Ecohydrology

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RESEARCH ARTICLE

Interactions Between Climate and Species Drive Future Forest Carbon and Water Balances

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ABSTRACT

Global change is altering forest carbon and water balances; however, the extent to which tree species shape ecosystem-scale responses to climate, particularly in biodiverse forests, remains unclear. To address this, we simulated the effects of an envelope of future climate conditions on watershed carbon and water balances and quantified the contributions of tree species based on their xylem anatomy. We accomplished this by incorporating species-level transpiration calculations into a landscape-scale ecosystem process model. Our revised model linked the effects of forest succession, species composition, and climate change on water and carbon. Calibration of forest water fluxes using sap flux measurements and catchment water balances captured variability in species transpiration and interannual ET in biodiverse, humid temperate forest catchments in the southern Blue Ridge Mountains, USA. Across wet and dry future climate projections, ET increased, and streamflow and net carbon uptake decreased, particularly under a scenario of increasing drought. Despite accounting for just 30% of current biomass, diffuse-porous tree species were the main driver of carbon and water flux responses now and in the future, thus intensifying the increase in ET and decline in streamflow. As diffuse-porous biomass continues to increase, these forests will be increasingly sensitive to drought, amplifying losses of carbon sequestration and freshwater delivery.

1 | Introduction

Forests provide essential ecosystem services, including carbon sequestration (Pan et al. 2011) and supplying clean and stable freshwater (Vose et al. 2016). The changing climate is altering forest carbon and water dynamics and, therefore, the delivery of ecosystem services. Increasing temperature has the potential to increase ET through higher evaporative demand (i.e., vapour pressure deficit; VPD) and through extending growing season length (Novick et al. 2016; Hwang et al. 2018). However, increased ET depends on water availability, which may become more limiting under future climate conditions (Denham et al. 2023; Short Gianotti et al. 2019). Warmer, more water-limited conditions may subsequently decrease gross primary production due to stomatal closure and increased respiration, but the combined effect on net carbon uptake is uncertain (Green et al. 2019; Oishi et al. 2018). Despite understanding the major atmospheric and ecophysiological drivers of changing carbon and water fluxes, the directions and magnitude of those changes remain difficult to predict, leading to uncertainty in the sustainability of ecosystem services under future climates (Fisher et al. 2018).

The influence of climate on carbon and water fluxes in vegetation varies depending on the species present. In particular, species water use traits dictate transpiration rates and drought responses. Among other traits, xylem anatomy and sapwood area

Summary

- Ecosystem model LANDIS-II NECN updated to include species-level transpiration
- Increasing ET was dominated by transpiration from diffuse-porous species.
- Climate change exacerbates impacts of mesophication on water and carbon fluxes.

are important drivers of species transpiration rates and sensitivity to water stress (Ford, Hubbard, and Vose 2011; Hawthorne and Miniat 2018). Transpiration rates of diffuse-porous species such as maples (*Acer* sp.) and tulip-poplars (*Liriodendron tulipifera*) are up to four times higher than similarly sized ring-porous species including oaks (*Quercus* sp.) and hickories (*Carya* sp.) and are over twice as sensitive to soil water stress (Ford, Hubbard, and Vose 2011). Under future climates, diffuse-porous species are expected to experience greater water stress and reduced productivity, and provision less water downstream compared to ring-porous species (Brzostek et al. 2014; Vose et al. 2016). However, in additional to a changing climate, species compositions are changing in ways that further complicate projections of future fluxes.

Long-term changes in species composition can alter the water-use requirements, carbon balance, and forest climate resilience. In eastern U.S. forests, multiple interacting ecosystem drivers including fire suppression practices during one of the wettest periods since 1500 CE led to a shift in dominant species composition from ring-porous, shade-intolerant species to diffuse-porous shade-tolerant species (McEwan, Dyer, and Pederson 2011; Nowacki and Abrams 2008; Pederson et al. 2015). In the absence of fire on the landscape, a positive feedback loop favouring the shade-tolerant species resulted in increasingly closed canopy forests where shade-intolerant species were outcompeted in a process called mesophication (Nowacki and Abrams 2008). Since the mid-1970s, this shift has been attributed to a 29% increase in ET and an 18% decrease in streamflow of select headwater catchments (Caldwell et al. 2016). These forests are expected to be more sensitive to rising temperatures, more frequent droughts, and wildfires expected under future climates, with the potential for reduced sustainability of ecosystem services (Vose and Elliott 2016).

Understanding how future climate and forests will impact carbon and water balances requires a model that incorporates succession with dynamic species-level carbon and water fluxes. Forest landscape models (FLMs) are frequently used to forecast change by combining forest stand dynamics with interactive and spatially explicit forest landscape processes (de Bruijn et al. 2014; Scheller et al. 2007; Seidl et al. 2012). However, simplified representations of hydrology are often implemented in FLMs as a computational trade-off to more complex overstory dynamics, resulting in models that do not simulate species-level transpiration (Scheller et al. 2011; Seidl et al. 2012). Hydrological models, on the other hand, include complex representations of hydrology but lack the necessary representation of forest landscape processes. Given these limitations, we expanded applicability to ecohydrology by updating the forest landscape model, LANDIS-II Net Ecosystem Carbon and Nitrogen (hereafter, LANDIS NECN) succession extension (Scheller et al. 2011) to incorporate species-level transpiration calculations, and applied it to capture interactions between climate and species (Supplementary Figure 1). LANDIS NECN simulates spatially interactive forest succession including species growth, mortality, competition, reproduction, and disturbance at landscape scales over long time periods. Therefore, it is an apt choice to study climate change impacts on forest ecohydrology.

Despite large species-level differences in the magnitude and sensitivity of carbon and water fluxes to climate variability, the extent that landscape scale carbon and water fluxes will be determined by species responses to climate change remains unclear, especially in diverse forests. This is particularly important to understand in eastern forests experiencing ongoing mesophication, and we hypothesize that the expansion of diffuse-porous species will play a dominant role in determining landscape-scale hydrologic responses to climate change. Therefore, out aims were to: (1) Calibrate the revised LANDIS NECN for ecohydrology using forest water fluxes at species and catchment scales. (2) Quantify carbon and water balances across two headwater catchments in the southern Blue Ridge Mountains, USA under an envelope of potential future climate based on species composition.

2 | Materials and Methods

Readers may reference Supplementary Table 1 to keep track of acronyms and their meanings.

2.1 | Study Area

We modelled two reference watersheds unmanaged since the 1930s (WS14 and WS18, total area 0.76 km^2) within the USDA Forest Service Coweeta Hydrologic Lab located in the southern Blue Ridge Mountains, U.S. with supplemental data from across the large basin (Miniat et al. 2021). The climate is marine, humid temperate (Peel, Finlayson, and McMahon 2007) with average annual temperature and precipitation of 13.6 °C and 2085 mm yr^{-1} (Miniat et al. 2015; Miniat et al. 2017). Elevation ranges from 670 to 1590 m across the whole basin with WS14 and WS18 from 710 to 1013 m. Forest composition in WS14 and WS18 has a canopy dominated by broadleaf deciduous trees with a high abundance of oak (*Quercus* sp.) and hickory (*Carya* sp.) but with an increasing abundance of mesophytic species like maple (*Acer* sp.) and tulip poplar (*L. tulipifera*) (Caldwell et al. 2016).

