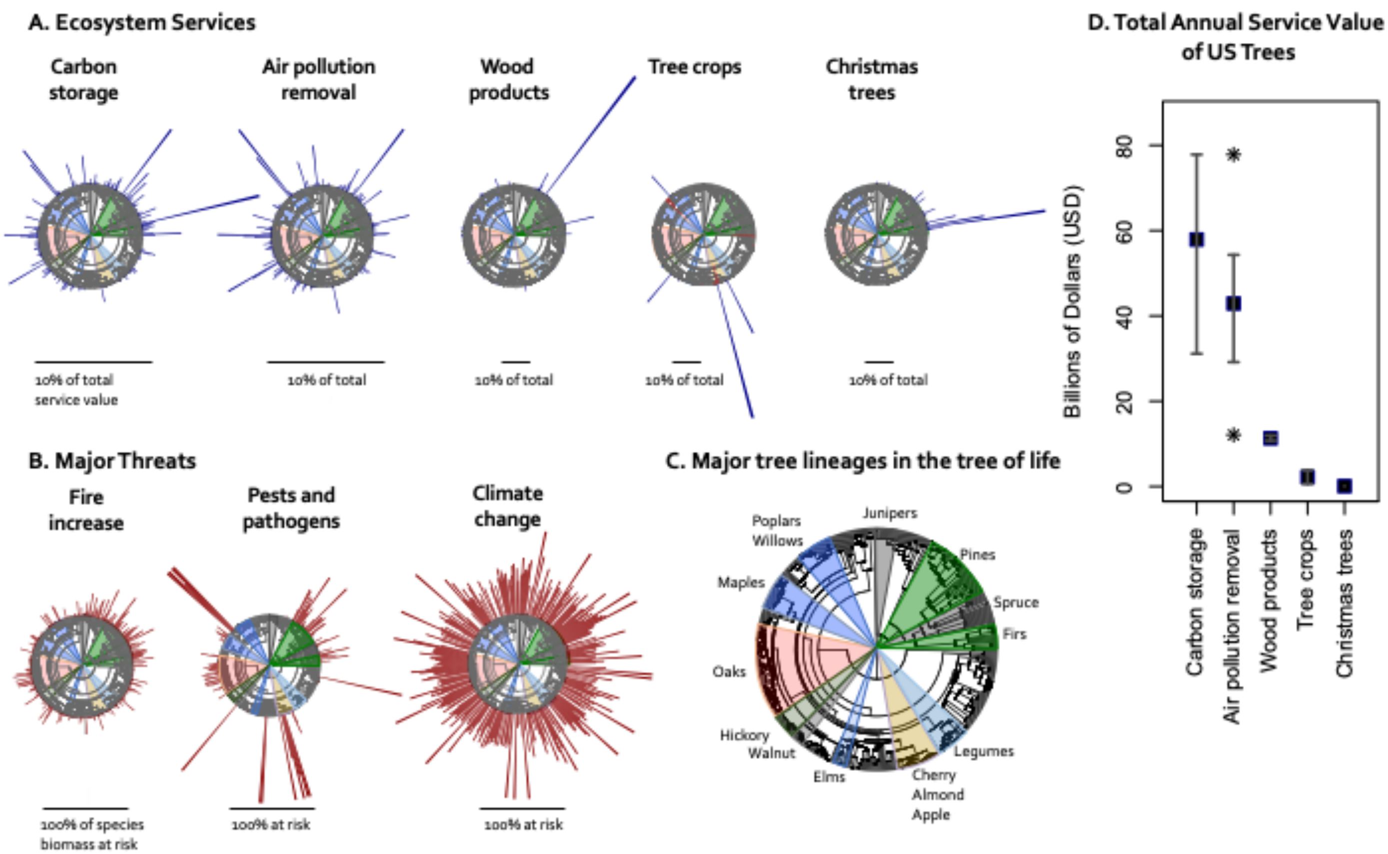

Figure 2.

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.

