



Linkage of forest productivity to tree diversity under two different bioclimatic regimes in Italy

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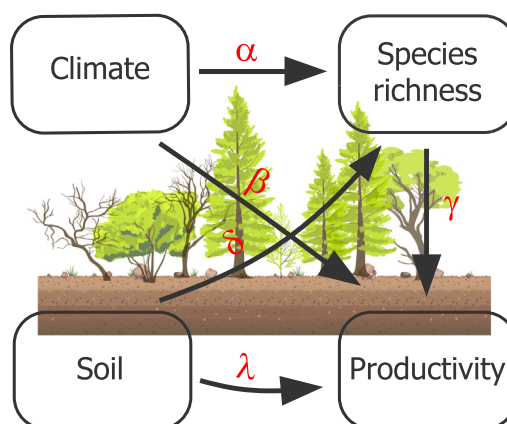
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HIGHLIGHTS

- Positive relationship between forest productivity and tree species richness
- Distinct relationships between bioclimatic domains exist.
- Predominant effect of biodiversity and climate on productivity in Mediterranean forests
- Variability associated with species richness greater than variability due to climate
- Tree diversity enhances the resistance of ecosystem to climate in the Mediterranean region.

GRAPHICAL ABSTRACT



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ABSTRACT

We analyzed the Italian National Forest Inventory data set to evaluate the interdependence of forest productivity, tree species richness (used to indicate biodiversity), climate, and soil factors. We tested the hypotheses that the relationship between biodiversity and forest productivity is positive and significant for all forests in Italy and whether the relationship is the same for forests growing in the temperate and Mediterranean bioclimatic domains (regions) of Italy. We used generalized additive models to explore the univariate response curves for the data and then performed structural equation modeling (SEM) and multi-group SEM analyses to evaluate the relationship between biodiversity and productivity. We found that the SEM model for the entire dataset explained about 60% of the variation in forest productivity. In addition, the variation associated with species richness was greater than variation due to climatic factors and the variation in climate factors was greater than the variation in soil factors (all relative to their contributions to productivity). The multi-group SEM showed a more predominant effect of biodiversity and climate on productivity in Mediterranean compared to temperate forests. In both cases, we observed a moderate effect of soil (factors) on forest productivity. Our results support the hypothesis that increasing tree diversity in forests could help reduce the effects of climate warming and enhance ecosystem productivity in the Mediterranean region.

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1. Introduction

A number of factors influence forest ecosystem functions, including local climatic conditions, soil fertility, biodiversity, and applied management practices. Understanding how these factors interact is challenging, particularly in a warming climate. However, an understanding of these interactions is needed to manage forests that provide ecosystem services, such as carbon uptake, water and nutrient cycling, soil protection, and commercial forestry products (e.g., timber and pulp) (D'Amato et al., 2011; Pilli and Pase, 2018).

Biodiversity has long been considered to be as an important component of ecosystem functioning (e.g. Pretzsch, 2005; Loreau, 1998). In fact, the effect of biodiversity on forest ecosystem functions and productivity has been the subject of numerous studies (Pretzsch et al., 2015; Paquette and Messier, 2011; Jucker et al., 2016; Poorter et al., 2017), all of which indicate that biodiversity is positively related to forest productivity. For instance, in a broad meta-analysis of 54 forest ecosystem studies, Zhang et al. (2012) found higher productivity in forests of mixed stands than in pure stands. Similarly, in a global survey on terrestrial biomes, Liang et al. (2016) documented a positive relationship between biodiversity and productivity, warning that in the face of climate change, widespread loss of forest biodiversity may undermine crucial forest functions, impair ecosystem processes, and promote a decline of forest productivity and economic losses at regional and global scales. The effect of biodiversity on ecosystem productivity has been interpreted as the consequence of several functional mechanisms, including competitive exclusion (Warren et al., 2009), niche complementarity (Loreau and Hector, 2001; Cardinale et al., 2007, 2012), species facilitation (Hooper et al., 2005), and resistance against pathogens (Latz et al., 2012). In addition, Leuschner et al. (2009) argued that high longevity of trees, complex forest structure, and environmental factors, particularly for forest growing in harsh climate environments, could confound our understanding of the biodiversity-productivity relationship.