2.2 | Modelling Framework

We used the Landscape Disturbance and Succession model, LANDIS-II (v7), a spatially interactive model that simulates forest growth, mortality, competition, reproduction, and disturbance at landscape scales (Scheller et al. 2007). It has been applied extensively to study the impacts of changing climate and drought (Duveneck et al. 2017; Gustafson et al. 2015; Scheller et al. 2018) on forest dynamics.

Forest succession, soil dynamics, water and nutrient exchange were simulated using the NECN (v6.7) extension to LANDIS-II (Scheller et al. 2011). NECN operates over large spatial extents and long time periods, making it an ideal choice for projecting

forest succession and species-to-landscape responses to climate change. NECN accounts for above and belowground carbon and nitrogen dynamics to simulate species responses to climate and disturbance via establishment and growth. A simple bucket model is used to track the water balance in each grid cell. Transpiration is based on soil moisture and PET, resulting in transpiration estimates disconnected from forest dynamics, like productivity, growth or species composition.

We revised the NECN extension to calculate transpiration for each species-age cohort based on the Photosynthetic/EvapoTranspiration model (PnET) (Aber and Federer 1992), as implemented within the LANDIS PnET Succession extension (de Bruijn et al. 2014). We opted to revise NECN instead of run the PnET extension to retain the comprehensive soil carbon and nitrogen dynamics from NECN, specifically the limiting effect of soil nitrogen on forest growth and transpiration. Following LANDIS PnET, dynamic water use efficiency (WUE) was a pure mass flux ratio (WUE = Mass flux of H_2O/Mass flux of CO_2) calculated as a function of soil water limitation, species-specific foliar nitrogen, atmospheric CO_2, temperature, and VPD. Gross primary productivity (GPP) (g C m^{-2} mo^{-1}) was calculated using a carbon use efficiency of 0.5 (GPP = NPP × 2), which is a common heuristic in temperate forests (Running and Coughlan 1988; Waring, Landsberg, and Williams 1998). Then GPP was converted to transpiration (mm m^{-2} mo^{-1}) using dynamic WUE (Transpiration = GPP/WUE). The updated transpiration calculation reflects species-level differences in water use rates and implicitly includes the effects of competition, age, climate, and available water and nutrients from the productivity calculation. The source code for the revised model can be found on GitHub (https://github.com/kmcquil/Extension-NECN-Succession). For additional information on modelled pools (C, N, H_2O), their interactions with climate, and outputs, see Scheller et al. (2011) or the NECN User's Manual (https://landis-ii-foundation.github.io/Extension-NECN-Succession/). See Supplementary Figure 1 to visualize the modelling workflow.

2.3 | Model Setup and Parameterization

The study area (WS14 and WS18, which are adjacent) was modelled at 30-m resolution (Supplementary Figure 2). NECN requires several inputs, which describe the landscape, species, and climate. First, a set of maps describe the landscape including forest composition, hydrology including stormflow and baseflow, and soil properties including depth, texture, drainage, field capacity, wilting point, carbon and nitrogen pools. The stormflow and baseflow maps describe the fraction of soil water in each cell allocated to stormflow and baseflow each month. While the model does not explicitly include lateral connectivity, slope and landcover were used as inputs to the stormflow and baseflow maps to implicitly include those influences on water availability across the landscape. Second, parameters were assigned to species as well as functional groups describing their unique characteristics. We chose three functional groups describing xylem anatomy (diffuse-porous, ring-porous, and tracheid) to capture differences in water-use rates and responses to heat and water stress (Supplementary Table 2). Robbins et al. (2022) calibrated a model for the Southern Blue Ridge ecoregion, which served as the primary source for parameters as well as the procedures to create input maps. Additional information detailing methods to parameterize species traits, including growth curves, shade tolerance, and regeneration, can be found in Robbins et al. (2022). A detailed explanation of the parameterization of this model can be found in the Supplementary Materials.

2.4 | Extension Calibration

We calibrated the landscape using water flux data at species and catchment scales to ensure the model accurately represented forest hydrology. While a flux tower is located at the bottom of the Coweeta basin, its footprint does not consistently include WS 14 and 18. Because of this mismatch, we opted not to calibrate using the flux tower. However, flux tower net carbon uptake from 2011 to 2015 (Oishi 2020) was used to ensure the modelled net carbon uptake was within a reasonable range.

We calibrated species-level transpiration rates using sap flux measurements (Supplementary Table 3, Supplementary Table 4). The magnitude of transpiration rates from single tree sap flux measurements are not directly comparable with modelled transpiration of a species-age cohort, so we instead focused on modelling relative species transpiration rates (i.e., How much water does a similarly sized oak use compared to a maple?). Monthly species transpiration rates (mm mo^{-1}) were estimated using measurements of sap flux, effective sapwood area (m^2 ha^{-1}), and basal area (BA, m^2 ha^{-1}) in WS32 (Figure 1) from 2017 to 2021. A description of the dataset and methods to process raw sap flux data and scale to WS32 can be found in the Supplementary Materials. WS32 was not used as the study area because it does not include a long-term stream gage record to estimate water balance. While it is outside of the study area, forest composition is similar. In WS32, WS14, and WS18, diffuse porous species, including maple and tulip poplar, and ring porous species, including oak and hickory, contribute the majority of basal area while tracheid species (i.e. pine) contribute little (Supplementary Table 3) (Caldwell et al. 2016). Topography is also similar, except for the aspect which is SE in WS32 and NW in WS14 and WS18. We included maple (*Acer* sp.), tulip poplar (*L. tulipifera)*, and oak (*Quercus* sp.), the most abundant species, in the calibration. We calculated the monthly transpiration rate relative to the BA, T_{rel} (mm mo^{-1}/m^2 ha^{-1}), and then using growing season months (May–September), found the mean and standard deviation for each species. We calculated the same metric for the modelled species but substituted biomass (g biomass m^{-2}) for the BA since the model does not calculate BA.

Following water at the species scale, we calibrated the watershed scale model using watershed-scale ET. ET was calculated separately for each catchment using a water balance approach following

$$ET + \Delta S = P - Q$$

where P is precipitation (mm yr^{-1}), Q is streamflow (mm yr^{-1}), and ΔS is the change in soil water storage (mm yr^{-1}). Water balance calculations were based on a 'vegetation year' that extends from the beginning of the growing season to the end of the following dormant season (Troch et al. 2009). Using a vegetation year from June to May allows us to calculate ET as *P-Q* with

