Forest Ecology and Management 460 (2020) 117881

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Bedrock type drives forest carbon storage and uptake across the mid-Atlantic Appalachian Ridge and Valley, U.S.A.

Warren P. Reed[a,b,*], Margot W. Kaye[a,b]

[a] Department of Ecosystem Science and Management, The Pennsylvania State University, University Park, PA 16802, USA
[b] Intercollege Graduate Degree Program in Ecology, The Pennsylvania State University, University Park, PA 16802, USA

ABSTRACT

Lithology influences forest carbon storage and productivity yet is often overlooked for forests of the eastern United States, a large and important carbon sink. This research explores the influence of two common lithologies of the Ridge and Valley physiographic province in the Appalachian Mountains, shales and sandstones, on live aboveground carbon storage, carbon uptake, forest community composition and their interrelationships. We couple forest inventory data from 565 plots from Pennsylvania state agencies with a suite of GIS derived landscape metrics including measures of climate, topography and soil physical properties to identify biotic and abiotic drivers of live forest carbon dynamics in relation to lithology.

Forests growing on shale bedrock store more live aboveground carbon compared to forests on sandstone when controlling for stand age, which ranged from 20 to 200 years. Furthermore, forests in the dominant ages (81–120 years) store more live aboveground carbon (108.1 Mg/ha vs. 86.5 Mg/ha) and uptake live aboveground carbon at a faster rate (1.32 Mg/ha/yr vs 0.85 Mg/ha/yr) on shale compared to sandstone respectively. Overall forest communities on both lithologies are dominated by oaks (*Quercus* spp.), however northern red oak (*Q. rubra*) is more dominant at shale sites compared to chestnut oak (*Q. prinus*), which dominates on sandstone. Most species in the forest tend to be more productive on shale, which may account for differences in carbon pools and fluxes across the landscape. Tree species richness is higher in sites on shale bedrock, but biodiversity-productivity relationships within lithologic classifications fail to account for differences in forest productivity. Modeled live aboveground carbon storage points to topography (elevation and aspect) and soil physical properties (% clay and available water capacity) as important influences on forest productivity that related back to lithology. Incorporating lithology into forest management strategies that are focused on a variety of ecosystem services can aid future site selection, and we demonstrate that forests on shale bedrock grow faster, store more carbon and have higher species diversity. The results presented here highlight the potential for underlying bedrock to exert differential influences on forest ecosystem structure and function across a region.

1. Introduction

Differences in forest growth and carbon storage are linked to factors that span biotic to abiotic realms including but not limited to forest community composition (Jonsson and Wardle, 2010), age demographics (Pugh et al., 2019), climate gradients (Gough, 2008) and interannual weather and climate (Barford et al., 2001). In the United States, forests have the potential to offset 12–19% of the annual fossil fuel emissions (Ryan et al., 2010), much owed to forest biomass increases in the eastern U.S. (USGCRP, 2018). Most of this region is dominated by temperate forests, which globally are estimated to store ~10% of the Earth's terrestrial carbon (Bonan, 2008). Moreover, recent studies have highlighted that second growth forests of the eastern U.S. may continue to increase the amount of carbon sequestered for decades (McGarvey et al., 2015; Gough et al., 2016), further bolstering the importance of understanding the potential controls on forest growth across the region.

Past work has highlighted that 25% of global temperate forests productivity can be explained by the combination of mean annual temperature, mean annual precipitation and forest age (Reich and Bolstad, 2001) leaving 75% of variation to explain. One key abiotic factor that may be missing is the underlying bedrock composition (lithology), which has recently been demonstrated to influence forest carbon storage (Morford et al., 2011; Hahm et al., 2014). Incorporating lithology into forest productivity models in the far northeastern United States and Southeastern Canadian region was notably important to modeling forest growth (Hennigar et al., 2017) and site index models of Maritime pine (*Pinus pinaster*) yielded different responses of growth in relation to bedrock type (Eimil-Fraga et al., 2014). Additionally, lithology can influence forest community composition and linked soil properties (Nowacki and Abrams, 1992; Searcy et al., 2003). While there seems to be a growing recognition and quantification of the lithologic influences on forests, no study to our knowledge has documented its degree of influence on carbon storage and uptake in the temperate deciduous forest region of the eastern United States.

To fill this knowledge gap, we present an analysis of public lands

* Corresponding author at: Intercollege Graduate Degree Program in Ecology, The Pennsylvania State University, 317 Forest Resources Building, University Park, PA 16802, USA.
E-mail address: wpr5005@psu.edu (W.P. Reed).

https://doi.org/10.1016/j.foreco.2020.117881
Received 30 September 2019; Received in revised form 20 December 2019; Accepted 6 January 2020
Available online 16 January 2020

across the Ridge and Valley physiographic province in the forested central Appalachian Mountains of Pennsylvania. We focus on two rock types characteristic of the region, shale and sandstones, which are commonly overlain by forests. Specifically, the objectives of this study are to 1) assess differences in storage and uptake of live aboveground forest carbon between shale and sandstone 2) explain how forest community composition, species growth rates and species diversity differ in relation to rock type 3) model live aboveground carbon storage using abiotic variables to understand the lithologic influence on forest growth and 4) categorize the abiotic features of forest sites underlain by shale and sandstone bedrock that we hypothesize would influence forest productivity. In this study we rely on forest inventory data that capture the spatial variability of differences in forest growth, structure and composition across the landscape. We pair forest sites with spatially explicit abiotic variables to illuminate patterns of forest productivity important at the local scale and explore drivers that may be important across more regional and global scales.

2. Methods

2.1. Study area

The Ridge and Valley physiographic province in Pennsylvania, USA is characterized by folded Paleozoic sedimentary rocks that result in a series of northeast trending linear sandstone ridges and intervening shale and carbonate valleys (Fig. 1). Soil properties and textures are linked to underlying bedrock and parent material (Ciolkosz et al., 1990). The mean annual temperature of the study area is 9.4 °C and mean annual precipitation is 1130 mm, relatively evenly distributed throughout the year. The elevation of study plots averages 449 m above sea level and ranges from 130 to 767 m.

The majority of forests in the region are typically second growth forests that have established following a period of tree harvesting from the late 1800 s into the early 1900 s and generally collocate with upland mountainous terrain, likely a relic of complex topography and poor soil fertility unsuited for agriculture. Sixty-five percent of the forest landscape is comprised of forests that are 81–120 years old, according to forest inventory data presented in this study. Forests are dominated by oaks, where 62.5% of the overall biomass is in a mix of oak species [chestnut oak (*Quercus prinus* L.), northern red oak (*Q. rubra* L), white oak *(Q.alba* L.), scartlet oak (*Q. coccinea* Muenchh), and black oak (*Q. velutina* Lam.) in order of oak dominance] and 89% of the total forest biomass across the landscape is comprised of 10 canopy tree species.

