Science of the Total Environment 793 (2021) 148399

Contents lists available at ScienceDirect

Science of the Total Environment

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

Similar tree species richness-productivity response but differing effects on carbon stocks and timber production in eastern US and continental Spain

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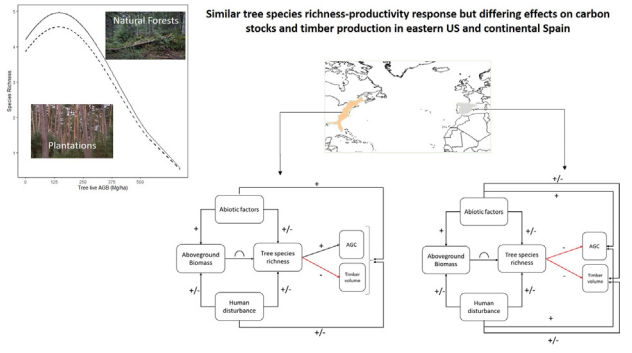
HIGHLIGHTS

- Humped-back relationship between tree aboveground biomass and species richness across bioregions
- Aboveground carbon stock and timber volume showed trade-off in eastern US forests
- Species rich plantations had less aboveground biomass but more timber volume
- Natural forests need more tree species to get the same aboveground biomass than plantations

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 5 March 2021
Received in revised form 8 June 2021
Accepted 8 June 2021
Available online 18 June 2021

Editor: Manuel Esteban Lucas-Borja

Keywords:
Forest carbon
Tree biomass
Species richness
Timber production
Ecosystem services trade-offs

ABSTRACT

Unimodal response of tree species richness to increases in aboveground productivity is evident in grasslands but to a lesser extent in forests, where confounding factors (e.g., abiotic factors and management regimes) may alter the response and compromise the delivery of ecosystem services. We hypothesize that unimodal response of biomass accumulation through increased species richness leads to greater tree above ground carbon (AGC) stocks and thus climate regulation but not necessarily higher timber volume production for human consumption across portions of North American and European forests. We first evaluated the biodiversity-productivity pattern and assessed if the addition of potential confounding variables altered the response. Afterwards, we integrated direct and indirect effects of species richness and confounding factors in the modelling of aboveground carbon stock and timber volume. We confirm an increase in carbon stocks concomitant with an increase in tree species richness up to an optimum biomass value in both regions. Tree species richness had a marginal effect on both aboveground carbon stocks and timber volume with a trade-off in the eastern US. Biomass accumulation is lower in tree plantations than in natural forests, although volume increased with species richness. Naturally-regenerated forests needed as much as double the number of tree species than plantations to reach the same carbon stocks. Distinct ecosystem services (AGC and timber volume) showed unique pathways of achieving their maximum provisioning. As increasing forest resilience to global change requires a fundamental understanding of how tree species combine with changing climatic conditions to drive the provisioning of various ecosystem services, further examination of this study's findings across additional biogeographical regions may lead the way to unraveling such dynamics and empowering adaptive management.

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https://doi.org/10.1016/j.scitotenv.2021.148399

1. Introduction

Forest managers and policy makers alike strive for more resilient forest systems against a backdrop of global change concerns regarding the loss of biodiversity. These concerns have attracted scientists and managers to the concept of species richness effects on forest stand productivity. Through recent decades studies around the globe have investigated the growth performance and characteristics of mixed versus pure stands (Amoroso and Larson, 2010; Pretzsch, 2018; Pretzsch et al., 2015), the effects of tree species diversity on stability of production (Morin et al., 2014; Ouyang et al., 2021) and the relationship between tree species richness and productivity (Fei et al., 2018; Liang et al., 2016; Pan et al., 2018; Wang et al., 2009; Zeller et al., 2018).

There are two possible pathways to explore the tree species diversity-productivity relationship (Waide et al., 1999). First, species richness is predicted as a function of productivity (SR-PR relationship) based on available energy for plant development (Currie and Paquin, 1987; Francis and Currie, 1998) or biogeographic history and regional factors (Latham and Ricklefs, 1993; Ricklefs and He, 2016). This approach is often used to explain the species richness pattern distribution (Gaston, 2000; Šímová et al., 2013) or to empirically analyze the unimodal response of species richness to increases in productivity, i.e. the so-called humped-back diversity-productivity pattern (Fraser et al., 2015). The second approach focuses on the prediction of productivity as a function of species richness, i.e. PR-SR relationship (Liang et al., 2016; Wang et al., 2009) or other measures of plant diversity (Paquette and Messier, 2011; Ruiz-Benito et al., 2014) if the research focus is on the complementary use of resources. Both approaches have been conducted at local, regional, and global scales with contrasting results ranging from no response, positive or negative linear relationships, and saturating or unimodal responses (Hooper et al., 2005). At large scales, the species richness effect can be confounded as abiotic drivers might be more influential (Vilà et al., 2013; Ali et al., 2020; Ouyang et al., 2019). As such, a unimodal or humped-back relationship is expected in response to large scale environmental gradients or successional stages (Waide et al., 1999). Additionally, the species richness effect may increase in strength when the same limiting factor affects both species richness and productivity. This may result in a decrease in ecosystem productivity due to the presence of competing species (Wardle, 2001).

Thus, in both the SR-PR or the PR-SR approaches several factors interact: energy-based factors (e.g., climate), local environmental gradients (e.g., water and nutrient availability), management factors (e.g., species selection), modification of competitive environments and homogenization of structure, biogeographic history and the available pool of functionally diverse species. All of these variables may be referred to as confounding factors that can alter the pattern observed and should be taken into account when modelling this relationship (Vilà et al., 2005).

