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Article

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Abstract

The spatial variation of forest ecosystem services at regional scales remains poorly understood, and few studies have explicitly analyzed how ecosystem services are distributed across different forest management types. This study assessed the spatial overlap between forest management types and ecosystem service hotspots in the Southeastern United States (SEUS) and the Pacific Northwest (PNW) forests. We used the InVEST suite of tools and GIS to quantify carbon storage and water yield. Carbon storage was estimated, stratified by forest group and age class, and literature-based biomass pool values were applied. Average annual water yield and its temporal changes (2001–2020) were modeled using the annual water yield model, incorporating precipitation, potential evapotranspiration, vegetation type, and soil characteristics. Ecosystem service outputs were classified to identify hotspot zones (top 20%) and to evaluate the synergies and tradeoffs between these services. Hotspots were then overlaid with forest management maps to examine their distribution across management types. We found that only 2% of the SEUS and 11% of the PNW region were simultaneous hotspots for both services. In the SEUS, ecological and preservation forest management types showed higher efficiency in hotspot allocation, while in PNW, production forestry contributed relatively more to hotspot areas. These findings offer valuable insights for decision-makers and forest managers seeking to preserve the multiple benefits that forests provide at regional scales.

Keywords: U.S. forests; hotspot analysis; carbon storage; water yield; InVEST model



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1. Introduction

Forests provide a wide range of ecosystem services, such as climate regulation, clean water supply, wood and non-wood products, and recreation and cultural enrichment [1,2]. Forests regulate climate by absorbing considerable amounts of atmospheric carbon dioxide through photosynthesis and sequestering carbon, thereby helping to mitigate climate change [3]. For instance, forests take up approximately 19% of the global carbon dioxide released through fossil fuel emissions and land-use changes each year [3,4]. In addition, forests make a substantial contribution to regulating and supplying water. Compared to other land cover types, forests provide a more stable and higher-quality water supply [5,6] and help to reduce downstream flood risk [7]. Forests supply over half of the United States'

(U.S.) water supply, although contributions vary due to regional differences in climate and forest management [5,8].

Land-use change, management practices, natural disturbances, and climate change drive forest dynamics and their associated ecosystem services [9,10]. The forest's natural disturbance regime, defined by the frequency, duration, timing, magnitude, and intensity of these drivers, both shapes and shifts forest structure and function [11]. Yet changes outside of the natural disturbance regime can fundamentally alter forest structure and function [9]. Anthropogenic disturbances can also affect forest ecosystem services [12,13]. The relative impacts of these driving forces on ecosystem services, however, are often complex. For example, Balist et al. [14] and Bai et al. [15] found that while changes in land use and climate influence ecosystem services, the sensitivity and response of ecosystem services to such drivers vary spatially and temporally.

Forest management practices, such as harvesting, reforestation, and intermediate interventions like prescribed fire, can alter the balance among ecosystem services, resulting in both synergies and tradeoffs [16]. These practices may lead to either synergies—when services increase or decline together—or tradeoffs, where improving one service comes at the expense of another [17,18]. A recent review revealed that plant functional traits influence the tradeoffs among forest ecosystem services, primarily occurring between regulating services (e.g., runoff control, climate regulation) and provisioning services (e.g., biomass production) [16]. For instance, thinning and clear-cut harvesting can reduce forest soil organic carbon stocks [19,20] but also increase water yield [21]. In general, higher intensity management tends to increase biomass production but often comes at the cost of other vital ecosystem services [22]. Numerous studies have quantified forest ecosystem services and their tradeoffs using spatially explicit models under various land-use or management scenarios e.g., [18,23,24]. Given the strong influence of management strategies on ecosystem services, a multifunctional perspective is needed to ensure the sustainable provision of ecosystem services [18]. Understanding the mechanisms behind ecosystem service synergies and tradeoffs is therefore essential for effective forest management.

Most studies that map ecosystem services have focused on relatively small spatial scales such as individual watersheds, catchments, or state-level scales. For example, Nelson et al. [25] modeled the impacts of land-use change on services such as carbon storage and water supply in the Willamette Basin of Oregon, and Hamel et al. [26] developed a sediment retention model for the Cape Fear catchment in North Carolina. Meanwhile, the spatial pattern in ecosystem services at macroscales (ranging from regional to continental extents, spanning hundreds to thousands of kilometers) remains poorly understood [27]. Understanding ecosystem services at macroscales requires integrating ecological processes, management strategies, and cross-scale dynamics into a social–ecological system [28]. However, macroscale analyses can reveal how differences in environment, regional policy frameworks, and ownership structures shape ecosystem service supply across diverse geographic and governance contexts. Furthermore, to our knowledge, no studies have explicitly analyzed how ecosystem services are distributed across different forest management types. This represents an important knowledge gap, especially in the context of U.S. forests, which span diverse climates, forest types, and ecological conditions [29] and are managed by public and private owners for multiple purposes [30]. Variations in environment and management practices are key drivers of forest dynamics, and, as a result, there will likely be profound long-term effects on associated ecosystem services [22,31]. Integrating forest management into large-scale ecosystem services provides a more comprehensive understanding of how management overlaps with and contributes to the multiple services.

This study aims to address these gaps by mapping ecosystem services and assessing spatial overlap between management types and ecosystem service hotspots at a regional scale. We focus on two critical services (water supply and carbon storage) in two ecologically distinct regions of the U.S. that exemplify diverse climates and different management and ownership patterns: the Southeast and the Pacific Northwest. This contrast provides a comparative framework for understanding spatial patterns and variability of ecosystem services at the regional scale and enables us to examine the interactions between ecosystem service provision and management. Importantly, the ecological and socioeconomic diversity between these regions enhances the replication of the methodological framework, making it applicable to other forested regions worldwide, where diverse forest management approaches exist and tradeoffs between ecosystem services are likely to occur. We aim to answer a key question: “How do ecosystem services and their synergies or tradeoffs vary spatially at the regional scale, and how do areas of high service value (hotspots) overlap with different forest management types?” Specifically, we aim to: (i) quantify the spatial distribution of annual water yield and carbon storage in each region and assess the sensitivity of these services to climate change, (ii) identify hotspot zones of water yield and carbon storage to highlight areas of ecological importance and evaluate tradeoffs and synergies between them, and (iii) examine the spatial overlap between identified hotspot zones and current forest management types. Results will provide insights for decision-makers and forest managers seeking to preserve the multiple benefits offered by forests at macro scales.

2. Materials and Methods

The Southeast U.S. (SEUS) and Pacific Northwest (PNW) forests collectively account for approximately 32% of the total forested lands in the U.S. (Figure 1), and they differ in terms of ownership and management practices [30]. The SEUS features a humid subtropical climate, with long, hot summers and mild winters. The average daily temperatures of the region range from over 21 °C in the south to 12.7–15.6 °C in its northern parts [32]. Mean maximum and minimum temperatures are 22 °C and 9 °C, respectively. Mean annual precipitation in the SEUS is fairly uniform across the region, ranging from approximately 1000 to 1250 mm, with some areas along the southern coast reaching over 1500 mm [32]. Topography is relatively modest, and extensive coastal plains and Piedmont dominate the region, while northern SEUS includes portions of the Appalachian Mountains that create cooler microclimates and higher rainfall pockets. Soils are primarily Ultisols and Inceptisols, which are highly weathered and moderately fertile [33]. Ecologically, the SEUS forests are a mix of fire-adapted pine ecosystems and broadleaf deciduous forests. *Pinus taeda* (loblolly pine), *Pinus elliottii* (slash pine), *Quercus alba* (white oak), *Quercus rubra* (red oak), and upland hardwoods are the most common forest types in the region [34]. The region’s warm climate and abundant rainfall support rapid forest growth, and much of the landscape (~85% of forest land) is privately owned and intensively managed for timber production [30].

The PNW encompasses a highly diverse climate, terrain, and forest structure. A precipitation gradient is evident from coastal areas in the west to the interior regions in the east. Coastal areas receive extreme rainfall (over 2000 mm annually, with local maximum > 3500 mm on windward mountain slopes) and have a cool, maritime climate with wet winters and dry summers [35]. In contrast, interior portions east of the Cascades lie in the rain shadow, with semi-arid conditions (<300 mm annual precipitation) and more extreme seasonal temperature ranges. The topography of the PNW is complex, ranging from flat coastal areas and valleys to high-elevation mountains, including the Cascade and Olympic ranges. Soils in the PNW are heterogeneous, reflecting this physiographic complexity. Inceptisols and Andisols are common in the mountainous and western forested

zones, along with some Spodosols in wet conifer forests; meanwhile, Mollisols and other dry-order soils appear on the eastern side [36]. Mountains create sharp climatic divides, sustaining temperate rainforests on their western slopes and shrub–steppe or ponderosa pine woodlands in the dry east. Old-growth stands, especially in coastal and montane areas, are notable for their exceptionally high biomass and carbon storage. About two-thirds of PNW forest land is publicly owned, and even privately managed forests tend to use longer rotation lengths (~70 years) than in the SEUS [30]. Coniferous forests dominate this region, with *Pseudotsuga menziesii* (Douglas fir), *Pinus ponderosa* (Ponderosa pine), and *Tsuga heterophylla* (western hemlock) as the most prevalent species [37].