Overall both theoretical and empirical evidence suggested that climate and soils influence aboveground biomass in natural forests either directly or indirectly via tree species richness and/or stand structural complexity. In a broad study of temperate and boreal forests in Eastern Canada, Paquette and Messier (2011) showed that biodiversity in stressful boreal environments may be more important in driving forest productivity (mostly via complementarity effects, i.e. beneficial interactions between species) than under more stable temperate conditions, where competitive exclusion is likely to be the dominant ecological mechanism driving productivity. Jucker et al. (2016) reported a relationship between productivity and species richness, which they found shifts from being largely positive at sites characterized by strong climatic constraints to being weakly negative at sites where climatic conditions are not limiting. Yet, results from structurally complex hyper-diverse tropical forests demonstrated that biomass stocks and dynamics are under strong (independent) control of forest attributes, including species diversity and community-weighted mean traits, more than environmental conditions (mainly soil fertility and water availability) (e.g., Poorter et al., 2017; Ali et al., 2019).

Environmental conditions experienced by forests are rapidly changing due to climate warming and the structure, diversity, and functioning of forest communities are expected to be impacted by intensifying droughts (Boisvenue and Running, 2006; IPCC, 2014). Therefore, climate warming could affect forest productivity through direct impacts on ecosystem processes and indirectly via changes in tree species composition (Clark et al., 2016). For example, in the Mediterranean region, selective effects on forest communities due to tree mortality may increase substantially with rising temperatures and more frequent and intense droughts (Allen et al., 2010; Gazol et al., 2018). Some drought effects could be somewhat alleviated by changing forest management practices. For example, a promising practice for improving forest resilience is to create more diversified forest stands with silvicultural

treatments (Spiecker, 2003; Metz et al., 2016). However, the relationship between biodiversity and productivity has not been extensively tested in forests growing under the drought-stressed conditions that prevail in Mediterranean regions. Therefore, to manage forests in this region better, data are needed to understand the importance of biodiversity on forest productivity and carbon sequestration.

Forest survey data sets can be used to explore the types and magnitudes of the relationships among various forest attributes (e.g., productivity) and environmental conditions, to assess how such relationships change over time, and as an essential support for spatial modeling (Nabuurs et al., 2003; Marchi and Ducci, 2018). In this study, we use data from the most recent Italian National Forest Inventory (NFI) to determine the inter-relationships among forest productivity, biodiversity, climate, and soil conditions. We use generalized additive models and structural equation modeling to test whether there is a positive relationship between biodiversity and productivity throughout Italy, which spans the temperate and Mediterranean macroclimates (Pesaresi et al., 2017). We asked the following question, is forest stand diversity more important in the harsher Mediterranean climate or in the more-moderate temperate climate? That is, we challenged the hypothesis that there is a stronger relationship between biodiversity and productivity in forests in more drought-stressed climatic regions.

2. Methods

2.1. Study area and forests

Our study area extends throughout Italy, from 35°29' N to 47°04' N and from 6°37' E to 18°31' E (total area is about 301,000 km²). Climate is highly variable throughout the study area; it is affected by latitude, topography, and coastal-inland gradients, ranging from warm Mediterranean to temperate cold climatic regimes (sensu Pesaresi et al., 2017). Forests cover >35% of the total land area, with >50% located in the Mediterranean region. The most commonly occurring forests are oak (evergreen and deciduous types), beech, mountain pine, Mediterranean pine, silver fir and Norway spruce (Pignatti, 1998).

2.2. Forest inventory data

We used geo-referenced data from the most-recent Italian National Forest Inventory (NFI) (<https://www.inventarioforestale.org/>). A detailed description of the NFI dataset, and procedures used to construct it is provided by Gasparini and Tabacchi (2011) and Tabacchi et al. (2011). The data set consist of 7272 forest plots sampled throughout the Italian peninsula. A suite of important forest characteristics was measured or estimated in each plot. For our purposes, we filtered out temporary un-stocked forest areas (e.g., burned areas) and forest tree plantations, leaving 6925 plots that we separated into two groups based on the bioclimatic classification of Pesaresi et al. (2017). One group consisted of forest plots growing in the Mediterranean domain of Italy; the other group consisted of forest plots growing in the temperate domain (Fig. 1).