Grassland experiments have demonstrated that biodiversity promotes ecosystem functioning and process stability (Loreau et al., 2001) with a high number of species needed to maintain functions and services across time and space (Isbell et al., 2011). Translation of grassland studies to forests have found similar effects of species richness on productivity either in ecological terms, i.e. wood biomass studies, (Li et al., 2018; Paquette and Messier, 2011; Ruiz-Benito et al., 2014; Vilà et al., 2003, 2013) or forestry-related production, i.e. wood volume (e.g., Zeller et al., 2018) or both (Vilà et al., 2007). In general, an increased number of species often leads to higher biomass and timber productivity, both easily transformed into carbon values. However, studies involving species richness and ecosystem services do not define wood volume in terms of individual tree quality or merchantable dimensions. Although all species in a forest contribute towards regulating climate through carbon sequestration, not all species or individuals contribute to timber production as not all species are merchantable nor do all individuals meet industrial standards for consumption. Thus, in a forestry context, not all species-rich forest ecosystems provide the same amount of functions and services (van der Plas et al., 2016).

Positive biodiversity-ecosystem functioning relationship has been largely explained as a consequence of complementarity and sampling or selection effects (Loreau and Hector, 2001) that determine the net biodiversity effect. Sampling effect occurs when random or stochastic processes drive the appearance of a high productive species within an assemblage in natural systems (Loreau and Hector, 2001). However, in human-altered ecosystems, like Southwest Europe and the Atlantic coast of the US, the selection effect could be more deterministic as the species selection effect is driven by human decisions rather than by random processes. For example, human preference is clearly demonstrated when tree species are selected for various ecosystem services such as esclerophyllous oak for acorn production in the Mediterranean, pine plantations in the southern US for dimensional lumber, or the promotion of spruce/fir in the eastern US for pulp mills.

We aim to expand the species richness-productivity debate to the delivery of ecosystem services in two highly human-altered regions with large within and between variation in terms of climate, local site conditions, biogeographic history, species pool, and forest management by investigating (i) the SR-PR pattern (unimodal, decreasing or increasing) using bivariate (linear modelling) and integrative methods (structural equation models), and (ii) the delivery of regulating and provisioning ecosystem services that typically exhibit trade-offs: aboveground carbon stock in trees (AGC) and production of quality timber volume (QTV).

Our main hypothesis is that all tree species contribute to carbon accumulation but not all of them contribute to quality timber volume inducing a trade-off between the ecosystem services of carbon sequestration and timber production. The trade-off is mediated by the diversity-production functional relationship.

2. Material and methods

2.1. Tree and site data

We used national forest inventories to investigate the SR-PR relationship in two contrasting regions in terms of large within and between climate variability, productivity and species composition variation with distinct biogeographical history. Inventory data sources include forests of the eastern US and continental Spain.

The Forest Inventory and Analysis (FIA) program of the US Department of Agriculture, Forest Service, has conducted an annual inventory of all US states since ~2000. The design is based on a spatially balanced sample of one plot every ca. 24 km^2 (Reams et al., 2005). Each inventory plot consists of four points arranged in a cluster with one point at the center and three points oriented from the central subplot at 0, 120, and 240 degrees (Bechtold and Scott, 2005). Each of these four points are referred to as subplots. The distance from the center of the central point to the center of the surrounding points is 36.58 m. These four points form the center of fixed-area plots used to tally live and standing dead trees in order to avoid boundary issues and plots straddling multiple forest conditions (USFS, 2018). A total of 15,752 forested plots (minimum crown cover 10%, median value 70%) comprising a single condition (e.g., forest type or land ownership) in the eastern US were considered in this study. Individual tree volume, biomass, and carbon are estimated using a component ratio method (Woodall et al., 2011) whereby regional volume models by species or species groups are used to estimate gross and sound volumes with apportionment to tree biomass components (e.g., limbs, boles, etc) via national-scale biomass equations. Data of plot elevation (m.a.s.l.), stand basal area, and stand establishment method (plantation or natural regeneration) were also extracted in both datasets. Fig. S1 displays the location of the plots in both regions.

The Spanish National Forest Inventory (SFNI) is a multi-objective cyclic inventory for national and large-scale assessment of forest resources (Alberdi et al., 2017). The sampling is performed approximately on a 10-

year cycle basis. Forest is defined in Spain as land covered by tree species with a crown cover at least 10% of crown cover with a minimum area of 0.5 ha (Alberdi et al., 2016). In this study we used the latest full inventory available (SNFI3) completed between 1997 and 2007 in continental Spain (excl. Canary and Balearic Islands) to avoid insular effects that might not be present in the other region. We used 56,345 plots with a median crown cover of 60%. Sample points are located on the nodes of the UTM 1 × 1 km grid. Four concentric plots (radii 5, 10, 15, 25 m) are sampled in each node and trees are measured if they reach a diameter at breast height (DBH) threshold: 7.5, 12.5, 22.5 and 42.5 cm. This implies that not all trees in the plot are measured, however all tree species present in the plot are recorded irrespective if they have been measured or not. We used the actual number of species to estimate SR whereas measured trees according to the above thresholds were used to estimate the forest variables expressed on an area basis (AGB, AGC and QTV). This might have under-estimated forest variables but it should have little impact on their functional relationship with SR because the estimation of per area forest variables, like basal area or volume, is more efficient in variable radius plots (Packard and Radtke, 2007). Trees are located, tallied, measured (DBH and height), and classified according to stem form quality. Volume over- and under-bark is estimated using allometric equations based on form quality, diameter, height, and species. Trees are also classified according to form and stem quality. We used the two better qualities and forms to estimate QTV, i.e., fusiform stems and more than 4 m of merchantable wood stem with a minimum top diameter of 7.5 cm (Alberdi et al., 2016). AGB was estimated using allometric equations for soft- and hardwood species (Ruiz-Peinado et al., 2012, 2011) and included stem, branches and foliage biomass. As not all species have specific biomass equations, those associated with species having similar wood density were used. Carbon values were obtained using dry matter to species-specific carbon ratio developed by (Montero et al., 2005) and used in the National Inventory of Green-House Gas Emissions.