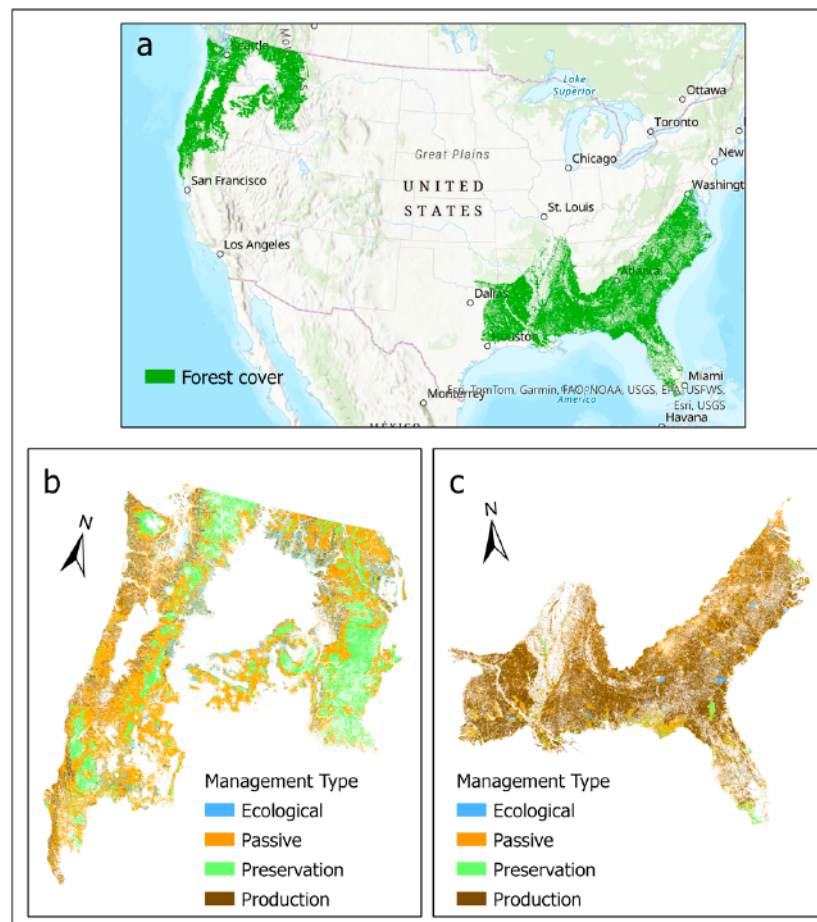


Figure 1. (a) United States forest cover in two study regions; (b) Pacific Northwest; (c) Southeast study region forested lands and their management types.

2.1. Ecosystem Services Assessment

We used the Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST) (Version 3.15.1) suite of tools to model carbon storage and water yield in the SEUS and PNW regions. InVEST was developed to map ecosystem services and assess tradeoffs among them [38], using a series of models with specific data preparation requirements. InVEST contains multiple modular models, each with specific data input requirements and assumptions. A key advantage of InVEST is its flexible spatial resolution, enabling applications from local to global scales depending on data availability and decision-making needs. In this study, we implemented two models within the InVEST framework: the carbon storage and sequestration model and the annual water yield model, which evaluate ecosystem services related to climate regulation and water provision, respectively (Figure 2).

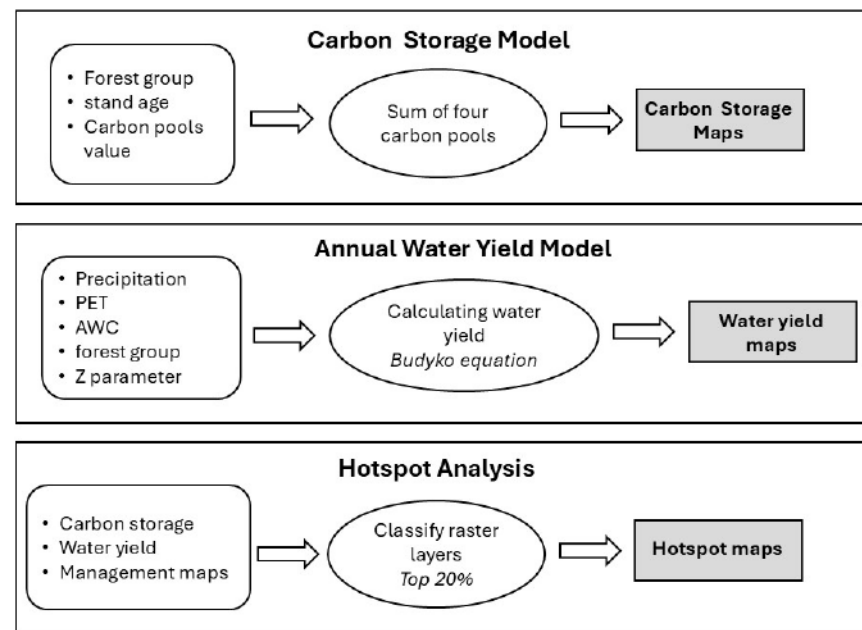


Figure 2. Model framework used to estimate forest carbon storage and annual water yield, and to identify ecosystem service hotspots.

Carbon Storage. The InVEST carbon storage and sequestration model estimates the amount of carbon currently stored in a landscape or the amount of carbon sequestered over time in four carbon pools: aboveground biomass, belowground biomass, soil, and dead organic matter pools [38]. Carbon storage plays a key role in regulating the climate by moderating atmospheric CO₂ levels. This model has been widely used for carbon storage and sequestration modeling in diverse regions and climatic zones [39,40]. We obtained carbon pool values from published estimates by the USDA Forest Service [40,41] for forest type groups and forest age classes (Table 1). We acquired the forest type group layer with a spatial resolution of 250 m, developed by the U.S. Department of Agriculture Forest Service [41]. The forest age map at a 250 km resolution was derived from Pan et al. [42]. These layers were integrated to create a composite input for carbon modeling, maintaining the 250 m spatial resolution throughout, in which each pixel represented both the forest group and its age class. This map, along with the corresponding carbon pool values, was used as input for the InVEST carbon storage model (Table 1 and Figure 2).

Table 1. Data used in the InVEST water yield and carbon storage and sequestration models.

Data	Source	Resolution
Stand age	[42]	250 m
Forest type groups	US Forest Service	250 m
Precipitation	PRISM	4 km
Reference ET	[43]	1 km
Root restricting layer depth	SSURGO	30 m
Plant available water content	SSURGO	30 m
Land use/cover	NLCD	30 m
Biophysical variables (CN, Kc, etc.)	Literature/InVEST documentation	-

The estimated total carbon storage was visualized using ArcGIS Pro software (version 3.3.6) to show the spatial distribution of total carbon across both regions. To assess the contribution of each forest group to total carbon storage, we used the Zonal Statistics tool

in ArcGIS Pro (Version 3.3.6) to calculate the total and mean carbon storage for each forest group in both regions.

Water Yield. The InVEST annual water yield model was applied to estimate the annual water yield, which represents the amount of water running off in the landscape. The model assumes that all water passing through a land parcel will eventually reach an outlet (i.e., a watershed's lowest point or a reservoir) [38]. The water yield model incorporates climate, vegetation, soil, and plant-available water content data to simulate the role of forests in regulating regional water yield [18]. We obtained annual precipitation data (mm) for the period 2001–2020 from the PRISM Climate Group (<https://prism.oregonstate.edu> (accessed on 1 October 2024)), with a spatial resolution of 4 km (Table 1). The average annual reference evapotranspiration was obtained from the Climatology Lab [43]. The model's inputs were the 20-year average precipitation and evapotranspiration. The root restricting layer depth and plant available water content were derived from the USDA Soil Survey Geographic Database, SSURGO/NRCS Soils (<https://data.nal.usda.gov/dataset/gridded-soil-survey-geographic-database-gssurgo> (accessed on 1 October 2024)). We utilized the forest type map, developed by the U.S. Department of Agriculture Forest Service [42], with a spatial resolution of 250 m. The maximum root depth per vegetated land use class was extracted from the Food and Agriculture Organization (FAO) guidelines [44] and Schenk and Jackson [45]. The evapotranspiration coefficient (Kc) was extracted from Allen et al. [44] and InVEST documentation. The InVEST water yield model resamples all input datasets to match the cell size of the forest group map. The forest group map had a spatial resolution of 250 m, and thus, all input layers were resampled to match this resolution. Consequently, the model's final output was also produced at 250 m. A detailed description of the equations and parameter derivations is provided in Appendix B.

We also analyzed temporal changes in water yield between 2001 and 2020 for both regions. We used 5-year average values of precipitation and evapotranspiration for two time periods: Period 1 (2001–2005) and Period 2 (2016–2020). Using average values helps to smooth out annual variability and reduce the influence of extreme weather events (e.g., drought). The InVEST model runs on an annual timestep; therefore, all model inputs and outputs were annual.