2.2. Forest inventory

Forest inventories conducted by the Pennsylvania Department of Conservation of Natural Resources Bureau of Forestry and the Pennsylvania Game Commission across state public lands within the Ridge and Valley physiographic province of Pennsylvania were combined in this study to quantify forest carbon storage. Plot locations were

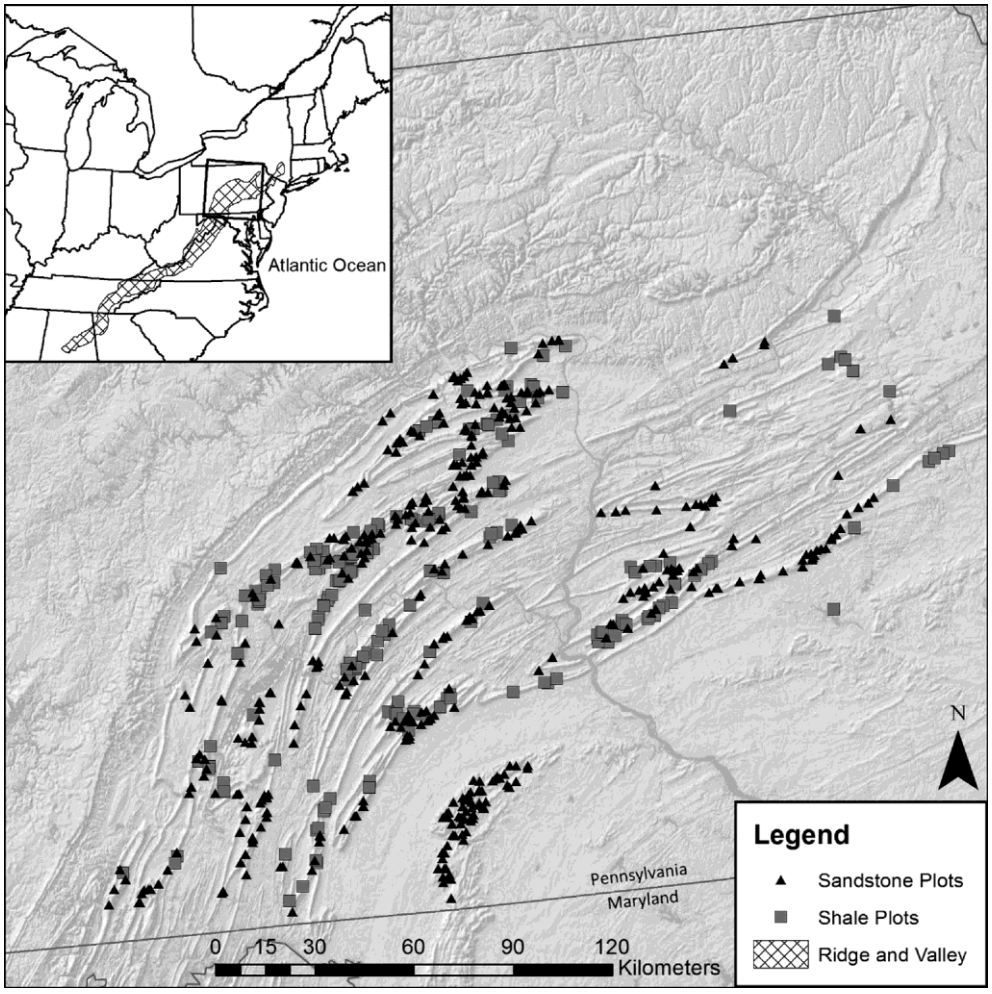

Fig 1. Forest inventory plots in the Ridge and Valley physiographic province in the eastern United States used in this study. Inventory plots are restricted to land owned and managed by the Pennsylvania Department of Conservation of Natural Resources Bureau of Forestry and the Pennsylvania Game Commission underlain by shale and sandstone bedrock.

selected by the state agencies to proportionally represent the major forest community types within the region and provide basic biological data on growth, mortality, structure, volume and change of public forest land. The sampling strategy of the inventories ensures that permanent plots are maintained and sampled multiple times, as well as continually adding newly established forest plots to inform short- and long-term forest management. Plots with repeated inventories were sampled after an average time period of 5.97 years, with a median of 6 and range from five to eight years prior.

Within the inventories, all trees with a diameter at breast height (DBH) ≥ 11.4 cm were measured and identified to species within 810.6 m^2 circular plots. Plots that experienced a documented disturbance (< 1% of eligible plots) or silvicultural manipulation (7% of eligible plots) were removed from the dataset in this study to focus on the influence of bedrock lithology on forest carbon accumulation. We only included data from living trees to calculate the live aboveground component of forest ecosystem carbon. Forest stand age was categorized from tree core samples of three dominant or codominant individuals and binned into 20-year windows spanning 21–200 years of age. Thirteen plots were categorized as mixed age stands because trees within a plot were different ages and were removed to more parsimoniously consider the effect of forest growth as stands age.

2.3. GIS and abiotic landscape metrics

Coordinates of inventory plot centers were mapped onto a geologic map of Pennsylvania (Berg et al., 1980; Miles and Whitfield, 2001) to identify the primary bedrock lithology of each plot. Forest plots growing on shale, sandstone and quartzite were selected for further analysis. Plots with primary lithology of sandstone or quartzite were lumped together and categorized as sandstone. To better quantify the geophysical and abiotic features associated with underlying bedrock a suite of topographic, climatic and soil metrics were compiled across the central Pennsylvania Ridge and Valley (Table 1). Topographic metrics were derived in ArcMap 10.5.1 from a 10-meter resolution digital elevation model (DEM). Thirty-year annual climate normals (1981–2010) across the landscape at 800-meter spatial resolution were sampled from the PRISM database (PRISM, 2004). Soil metrics were derived in ArcMap using the Soil Data Development Toolbox from the Gridded Soil Survey Geographic Database (gSSURGO).

2.4. Data analysis

The analysis included 565 forest plots containing 23,119 trees from the most recent fully completed and available forest inventory data that were sampled between the years 2009 and 2015. Within the dataset 381 plots were on sandstone bedrock and 184 were on shale, a fairly similar ratio to the amount of Pennsylvania public land on each bedrock type in the Ridge and Valley (328,995 ha on sandstone vs 106,038 ha on shale). Estimates of aboveground individual whole tree biomass, or all of the tree material aboveground, were made from species group allometric equations (Jenkins et al., 2003) and then scaled to carbon by assuming a 48% carbon content of broadleaved trees in temperate forests (IPCC, 2006). Live aboveground forest carbon storage at the plot level was calculated as the sum of carbon content of all live trees divided by the plot area to produce values in Megagrams C per hectare (Mg/ha). Three hundred and sixteen plots ($n_{sandstone}$ = 219 and n_{shale} = 97) with repeated inventory measurements were identified from the 81–120 year age class range, the most representative of the broader forest landscape (65% of plots), to understand the general patterns of forest carbon accumulation in the region on different bedrock types through time. Carbon accumulation at the plot level was calculated as

$$\Delta C = Carbon_{t2} - Carbon_{t1} / t2 - t1$$

where t2 is the year of the most recent inventory and t1 is the year of the prior inventory, and is represented in Megagrams per hectare per year (Mg/ha/yr). Herein, we use the terms "store" and "storage" to represent aboveground carbon stock and "accumulation" and "uptake" to represent net live aboveground carbon accumulation rate. Live aboveground forest carbon storage and live aboveground carbon accumulation were calculated for the top 10 dominant species in the region to better quantify differences in community composition and species growth. Despite removing plots with documented disturbances from the analyses, some plots had negative carbon accumulation values and are assumed to have experienced tree mortality not visually attributable during field sampling to a specific disturbance (e.g windthrow, harvesting).