2.2. Climate data

Bioclimatic variables derived from monthly temperature and precipitation for inventory plot locations were extracted from WorldClim database (https://www.worldclim.org/data/bioclim.html). We used variables describing annual trends as well as climatic variability: mean annual temperature (BIO1), annual precipitation (BIO12); temperature seasonality (standard deviation ×100) (BIO4), precipitation variability (coefficient of variation) (BIO15) and precipitation of driest quarter (BIO17) were selected. Bioclimatic variables were extracted using spatial analyst in ArcMap™ 10.5 and map creation using ArcGIS® software. Copyright © Esri.

2.3. Statistical analyses

All statistical analyses were performed in R (R Core Team, 2018). We first conducted a correlation analyses to analyses bivariate relationship between considered variables. We focused the remainder of the analyses on those variables that exhibited stronger correlation with the target variables: SR, AGB, AGC. The linear or humped-back relationship between SR and productivity, estimated as AGB, was first tested fitting a generalized linear model (GLM) model to count data using a Poisson distribution model or a negative binomial model in case of overdispersion (Zuur et al., 2009). The linear (SR = f(AGB)) and humpbacked hypothesis (SR = f(AGB, AGB^2)) were compared with an information criterion approach using the function *model.sel* of the *MuMIn* package (Barton, 2019). A negative significant quadratic term (AGB^2) would indicate concave downward pattern consistent with a humped-back relationship. Confounding factors associated with climate (precipitation and temperature mean value and variability), elevation, and stand origin (1 for plantations, 0 for natural regenerated forests) were added subsequently. In order to avoid multicollinearity we applied a global variance inflation factor analyses keeping those variables that demonstrated a GVIF < 3. Once we fitted and selected an appropriate model, we expanded our analyses to account for potential nested effects of plots within ecoregions regions and applied a Generalized Linear Mixed Model with a random intercept. In Spain, we divided the study area according to bio-geo-climatic regions (Elena-Rosselló et al., 1997). In the eastern US we used the ecological classification at the province level (Bailey, 1983).

In order to analyze the trade-offs between AGC and QTV based on SR-PR relationship, we performed an integrative modelling approach (Grace et al., 2016) fitting a structural equation model (SEM). We tested if aboveground carbon and quality timber volume is the result of direct effects of species richness and abiotic factors and indirect effects of aboveground biomass, human disturbance regime, and abiotic factors mediated by species richness. Different signs in the total effect would indicate trade-offs between target variables. SEM required that all relationships be linear and multivariate normally distributed which are assumptions hardly attainable with extensive forest inventory data. We took advantage of the *piecewiseSEM* package (Lefcheck, 2016) that allows for a simultaneous fit of models to data showing departures from assumptions (e.g. nested structure and count data). We evaluated the piecewise SEM goodness of fit using the Fisher's C statistic to test if relationships (paths) are consistent with data (Lefcheck, 2016; Shipley, 2016). At the time of analyses, the *piecewiseSEM* algorithm did not allow for reciprocal analyses, i.e. simultaneous PR-SR and SR-PR relationship.

This second analyses focused on the integrative modelling approach to analyze if species richness mediated the amount of AGC and QTV, either directly or indirectly through biomass accumulation (Fig. 1). The set of models in the SEM includes a SR-PR model fitted using a Poisson distribution and two mixed-effect relationships (1) AGB as a function of species competition, stand origin, and climate attributes; 2) AGC and timber volume as a function of species richness and stand origin.

3. Results

Although the lower limit of the crown cover to define forests is comparable in both countries (i.e., 10%), there was a larger proportion of understocked plots in the Spanish dataset compared to the FIA that led to large differences in mean crown cover in both datasets (57.6% and 80.7% respectively). This difference affected the SEM fitting procedure in the case of continental Spain (Section 3.3). The SEM model showed little significance and the model estimates were only near to the optimum using all data points (56,345 plots) as evidenced by warning messages in the program output. We performed a sequential analysis based on a 10% increment of crown cover threshold until the fit was consistent and without warning messages. A threshold of 40% in the Spanish dataset (44,626 plots) led to consistent fit results and raised the mean crown cover to 69.8%.

In the following, we present results using this threshold to preserve consistency and further discuss the implications for this approach in analysing trade-offs. In the supplementary material we show a summary of the analyses with the original 10% crown cover threshold including the humped-back relationship (Fig. S5 and Tables S2 and S3).

3.1. Correlation analyses of species richness with stand and abiotic factors

Correlation analysis (Fig. S2) indicated that tree species richness was positively correlated with stand variables (stand basal area (SBA), AGB, AGC and QTV) in both regions, with the highest in the eastern US than in continental Spain (e.g. $r_{pearson}$ between SR and AGB is 0.43 in eastern US and 0.12 in continental Spain, $p < 0.001$). Precipitation seasonality (BIO15, Prec.Season.), which is associated with longer dry periods, showed negative correlation with species richness in both regions ($r_{pearson}$ − 0.35 in continental Spain and -0.43 in eastern US, $p < 0.001$). However, annual precipitation had a positive correlation in Spain ($r_{pearson}$ 0.21, $p < 0.0001$) and a weak negative correlation in