2.2. Model Validation

We calibrated the InVEST water yield model insofar as adjusting it to region-specific inputs, but the model itself does not use site-specific calibration parameters. To build confidence in the model outputs, we performed a validation of the model output against an independent dataset. The most important parameters for analyzing model accuracy are climate variables, including annual precipitation and potential evapotranspiration [26]. Among the water yield model outputs, actual AET has been measured at various spatial and temporal scales using multiple methods, including remote sensing techniques, eddy covariance flux towers, and hydrological modeling approaches. For example, Yin et al. [46] validated AET estimates from the InVEST model by comparing them with observed data, demonstrating strong agreement ($R^2 = 0.95$). We compared the AET simulated by the InVEST model to AET estimates derived from remote sensing data from the Operational Simplified Surface Energy Balance (SSEBop) database [47]. Because the MODIS AET data are available at a coarser spatial resolution (~1 km), we resampled our modeled AET output to 1 km to enable a direct pixel-by-pixel comparison. Validation was conducted across all forested pixels in both the SEUS and PNW, which enables the evaluation of the performance and spatial accuracy of the modeled outputs.

2.3. Hotspot and Coldspot Analysis

InVEST provides spatially explicit outputs that estimate ecosystem service values for each pixel. For example, the model simulated the annual water yield for a spatial unit in this study (250 m × 250 m spatial resolution). We were particularly interested in identifying hotspots and coldspots that have the highest or lowest values of ecosystem services in each pixel [48,49]. These are commonly defined based on biological thresholds or quantitative cutoffs [50]. We classified the ecosystem services maps into five classes using the quantile classification method in the ArcGIS environment. We designated areas falling within the top 20% of values for each service as hotspot areas and the bottom 20% as cold spots [48]. Areas where both the 20-year average water yield and carbon storage simultaneously ranked in the top 20 percent of their distributions were identified as multiple ecosystem services hotspot areas, and the bottom 20% as coldspots. Because both ecosystem service outputs—carbon storage and water yield—were generated at the same resolution (250 m), they were directly comparable and spatially aligned, ensuring consistency for the hotspot and coldspot analyses.

Finally, we assessed the distribution of hotspot zones across different forest management types to examine management effects. We used four classified forest management maps for the SEUS and PNW, available from Marsik et al. [30]. These maps categorized forested lands into four management types: (1) production, (2) ecological, (3) passive, and (4) preservation management types (Table 2). The management maps were derived using a random forest classifier applied to 16 years of MODIS satellite Enhanced Vegetation Index (2000–2015), combined with ancillary data such as forest ownership, roads, and wilderness areas. Non-forest pixels were removed, and management types were assigned to pixels where at least 80% of the data sources reached complete or majority consensus. An overall classification accuracy of ~89% (from 10-fold cross-validation of the model) and ~67% accuracy against an external ground truth dataset were reported for the SEUS, and ~91% (cross-validated) and ~70% external for PNW.

Table 2. Management types in SEUS and PNW regions.

Management Type	The Primary Goal of Management	% Regional Area	
		SEUS	PNW
Production	To extract wood products for economic gain.	67	10
Preservation	To promote ecological diversity by minimizing human consumptive services and maximizing other ecosystem services.	4	27
Ecological	To balance wood product extraction with the maintenance of other ecosystem services.	1	12
Passive	Rather than a goal, forests are primarily left alone—too wet to harvest or to protect sensitive species (riparian areas)—or owned by people who enjoy their aesthetics or simply neglected.	28	51

These management maps represent long-term, dominant management regimes rather than short-term or year-to-year management events. However, the use of diverse input data (seasonal vegetation dynamics, ownership and infrastructure data, etc.) helps capture different facets of forest management, from harvest rotations to the presence of roads and conservation status. Thus, they provide a valuable and consistent spatial foundation for regional-scale forest management types. Additional methodological detail on data sources, variable selection, classifier accuracy, and validation metrics (including kappa statistics) is provided in Marsik et al. [30].

We converted the categorical management maps into a binary raster and calculated the proportion of each management type that overlapped with identified hotspot zones using

the raster calculator tool. This allowed quantification of how different management types contribute to high ecosystem service provision zones in each region. We also calculated a “hotspot contribution ratio” (percentage of regional hotspots divided by percentage of area for each management type) to quantify the relative allocation of hotspots in each management type per unit area.

3. Results

3.1. Carbon Storage

Our InVEST model results indicated that in the SEUS, carbon storage ranged from approximately 60 to 326 t ha^{−1}, with varying spatial distribution. Overall, carbon storage was higher in the east than in the west of the SEUS region. Higher values of carbon were concentrated in parts of northern Florida, coastal South Carolina, and Appalachia (Figure 3). Among forest types, Loblolly/Shortleaf Pine forests had the largest contribution to carbon storage in the SEUS, accounting for 35.7% of the total carbon stored (Table 3). However, the highest mean carbon storage per unit area was for Oak/Gum/Cypress forests, with an average of 189 t ha^{−1}. Oak/Hickory and Longleaf/Slash Pine Forest groups also greatly contributed to the carbon storage of the SEUS. The remaining forest groups had smaller shares and together accounted for less than 10% of the total SEUS carbon.

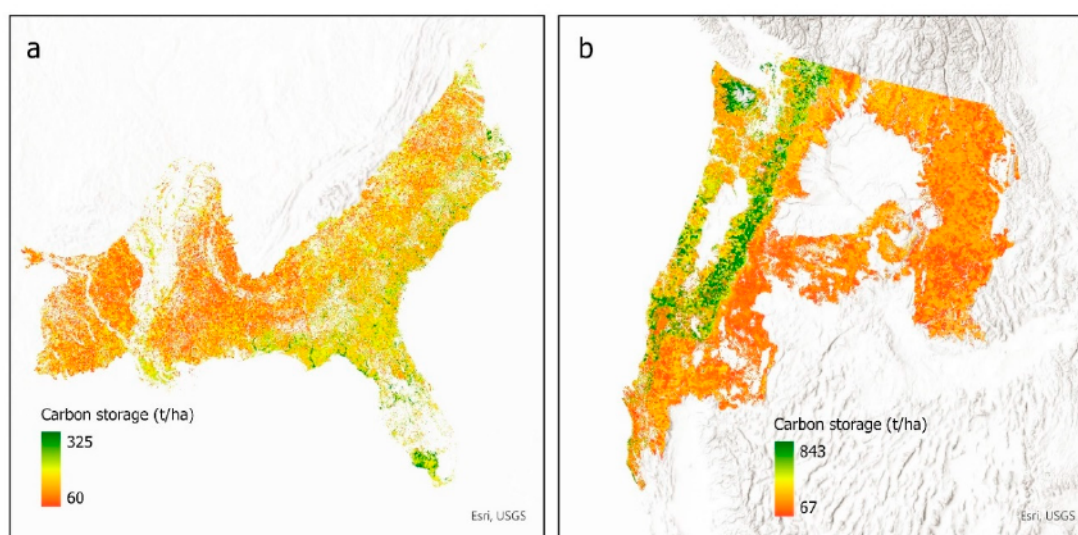


Figure 3. Spatial distribution of carbon storage in the (a) SEUS and (b) PNW regions.

Table 3. Carbon storage by the forest group in the SEUS region.

Forest Type Group	Area (%)	Mean (t ha ^{−1})	Standard Deviation	Sum (MT)	Sum (%)
Loblolly/Shortleaf Pine	41.65	130.6	41.1	3451.9	35.74
Oak/Gum/Cypress	16.41	189.0	64.5	1964.4	20.34
Oak/Hickory	23.60	127.6	46.4	1924.4	19.93
Longleaf/Slash Pine	9.38	175.5	39.0	1318.1	13.65
Oak/Pine	7.64	133.1	44.0	730.6	7.56
Elm/Ash/Cottonwood	1.29	154.8	47.1	164.4	1.70
Other Eastern groups	0.03	154.8	45.2	23.1	0.24

Results from our InVEST model indicated that the forests of the PNW region exhibited a wider range of carbon storage than the SEUS, ranging from 67 to 845 t ha^{−1} (Figure 3). Carbon storage in the PNW was less uniformly distributed and displayed a distinct trend

from west to east. The highest concentrations of carbon were found in the dense, temperate rainforests along the western slopes of the Cascade Range and coastal forests of Oregon and Washington. In contrast, the interior and eastern parts of the PNW exhibited considerably lower carbon storage due to drier conditions and lower forest productivity. Douglas Fir forests contributed a significant portion of the total regional carbon (~52%), followed by Fir/Spruce/Mountain Hemlock and Ponderosa Pine forests (Table 4). Although Hemlock/Sitka Spruce forests accounted for only 6.6% of the total carbon storage in PNW, this forest group had the highest mean carbon storage among major forest types, showing their great potential for carbon storage.

Table 4. Carbon storage proportion by the forest group in the PNW region.