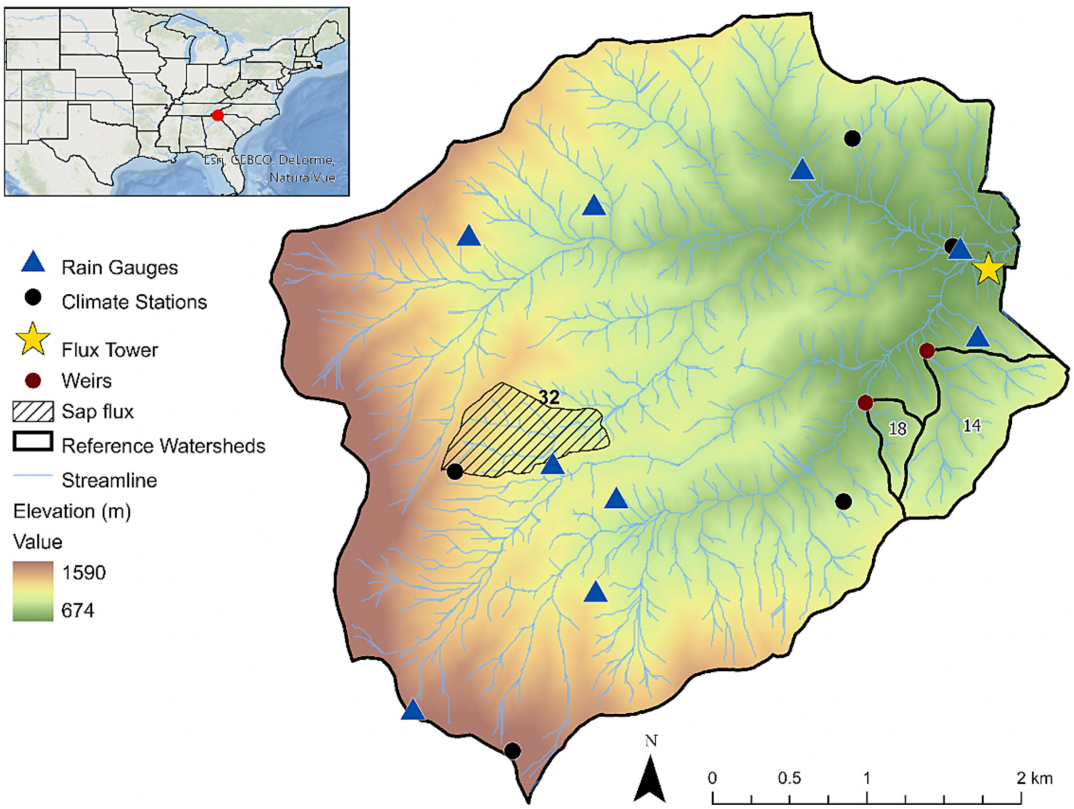

FIGURE 1 | Map of the study area at Coweeta Hydrologic Laboratory.

the assumption that precipitation during the dormant season recharges soil water depletion from the growing season in the deciduous forest without a permanent snow pack, making storage negligible (Hwang et al. 2018; Troch et al. 2009).

Parameters that determine productivity rates and foliar nitrogen, including the species maximum aboveground net primary productivity (ANPP) rates and leaf C:N ratios, were adjusted until modelled transpiration reflected the relative differences in species transpiration rates based on sap flux measurements, modelled annual ET magnitudes reflected average annual ET from catchment water balance calculations, and modelled annual net ecosystem exchange (NEE) magnitudes reflected average annual NEE from the flux tower. Parameters controlling growth responses to temperature and moisture were adjusted until modelled annual ET reflected interannual variability in ET from catchment water balance calculations.

2.5 | Model Performance

We compared the performance of the original version of NECN with our updated version at the watershed scale, calculating the bias, RMSE, and R^2 of the annual watershed water balance and modelled ET at WS14 and WS18. For simplicity, we will refer to the watershed water balance ET as "observed" flux. We also assessed model performance simulating change in ET and NEE across environmental gradients, including elevation, hillslope, and forest composition. Elevation data was retrieved from USGS National Elevation Dataset (NED) at 30-m resolution. The topographic wetness index (TWI), calculated from elevation, was used to represent the hillslope gradient (Beven and Kirkby 1979).

2.6 | Landscape Simulations

To assess the influence of species on watershed scale carbon and water balances, we ran simulations using an envelope of four climate change scenarios. We selected climate scenarios to capture species interactions with a range of changes in temperature and precipitation. To select these models, we analysed the change in annual and growing season (GS, May–September) temperature (T °C), precipitation (P mm yr^{-1}), and dryness between the historic period (2001–2020) and future period (2041–2060) for all RCP 8.5 downscaled general circulation models included in the MACAv2-METDATA at 4-km resolution. Dryness was calculated as the ratio of annual P to PET (P:PET) (Robbins 2022). Scenarios were selected to represent an envelope of future dryness conditions and included one wetter scenario, CSIRO-Mk3-6-0 (CSIRO), one scenario with a minimal increase in dryness, CNRM-CM5 (CNRM), and one scenario with a large increase in dryness, HadGEM2-ES365 (HadGEM2). The fourth scenario represents no change in climate (No Change). We created this time series by randomly sampling years with replacement from the climate record between 1995 and 2021 (Scheller et al. 2018). Each scenario was run using the modern climate measured at Coweeta (2001–2020), followed by the climate scenario from 2021 to 2060. Using a water balance approach ($Q = P$-ET), we calculated annual streamflow (Q mm yr^{-1}) in each watershed.

While simulations are run from 2001 to 2060, we use the future period (2041–2060) to make comparisons across scenarios. We assessed differences in species biomass, ET, *Q*, and NEE during the future period between climate scenarios. Comparisons against the No Change scenario using a Wilcoxon Signed Rank Test reveal the relative effects of climate change between scenarios and help reduce the effects of model uncertainties on results.

3 | Results

3.1 | Calibration

Modelled T_{rel} agreed well with observations (Figure 2). Observations showed that transpiration rates of diffuse-porous *Acer* sp. and *L. tulipifera* were 4.5 times higher than ring-porous *Quercus* sp. per unit BA (Figure 2). In comparison, modelled transpiration rates of diffuse-porous species were 3.5 times higher than ring-porous species per unit biomass. Modelled transpiration rates of tracheid species were similar to diffuse-porous species and about 3.5 times higher than ring-porous species (Figure 2). Due to the small proportion of tracheid species (i.e. *Pinus* sp.) on the landscape, we did not include them for comparison to diffuse-porous and ring-porous species. However, other studies have found similar transpiration rates between tracheid and diffuse-porous species (Vose et al. 2016). The original NECN model was not compared to sap flux observations because it does not calculate species-level transpiration estimates.

The updated model performed better simulating annual watershed ET than the original model. Bias in the updated model is lower compared to the original, averaging 9% in the updated model and 28% in the original model (Table 1). Similarly, RMSE from the updated model was almost half of the original model, averaging 182 mm yr^{-1} compared to 310 mm yr^{-1} (Table 1). The R^2 for both models are low (0.04–0.16). *P* ranged from 1653 mm yr^{-1} to 2685 mm yr^{-1} with an average of 2128 mm yr^{-1} and *T* ranged from 11.9 °C to 14.0 °C with an average of 13.1 °C. Both the original and updated model overestimate ET during the wettest year in the calibration period, 2018 (Figure 3). Excluding 2018, the updated model captured almost twice as much of the interannual variability compared to the original model, with an average R^2 of 0.58 compared to 0.33 (Table 1).

Mapped ET highlights improvements to the updated model as it reflects variability across the study area (Figure 4). While the updated model predicts higher ET rates at low elevations, downslope positions, and forests with a greater abundance of diffuse-porous BA, the original model predicts similar ET rates across these gradients (Figure 5). In contrast, both the updated and original models capture the variability of NEE across environmental gradients. Higher net carbon uptake is predicted at low elevations, downslope positions, and forests with more diffuse-porous BA (Figure 5).