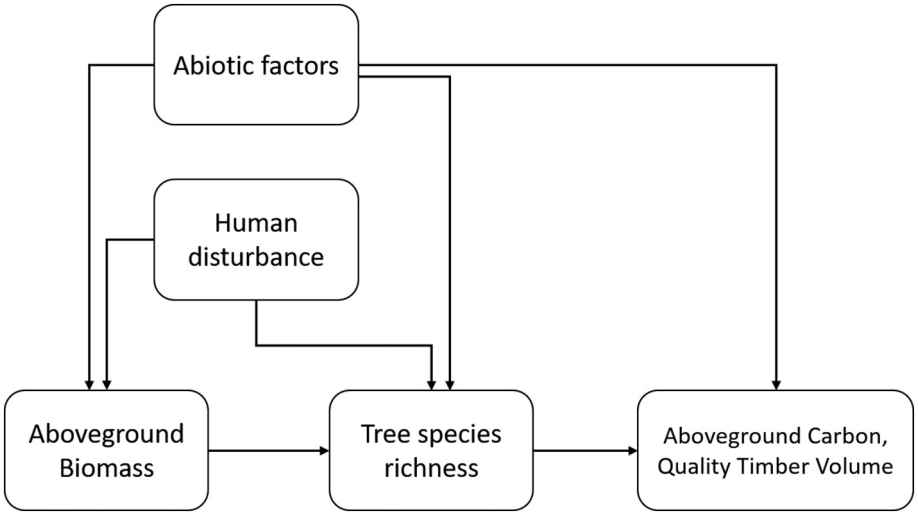

Fig. 1. Study hypothesis conceptualization: aboveground carbon and quality timber volume is the result of direct effects of tree species richness and abiotic factors and indirect effects of aboveground biomass, human disturbance regime (plantation, natural regeneration, stocking control), and abiotic factors (climate regime) mediated by species richness. Different signs in the total effect (direct + indirect) would indicate trade-offs between target variables.

eastern US ($r_{pearson} - 0.10$, $p < 0.001$) probably due to a positive correlation between MAP and BIO15. Mean annual temperature (MAT) had a negative correlation with species richness in US ($r_{pearson} - 0.21$, $p < 0.001$) but negligible in Spain ($r_{pearson} - 0.09$, $p < 0.0001$). The highest positive correlation with species richness in Spain was with precipitation of the driest quarter ($r_{pearson}$ 0.40, $p < 0.001$) which is also correlated with species richness in eastern US but to a lower extent ($r_{pearson}$ 0.17, $p < 0.001$). Temperature seasonality exhibited reverse correlation values in both regions for species richness. Correlation was negative in continental Spain ($r_{pearson} - 0.23$, $p < 0.001$) and positive in the eastern US (0.19, $p < 0.001$). Species richness was positively correlated with elevation in the US ($r_{pearson}$ 0.25, $p < 0.001$ in US) and negative in continental Spain ($r_{pearson} - 0.15$, $p < 0.001$). In general, climate attributes related to precipitation regime were more closely correlated with species richness in continental Spain whereas stand attributes were more closely correlated in the eastern US.

3.2. Is there a unimodal relationship between species richness and aboveground biomass?

In both regions the unimodal Poisson model performed better than the linear relationship; however, over-dispersion was high in both regions (ratio 1.5 in Spain and 1.2 in the eastern US). After fitting a binomial model to overcome over-dispersion the unimodal relationship was still superior. This unimodal pattern persisted even after the inclusion of potential climate attributes and the confounding factor of management (stand origin). However, covariates differed between regions. In continental Spain, species richness decreased with temperature and precipitation seasonality whereas in the eastern US species richness increased with higher precipitation during the driest quarter (BIO17) and decreased with mean annual temperature. In both regions, elevation and plantations had a negative impact on species richness (Table S1). Visual inspection of residuals indicates that there were some random variations across ecological regions within each bio-geographic area (Fig. S4). A generalized mixed model with ecoregion in Spain (Elena-Rosselló et al., 1997) and ecological province in US (Bailey et al., 1997) as a random effect in the intercept performed better than the fixed-effect model. In this latter model the independent variables were scaled to reach convergence. We repeated the analyses using a Poisson distribution assumption with all fixed effects and a random component in the intercept indicating that over-dispersion was not an issue anymore (ratio 1.01 and 0.85 in Spain and US, respectively). We used the Poisson model (Table S1) to depict the unimodal response (Fig. 2) where environmental variables were set to their mean value. In both regions less species are needed in plantations to grow the same amount of biomass than in naturally regenerated forests.

3.3. Is aboveground carbon and timber volume mediated by species richness?

The unimodal SR-PR response is also predicted by the piecewise SEM in both regions (negative AGB quadratic). SR mediated the relationship between both AGC and QTV, but the effect is context-dependent. In the eastern US, SR has a positive effect on aboveground carbon (Fig. 3) whereas it has a negative direct effect on timber volume (Fig. 4) confirming our hypothesis that all species contribute to carbon accumulation but not to timber production. However, in continental Spain SR has a negative direct effect on both AGC and QTV (Figs. 5 and 6).

In the eastern US, MAT exhibited a negative direct effect on species richness (−0.0745), but a positive indirect effect via aboveground biomass (0.1284×0.4401) leading to a negative total effect on species richness (−0.018). However, temperature has a positive direct and total effect on aboveground carbon (0.1311 and 0.1308 respectively). Precipitation during the driest quarter had a positive effect on species richness, an indirect effect on AGC via SR and no effect on above ground biomass (Figs. 3 and 4).

Stand basal area has a direct and total positive effect on AGC and timber volume although the mediation of SR led to indirect negative effects on AGC in Spain and QTV in both regions. Abiotic factors affecting target variables differed. Whereas elevation is not significant for volume in eastern US it has a total positive effect on AGC and negative effects on species richness and consequently a negative indirect effect on AGC. In Spain, elevation has a positive direct effect on volume and indirect effect on AGC (Figs. 5 and 6).

Stand origin (plantations) had a negative effect on both AGC and QTV in eastern US, whereas plantations had a positive effect on QTV and a negative total and direct effect on AGC in continental Spain.