Forest Type Group	Area (%)	Mean (t ha ⁻¹)	Standard Deviation	Sum (MT)	Sum (%)
Douglas Fir	42.29	353.7	202.1	5530.0	52.30
Fir/Spruce/Mountain Hemlock	19.87	265.5	128.8	1938.8	18.34
Ponderosa Pine	13.95	148.0	39.0	751.3	7.10
Hemlock/Sitka Spruce	4.64	408.3	242.1	698.1	6.60
California Mixed Conifer	6.01	224.7	83.9	500.0	4.73
Lodgepole Pine	4.42	158.9	55.1	257.5	2.44
Alder/Maple	2.06	335.8	140.5	255.0	2.41
Tanoak/Laurel	1.88	213.7	139.0	148.1	1.40
Western Oak	1.80	207.9	74.0	137.5	1.30
Pinyon/Juniper	2.21	154.7	31.4	124.4	1.18
Redwood	0.64	478.3	185.1	113.1	1.07
Other Western groups	0.22	238.6	90.1	92.5	1.13

3.2. Water Yield

In the SEUS, our InVEST model results indicated that the 20-year average annual water yield (2001–2020) exhibited considerable spatial variability, ranging from less than 200 mm yr⁻¹ to nearly 1000 mm yr⁻¹ (Figure 4). Northern parts of the SEUS, particularly the mountainous regions, and coastal zones of Alabama, Mississippi, and western Florida had higher water yield. Conversely, southern Florida exhibited low rates of water yield. Other regions with low water yield were eastern Texas, the interior areas of the SEUS region, and southwestern Georgia. From 2001 to 2020, the total regional water yield in the SEUS increased; however, this change was inconsistent across the region. Some areas, particularly in the western, northwestern, and northeastern portions of the SEUS, experienced increases in water yield. In contrast, northern Florida, Georgia, and some central parts of the region experienced declines in water yield.

In the PNW, the estimated water yield showed a wider range than the SEUS, varying from less than 100 mm yr⁻¹ to nearly 2000 mm yr⁻¹ (Figure 5). The western areas, particularly mountainous areas, had the highest water yields, whereas the eastern and interior portions of the region had much lower water yields. Like the SEUS region, total water yield in PNW increased between 2001 and 2020. Coastal areas in the west typically experienced an increase in water yield, whereas northern California experienced the biggest decreases.

3.3. Hotspot Zones

In the SEUS, carbon storage hotspots were predominantly distributed across central, northeastern, and eastern parts of the region (Figure 6a). Water yield hotspots appeared more concentrated in the southern portion of the region, especially along the Gulf Coastal Plain and parts of Florida. Only about 2% of the region contained hotspots for both ecosystem services, carbon storage and water yield (i.e., falling within the top 20% for

both water yield and carbon storage) (Figure 6a). Co-occurring hotspot areas in the SEUS were mainly found along the Gulf Coast, with small portions in northern Florida and mountainous regions.

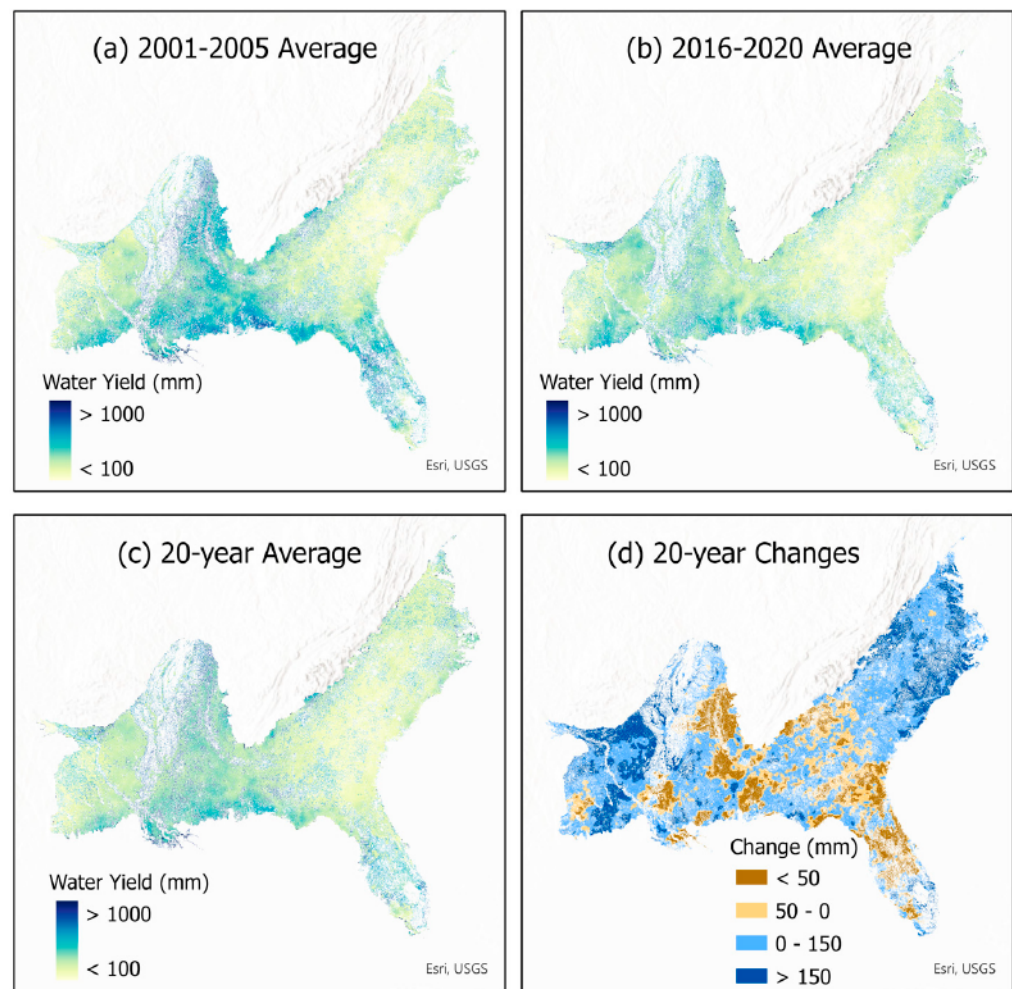


Figure 4. Spatial distribution and temporal changes in annual water yield across the Southeastern United States (SEUS) from 2001 to 2020: (a) Average water yield for the period 2001–2005; (b) average water yield for the period 2016–2020; (c) 20-year average water yield from 2001 to 2020; (d) change in water yield between the first and last 5-year periods (2016–2020 minus 2001–2005).

In contrast, the PNW contained many more co-occurring hotspots, with approximately 11% of the region classified as simultaneous hotspot zones for both water yield and carbon storage. Hotspots were primarily located along the western slopes of the Cascade Range and in coastal forests (Figure 6b). Both carbon storage hotspots and water yield hotspots were widespread in western Oregon and Washington (coastal and mountainous areas) (Figure 6b). However, water yield hotspots were more scattered across the region, appearing along a few spots in the eastern side with greater precipitation. Approximately 2% of the SEUS and 7% of the PNW were classified as coldspots for multiple ecosystem services, where both water yield and carbon storage fell within the bottom 20%. In both regions, areas with either high carbon storage or high water yield (only one ecosystem service as a hotspot) were widely scattered throughout each region.