2.5. Statistical analysis

To compare the amount of live carbon stored in forests growing on shale and sandstones we conducted an analysis of covariance that considers the effect of bedrock and stand age class using the Anova function with a type II test to address an unbalanced design (Langsrud, 2003) in the car package (Fox and Weisburg, 2011) in R (R Core Team, 2018) on all forest plots in the dataset. Initially the linear model included the interaction of the two factors, however there was no significant interaction between bedrock and stand age class ($p = 0.37$) so henceforth the interaction was not included. To understand differing rates of carbon accumulation on shale and sandstone bedrock, the subset of 316 forest plots from stands aged 81–120 years of age (the age of 65% of the forests in the study area) with carbon change data were compared using a Wilcoxon rank sum test after confirming the lack of normality using a Shapiro-Wilk normality test ($W = 0.78$, $p < 0.0001$). Results within this study are considered statistically significant at $\alpha = 0.05$, with correction for multiple comparisons when needed.

To test for differences in carbon storage and accumulation for species between the two lithologies, bootstrap confidence intervals were

Table 1
List of landscape metrics associated with forest inventory plot centers derived from GIS and source databases.

Variable	Category	Source
Primary rock type	Lithologic	Berg et al. (1980), Miles and Whitfield (2001)
Elevation	Topographic	Derived from PAMAP program
Compound Topographic Index	Topographic	Geomorphometry and Gradient Metrics ArcToolbox, Evans et al. (2014)
Slope	Topographic	3D Analyst Tools, ArcToolbox
Aspect	Topographic	3D Analyst Tools, ArcToolbox
Mean Annual Temperature	Climate	30-year climate normal, PRISM (2004)
Mean Annual Precipitation	Climate	30-year climate normal, PRISM (2004)
Available Water Content	Soil	Gridded Soil Survey Geographic Database
Percent Sand	Soil	Gridded Soil Survey Geographic Database
Percent Clay	Soil	Gridded Soil Survey Geographic Database
Bedrock Depth	Soil	Gridded Soil Survey Geographic Database
pH	Soil	Gridded Soil Survey Geographic Database

Table 2
Top ten dominant species by biomass in 81–120 year old forests, species codes and common names.

Species	Code	Common name
Quercus prinus	QUPR	Chestnut oak
Quercus rubra	QURU	Northern red oak
Acer rubrum	ACRU	Red maple
Betula lenta	BELE	Black birch
Quercus alba	QUAL	White oak
Nyssa sylvatica	NYSY	Black gum
Liriodendron tulipifera	LITU	Tulip poplar
Quercus coccinea	QUCO	Scarlet oak
Pinus strobus	PIST	Eastern white pine
Quercus velutina	QUVE	Black oak

calculated using the boot package in R (Canty and Ripley, 2017) with 5000 replicates on plot level estimates from 81 to 120 year old forests. We analyzed the data for the top 10 dominant species in this age class (Table 2). We account for multiple comparisons between lithologies across the 10 species by using a Bonferroni correction and calculated 99.5% bootstrap confidence intervals. When confidence intervals do not overlap, differences between species are considered statistically significant.

To further quantify indirect relationships between lithology and forest productivity we examined the relationship between biodiversity and productivity and tested for differences in the average number of species within a plot (species richness) by bedrock type and performed a correlation analysis between species richness and the rate of live aboveground carbon accumulation for all 316 forest plots included with multiple measurements. Because there may be differences in the biodiversity-productivity relationship between more and less productive forest ecosystems (Paquette and Messier, 2011), we separately compared species richness and the correlation with productivity for both rock types. To test for differences in species richness between shale and sandstone a Wilcoxon rank sum test was conducted after confirming the lack of the assumption of normality from a Shapiro-Wilk normality test ($W = 0.78$, $p < 0.0001$).

To better understand how forests differ between the two rock types, we summarized a set of forest structural characteristics for plots in the 81–120 year old category from 367 available plots of the most recent inventories. Tree stem density (stems/ha) and basal area (m^2/ha) were calculated at the plot level and averaged for each rock type. Additionally, we isolated the tallest and largest (DBH) individual trees from each plot and compared the average maximum tree height (m) and average maximum DBH (cm) by rock type. Statistical differences in stem density, basal area and maximum DBH were tested using Wilcoxon rank sum tests after testing the assumptions of normality with a Shaprio-Wilk normality test in which all sample groups had a p-value < 0.05 with the exception of tree stem density growing on sandstone. Maximum tree height data were normally distributed for forests growing on shale and sandstone bedrock (Shapiro-Wilk normality test, $p = 0.78$ and $p = 0.14$ respectively) and differences between rock types were tested using a Welch 2 sample *t*-test.

Linear models were constructed using backward stepwise regression to understand which abiotic variables contribute to live carbon accumulation and the direction of influence within and between bedrock types. We compared and confirmed variable selection with the results from a step function in R based on AIC (R Core Team, 2018). We built significant models using stand age and 11 GIS derived geophysical variables (Table 1). The importance of each variable was assessed by ranking significant predictors using the varImp function in the caret package in R (Kuhn et al., 2018) based on the absolute value of the t-statistic for each model parameter. Finally, to more fully understand which of the 11 geophysical variables are characteristic of each rock type, and potentially drivers of forest differences, we built classification and regression trees for all sites using the rpart package (Therneau et al., 2009) in R. The classification and regression tree was pruned to minimize the cross-validated error to avoid overfitting the data and for parsimony in interpretation.

2.6. Allometric limitations

Estimating forest biomass using generalized species group allometric equations, as with all allometric estimates, yields tradeoffs. Localized site- and species-specific equations are preferred when focusing on small study areas because they model local tree growth. However, parameters developed at one site may not apply to another due to variability in growing conditions and many of the published equations are often developed from relatively few trees (i.e. 10–20 individuals). The study area detailed here spans ~4,000,000 ha and is suited for the use of generalized equations that have been developed from many equations (i.e. 36–49) for each tree species group (Jenkins et al., 2003), which may represent more of the variability encompassed by ~23,000 trees than that of site and species specific equations. Additionally, a potential shortcoming of the equations used to predict biomass is the exclusive use of tree diameter and omission of tree height, which may alter the accuracy and precision of our forest carbon estimates by not capturing differences in tree architecture due to bedrock mediated site properties. However, other equations predicting tree biomass in temperate forests have found only very slight improvements by including height and recommend using DBH only equations, particularly for total biomass estimation (Wang, 2006). Furthermore, Smith et al. 2017 estimated a 10% uncertainty of biomass estimates from the sum of measurement, model prediction, and model selection uncertainty at a watershed scale in the Pennsylvania Ridge and Valley. They did not include sampling uncertainty due to their census of trees in the watershed, which means their 10% uncertainty can be considered a conservative estimate for results presented here that include sampling uncertainty. Lastly, this study focuses solely on the live aboveground carbon in trees and does not include belowground components of forest ecosystem carbon such as soil organic carbon, which has the potential to constitute more than half of total forest carbon stock in the United States (Domke et al., 2017).