4. Discussion

At the heart of the growing number of investigations about the relationship between species richness and forest productivity is the fundamental need of society to unravel the key drivers of forest ecosystem

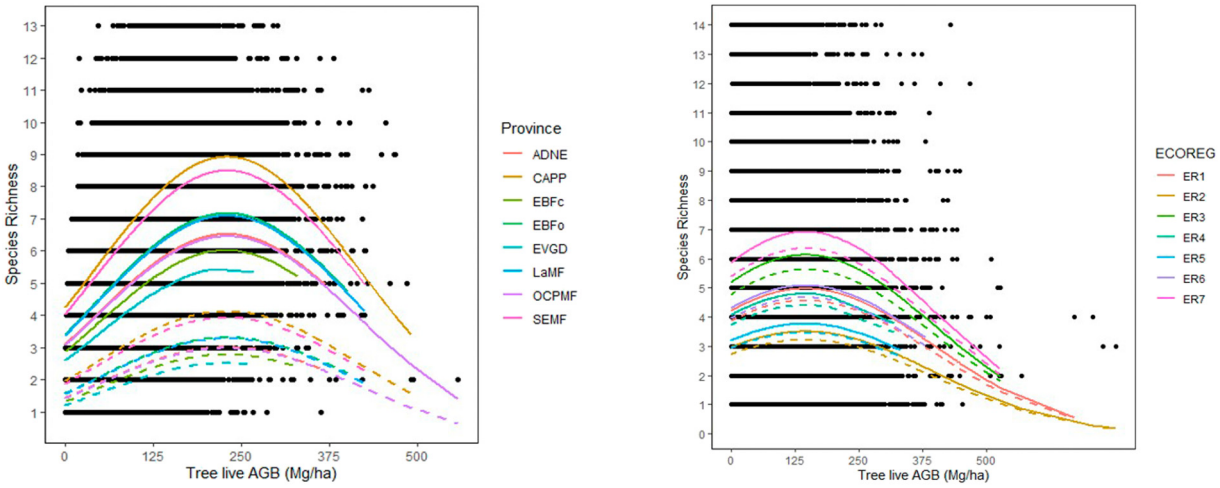

Fig. 2. Unimodal relationship of species richness and tree live aboveground biomass in the eastern US (left panel) and continental Spain (right panel). US ecological provinces codes are ADNE: Adirondack-New England Mixed Forest-Coniferous Forest-Alpine Meadow, CAPP: Central Appalachian Broadleaf Forest-Coniferous Forest-Meadow; EBFc: eastern Broadleaf Forest (Continental); EBFo: eastern Broadleaf Forest (Oceanic); EVGD: Everglades, LaMF: Laurentian Mixed Forests; OCPMF: Outer Coastal Plain Mixed Forest; SEMF: Southeastern Mixed Forest. ES biogeographical ecoregions are ER1: Galaico-Cantabrica, ER2: Duriense, ER3: Catalano-Aragonesa; ER4: Litoral Mediterránea: ER5: Extremadurense; ER6: Manchega; ER7: Bética. Solid lines are naturally regenerated forests and dashed lines are planted forests. Minimum crown cover in the eastern US was 10% whereas in continental Spain it was 40%. Fig. S5 shows the same unimodal pattern using alternative crown cover thresholds.

functions and their services. Across two contrasting forests in regions with different biogeographical histories, management regimes, and abiotic factors, our study identified a humped-back pattern between aboveground biomass and species richness. This pattern exhibited an initial increase in species richness up to an optimum value with increasing aboveground biomass and then turning into a tendency to decrease. This pattern is evident worldwide in grasslands (Fraser et al., 2015) and in forest ecosystems at local scales (Vilà et al., 2013). However, there are also examples of a lack of unimodal patterns because of effects of the biodiversity measure used (Brun et al., 2019) and the working scale (Mittelbach et al., 2001; Zhang et al., 2011). Our study runs at a subcontinental scale where the unimodal pattern for species richness was common but the mechanisms behind this response differed.

In both regions, the AGB is a proxy for net primary productivity (Fraser et al., 2015; Mittelbach et al., 2001) with the increasing part of the curve reflecting the amount of energy captured by the system and transformed into dry matter following the energy-diversity theory (Currie and Paquin, 1987) whereas competition is stronger at higher productivity levels leading to competitive exclusion (Rajaniemi, 2003) and decreasing the number of species. The unimodal response based on energy availability was first proposed by O'Brien (1998) where water availability increases the number of species and available energy

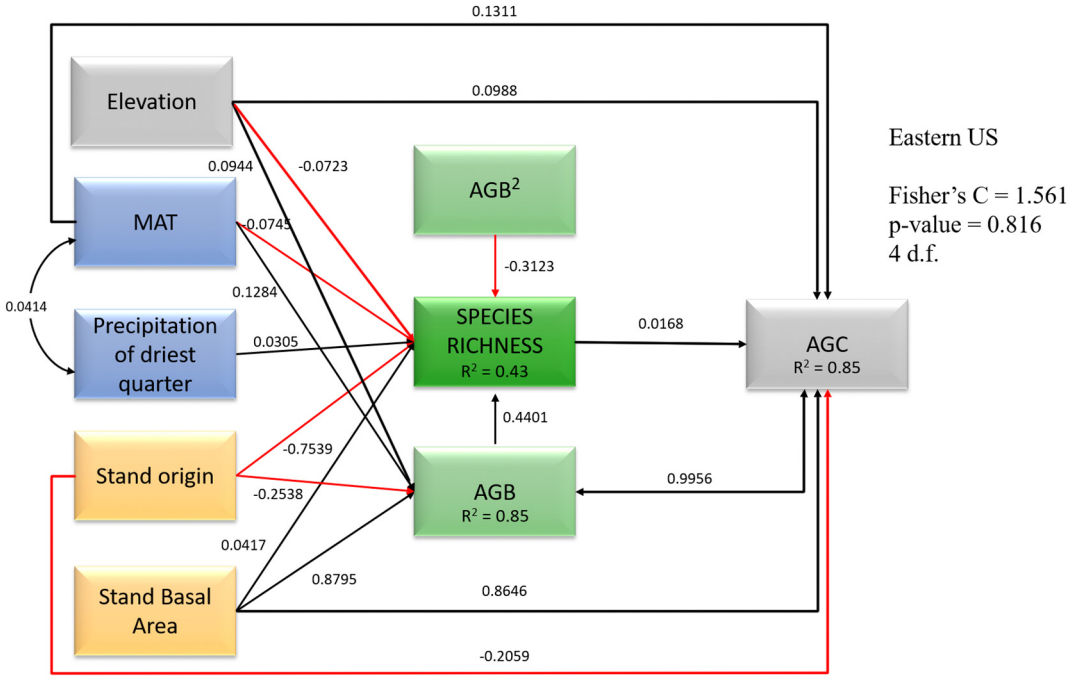

Fig. 3. Structural equation model of aboveground carbon predicted by species richness, abiotic factors and management regime. MAT: Mean annual temperature, AGB and AGB^2: aboveground biomass and quadratic term, AGC Aboveground carbon. Black lines are positive effects; red lines indicate negative effect. Effect value over or close to the paths. Missing paths are not significant. Curved paths are correlations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