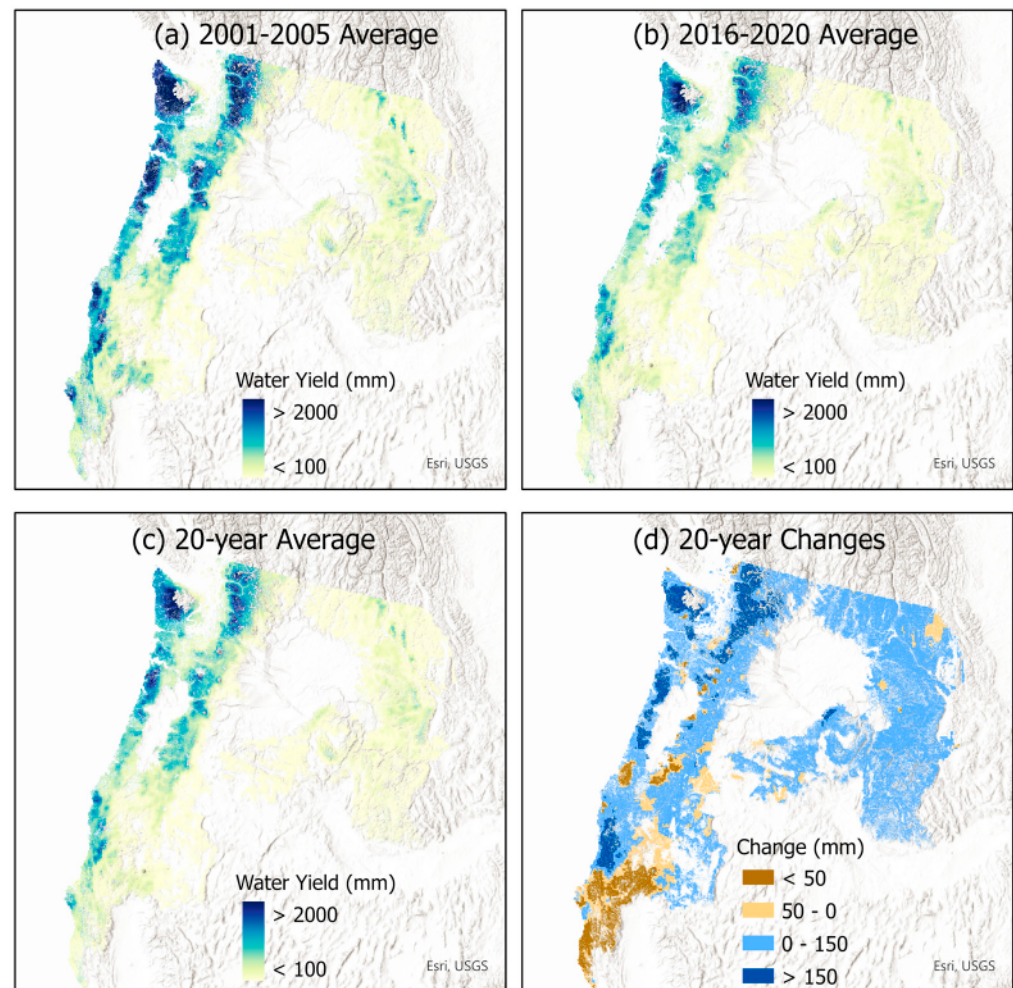


Figure 5. Spatial distribution and temporal changes in annual water yield across the Pacific Northwest (PNW) from 2001 to 2020: (a) Average water yield for the period 2001–2005; (b) average water yield for the period 2016–2020; (c) 20-year average water yield from 2001 to 2020; (d) change in water yield between the first and last 5-year periods (2016–2020 minus 2001–2005).

We also conducted a correlation analysis for ecosystem services. The results revealed a very weak negative correlation between carbon storage and water yield in the SEUS region ($r = -0.042$), while the PNW region showed a moderate positive correlation ($r = 0.437$) (Table 5), implying that increases in carbon storage are associated with increased water yield. Correlation coefficients between carbon storage and water yield by forest management types were also substantially different. In the SEUS, all forest management types exhibited similarly weak and negative correlations, suggesting that current forest management strategies in the SEUS may not promote strong synergies between carbon storage and water yield. Areas in passive management had the weakest negative correlation, whereas areas in production and ecological management had slightly stronger negative correlations. In contrast, in the PNW, all four management types showed positive correlations, with the strongest observed under preservation ($r = 0.590$) and passive ($r = 0.396$) management. These results highlight that protected and less intensively managed forests are more effective at maintaining co-benefits between carbon and water services.

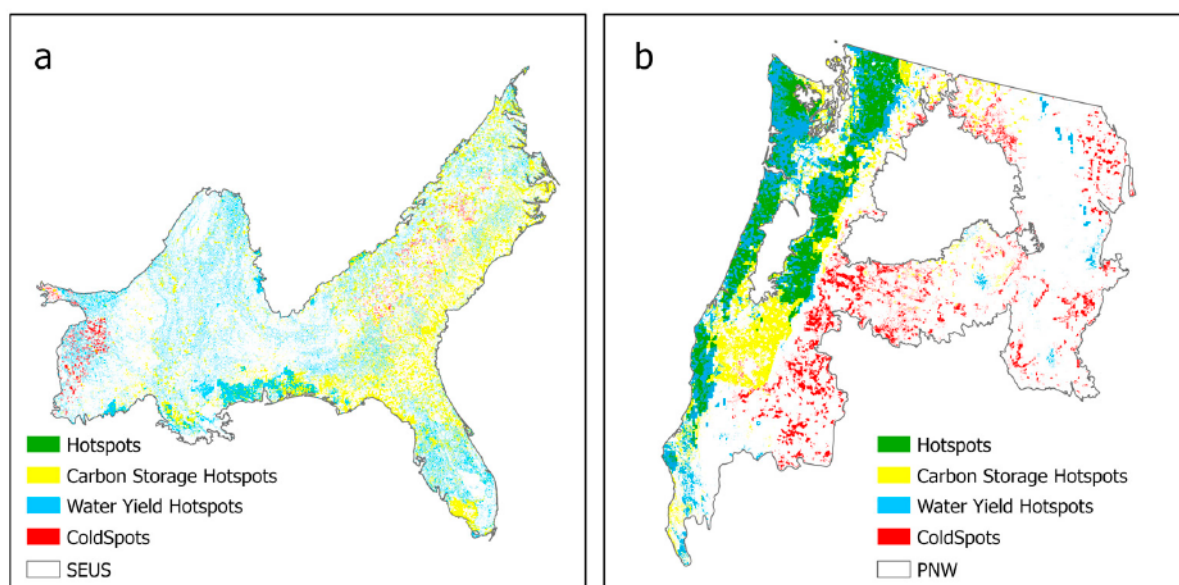


Figure 6. Maps of hotspots (green) and coldspots (red) for two ecosystem services in the (a) SEUS and (b) PNW regions. The green areas represent regions where both water yield and carbon storage are hotspots, while the red areas represent regions where both are coldspots. Additionally, areas where only water yield or carbon storage is a hotspot or coldspot are indicated.

Table 5. Pearson correlations between carbon storage and water yield in the SEUS and PNW regions by management type.

Region	Management Type	Correlation Coefficient
SEUS	Ecological	−0.075
	Passive	−0.019
	Preservation	−0.042
	Production	−0.074
	Overall	−0.042
PNW	Ecological	0.341
	Passive	0.396
	Preservation	0.590
	Production	0.223
	Overall	0.437

3.4. Management Types

The two regions showed key differences in the ratio of carbon hotspots to regional areas. In the SEUS region, production and passive management types cover 67% and 28% of the forested lands, respectively. However, production forestry contributed a disproportionately lower amount (54%) toward carbon hotspot zones, while passive contributed a slightly higher amount (32%) (Table 6). On the other hand, preservation and ecological forestry together cover 5% of the region, while they contributed disproportionately higher amounts (14%) to carbon hotspot zones. The ratio of carbon hotspot proportion to regional area covered indicated that ecological management (with a ratio of 4:1) had the highest allocation, followed by preservation (with a ratio of 2:1) in the SEUS. In contrast, production forestry had the lowest contribution ratio in hotspots (0.8) among the four management types.

In the PNW, passive and preservation management types dominate the region (51% and 27%, respectively), and they also accounted for the highest proportions of carbon hotspots (53% and 27%, respectively), contributing roughly proportionate amounts, as indicated by ratios close to 1. Ecological forestry covers 12% of the PNW's forests but

accounted for a lower amount (8%) of carbon hotspots, yielding a ratio of 0.6, while production forestry covers 10% of the area but accounted for a higher (12%) amount of the hotspot zones, giving a ratio of 1.3.

Table 6. Distribution of forest management types in contributing to carbon and water yield hotspots in the SEUS and PNW regions.

Region	Management Type	% Regional Area	Proportion of Regional Carbon Hotspots	Ratio (Carbon Hotspot–Area)	Proportion of Regional Water Yield Hotspots	Ratio (Water Hotspot–Area)
SEUS	Ecological	1	4	4	2	2
	Passive	28	32	1.1	32	1.1
	Preservation	4	10	2.1	4	1.0
	Production	67	54	0.8	62	0.9
PNW	Ecological	12	8	0.6	10	0.8
	Passive	51	53	1.0	45	0.9
	Preservation	27	27	1.0	28	1.0
	Production	10	12	1.3	17	1.7

In the SEUS, production management accounted for 62% of the water yield hotspot zones (Table 6). Its ratio of hotspot proportion to area covered (0.9) represents a slightly lower contribution to water yield hotspots relative to its regional area. Ecological forestry (1% of the land area) contributed 2% to the water yield hotspots, thus resulting in the highest ratio (2.0) among all management types in the SEUS. Preservation and passive forestry had a balanced contribution, with a ratio of 1. In the PNW region, passive management contributed the most to water yield hotspots (45%); however, this amount was slightly lower than its area (51%), yielding a ratio of 0.9. Similar to the results with carbon hotspots, ecological management has a lower ratio (0.8), indicating a disproportionately lower contribution to PNW water yield hotspots, whereas preservation management contributions were proportionate (ratio = 1). Production forestry had the highest ratio (1.7) among all management types, showing its higher relative contribution per unit area to overlap in high water yield zones in the PNW.

4. Discussion

This research explored the question: “How do ecosystem services and their tradeoffs or synergies vary spatially at the regional scale, and how do areas of high service value (hotspots) overlap with different forest management types?” We found that the production of ecosystem services varied spatially at a regional scale, reflecting the combined influence of biophysical characteristics, climate patterns, forest type and age, and management strategies. At the regional scale, we observed clear spatial differences in the extent of overlapping service hotspots and found that tradeoffs and synergies between ecosystem services are not only regionally distinct but are also shaped by forest management approaches.