3. Results

3.1. Live aboveground carbon storage and growth by bedrock lithology

Forests growing on shale bedrock store more live aboveground carbon when compared to forests growing on sandstone after considering the effect of stand age spanning 21–200 years ($F_{1, 562} = 74.4$, $p < 0.001$). Carbon storage is 25% higher in forests on shale that are 81–120 years of age (107.9 Mg/ha ± 2.5 Standard Error of the Mean, from here on SEM, $n = 113$), the demographic of the majority (65%) of forests in the region compared to those on sandstone (86.5 Mg/ha ± 1.7 SEM, $n = 249$) (Fig. 2). Additionally, forests growing on shale bedrock are accumulating carbon approximately 55% faster (1.32 Mg/ha/yr, ± 0.11 SEM, n = 97) than their sandstone counterparts (0.85 Mg/ha/yr ± 0.10 SEM, $n = 219$) ($W = 7932$, $p < 0.001$) (Fig. 3). Carbon accumulation was also examined across all age classes and because of the low number of plots on the tail ends of the age distribution we binned the data into wider age classes (0–80, 81–120, 121–200 years old) (Fig. 3, Supplementary Fig. 1). The trend of higher carbon uptake on shale increased from younger to older forests.

3.2. Forest community and forest carbon accumulation rates by species

Overall, forest species composition differed between shale and sandstone. For three of the ten tree species examined in this study, carbon storage was statistically different between the two bedrock types (Supplementary Table 2). Two species, chestnut oak and northern red oak, constitute 49% of all of the forest biomass in 81–120 year old

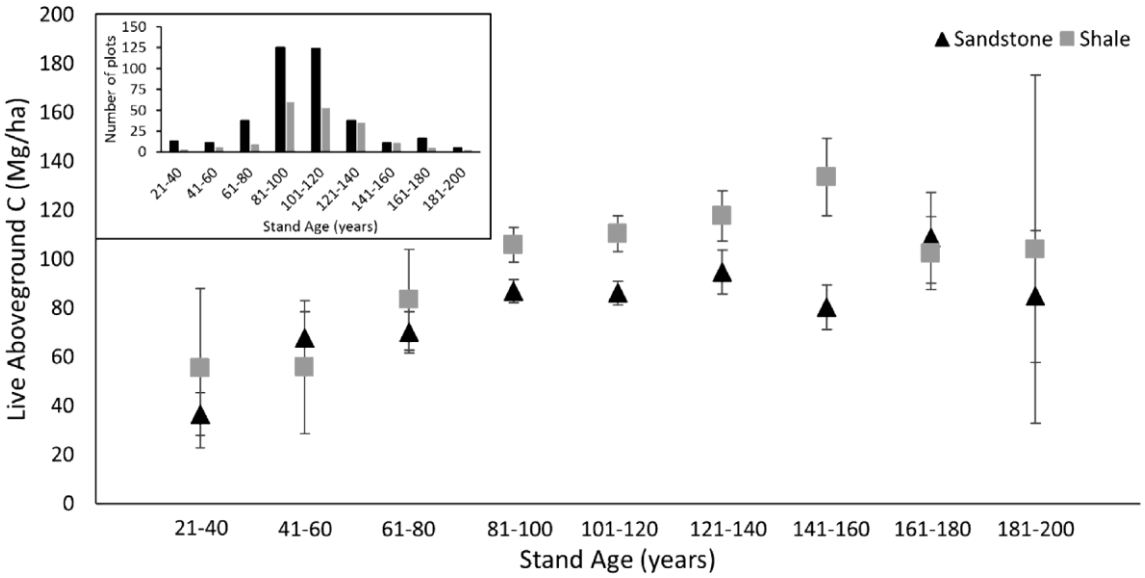

Fig. 2. Average live aboveground carbon (Mg/ha) across 21 – 200 year old forests by rock type, with inset of distribution of forest age classes. Gray squares represent forests growing on shale, black triangles represent forests growing on sandstone. Error bars represent 95% confidence intervals. $Sandstone_n = 381$, $Shale_n = 184$.

forests on shale and sandstone combined. However, the dominance of these two species on each bedrock type follows a contrasting pattern. Chestnut oak on shale has 18.8 Mg/ha (99.5% CI 13.0–24.0) of live aboveground carbon on average in contrast to 32.0 Mg/ha (99.5% CI 26.9–36.7) on sandstone, a difference of 52%. The inverse relationship exists for northern red oak. On shale northern red oak has 29.1 Mg/ha (99.5% CI 18.3–37.5) of live aboveground carbon on average compared to 17.2 Mg/ha (99.5% CI 13.1–20.8) on sandstone, however differences were not significant (Fig. 4, Supplementary Table 2). In addition to chestnut oak, two of the other ten dominant species store more carbon on a given bedrock type. White oak and tulip poplar (*Liriodendron tulipifera* L.) store more carbon on average in plots growing on shale bedrock, a difference of 102% and 183% respectively (Fig. 4, Supplementary Table 2).

Six of the ten species considered had an average carbon accumulation rate that was higher on shale bedrock compared to sandstone (Supplementary Table 3). However, only black gum (*Nyssa sylvatica* Marsh.) had significantly higher carbon accumulation rate on sandstone, owing to considerable variation in species growth rates across the study area (Fig. 5). Black gum accumulates carbon on sandstone at a rate of 0.13 Mg/ha/yr (99.5% CI 0.09–0.16) and is present in 64% of plots compared to 0.02 Mg/ha/yr (99.5% CI −0.02–0.08) and is present in 56% of plots on shale (Fig. 5). The two dominant species, northern red oak and chestnut oak, had the highest average rate of carbon accumulation on shale. Despite faster growth, rates were highly variable and not significantly different between bedrocks. For example, chestnut oak growing on sandstone has a confidence interval more than two times the species' average annual rate on that lithology (Supplementary Table 3).

3.3. Biodiversity productivity relationships and forest structural characteristics

Tree species richness is higher on shale compared to sandstone ($W = 1399$, $p < 0.0001$). The number of species per plot averaged 6.4 and ranged from 2 to 12 in plots on shale bedrock compared to an average of 5.4 (range 1 to 11) for sandstone bedrock. Within both shale and sandstone, there is no evidence of a positive relationship between species richness and forest productivity ($R = 0.03$, $p = 0.81$ and $R = 0.09$, $p = 0.17$ respectively) (Fig. 6).