3.2 | Landscape Simulations

We ran simulations using four future climate scenarios and compared climate between historic (2001–2020) and future periods (2041–2060) (Figure 6). Under the No Change scenario, the average climate remained unchanged with an average annual *T* of 12.9 (s.d. ±0.5)°C, *P* of 1987 (s.d. ±404) mm yr^{-1}, and *P*:PET of 2.8 (s.d. ±0.6). Under the wetter scenario (CSIRO), *T* increased (1.7 °C annual, 2.3 °C GS), *P* increased (2% annual, 4% GS), and *P*:PET decreased (7% annual, 7% GS). Under the moderately drier scenario (CNRM), *T* increased (1.9 °C annual, 1.9 °C GS), *P* decreased (0% annual, 5% GS), and *P*:PET decreased (9% annual, 12% GS). Under the driest scenario, *T* increased (3.6 °C

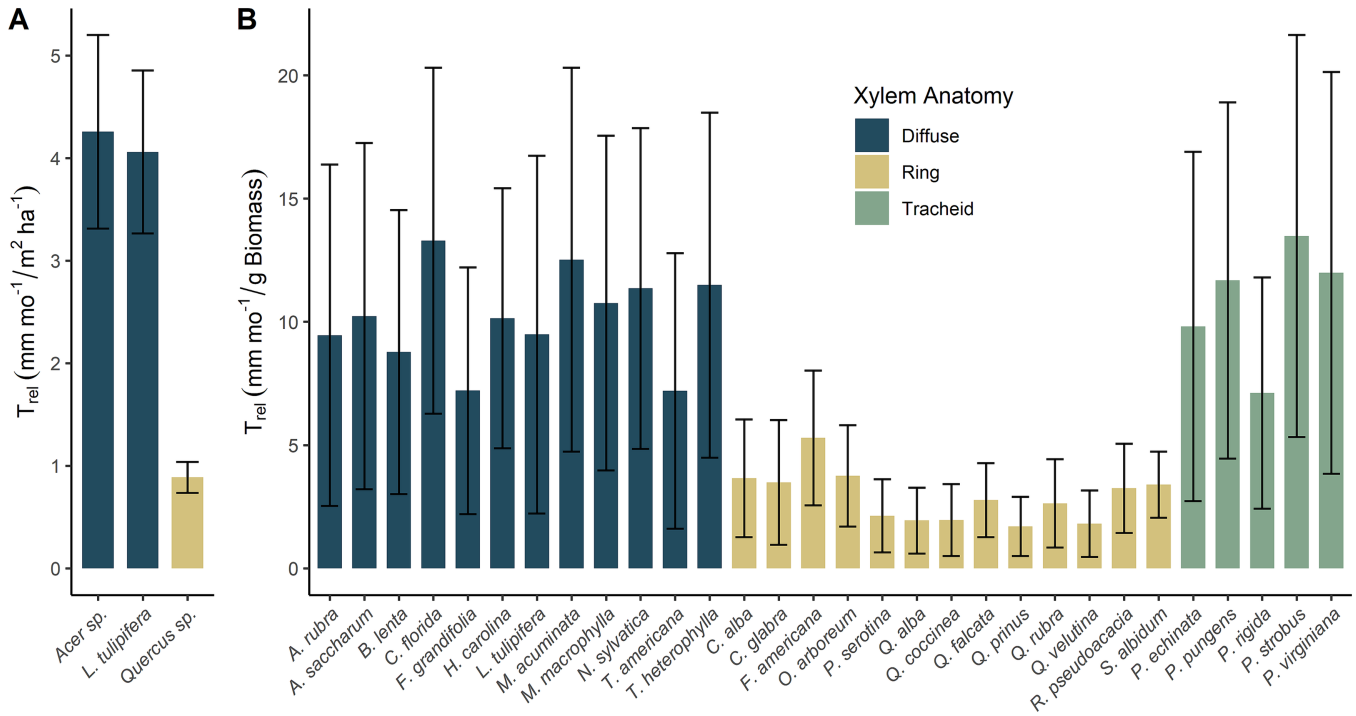

FIGURE 2 | A. Observed and B. modelled average relative species transpiration rates (T_{rel}) ±1 SD. Species are grouped by xylem anatomy.

TABLE 1 | Performance statistics of the original and updated model simulating watershed ET (mm yr^{-1}) from vegetation year 2011–2020.

	R^2		R^2 (excluding 2018)		RMSE (mm yr^{-1})		Bias (%)	
	Original	Updated	Original	Updated	Original	Updated	Original	Updated
WS14	0.16	0.10	0.34	0.61	358.1	205.3	31.9	17.0
WS18	0.11	0.04	0.31	0.55	261.3	158.1	23.3	1.2

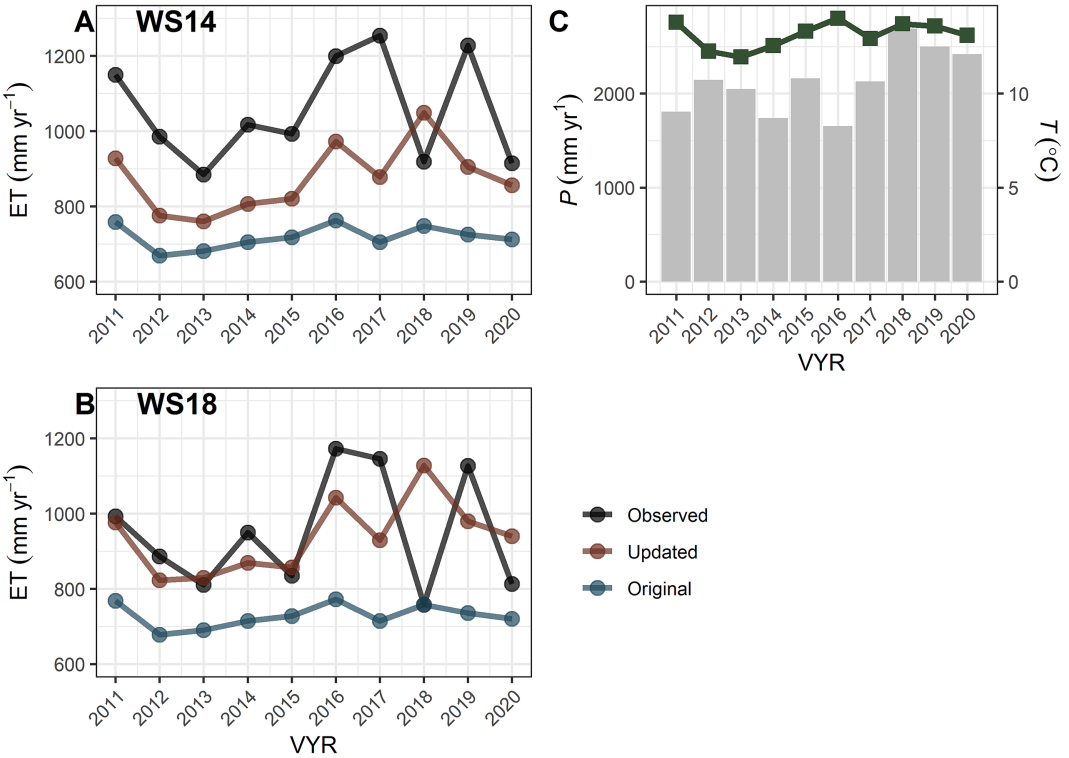

FIGURE 3 | Vegetation year (VYR) comparison of watershed ET from the original and updated model for A. WS14 and B. WS18. C. Interannual variability of P (mm yr^{-1}) and T (°C) averaged from WS14 and WS18. P is represented by grey bars and T is represented by the green line.