4.1. Carbon Storage

The results of this study showed pronounced spatial variation in carbon storage across the SEUS. This variation is influenced by factors such as forest structure, climate patterns, soil characteristics, and management practices [49,51–53]. In particular, total carbon storage was higher in the eastern portion of the SEUS, with notable differences in soil organic carbon (Figure A1, Appendix A). The higher soil organic carbon (SOC) levels are likely driven by a combination of climatic, topographic, and soil conditions [54]. SOC generally increases with increasing precipitation but decreases with rising temperatures and steeper slopes [54]. In addition to these parameters, land-use and forest management practices, particularly harvesting and reforestation, can affect the SOC level depending on the intensity and frequency of management interventions [55,56]. In the SEUS, forest age and rotation cycles,

particularly in intensively managed pine plantations with harvest intervals of ~25–30 years, can limit long-term carbon storage. These frequent harvests limit biomass accumulation, which decreases their potential to reach the higher carbon storage levels often achieved in older or unmanaged forests [57,58].

The PNW region displayed a more heterogeneous carbon storage pattern, reflecting its sharp climatic gradients, complex topography, and diverse forest composition. The coastal temperate rainforests of the western PNW contained the highest carbon storage values, benefiting from abundant precipitation, mild temperatures, and the dominance of long-lived, high-biomass species such as Douglas fir and western hemlock. In contrast, the interior and eastern portions of the region exhibited substantially lower carbon storage levels, primarily due to drier conditions, which limit biomass accumulation and carbon sequestration. A distinct west-to-east gradient in precipitation reflects the influence of the rain shadow effect, where the Cascade Range and other major mountains create drier conditions on their eastern (leeward) slopes compared to the western (windward) slopes of the PNW [59–61]. Also, the average harvest rotation period in the PNW is approximately 70 years [62], which allows trees to sequester high levels of carbon before harvest.

These findings are consistent with those of Pan et al. [3], who emphasized the influence of climatic gradients and forest structure on regional variability in carbon storage, with carbon density being highest in forests with warm, moist climates. They also highlighted the importance of forest management, disturbance regimes, and land-use changes on carbon storage and sequestration. Similarly, Hoover et al. [63] noted that forest type and stand age are key determinants of carbon storage and sequestration across the US forests. At a global level, a comprehensive analysis of forest carbon-flux databases showed that old-growth forests, particularly in the boreal and temperate regions of the Northern Hemisphere, store larger quantities of carbon [64].

4.2. Water Yield

Our results demonstrated that water yield across both the SEUS and PNW regions varied spatially and temporally over the 20 years. These patterns suggest that forest water yield in both regions was sensitive to climate, particularly temperature and evapotranspiration. In the SEUS, mountainous areas exhibited higher water yield, primarily due to greater precipitation and lower evapotranspiration rates associated with cooler temperatures. In contrast, southern Florida demonstrated lower water yield despite high precipitation levels, which can be attributed to high evapotranspiration rates under warmer temperatures. These findings are consistent with those of Sun et al. [65] who reported substantial spatial variation in forest water yield across the SEUS, with mountainous watersheds producing the highest water yield due to high rainfall levels and reduced evapotranspiration losses in cooler environments. In addition to climate, forest structure also plays a critical role in regulating water yield. For instance, Acharya et al. [66] found that forest management influenced local water yield variability through its effects on leaf area index (LAI). They demonstrated that higher LAI increased evapotranspiration and interception, thereby reducing the water yield. These mechanisms, along with topographic variation (e.g., elevation differences between mountainous and coastal areas), may explain some of the spatial variation in water yield observed in our study, where differences in forest composition, management, and topography likely contribute to the water yield patterns.

Like carbon storage, water yield in the PNW exhibits greater spatial contrasts, driven by the region's complex topography and sharp climatic gradients. As noted, due to the rain shadow effect, the western slopes of the region receive high precipitation, leading to greater water yield, while the interior and eastern areas have drier conditions, resulting in lower water yield. Additionally, forest age and local variations in bedrock geology

can contribute to streamflow patterns in the PNW [67,68]. A study analyzing 60 years of daily streamflow records in Oregon found that older forests, dominated by species such as Douglas fir, western hemlock, and other conifers, had 50% higher summer streamflow compared to younger (34–43 years old) Douglas fir plantations [68]. This difference was attributed to higher evapotranspiration rates in younger plantations, driven by greater sapflow per unit of sapwood area and a lower physiological capacity to limit transpiration.

Our findings also revealed temporal changes in water yield over a 20-year study, likely linked to climate change. Although the total water yield increased in both regions overall, certain areas, such as northern Florida and northern California, experienced declines. Reductions in these regions were likely due to decreased precipitation and increased evapotranspiration under warming conditions. In contrast, increases observed in parts of the SEUS and PNW appear to be associated with rising precipitation amounts. Between 2001 and 2020, total average annual precipitation increased by approximately 13% in the SEUS and 17% in the PNW, contributing to these regional shifts in water yield. In a recent study, Duarte et al. [69] reported that water yield across much of the conterminous U.S. has been influenced by climate change and is projected to decline, particularly in the central and southeastern regions. Similarly, Liu et al. [70] analyzed the spatial and temporal variations in runoff in response to the changing climate in the PNW. Their results indicated both positive and negative trends, with runoff decreasing in warmer, drier areas and increasing in colder, wetter areas. These temporal changes in water yield, particularly in drier regions, emphasize the need for sustainable and adaptive forest management strategies to ensure long-term water provision under future climate scenarios.

4.3. Hotspots and Coldspots

In the SEUS, only about 2% of the region was classified as a hotspot for multiple ecosystem services, mostly located along portions of the Gulf Coast and small areas in northern Florida. These forests are generally characterized by relatively flat terrain and a mix of pine and hardwood forest types. The limited extent of hotspots in the SEUS may be attributed to more intensive forest management, shorter rotation lengths, and higher evapotranspiration rates, all of which constrain the ability of forests to simultaneously support high levels of both carbon storage and water yield. In contrast, approximately 11% of the PNW was classified as a hotspot for multiple ecosystem services, mainly along the western slopes of the Cascade Range and in coastal temperate rainforests. Dense, high-biomass coniferous species, such as Douglas fir and western hemlock, dominate forests in these areas. These substantial regional differences between SEUS and PNW suggest that forest management strategies, harvest intensity, and climatic conditions in the PNW are more favorable for delivering co-benefits in the provision of both regulating and provisioning ecosystem services. However, the percentage of coldspots for multiple ecosystem services was higher in the PNW (7%) than in the SEUS (2%), which suggests that while the PNW contains more highly productive areas (hotspots), it also includes larger regions with simultaneously low carbon storage and water yield due to its heterogeneous climatic and environmental condition.

Areas that provide only a single ecosystem service hotspot, either carbon storage or water yield, were scattered across both regions. These spatial patterns likely reflect differences in underlying biophysical characteristics (such as soil and climate) and forest management practices, which often favor one service at the expense of the other. For example, forest management practices such as thinning and canopy removal in harvested forests reduce leaf area and transpiration, which can enhance water yield by allowing more precipitation to contribute to runoff. However, these practices typically reduce aboveground biomass and soil organic matter, thereby limiting the forest's ability to store

carbon [71]. Previous studies have supported this tradeoff dynamic. For instance, increasing forest cover globally often enhances carbon storage but can simultaneously decrease water yield, especially in water-limited ecosystems [72]. Similarly, afforestation intended for climate change mitigation may reduce water availability due to increased transpiration, with tradeoffs being especially prominent in drier regions, semi-arid tropics, and intensively managed systems [73]. In a study conducted in the SEUS forest, Pisarello et al. [74] found that management practices such as increased thinning and shorter rotation cause greater water yield while decreasing biomass.

4.4. Management Types

We utilized four classifications to describe forest management approaches currently implemented in the SEUS and PNW regions (Figure 1). In the SEUS, the majority of forested lands are managed under production and passive management types (Table 2). Production management typically uses common silvicultural practices such as clear-cut harvesting, even-aged stand management, and site preparation to maximize wood production and economic returns [30]. However, these practices often come at the expense of other ecosystem services [75]. In contrast, ecological and preservation forestry aims to enhance and support a wider range of ecosystem services. In the SEUS, only a small portion of forests (~5%) are currently managed for ecological or preservation forestry. Our analysis shows that this small proportion of forests under these management types exhibited a greater spatial overlap with carbon storage hotspots compared to areas under production or passive management, which highlights the critical role that ecological and preservation management play in enhancing long-term carbon sequestration and storage. This result is consistent with the work of Karimi et al. [49], who found that switching to preservation management led to the greatest increase in forest productivity relative to other management types in the SEUS forests. Similarly, the influence of landscape-scale conservation initiatives on ecosystem services was examined in England and Wales, and it was shown that conservation management enhances the provision of carbon storage [76]. In the PNW, production forestry contributed greatly to carbon hotspots, primarily because low-elevation forests in the western part of the region are located in areas with favorable climatic and ecological conditions, which are managed for production with a long harvest rotation period (Figure 1). Overall, ratios describing the hotspot area to management area in the SEUS varied widely across management types, indicating the uneven contributions of management to hotspots, while in the PNW, most management types showed ratios closer to 1, reflecting a more proportional relationship between the regional percentage of management type and hotspots. Our spatial overlay of ecosystem service hotspots with forest management types is among the first of its kind at a regional scale in U.S. forests. This approach addresses a key knowledge gap by revealing how current management practices influence the spatial distribution of ecosystem services and their hotspots, which provide valuable insights for prioritizing sustainable forest management and conservation.