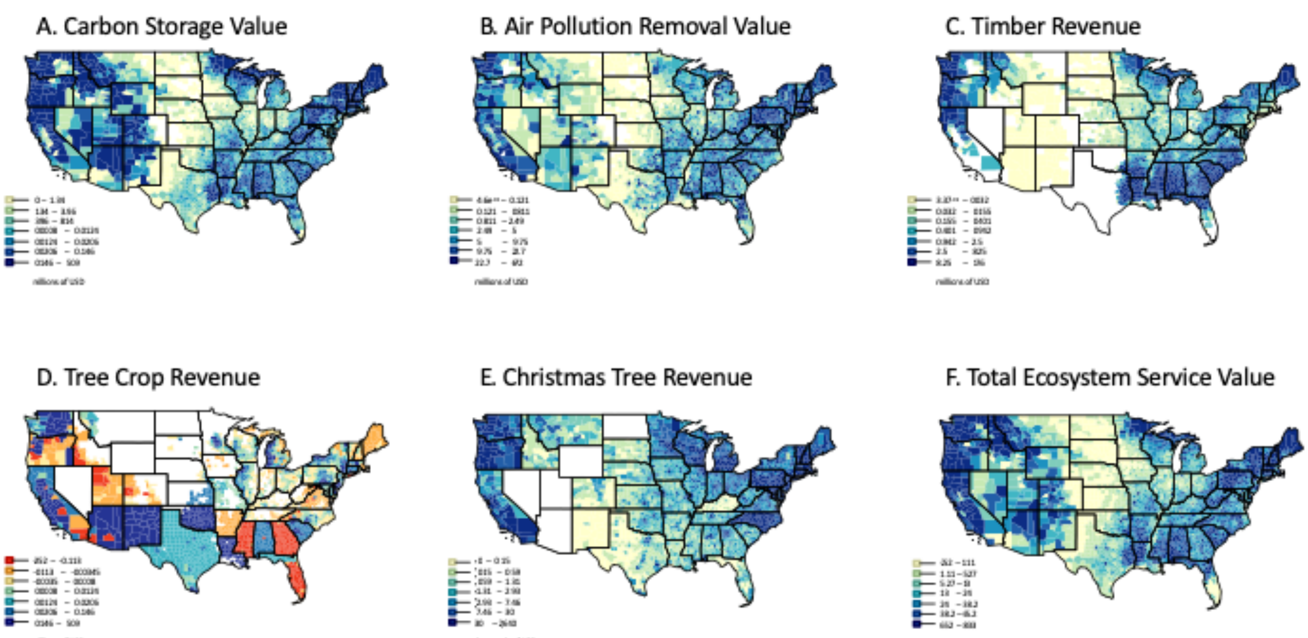

Figure 3.

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 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.

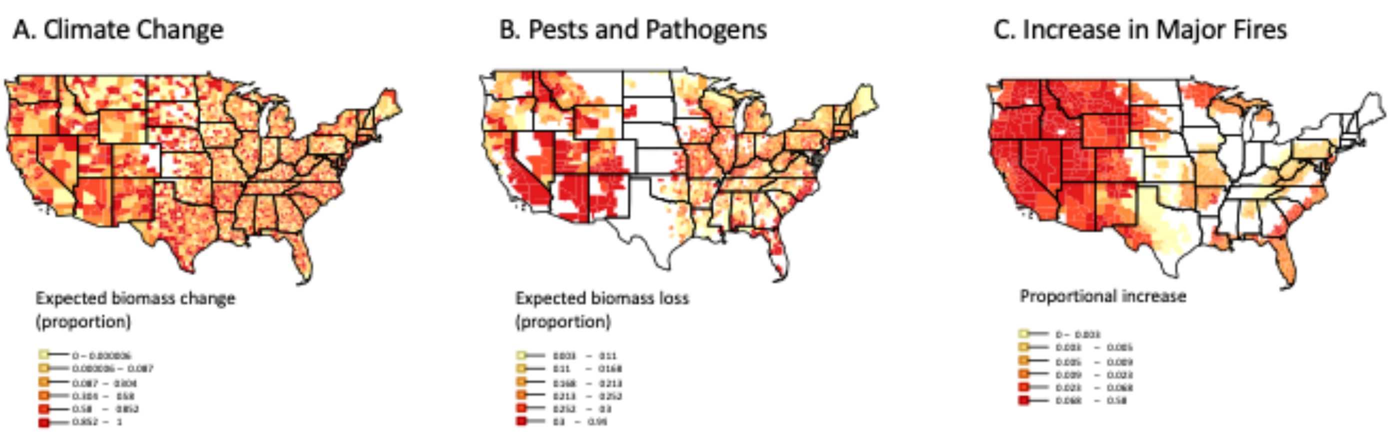

Figure 4.