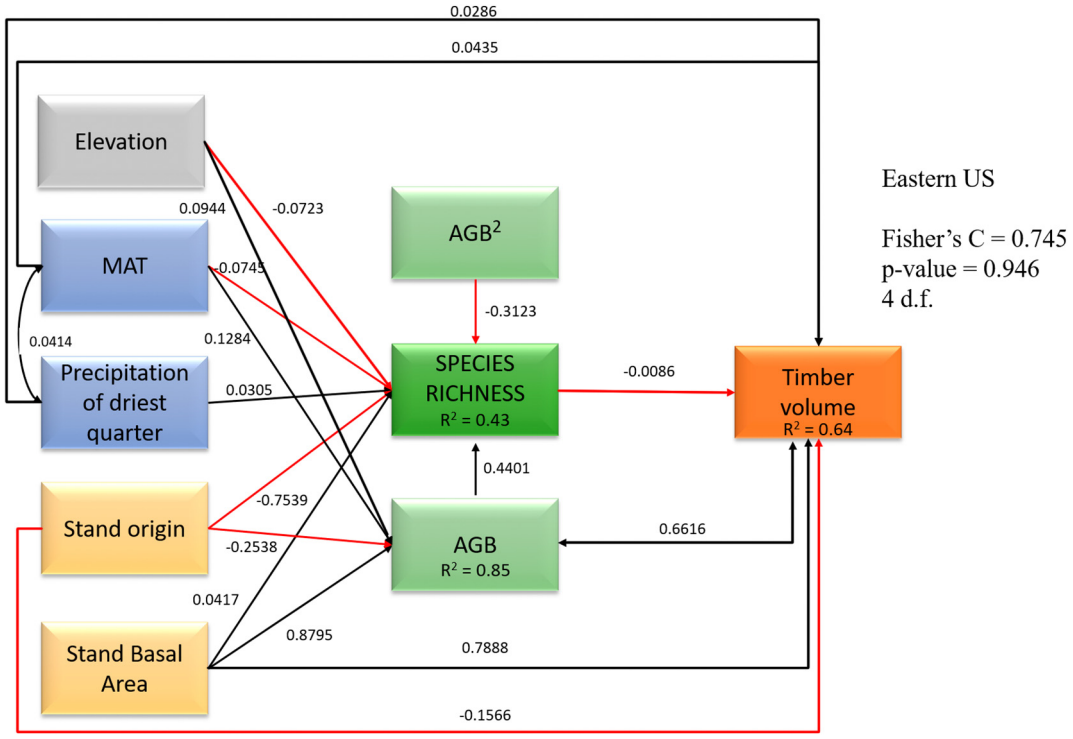

Fig. 4. Structural equation model for quality timber volume (net volume) in eastern US as a function of species richness, abiotic factors and management regime. MAT: Mean annual temperature, AGB and AGB^2: aboveground biomass and quadratic term, AGC: Aboveground carbon. Black lines are positive effects; red lines indicate negative effect. Effect value over or close to the paths. Missing paths are not significant. Curved paths are correlations. Minimum crown cover limit is 10% and mean is 80.5%. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

is responsible for the humped-back pattern. This mechanism seems to partially operate in the eastern US where precipitation of the driest quarter (BIO17) had a positive influence on species richness. However, higher mean annual temperature (BIO1) had a negative impact on the number of species. Temperature is associated with high energy levels and high productivity, that corresponds to the peak of the humped-back relationship between species richness and productivity. Wang et al., 2009 found positive effects of temperature on species richness in the U.S. and China, whereas Liu et al. (2019) demonstrated that increased temperature hampered species richness recovery in Chinese

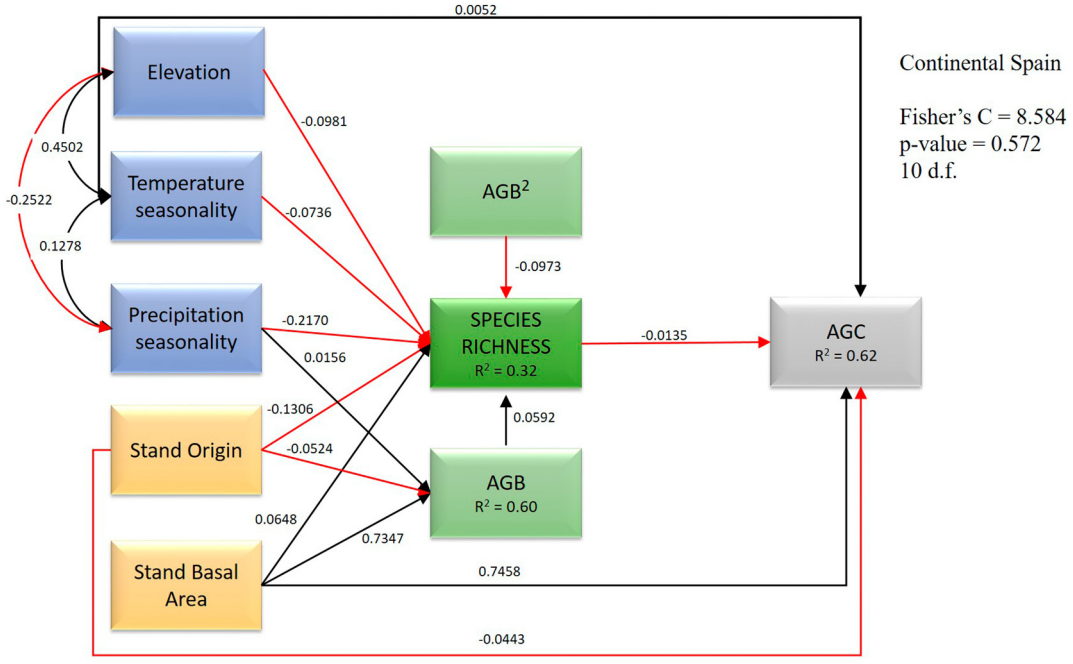

Fig. 5. Structural equation model of aboveground carbon as a function of species richness, abiotic factors and management regime in continental Spain. AGB and AGB^2: aboveground biomass and quadratic term, AGC_ Aboveground carbon. Black lines are positive effects; red lines indicate negative effect. Effect value over or close to the paths. Missing paths are not significant. Double-arrowed paths are correlations. Minimum crown cover is 40% and 66.7%, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