Water yield hotspots in the SEUS were predominantly located in production and passive management types, which together account for approximately 95% of the forested lands (Table 2). However, ecological management exhibited the highest relative contribution to water yield hotspots (ratio = 2.0), indicating that this management may have higher capability for water yield provision. In the PNW, areas managed under passive forestry, which dominates the region, contained a substantial number of water yield hotspots. Interestingly, production forestry areas, although limited to only about 10% of the region's forests, made a relatively high contribution to water yield hotspots. Higher relative contribution of production and ecological forestry in both regions may be attributed to clear-cutting and harvesting, which reduce canopy cover and lower evapotranspiration, thereby increasing

water yield. Previous studies have reported that forest management practices such as reforestation and afforestation, tree harvesting, and stand thinning influence watershed water yield by altering the hydrological cycle [77,78]. For instance, Sun et al. examined the influence of forest removal on water yield across the U.S. and found that a 70% reduction in leaf area index can increase water yield up to 50% in some regions [77].

Although the model applied in this study did not directly evaluate the impact of forest thinning and clear-cutting on water yield, our findings reinforce the conclusion that both production and ecological forestry, which reduce stand density and increase structural openness, can enhance water yield. However, such gains in water yield under production forestry may come at the cost of other ecosystem services, such as carbon storage, nutrient retention, soil conservation, and habitat quality for biodiversity [75]. The consistent contribution of ecological management in both regions strengthens the potential of multifunctional forestry to support multiple ecosystem functions and services. As climate change continues to alter precipitation patterns and increase evapotranspiration demand, forest managers may adopt strategies that balance timber production with providing other vital ecosystem services, particularly in vulnerable and intensively managed areas.

4.5. Implications for Forest Management and Planning

Our findings have important practical implications for forest management strategies. By identifying carbon storage and water yield hotspots, the results provide valuable information for policymakers and forest managers aiming to maximize the co-benefits of forests. These findings can also help ensure that high-value ecosystem service areas are prioritized for conservation or sustainable management, aligning with existing literature that emphasizes the integration of ecosystem services into land-use planning and conservation strategies [79]. Given the regional scale of our analysis and the spatial resolution of some input data, these results are not intended to inform local or stand-level management decisions. Instead, they are most applicable to regional agencies, state forest services, and policymakers seeking to incorporate ecosystem service considerations into broad-scale land management and policy development.

Importantly, our findings demonstrate that not all management strategies are equally effective in delivering ecosystem service hotspots. Preservation and ecological forestry were associated with higher occurrences of co-occurrence hotspots, particularly in the SEUS. Policymakers can use these insights to guide management priorities and expand programs that promote a shift from intensive production to more ecological or preservation-focused practices in some locations. This does not mean eliminating timber production but rather optimizing the landscape. For example, intensive production could be concentrated in areas with minimal impact on other critical ecosystem services and biodiversity, while ecological approaches could be prioritized where co-benefits are highest. This aligns with sustainable planning frameworks that aim to balance multiple landscape values [80].

Furthermore, our study supports forest policies focused on climate change mitigation. The carbon hotspots that were identified are natural assets for climate mitigation. Preserving these forests can substantially contribute to carbon sequestration. Simultaneously, water yield hotspots are critical for water security under climate change, as they are likely to be sources of stable flow. Protecting forests in those watersheds could be a key climate adaptation strategy. There is increasing recognition that land management decisions must account for ecosystem service tradeoffs in a changing climate [81].

4.6. Limitations and Future Research

To assess ecosystem services at regional scales, models and assumptions are necessary, and all models have limitations. Here, we discuss the uncertainty and assumptions inherent in the InVEST carbon and water yield models and how they might affect our findings. Carbon storage and water yield models simplify hydrological and ecological processes, and uncertainty may arise from multiple sources. Inherent constraints of the InVEST model and the availability of input data prevent us from addressing every limitation. For example, the carbon storage model estimates carbon stocks based primarily on land use/land cover (LULC) classifications and the average carbon content within four carbon pools. However, carbon storage can vary significantly even within a single LULC type, such as forest cover, due to differences in species composition, forest type, and stand age [82,83]. We improved carbon storage estimation by disaggregating land cover types into forest groups and stand ages and revealed the substantial influence of these factors on carbon storage and sequestration by capturing more spatial heterogeneity and variability within forested lands, particularly on smaller scales. Still, there will be variability within the types of forests due to differences in stand density, management history, and/or site fertility. Also, due to the lack of multi-temporal forest group/age layers, potential changes in carbon between 2001 and 2020 (e.g., growth and/or harvests) were not dynamically modeled, with estimated carbon and hotspots assuming relatively stable forest cover. In other words, areas that were disturbed in the last 20 years could have less (or more) carbon than our map indicates. While we believe this effect is minor at the regional scale, it could impact specific locations. In terms of uncertainty, we did not validate the carbon model outputs against field data. However, given that we acquired carbon pools established by the U.S.D.A. Forest Service, it is expected that these values are unbiased at larger scales. Carbon hotspot identification should be robust, as it describes areas that exhibit high values across broad scales.

The water yield model assumes that long-term annual runoff is the sum of precipitation and evapotranspiration. This model also simplifies hydrological processes, and thus, one of the key limitations of the model is that it does not capture landscape complexities, such as land-use patterns or underlying geology, which can result in complex water balances [26]. Additionally, the model does not account for interannual variation in water yield, which may be influenced by seasonal flow dynamics and peak flows throughout the year [38]. In the SEUS region, which has year-round rain, seasonal effects are likely small; however, some areas of the PNW with high water yield experience dry summers. Integrating seasonal dynamics would provide a more detailed and comprehensive understanding of water yield as an ecosystem service, especially in regions characterized by distinct wet and dry periods. We recommend that future research incorporates seasonal variability into water yield estimation. Despite these simplifications and limitations, validation efforts, such as comparing the InVEST AET to satellite-based AET, as well as past studies, suggest the model performs well for our application. Validation results of our water yield model indicated generally good performance, with better accuracy observed in the SEUS compared to the PNW (Appendix C). The model tended to overestimate actual evapotranspiration (AET) in higher elevation areas, especially in the PNW region. This overestimation is likely attributable to the model's simplified water balance approach, which does not account for snow accumulation or topographic influences. Additionally, the greater climatic and topographic heterogeneity in the PNW likely contributed to more widespread AET overestimation. Prior studies have also compared InVEST outputs with those from other models and observational data and found acceptable agreement between the model outputs and observed measurements, as well as outputs from more complex hydrological models. For example, Hamel et al. [84] found that InVEST Water Yield

Model estimates were similar to the Soil and Water Assessment Tool (SWAT), which is a more sophisticated, process-based hydrological model. In addition to limitations related to the model structure, there may be limitations associated with the input datasets and their spatial resolutions. Uncertainty may arise from climate and soil parameters, which propagate into the output. A previous sensitivity analysis demonstrated that precipitation and potential evapotranspiration are dominant drivers of water yield uncertainty, while soil depth and plant available water also contribute to variability [26]. In our case, using a 20-year average climate reduces year-to-year uncertainty.

In our analysis, we used spatial datasets of varying resolutions (from 30 m to 4 km). As noted, for the carbon storage model, both the forest group and forest age maps were originally at 250 m resolution, which were integrated to create a composite input for carbon modeling, maintaining the 250 m spatial resolution throughout. However, a wider range of resolutions was used for the water yield model, in which the model resampled all input datasets to match the forest group, and consequently, the model's final output was also produced at 250 m. Although this makes water yield maps comparable to carbon storage, which was crucial for hotspot overlap analysis, resampling the dataset may affect the accuracy of water yield hotspots. Resampling high-resolution data (e.g., 30 m soil properties) may obscure fine-scale ecosystem heterogeneity. Likewise, downscaling precipitation to a 250 m pixel assigns the same rainfall total to many smaller pixels, which ignores any microclimate variation within that area. This is especially important in the PNW region, where topographic effects substantially influence local precipitation patterns. Thus, a small area with high water yield might not be captured as a hotspot, and the model underestimates localized hotspots. However, identifying hotspot areas at 250 m is acceptable given our regional-scale focus. The high carbon and water yield areas we identified align with known mature, old-growth forests and high-rainfall zones, respectively, and the influence of management we observed agrees with findings from literature and field studies (e.g., that intensive harvest reduces carbon and can increase water yield). Thus, while we acknowledge model limitations, we believe our approach is appropriate for our research question and study objectives.