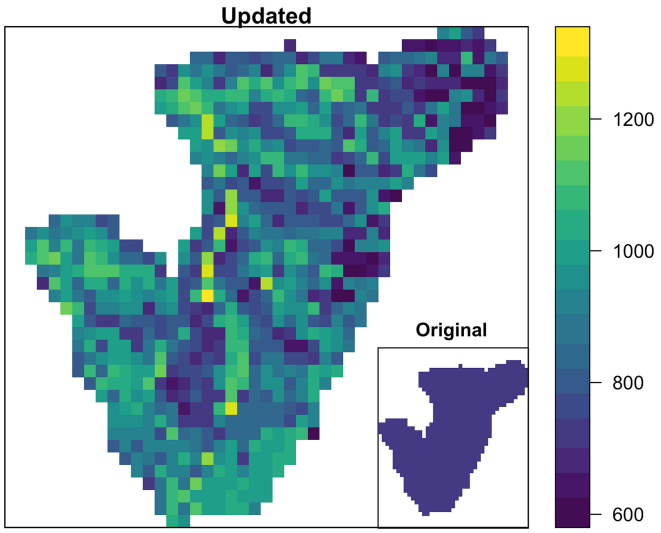

FIGURE 4 | Average annual ET (mm yr^{-1}) from 2011 to 2021 mapped using outputs from the original and updated models.

annual, 4.8 °C GS), P decreased (8% annual, 20% GS), and P:PET decreased (27% annual, 38% GS).

Initial biomass on the landscape was dominated by ring-porous species (66%), followed by diffuse-porous species (31%), and tracheid species (3%) (Figure 7). Biomass changed similarly across all scenarios from 2000 to 2060. Averaged across all scenarios, ring-porous biomass decreased to 62%, diffuse-porous biomass increased to 34%, and tracheid biomass increased to 4% over the duration of the simulation. Biomass of species cohorts established after the start of the simulation, referred to as new biomass, was also similar across scenarios. Diffuse-porous biomass accounted for the largest portion of new biomass (51%), followed by ring-porous (28%) and tracheid (21%).

Compared to the No Change scenario, ET increased more under the moderately dry scenario (10%) than the wet scenario (4%) and Q decreased more under the moderately dry scenario (−6%) than the wet scenario (−2%). The largest changes in Q were

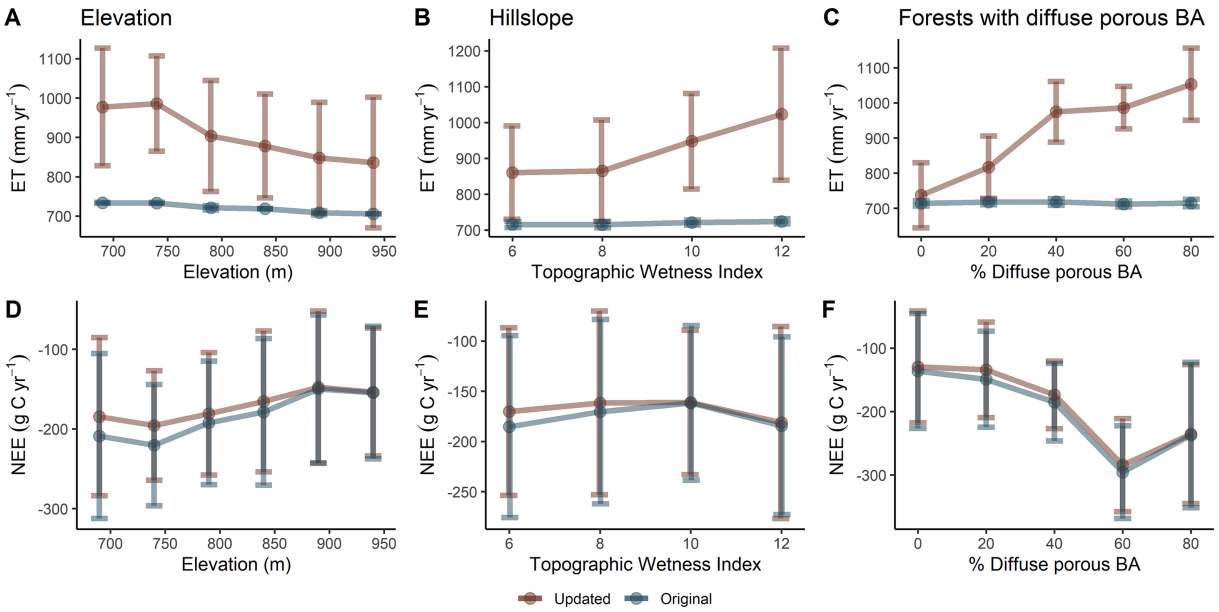

FIGURE 5 | Average annual ET (mm yr^{-1}) (A, B, C) and NEE (g C yr^{-1}) (D, E, F) binned along environmental gradients including elevation (A, D), topographic wetness index (TWI) (B, E), and the % BA belonging to diffuse-porous species (C, F). The hillslope is represented using TWI, with lower values corresponding to more downslope positions. Forest composition is quantified according to the percentage of forest BA that belongs to a diffuse porous species, with higher percentages corresponding to forests with more diffuse porous BA.

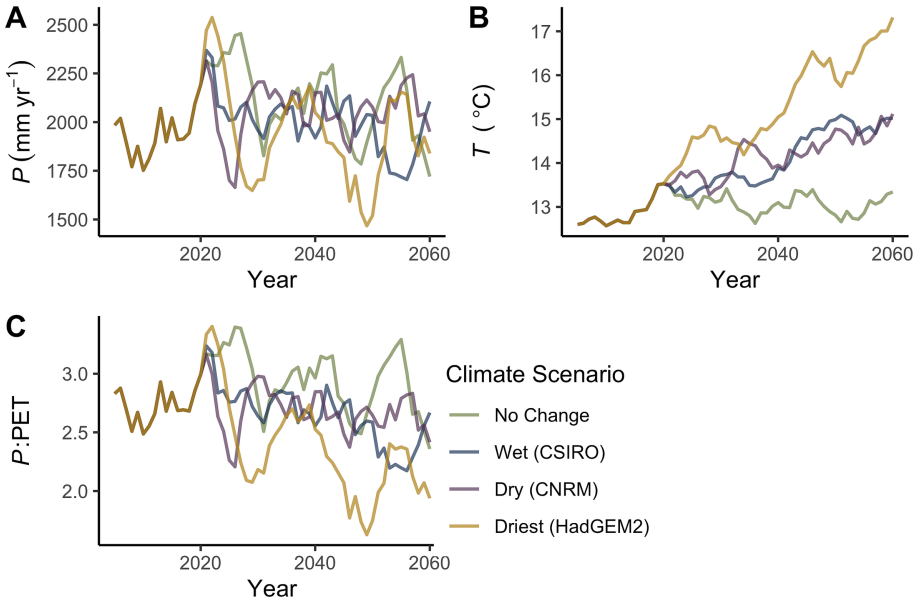

FIGURE 6 | Downscaled climate used for the landscape simulations from 2000 to 2060 visualized as a five-year rolling average including A. precipitation (mm yr^{-1}), B. temperature (°C), C. *P*/PET ratio. All landscape simulations use the same climate observed at Coweeta from 2000 to 2020.