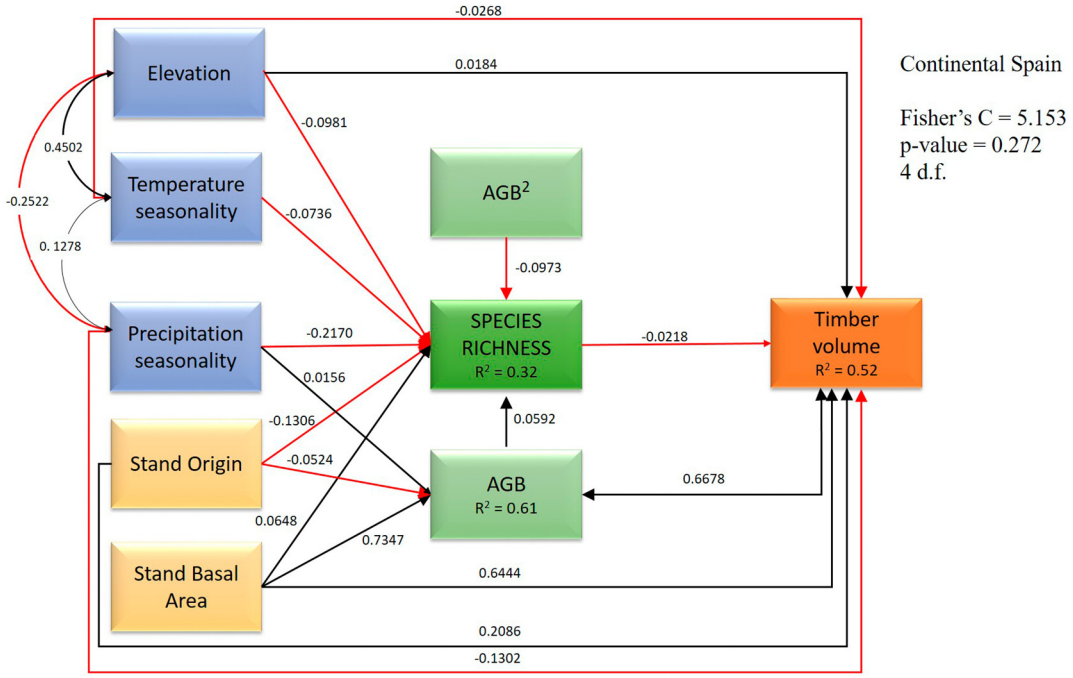

Fig. 6. Structural equation model of quality timber volume as a function of species richness, abiotic factors and management regime in continental Spain. AGB and AGB^2: aboveground biomass and quadratic term, AGC: Aboveground carbon. Black lines are positive effects while red lines indicate negative effects. Effect values are indicated over or close to the paths. Missing paths are not significant. Minimum and mean crown cover are 40% and 66.7%, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

secondary forests. In Australian rainforest and eucalyptus stands, temperature had a complex positive effect on species richness but it was dependent on precipitation and topographic effects (Austin et al., 1996). Globally, species richness response to temperature alone is not conclusive and it should be analyzed along with water availability (Pausas and Austins, 2001).

In continental Spain we did not find positive effects of mean climate metrics on species richness, rather it is climatic variability which decreased the number of species. Both precipitation seasonality (BIO12) which is associated with long drought periods (Ricklefs and He, 2016) and temperature seasonality (BIO4), which exacerbates drought effects through increased heating, reduced species richness. Whereas climatic stability leads to more species through specialization and smaller niche width (Currie, 1991; Huggett, 2004) a higher level of weather variability might compromise tree species richness in continental Spain.

Both regions exhibited a negative causal effect of elevation on species richness. This effect is stronger in continental Spain, probably because altitudinal gradient is 50% higher. Increasing elevation reduces species richness through decreasing energy or available area for species, although other patterns have been also described. Nogués-Bravo et al. (2008) demonstrated that the scale of gradients may change the relationship from negative to unimodal. Our study is not performed along pure gradients as plots are deployed in forest areas using systematic grids. However, National Forest Inventory data cover a broad spectrum of forested elevation classes from sea level to high altitude (0–1753 m in US and 0–2448 m in Spain). The representation of plots in particular elevation classes suggests that plots located at high elevations, more than 1000 m in US and 1500 m in Spain, are low compared to plots at lower elevations (2.2% in US and 5.4% in Spain). The median of species richness also decreased in these plots compared to lower elevation plots (2 vs. 4 species in the continental Spain that might indicate a species area effect, whereas the species response with elevation has an optimum in continental Spain (Fig. S3). The inconsistent relationship of elevation with species richness in the eastern US is a good example of the importance of integrative approaches in disentangling causal relationships (Grace et al., 2016).