Finally, we recommend that future studies map a wider range of ecosystem services, such as soil erosion control, habitat quality, and timber production, and analyze their spatial overlap with existing management practices. This approach could help identify areas of synergy and tradeoff, as well as identify multifunctional hotspot zones. Mapping multiple ecosystem services can also guide more strategic and optimized forest management practices, as our results suggest that certain areas may currently be under- or mismanaged in terms of their potential to deliver diverse and sustainable ecosystem services. Such analyses would support more adaptive and integrated forest management decisions and policies.

5. Conclusions

This study mapped the spatial distribution of ecosystem services and examined how hotspot zones intersect with different forest management types. The results showed significant spatial variability in the provision of carbon storage and water yield across the forested land of the SEUS and PNW regions, driven by differences in climate, topography, forest composition, and management practices. The PNW demonstrated higher potential for co-provisioning of ecosystem services, while SEUS showed more limited multifunctionality, with only a small portion of its landscape identified as hotspot zones for both carbon storage and water yield. Moreover, the results showed that forest management plays a key role in ecosystem service provision, where preservation and ecological forestry generally support higher levels of services, particularly in the SEUS region. These outcomes underscore the importance of forest structure and climate in shaping spatial patterns of ecosystem services

and highlight the potential of preservation and ecological practices to enhance ecological functions and services.

By mapping ecosystem services across diverse conditions and identifying areas with high potential for carbon storage and water provision, our research provides valuable insights for policymakers, land managers, and environmental authorities seeking sustainable water management and climate mitigation strategies. Forest managers should prioritize preservation and ecological approaches in regions with high multi-service potential, particularly where climate mitigation and water regulation are key objectives. Also, policymakers should support multifunctional forest management, especially in intensively managed landscapes. Finally, land managers can use spatial hotspot maps to guide conservation prioritization and adaptive policy development under climate change. While our primary focus was on the SEUS and PNW forests, the comparative analysis of these two ecologically and socioeconomically distinct regions provides a framework that can be applied to other U.S. forested lands. This will contribute to the advancement of integrated water resource management, climate mitigation, and ecosystem service evaluation at both national and global scales. The methodological framework presented in this study is also replicable in other forested regions globally, especially where forest management is heterogeneous and tradeoffs between carbon sequestration and water availability can occur under land-use changes and management strategies. Ultimately, our findings offer valuable insights into management policies and refinements that foster adaptive management strategies, aligning ecological capacity with social needs and environmental conservation.

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Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

InVEST	Integrated Valuation of Ecosystem Services and Tradeoffs
SEUS	Southeast United States
PNW	Pacific Northwest
DEM	Digital Elevation Model
U.S.	United States of America

Appendix A. Maps of Carbon Storage Pools in the SEUS and PNW Regions

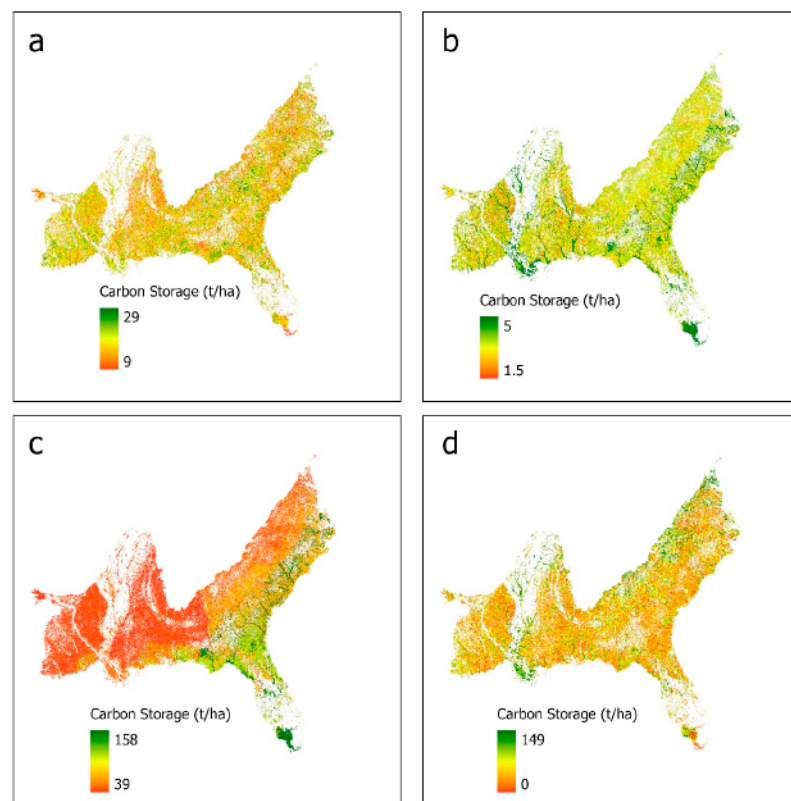


Figure A1. Spatial distribution of carbon storage pools in the SEUS region: (a) dead organic matter, (b) belowground biomass, (c) soil organic carbon, (d) aboveground biomass.



Figure A2. Spatial distribution of carbon storage pools in the PNW region: (a) dead organic matter, (b) belowground biomass, (c) soil organic carbon, (d) aboveground biomass.

Appendix B. Water Yield Model Equations and Parameters

The InVEST annual water yield model estimates the annual volume of water produced in each pixel as a function of climate, vegetation, soil, and topographic characteristics. The model is based on an annual water balance approach, which describes the relationship between precipitation and actual evapotranspiration (AET). The annual water yield equation for pixel i on LULC j , Y_{ij} (mm yr^{-1}), is as follows:

$$Y_{ij} = \left(1 - \frac{AET_{ij}}{P_i}\right) P_i \quad (\text{A1})$$

where AET_{ij} (mm yr^{-1}) is the actual annual evapotranspiration for pixel i on LULC j , and P_i (mm yr^{-1}) is the annual precipitation for pixel i .

For vegetated LULC, the evapotranspiration portion of the water balance, $\frac{AET_{ij}}{P_i}$, is based on an expression of the Budyko curve [85] (Equation (A2)).

$$\frac{AET_{ij}}{P_i} = 1 + \frac{PET_{ij}}{P_i} - \left[1 + \left(\frac{PET_{ij}}{P_i}\right)^{\omega_i}\right]^{\frac{1}{\omega_i}} \quad (\text{A2})$$

where PET_{ij} is the potential evapotranspiration for pixel i on LULC j (Equation (A3)), and ω_i is a non-physical parameter that characterizes the natural climatic–soil properties for pixel i (Equation (A4)):

$$PET_{ij} = K_{ij} ET_{0,i} \quad (\text{A3})$$

$$\omega_i = Z \frac{AWC_i}{P_i} + 1.25 \quad (\text{A4})$$

where K_{ij} is a vegetation-specific coefficient that adjusts reference evapotranspiration for land use/land cover type j , $ET_{0,i}$ is the reference evapotranspiration for pixel i , Z is a dimensionless constant ranging from 1 to 30, and AWC_i (mm) is the volumetric plant available water content for pixel i .

Appendix C. Validation of InVEST-Modeled AET Against Modis-Based Observations in the SEUS and PNW

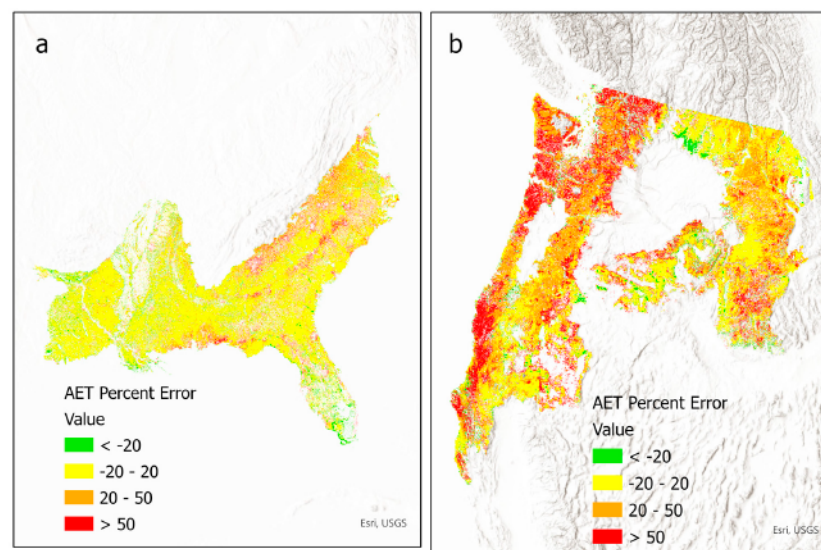


Figure A3. Percent error map of actual evapotranspiration (AET) in the SEUS (a) and PNW (b), comparing InVEST-modeled AET to MODIS AET. Positive values indicate overestimation by the model, while negative values represent underestimation.

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