observed under the driest scenario, with a 9% increase in ET and a 23% decrease in *Q* compared to a scenario of no change in climate. Changes in *Q* are driven by changes in *P* and ET. In this case, the decrease in *Q* is larger than the increase in ET due to simultaneous decreases in *P* under the driest scenario. NEE was more sensitive to changes in climate than ET and *Q* (Figure 8). While NEE increased under the wet (27%) and moderately dry (34%) scenarios, it decreased under the driest scenario (−64%), indicating it was becoming less of a carbon sink. This was due to a combination of changes in productivity and respiration under hot and dry conditions (Supplementary Figure 3). The variability of ET and NEE increased the most under the driest scenario. Leaf area index (LAI) remained relatively unchanged in the wet and dry scenarios but decreased by 6% in the driest scenario (Figure 8).

Species transpiration dynamics varied by xylem anatomy. Diffuse-porous species had the highest water use rates and on average contributed 56% of total annual transpiration while accounting for just 34% of the biomass (Figure 9). Tracheid species

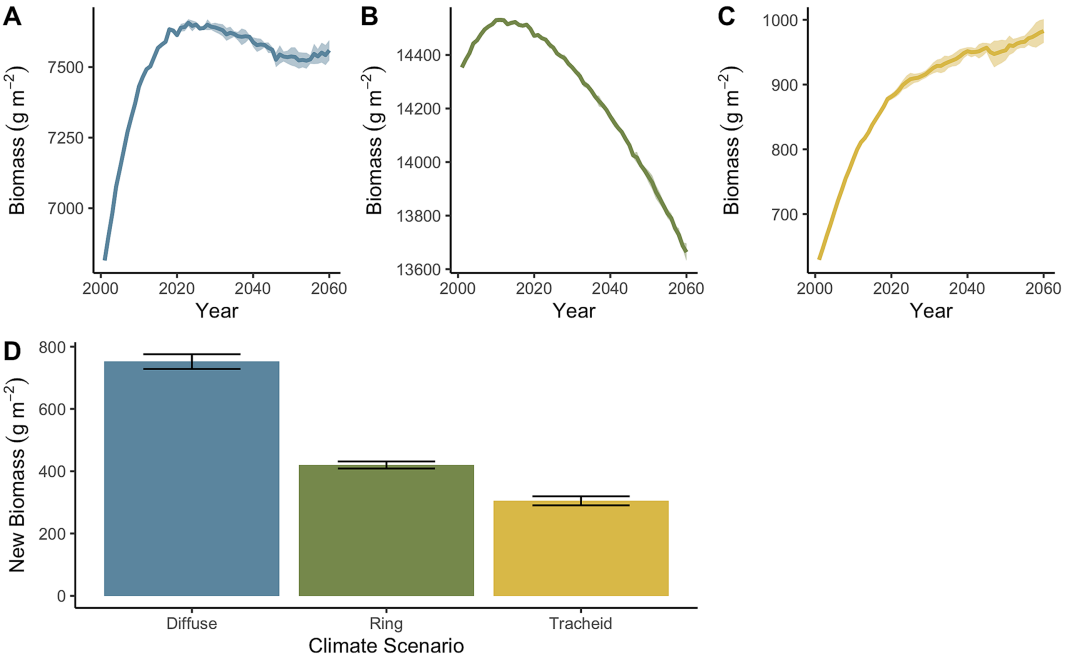

FIGURE 7 | Biomass (g m^{-2}) aggregated according to xylem anatomy from 2001 to 2060, including A. diffuse-porous species, B. ring-porous species, and C. tracheid species. D. Total biomass (g m^{-2}) of new cohorts at the end of each simulation aggregated according to xylem anatomy. New cohorts refer to cohorts that were not present at the start of the simulation.

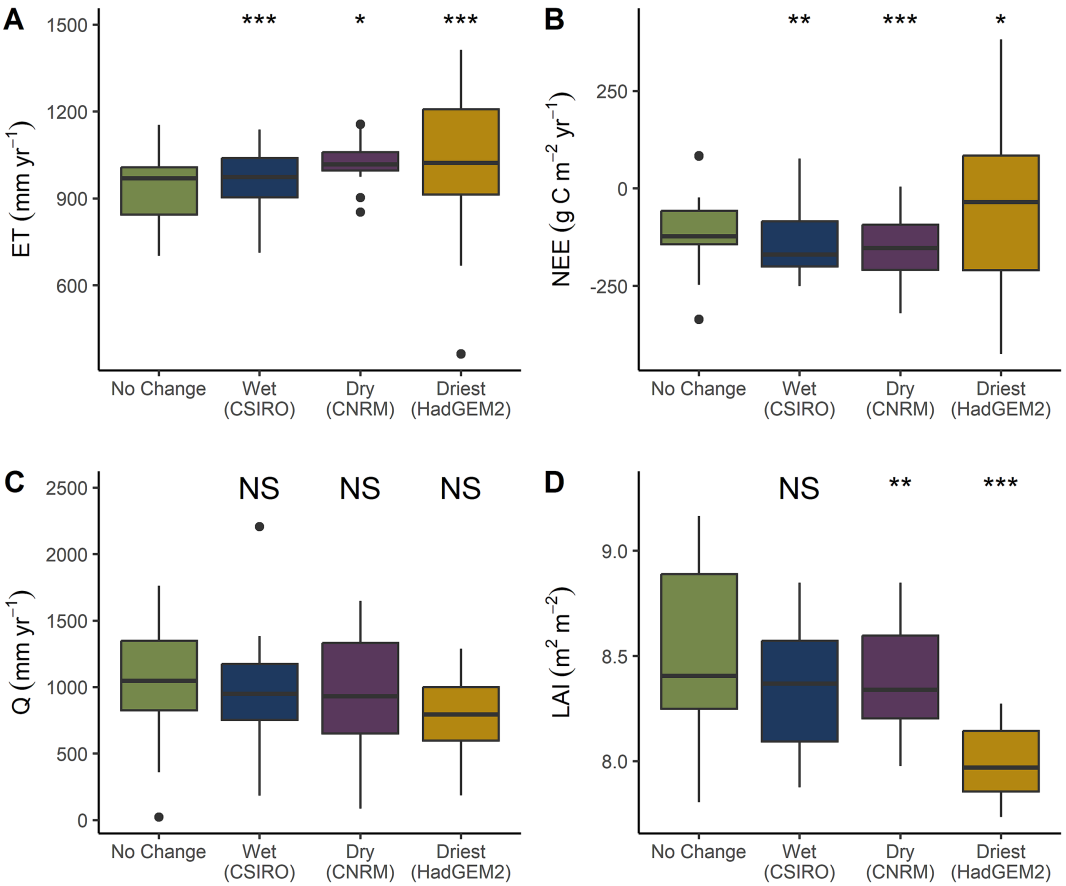

FIGURE 8 | Annual A. ET (mm yr^{-1}), B. NEE (g C yr^{-1}), C. Q (mm yr^{-1}) and D. LAI (m^2 m^{-2}) during the future period (2041–2060) according to climate scenario. Statistical differences compared to the No Change scenario noted as 'NS': $p > 0.05$; *$p \leq 0.05$; **$p \leq 0.01$; ***$p \leq 0.001$.