The global negative effect of stand origin on species richness is a result of human homogenization of forest stands. Plantations of a single species for production is common in both regions for timber production with native single-species and exotic fast-growing species. Plantations may play a role to produce timber in the near future as 50% of timber is expected to be obtained from them (Kanninen, 2010). Although the majority of timber plantations are single-species, studies have showed that planting more than one species might enhance the performance of plantations in terms of timber production due to complementary use of resources (Forrester et al., 2017) or facilitation through improvement of the growing conditions by adding N-fixing species (Forrester et al., 2006) not to mention potential resilience to future global change. There may be two main concerns preventing forest managers and owners from increasing the abundance of mixed-species plantations for timber production. First, the reduction of area for production of industrial timber and second the lower quality of timber associated with mixtures (Pretzsch and Rais, 2016; Zeller et al., 2017). The integrative approach used in this study exhibited a negative path between species richness and high-quality timber production in both regions. However, stand origin can modify the sign of this effect. In both regions species-rich plantations have a positive effect on timber volume as evidenced by a positive indirect effect of stand origin on timber volume mediated by species richness. However, in the eastern US we found a strong negative direct effect of plantations on timber volume production, probably due to the prevalence of monocultures across timberland areas. The potential compensation of increasing species richness and/or changing the species used in plantations to mitigate the negative effect of plantations in timber volume production is outside the scope of this work.

In the case of continental Spain, the total effect of plantations on timber production was positive due to a strong direct effect; however, it is noticeable that plantations with several species also increased timber volume in accordance with other studies in the tropics (Amazonas et al., 2018; Petit and Montagnini, 2006) and boreal plantations (Kabzems et al., 2016). This can have an impact on the current plantation forestry paradigm as plantations of highly productive single-species can move towards mixed-species plantations potentially

without losing timber production while gaining resilience to climate change through risk-spreading (Pawson et al., 2013).

Our results illustrated how climate and management can affect the trade-offs between two important ecosystem services at a subcontinental scale: aboveground carbon (or aboveground biomass) stocks and timber production. Often timber and biomass production have been used vaguely and interchangeably leading to positive effects of species richness. However, although all species contribute to biomass production and carbon sequestration not all species contribute to timber production, at least in the case of eastern US. On the contrary, species richness did not have positive direct effect on AGC and timber volume in continental Spain, opening the question if other diversity measures like functional diversity or species identity are more important than species richness to explain AGC and timber volume. Ziter et al., (2013) found that functional diversity in unmanaged forest patches had a positive relationship with total aboveground carbon whereas management reduced the role of functional diversity. Evidence also suggests that long-term positive effect on carbon sequestration of mixed-species plantations can be increased by using the native regional pool of species (Cunningham et al., 2015; Rodríguez-Loinaz et al., 2013) whereas species-identity effect can modulate processes and patterns like overyielding (Steckel et al., 2019). Of particular note, natural forests need as much as double the number of species to reach the same amount of aboveground biomass in the eastern US (e.g., in the CAPP region only 4 species are needed to reach 250 Mg/ha of AGB in planted forests whereas 9 species are needed in natural forests). Such a difference is lower in the continental Spain region where 1 or 2 species more are needed in natural forests to reach the same aboveground biomass than in plantations. Further studies should incorporate more detailed information to provide sound management guidelines in order to minimize the trade-off between biomass and timber quality production.

One significant warning in our work is the computational hurdle in the structural model approach that we found in the case of the continental Spain dataset. Although both national forest inventories defined forested plots with the same crown cover threshold, i.e. 10%, the difference in the distribution of plots along crown cover classes is large. In the Spanish national forest inventory plots with less than 40% of crown cover amounts to 21.1% whereas in the FIA dataset it is 7.6%. The FIA dataset had a larger percentage (65.9%) of well stocked stands with a crown cover over 80% than the SNFI where the percentage was 23.2%. When crown cover is included as a predictor convergence is not reached in both datasets. AGC in sparse stands may be controlled by an abundance of a few tree species (McNicol et al., 2018) or large-sized trees that can result in non-significant SR-AGC relationship mediated by stand structure (Mensah et al., 2020). The integrative analyses of aboveground carbon and timber volume should be performed with caution in datasets with a significant number of understocked plots where mechanisms in the SR-AGC relationship may differ.

Overall, divergences between the pathways of aboveground carbon stocks and timber production via direct and indirect effects of species richness coupled with stand and site variables (such as climate) suggest new paradigms of ecosystem management may be needed in the face of global change. As this study builds upon robust datasets covering divergent and extensive forest ecosystems, it is inherently rooted in past climate conditions. In a future of increasing temperatures and associated episodic precipitation we can hypothesize that the abundance of unique species available to managers for delivery of critical forest ecosystem services (clean water, bioenergy feedstocks, or construction materials) may dwindle.

The emergence of forest ecosystem resilience concepts and associated adaptive management practices requires a fundamental understanding of how various tree species combine with changing climatic attributes to drive the provisioning of an array of diverse ecosystem services. Although we found confirmation of a hump-backed pattern of increasing above-ground tree biomass and increasing species richness across distinct biogeographical regions, it is the divergence of this influence on the production of merchantable volume and above ground carbon stocks, in combination with a host of climatic and stand attributes, which suggests every distinct ecosystem service may have a unique pathway of achieving its maximum provisioning. Our results suggest that detailed examination of separate ecosystem services (e.g. AGC versus timer volume) across different biogeographical regions may lead the way to unraveling such dynamics.

CRediT authorship contribution statement

ABO and CW conceived and conducted the study and did the first draft. DK and IA contributed with GIS information and helped with SNFI data handling. All authors reviewed and commented on the original manuscript and the revised version.

Declaration of competing interest

The authors declare no competing interests.

Acknowledgments

Andrés Bravo-Oviedo acknowledges the receipt of a fellowship from the OECD Co-operative Research Programme: Biological Resource Management for Sustainable Agricultural Systems in 2019. The U.S. Department of Agriculture, Forest Service International Programs and Research and Development facilitated his research visit. A.B.O and I.A. thanks to E. Robla and V. Sandoval of the Spanish Ministry of Ecological Transition for kindly providing access to the full SNFI data-sets and to the field teams of TRAGSATEC.

Data availability

Raw data from the US national forest inventories is available via Institutional data retrieving systems and upon request. Raw data from the Spanish national forest inventory is likewise available via institutional data retrieving systems but authors are not authorized to share the downloaded data to third parties.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.148399.

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