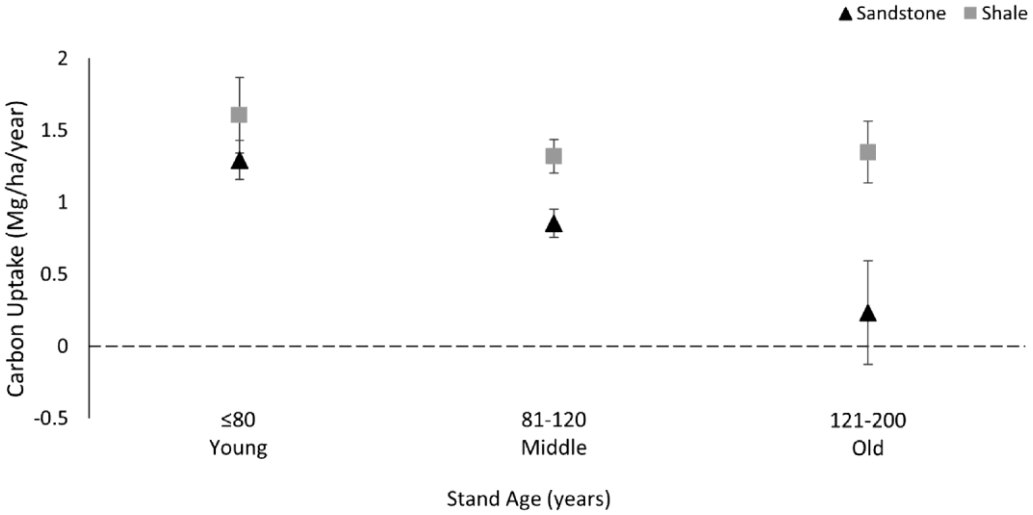

Fig. 3. Average rate of carbon uptake by rock type and stand age. Error bars represent the standard error of the mean (± SEM). Forests with ages 81–120 compared in analysis. Sandstone $n_{young} = 82$, sandstone $n_{middle} = 219$, sandstone $n_{old} = 49$, shale $n_{young} = 28$, shale $n_{middle} = 97$, shale $n_{old} = 41$.

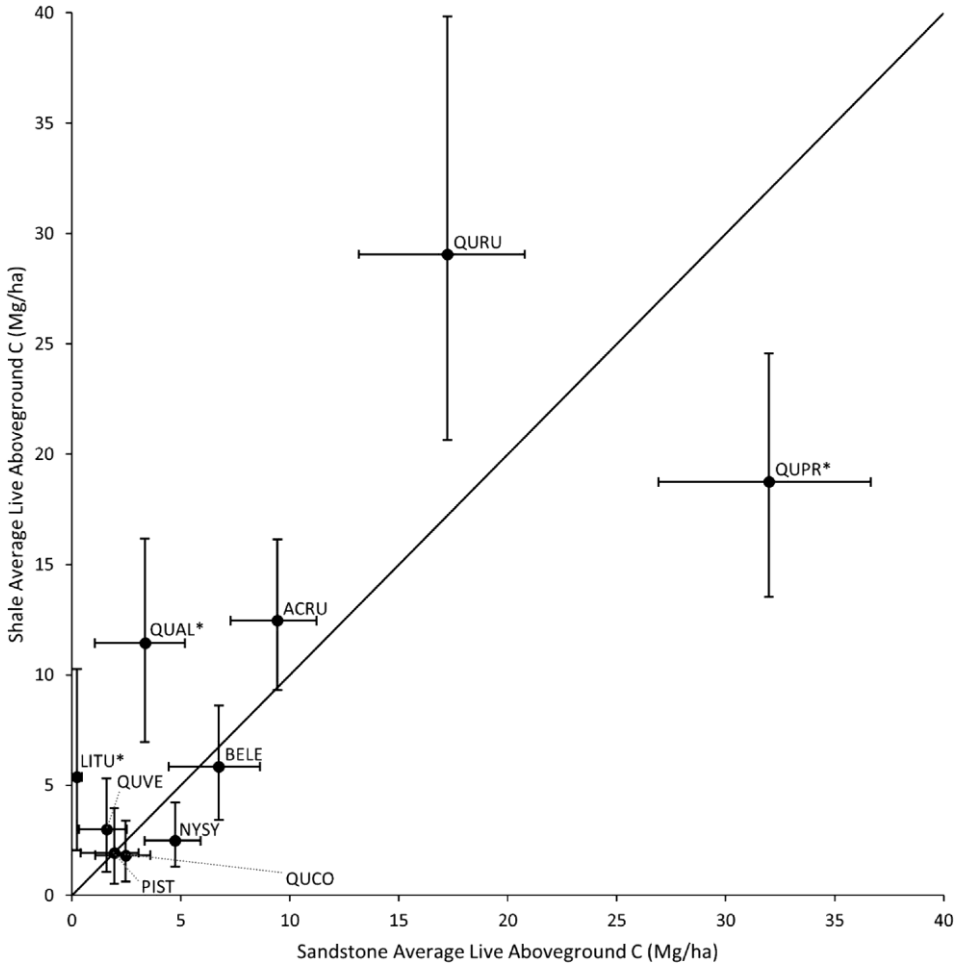

Fig. 4. Average live aboveground carbon by species and rock type, $n_{sandstone}$ = 97, n_{shale} = 219. Error bars in both directions are 99.5% bootstrap confidence intervals and correspond to the bedrock type represented on the parallel axis. Species with asterisks represent statistically significant differences between shale and sandstone. The solid 1:1 line represents the theoretical relationship of equivalent biomass on shale and sandstone. Species codes correspond to nomenclature in Table 2.

Forest structure differed between the two rock types. Average stem density in forests growing on sandstone is higher than that on shale (W = 19154, p < 0.0001). In contrast, other forest metrics were higher on shale. Basal area (W = 63.1, p < 0.0001), average maximum tree height (t = −12.79, df = 212.56, p < 0.0001) and average maximum tree DBH (W = 7371, p < 0.0001) are higher on shale compared to sandstone (Table 3). On shale the average maximum tree height was six meters taller and the average maximum tree diameter was 20% larger.

3.4. Multivariate analyses

Twelve variables were regressed to model live aboveground carbon stored in forests on shale and sandstone separately. Significant models for shale ($F_{4, 179}$ = 10.47, p < 0.0001) and sandstone ($F_{4, 376}$ = 22.53, p = < 0.0001) were produced from just four variables. Stand age and elevation were significant in both models (p < 0.001) (Table 4). Age was the most important predictor of live aboveground carbon stored in forests on both shale and sandstone and was positively related to live carbon stored. Elevation, which has a significant negative influence for both rock types, was more important to modeled live aboveground carbon on sandstone compared to shale (Table 4). In the shale model, aspect and percentage of clay in the soil (% clay) were the other two significant predictors of live aboveground forest carbon (p = < 0.01 and 0.04, positive and negative relationships respectively). In the sandstone model, mean annual temperature (Tmean) and available water capacity (AWC) were also significant predictors of live aboveground forest carbon (p = 0.03, both variables, negatively and positively related respectively). The percent of variance explained for models on both lithologies was similar (R^2 = 0.17 and R^2 = 0.18, for shale and sandstone respectively).