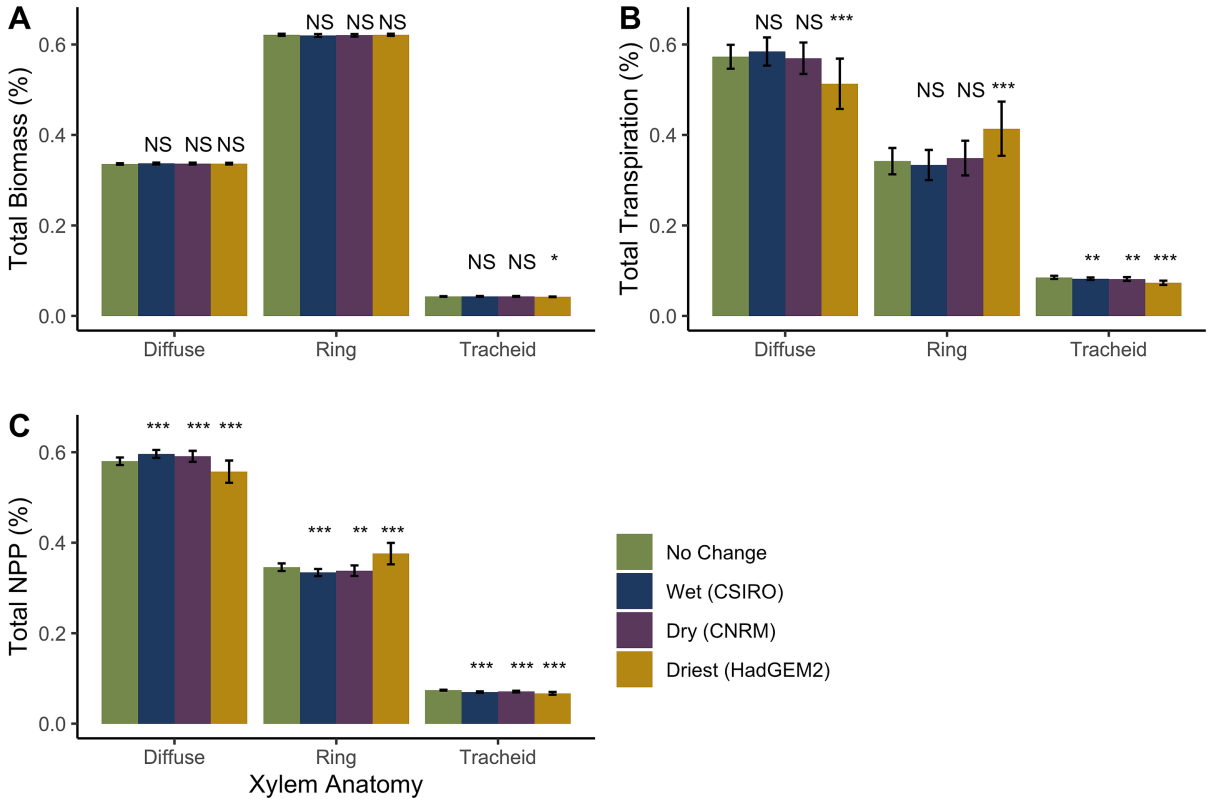

FIGURE 9 | The fraction of A. annual biomass, B. transpiration, and C. NPP contributed by each species group averaged during the future period (2041–2060). Error bars represent ±1 SD. Differences compared to the No Change scenario noted as 'NS': $p > 0.05$; *$p \leq 0.05$; **$p \leq 0.01$; ***$p \leq 0.001$.

have a similarly outsized contribution to transpiration (8%) relative to biomass (4%). In contrast, ring-porous species have the lowest water use rates and on average contributed 36% of total annual transpiration while accounting for 62% of biomass. Species NPP dynamics were similar to transpiration dynamics (Figure 9).

The relative species contributions to annual transpiration and NPP were sensitive to dryness. Diffuse-porous species contributed less to total transpiration and NPP as dryness increased while ring-porous species contributed more (Supplementary Figure 4). This trend was reflected in the relative contributions of diffuse-porous and ring-porous species under future climate scenarios (Figure 9). Diffuse-porous species contributed slightly more (1%) and ring-porous species contributed slightly less (1%) to total transpiration under the wetter scenario (Figure 9). In contrast, diffuse-porous species contributed 6% less while ring-porous contributed 7% more to total transpiration under the driest scenario. Variability of relative contributions increased the most under the driest scenario, with the largest deviations from the average found during the driest years. The relative contributions of species to NPP followed similar patterns but were less sensitive (Figure 9).

4 | Discussion

Future forest carbon and water dynamics are dependent on interactions between species and climate. We find shifts in carbon and water dynamics of Southern Appalachian forests determined by a continual increase in diffuse-porous species biomass, further amplifying drought sensitivity and reducing forest resilience. Our results show that diffuse-porous species used more water per unit biomass than ring-porous species across watersheds (Figure 2), due to comparatively deeper sapwood (Ford, Hubbard, and Vose 2011). And, despite accounting for approximately half the total biomass as ring-porous species, diffuse-porous species dominated the transpiration flux across current and future climates (Figure 9). However, diffuse-porous transpiration was also more sensitive to reductions during drought than ring-porous transpiration, leading it to contribute a smaller fraction of the total transpiration flux relative to ring-porous transpiration under increasingly dry conditions (Supplementary Figure 4).

Our results are consistent with plot-based studies from a variety of ecosystems. Diffuse-porous species found in the southern Appalachians can be over twice as sensitive to soil drying compared to ring-porous species (Elliott et al. 2015; Meinzer et al. 2013). Even with this sensitivity, diffuse-porous species often maintained higher transpiration rates compared to ring-porous species during drought (Hawthorne and Miniat 2018; Hwang et al. 2020). Similarly, a tropical rainforest sap flux study showed that while drought-sensitive trees dominated total water fluxes, they were also the most sensitive to soil drying (Werner et al. 2021). Ultimately, the proportion of drought-sensitive species on the landscape determined ecosystem-scale susceptibility to drought. We found this pattern persisted across climate

scenarios; even as diffuse-porous transpiration decreased, it remained a larger proportion than ring-porous species representing a fraction of the biomass (Supplementary Figure 4).