Associations between annual net ecosystem service values of tree species in the US and their predicted threats and drivers of change. A) The correlation matrix shows the r value of species-level correlations between annual net ecosystem service value and predicted threats. B) The correlation matrix shows 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.

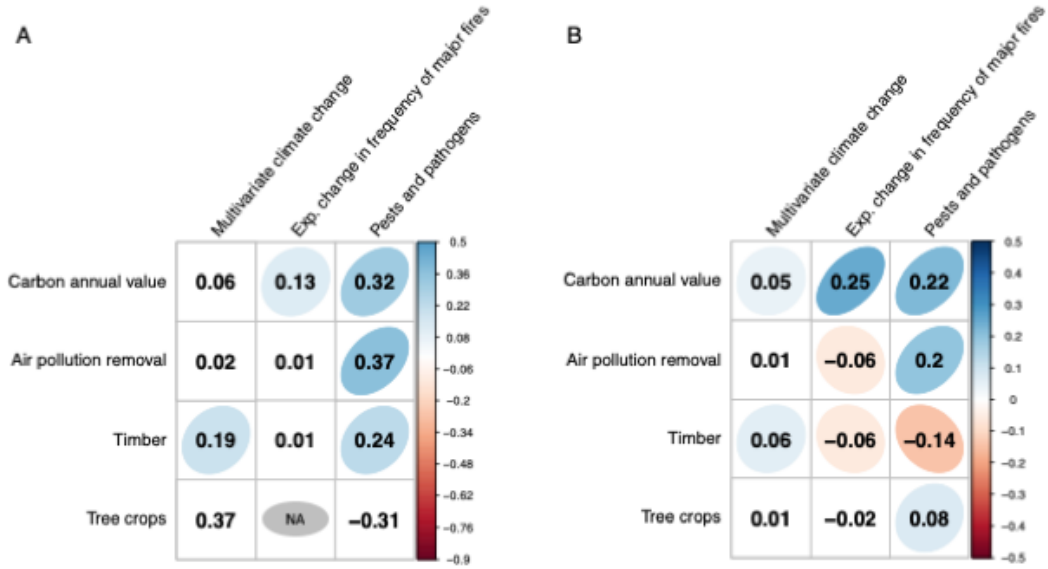
A
Multivariate climate change
Exp. change in frequency of major fires
Pests and pathogens
Carbon annual value
0.06
0.13
0.32
Air pollution removal
0.02
0.01
0.37
Timber
0.19
0.01
0.24
Tree crops
0.37
NA
−0.31
B
Multivariate climate change
Exp. change in frequency of major fires
Pests and pathogens
Carbon annual value
0.05
0.25
0.22
Air pollution removal
0.01
−0.06
0.2
Timber
0.06
−0.06
−0.14
Tree crops
0.01
−0.02
0.08

Table 1. Similarities among species (A) and phylogenetic lineages (B) in the trees that contribute to ecosystems in different ecodivisions (C) of contiguous US forests. Shown are the mean, median and standard deviation of pairwise similarities across ecodivisions 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 ecodivisions (1=all of the same species or lineages contribute), while lower values indicate different species or lineages contribute to an ecosystem service in different ecodivisions (0=none of the same species or lineages contribute). Ecodivisions are defined by the USDA Forest Service (C). See SI Figure S1 for details.

	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. Ecodivisions in US Forests

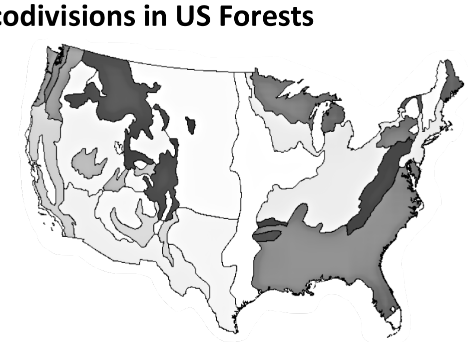

Table 2.

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		