A classification and regression tree was built using the 11 geophysical landscape variables for all sites in the forest inventory dataset to predict rock type. Trees were pruned by minimizing the cross-validated error. Only two variables, elevation and percent clay in the soil, were important to the classification of lithology (Supplementary Fig. 4). The classification and regression tree model preformed relatively well with a percentage of misclassified rock type based on these two variables of 18% for sandstone and 12% for shale plots.

4. Discussion

Forest carbon storage, carbon uptake and community composition differ in relation to underlying bedrock across the central Pennsylvanian Ridge and Valley. Specifically, forests that grow on shale store more live aboveground carbon in trees across forest age classes than those on sandstone. Forests within the most common age class (81–120 years old) are accumulating live aboveground carbon at a rate 55% higher on shale than those on sandstone. Despite greater forest growth on shale sites, none of the ten dominant tree species alone had significantly greater growth on shale. This finding combined with other statistical model results suggests that individual species are not driving

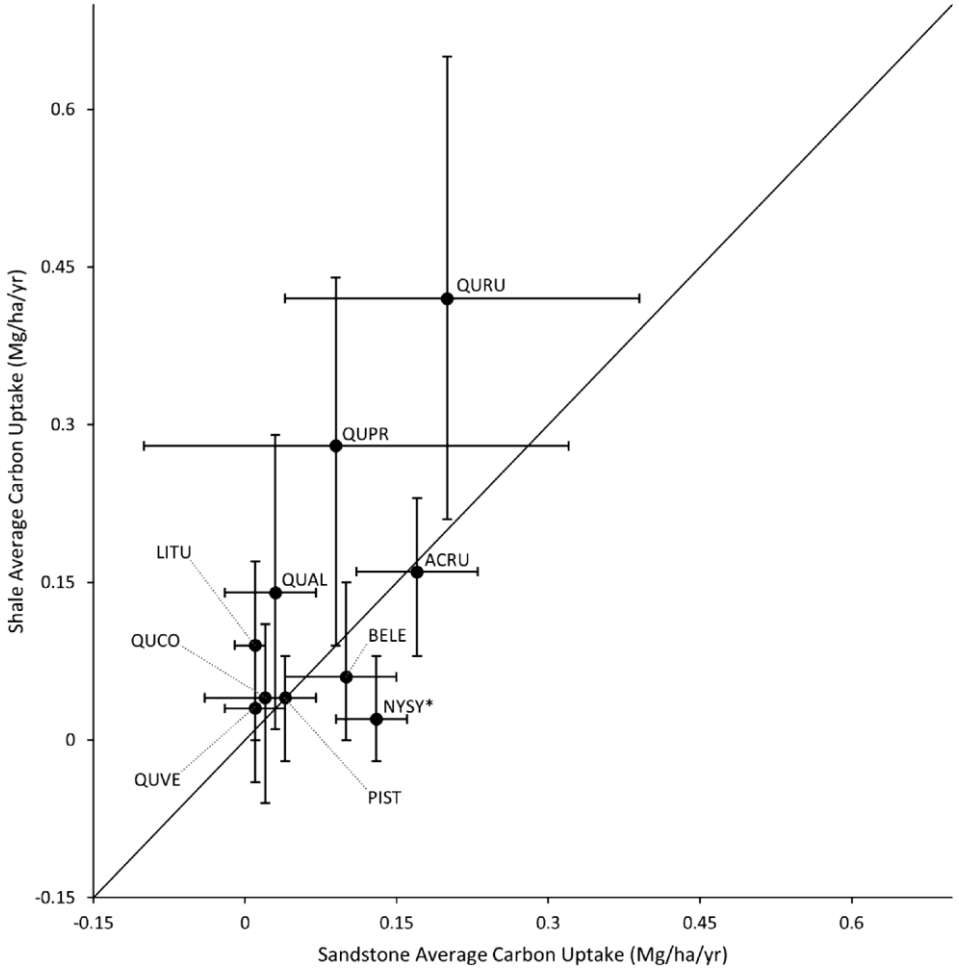

Fig 5. Average annual carbon uptake rate by species and rock type, $n_{sandstone}$ = 97, n_{shale} = 219. Error bars in both directions are 99.5% bootstrap confidence intervals and correspond to the bedrock type represented on the parallel axis. Species with asterisks represent statistically significant differences of carbon accumulation rates between shale and sandstone. The solid 1:1 line represents the theoretical relationship of equivalent carbon accumulation rates on shale and sandstone. Species codes correspond to nomenclature in Table 2.

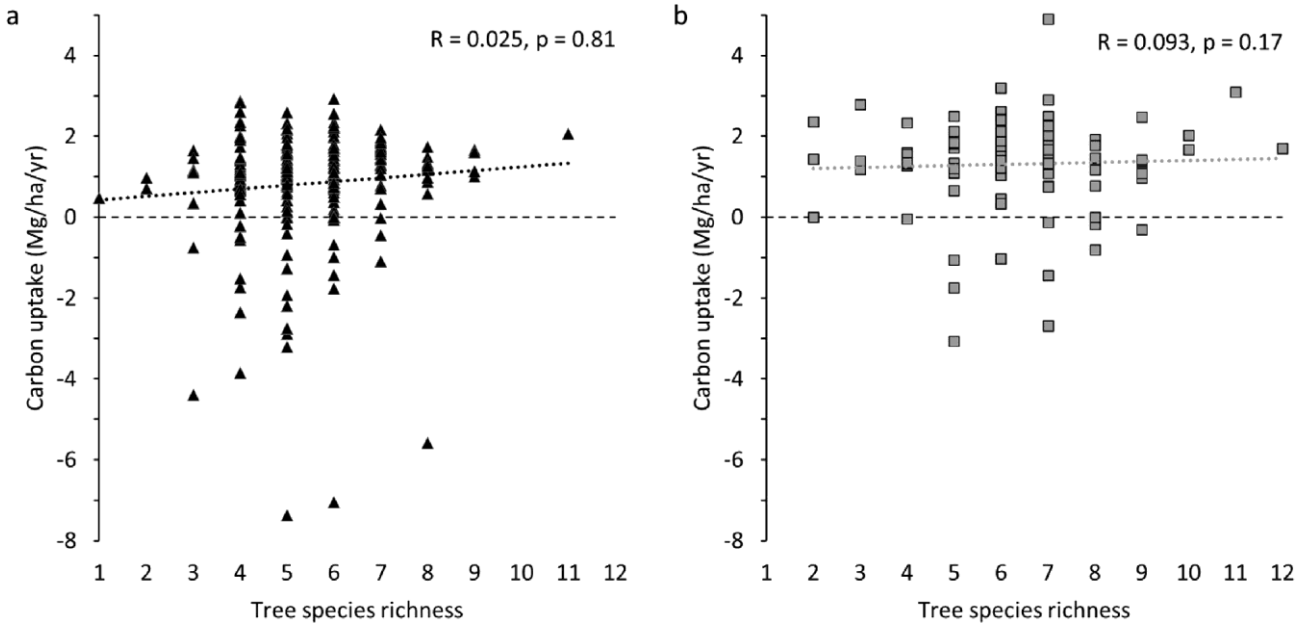

Fig. 6. Species richness and carbon uptake rates for forests on sandstone bedrock (a) and forests on shale bedrock (b). $n_{sandstone}$ = 219, n_{shale} = 97.