Our data indicates that climate change exacerbates the effects of mesophication on forest carbon and water cycles (Figure 8). Due to high water use rates of diffuse-porous species, when those species expand across the landscape and are able to take advantage of warming temperatures, it leads to larger increases in ET and reductions in streamflow. Each of our climate scenarios project a continuation of mesophication, with the majority of new species cohorts belonging to diffuse-porous species and an increase in diffuse-porous biomass over time (Figure 7). Diffuse-porous species are expected to reduce productivity and increase transpiration under future climates (Brzostek et al. 2014; Vose et al. 2016), supporting our projections of increasing ET and decreasing net carbon uptake (Figure 8). Forest composition in WS14 and WS18 has been surveyed repeatedly over the past century, revealing an increasing proportion of diffuse-porous species and decreasing proportion of ring-porous species (Caldwell et al. 2016; Elliott and Swank 2008; Elliott and Vose 2011). In comparison to the historical survey data, modelled increases in the future proportion of diffuse-porous biomass are small, and these findings could represent a best-case scenario to the extent that actual trends may push mesophication further. Streamflow decreases of up to 18% have been attributed to mesophication since the 1980s (Caldwell et al. 2016), and we projected similar decreases in the future period, suggesting this trend will continue (Figure 8).

We found that future change in net carbon uptake is sensitive to dryness because while net carbon uptake increased under the wetter and moderately dry scenarios, it decreased under the driest scenario (Figure 8). This aligns with the theory that despite greater vegetation growth associated with increasing temperatures (Keenan et al. 2014), net carbon uptake will not increase (Davi et al. 2006; Dow et al. 2022). This was seen at the Coweeta flux tower from 2011 to 2015, when hotter temperatures decreased net carbon uptake due to increased respiration but did not decrease ET (Oishi et al. 2018). While water limitations often reduce respiration (Oishi et al. 2013; Schindlbacher et al. 2012), when combined with high temperatures, respiration may increase, exacerbating drought impacts on net carbon uptake (Yuan et al. 2016). Under the driest scenario, large reductions in productivity and comparatively smaller reductions in respiration cause the watershed to switch from a sink to a source between wet and dry years (Supplementary Figure 3). Diffuse-porous species experience the largest decreases in productivity under the driest scenario and therefore, are important drivers of whether the landscape acts as a carbon sink or source under future climates. Despite being more drought-sensitive, diffuse-porous species also contribute to larger soil water deficits due to their high transpiration rates, especially compared to more drought-tolerant ring-porous species (Au et al. 2020; Hwang et al. 2020). These findings suggest that diffuse-porous species responses to changing temperature and moisture limitations could result in a reduced potential for carbon sequestration and streamflow generation in the future, even on landscapes historically considered water-rich. We present a novel method to simulate forest dynamics under different climate scenarios connecting interactions among climate change, species composition, and transpiration: an important approach to understanding changing forest water dynamics (Sun et al. 2023). Incorporation of species influence on transpiration improved the accuracy and spatial representation ET across the landscape compared to previously homogeneous estimates in the original model (Table 1, Figure 4). While NECN cannot route water between cells to simulate lateral flow, modelled outputs reflect the expected spatial variability of ecosystem function (Figure 5). Even so, future work incorporating more complex soil water dynamics, like lateral flow and rooting depth, would be helpful in representing forest water dynamics.

It is important to consider findings from FLMs in the context of their uncertainties. The updated model performed poorly in 2018, overestimating ET in both watersheds (Figure 3). Changes in the storage term of the water balance which are not fully accounted for in water balance calculations of ET introduce uncertainty into the watershed scale ET record used for calibration. For example, violations of the assumption of steady-state water-balance have been observed at Coweeta in watersheds with deep storage and large interannual precipitation variability (Nippgen et al. 2016). Therefore, it is possible that the model was not overestimating ET in 2018 but the 'observed' record was underestimating ET. There is some evidence for this in the relatively large model underestimations of ET in 2017 and 2019, suggesting differences in soil water storage at the end of each year led to discrepancies in estimated ET based on the calendar year. The year 2017 had below-average annual precipitation with particularly low precipitation in November and January (146 mm or 9% of annual total), which likely delayed the time until soil was fully recharged. Furthermore, 2018 was the wettest year in the calibration time period (Figure 3) and had high precipitation near the end of the year (582 mm total for November through December), which likely contributed to soil recharge. Despite this uncertainty, modelled and observed relative species water use rates and average annual ET and were similar. Over the calibration period, the average annual modelled ET was within 13% of the observed. Given that our study focused on differences in average carbon and water fluxes among climate scenarios, we concluded this model calibration was sufficient.

Other uncertainties should be considered as well. Inputs to LANDIS NECN describing the initial landscape condition (Ex. Forest composition, soil carbon and nitrogen) introduced uncertainty because they are impossible to measure everywhere, and therefore, must be represented using estimates from other models. Additionally, the sap flux dataset used for calibration was limited to three species. While data for additional species would improve the calibration, these three species were useful because they represented one species from each of the functional groups. FLM calibration would ideally encompass a wide range of climate conditions although that is not always possible, given constraints on the availability of in situ data. In this case, calibration did not include periods of extreme drought stress, leading to uncertainty in the projections of ecosystem responses to future drought stress. Finally, lateral flow is an important component of montane hydrology not simulated in NECN, leading to uncertainty in the evolution of water availability across the landscape that has been shown to influence forest drought responses (Hawthorne and Miniat 2018; Hwang et al. 2020; McQuillan, Tulbure, and Martin 2022).

5 | Conclusion

Our study highlights the importance of species in determining the watershed-scale carbon and water balances under future climate. We demonstrated that ET increased, streamflow decreased, and net carbon uptake decreased under a range of future climate projections, largely due to the dominance of diffuse-porous species driving carbon and water fluxes. Diffuse-porous species influence on carbon and water fluxes was outsized relative to its total biomass on the landscape and was exacerbated by climate change. Our research shows the importance of considering species composition in the context of future forest ecosystem services, particularly in humid eastern forests experiencing ongoing mesophication. Future work could leverage this modelling framework to explore the changing ecohydrology of temperate forests globally as well as the potential of forest management to increase forest resilience to future climate.

Author Contributions

KAM: conceptualization, formal analysis, methodology, software, visualization, writing–original draft, writing–review and editing. ACO: data curation, writing–review and editing. ZJR: methodology, writing–review and editing. RS: writing–review and editing. KLM: conceptualization, writing–review and editing.

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Data Availability Statement

Datasets used for climate included GRIDMET (https://doi.org/10.1002/joc.3413), MACA (https://doi.org/10.1002/joc.2312), and in situ data from Coweeta including precipitation (https://www.fs.usda.gov/rds/archive/Catalog/RDS-2017-0031) and other meteorological data (https://doi.org/10.2737/RDS-2015-0042). Datasets used for calibration included flux tower ET and NEE (https://ameriflux.lbl.gov/sites/siteinfo/US-Cwt) and daily streamflow (https://doi.org/10.2737/RDS-2016-0025). Sap flux dataset is included in the Supplementary Material. The revised version of LANDIS-II NECN which includes species-level transpiration is available on GitHub (https://github.com/kmcquil/Extension-NECN-Succession). Landscape scenarios and code to create figures are also available on GitHub (https://github.com/kmcquil/Ch3_Landis_Climate_Species_Interactions).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.