Table 3
Structure of 81–120 year old forests on sandstone (n = 253) and shale (n = 114) in the Ridge and Valley province of Pennsylvania. Mean, median, and standard error of the mean (S.E.M.) are included. P-values correspond to results from Wilcoxon rank sum tests and Welch two sample *t*-test in the case of average maximum tree height.

	Sandstone		Shale		
Structural metric	Mean (S.E.M.)	Median	Mean (S.E.M.)	Median	p-value
Stem density (trees/ha)	507.6 (9.4)	505.8	426.3 (11.7)	431.8	< 0.0001
Basal area (m^2/ha)	25.4 (0.40)	25.0	29.2 (0.56)	28.1	< 0.0001
Maximum tree height (m)	23.0 (0.26)	22.9	29.0 (0.39)	29.0	< 0.0001
Maximum tree DBH (cm)	48.0 (0.61)	47.2	57.6 (1.02)	56.1	< 0.0001

Table 4
Regression coefficients (b) standard error (SE) and p-values for multiple linear regression on live aboveground carbon stored based on final models containing only significant variables. Model fit is expressed in R^2. See Table 1 for variable sources. *Aspect is Beers' transformed aspect (Beers et al., 1966). Variable importance ranked from top to bottom for both rock types in the table.

Bedrock Lithology	N	Variable	b	SE	p-value	R^2
Shale	184	Intercept	87.11	14.57	< 0.001	0.17
		Stand age	3.71	0.74	< 0.001	
		Aspect*	7.95	2.91	< 0.01	
		% clay	−0.71	0.35	0.04	
		Elevation	−0.05	0.02	< 0.05	
Sandstone	381	Intercept	107.17	20.2	< 0.001	0.18
		Stand age	2.84	0.44	< 0.001	
		Elevation	−0.08	0.01	< 0.001	
		Tmean	−3.65	1.66	0.03	
		AWC	171.34	79.78	0.03	

the observed pattern of greater productivity on shale, and the differences can be indirectly accounted for through bedrock mediated soil and topographic properties such as soil texture (i.e. percent clay in the soil) and elevation that affect tree growth.

While other studies in the western United States have isolated more direct links between bedrock-derived essential nutrients and contrasting forest productivity through field measurements (e.g. Morford et al., 2011; Hahm et al., 2014), this study opportunistically capitalizes on a dataset comprised of hundreds of forest plots, many with repeated measurements linking forests with bedrock. Because we have not measured nutrient concentrations in bedrock and soils at these sites, we cannot account for the possibility that shale is higher in essential nutrients such as nitrogen or phosphorous that could limit carbon pools and fluxes in our study area. Somewhat counterintuitive, higher concentrations of phosphorous in sandstone-derived soils compared to those of shale have been reported in central Pennsylvania (Li et al., 2018) at sites where similar patterns of live aboveground carbon storage between shale and sandstone bedrock to this study have been documented (Brubaker et al., 2018). The bedrock type and phosphorous pattern found at critical zone field sites within this study region are different than what would be expected at larger scales for shale and sandstone rock types where larger grain sizes typically result in lower phosphorous concentrations (Porder and Ramachandran, 2013). Additionally, significantly lower soil moisture contents throughout the year are found in sandstone derived soils compared to those derived from shale (Li et al., 2018), which may limit forest growth and lead do the differences outlined here.

4.1. Estimates of live aboveground storage and productivity in context

Average live aboveground carbon storage estimates for forest on shale (108.1 Mg/ha for 80–120 year old forests) are more similar than sandstone (84.4 Mg/ha) to second growth forests in the northeastern United States that range from 100 to 116 Mg/ha (Barford et al., 2001; Siccame et al., 2007; Hoover et al., 2012) (Fig. 2). However, this general pattern is consistent with results from two forested watersheds in central Pennsylvania on shale (82 to 146.4 Mg/ha) and sandstone (58.1 to 91.9 Mg/ha) from ridgetop to valley bottom (Brubaker et al., 2018). Recent studies have highlighted variability in forest productivity across complex topography in the region at the watershed scale (Smith et al., 2017) and in other temperate forests of the mountain west (Swetnam et al., 2018). This study provides evidence that the spatial patterns of underlying bedrock contribute significantly to variability of forest carbon pools and fluxes within the Ridge and Valley physiographic province.

Forest carbon accumulation on shale was also more similar to other northeastern US forests than sandstone (this study: 1.32 and 0.85 Mg C/ha/year; other studies: 1.30 to 2.92 Mg C/ha/year, Barford et al., 2001; Curtis et al., 2002; Siccame et al., 2007). Furthermore, an inventory of forest productivity reported county-level estimates to range from 1.0 to 2.9 Mg/ha/year in the central Pennsylvanian region of our study (Brown and Schroeder, 1999). Similar to the pattern illuminated here for live aboveground carbon storage, carbon accumulation rates for forests growing on sandstone are low for what would be expected from other estimates. However, without taking into account rock type and forest age the overall average accumulation rate for 350 forest plots with repeated measurements that are 0–200 years old is 1.03 Mg/C/ha/year (±0.8 S.E.M).

For forests on both rock types within this study, lower carbon storage and uptake estimates could be a relic of increased forest stress from exotic pests (i.e. gypsy moth and others) (Lovett et al., 2006). Forests containing chestnut oak on sandy dry ridges (particularly consistent with sandstone sites for forest in this study) are susceptible to gypsy moth, but tend to exhibit low levels of mortality (Houston and Valentine, 1977). To minimize the influence of disturbance and focus on forest productivity in relation to bedrock, we removed stands that were deemed to have experienced a 'natural disturbance' from the dataset, which made up just 0.5% of the initially considered plots. The vast majority of 81–120 year-old stands experienced positive carbon accumulations over the measurement periods, however, some stands exhibited decreases in standing live carbon (Fig. 6). Plots with negative accumulation rates that were not visually deemed disturbed in field inventories could result from the death of one to a few large trees, consistent with observations of low mortality rates in other published literature from temperate deciduous forests of the eastern United States (Gonzalez-Akre et al., 2016). Within stands that experienced negative live carbon accumulation rates chestnut oak and northern red oak, the two dominants, experienced the greatest amount of live carbon loss. The average change for chestnut oak and northern red oak on sites that lost live carbon on sandstone was −1.48 and −0.52 Mg/ha of live carbon compared to −0.11 and −0.41 on shale sites respectively. These findings fit with the understanding that mortality is generally the product of short- and longer-term stress, and that trees with slower growth rates are more likely to experience mortality regardless of disturbance (van Mantgem et al., 2003). The mortality in this study could be caused by exogeneous agents such as forest pests (e.g. gypsy moth) or by mid-successional forest dynamics transitioning to gap-dynamics, but likely reflect an indirect connection to underlying bedrock through

species composition and physical stress.

4.2. Species growth and community

Only one species in this study, black gum, accumulated more carbon for a given rock type. Counterintuitively, black gum trees accumulate more carbon on sandstone, the rock type with lower overall forest productivity. Black gum is known for its almost ubiquitous presence across an extreme gradient of moisture availability, however, is almost always a small component of any forest type across its range (Abrams, 2007). Faster carbon accumulation rates on sandstone for black gum are likely a testament to the harshness of the growing conditions on some of the sites, where the species' reputation for extreme tolerance is expressed in the forest community compared to more productive sites on shale.

Environmental harshness has been hypothesized to limit species diversity in temperate forests across North America and co-vary with maximum tree height (Marks et al., 2016), which is sometimes used as a proxy for high levels of forest biomass and productivity (Fricker et al., 2019). Forests in this study region parallel this pattern, where maximum tree height (Table 4) and species richness are lower on sandstone. Despite a lack of relationship between species richness and forest productivity found here, the lower observed patterns of diversity, shorter maximum tree height, lower standing carbon, and lower productivity of forests on sandstone bedrock generally point to poorer growing conditions mediated through abiotic characteristics of bedrock (i.e. soil texture and topography) in relation to those on shale.

4.3. Bedrock linked topographic and soil properties

Sandstone bedrock in the Ridge and Valley is often found on ridges (Nowacki and Abrams, 1992; Li et al., 2018), and is generally at higher elevation due to increased resistance to erosion. In the southern Appalachians, average temperatures were found to be cooler at valley bottoms than at sideslopes and higher elevations (Boldstad et al., 1998) and while less extreme differences in elevation exist in the mid-Atlantic region, similar patterns likely exist here. Elevation is negatively related to the amount of live aboveground carbon across the forest of central Pennsylvania and was the first branch of the classification and regression tree predicting bedrock from geophysical characteristics of the forest plots in this study (greater elevations associated with sandstone bedrock). Patterns of lower productivity in these forests at higher elevation align with other observations of forest productivity and leaf area index in the Appalachian Mountains (Bolstad et al., 2001). While elevation may be confounded with the impact of rock type on forest growth, the inherent properties of bedrock are what sets the template for topography. In forests on shale and sandstone bedrock with overlapping elevation, patterns of live aboveground carbon storage and uptake parallel those from the entire dataset however are somewhat less pronounced for carbon uptake (Supplementary Fig. 5 and Supplementary Table 6). This supports our conclusion that the differing abiotic characteristics between shale and sandstone bedrock are driving differences of forests and the carbon cycle but still leaves open the possibility that within forests at higher elevations productivity may also negatively interact with bedrock and other exogenous stressors (e.g gypsy moth, acid deposition, and more variable and extreme microclimatic effects).

The amount of clay in soils derived from the two rock types can have contrasting impacts on forest growth by being at both extremes of plant available water (Brady and Weil, 2002). The percentage of clay in the soil was negatively associated with modeled live aboveground carbon for forests growing on shale and was the only other important branch of the classification and regression tree predicting bedrock type (Supplementary Fig. 4). On the other side of the spectrum, available water capacity (linked to soil texture) was positively related to regressed live aboveground carbon on sandstone bedrock. Both scenarios are inherently linked to the physical properties of underlying bedrock; sandstones produce coarser-grained soils with less clay than shales. These properties of bedrock likely exert an indirect influence on modern day forest growth through long term pedogenic processes. The relative control of tree growth (specifically tree height) by soil properties, parent material and geology across elevation gradients in the Sierra Nevada has been difficult to disentangle (Fricker et al., 2019) and similar challenges exist in this study.

5. Management implications

Forest provide a wide range of ecosystem services, with carbon storage and uptake manifesting as one of the many assets of forests in the central Appalachians. In addition to carbon storage and uptake, these oak-dominated forests produce economically important wood products (Luppold and Bumgardener, 2006), support wildlife populations (McShea et al., 2007), and provide recreation and tourism opportunities as well as other services (Krieger, 2001). As future forests grow and respond to warming, shifts in precipitation patterns, and invasive species across "complex hydrobiogeochemical templates" (Groffman et al., 2012), managers will benefit from incorporating lithological influences on forest composition and productivity. For example, identifying and conserving forests with higher species diversity will likely lead to greater resilience in the face of exogeneous perturbation (Peterson et al., 1998; DeClerck et al., 2006) and forests with more vigor due to site conditions have been shown to be more resilient to climatic stressors (Camarero et al., 2018). Additionally, geology can mediate soil organic carbon, another large and important carbon sink, and patterns of carbon storage and uptake likely exist belowground as well (Barré et al., 2017; Angst et al., 2018). Forests underlain by shale in this region may be seen as higher priority for management or conservation, particularly in light of the fact that they make up a smaller portion of the landscape, typically have a higher species richness, as well as store and uptake carbon at a faster rate, characteristics that will likely persist as forest respond to global change.

6. Conclusion

In the Ridge and Valley province of Pennsylvania forest carbon storage is 25% greater and annual uptake is 55% higher in forests growing on shale bedrock compared to sandstone. This difference is often overlooked despite the dominance of these rock types within a large and important carbon sink. The Ridge and Valley spans the Appalachian mountain chain from southern New York to northern Alabama where much of the forested upland topography is dictated by similar geologic patterns to the study area presented here. Although there are confounding factors associated with the geography of topographic and soil related features in relation to lithology, bedrock geology maps are readily available. As forest managers adapt to meet a variety of ecosystem services, including sequestering atmospheric CO_2, incorporating potential influences of lithology on forests into management plans can help target areas such as those underlain with shale that have higher diversity and faster growth, features that may add up to longer-term resilience.

Acknowledgements

Financial Support was provided by National Science Foundation EAR – 1331726 (S. Brantley) for the Susquehanna Shale Hills Critical Zone Observatory, the Intercollege Graduate Degree Program at Penn State and by the USDA National Institute of Food and Agriculture Federal Appropriations under Project PEN04658 and Accession number 1016433. Additionally, this study greatly benefited from conversations with E. Maynard-Bean, X. Chen and B. Holderman. Valuable advice through the development of this project was provided from R. DiBiase, J. Kaye and L. Leites. Thanks to Pennsylvania's Department of

Conservation and Natural Resources Bureau of Forestry and the Pennsylvania Game Commission for access to forest inventory datasets.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.117881.

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