For each plot, we extracted the following variables: aboveground biomass of living trees (B_{live} , Mg ha⁻¹), aboveground biomass of dead trees (B_{dead} , Mg ha⁻¹), and mean annual growth increment (I_{cur} , Mg ha⁻¹y⁻¹). In addition, for each plot we calculated the number of live tree species (S_{live}), and the number of dead tree species (S_{dead}). The variability of these forest characteristics in our data set is provided in Fig. A1 in the Appendix.

2.3. Climatic and soil data

Mean annual temperature (T) and mean annual precipitation (P) were extracted from the.

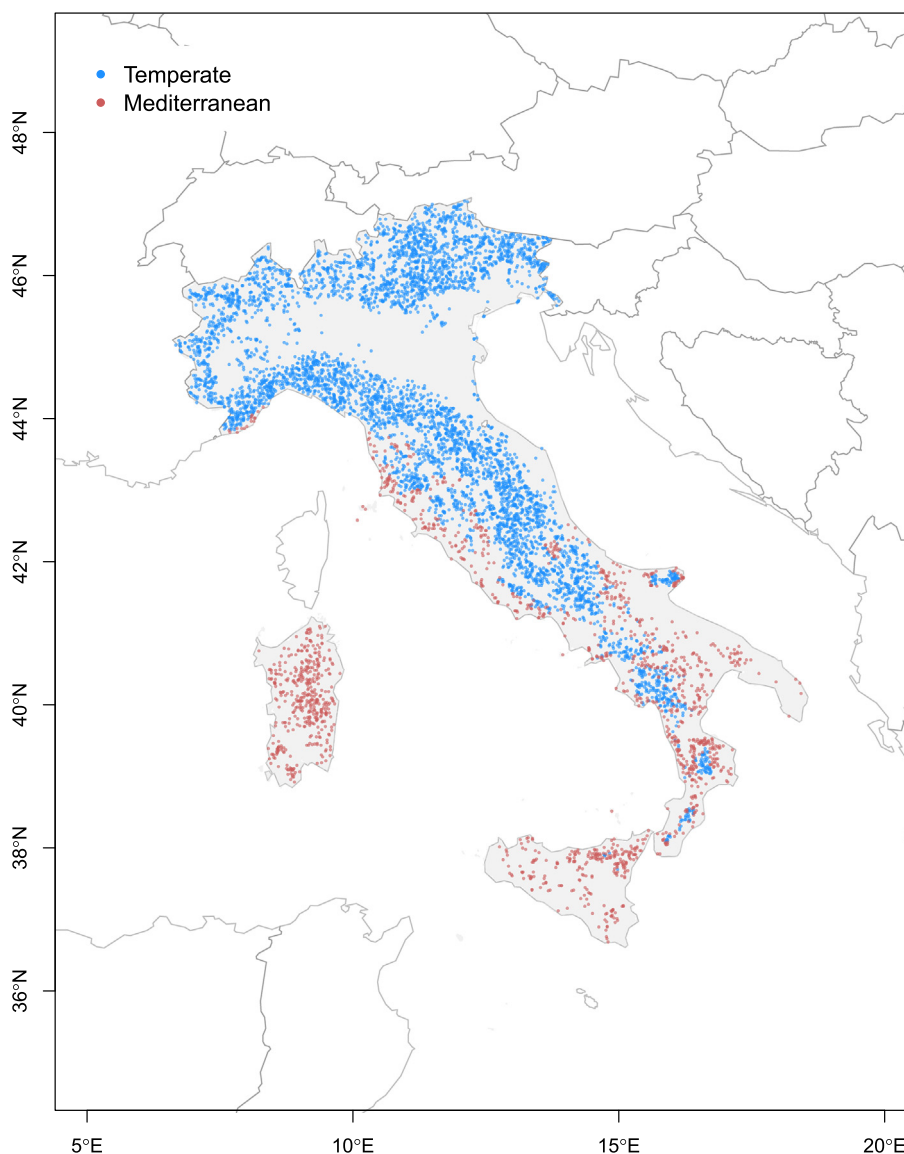


Fig. 1. Geographical distribution of NFI forest plots considered in our study, subdivided between temperate and Mediterranean bioclimatic domains, according to the classification proposed by Pesaresi et al. (2017).

WorldClim v.2 dataset (<http://www.worldclim.org/>), which provides climatic variables at a spatial resolution of approximately 1 km² for the period for 1970–2000 (Hijmans et al., 2005). Soil characteristics were obtained from the World Inventory of Soil Emission Potentials WISE30sec data set (<https://www.isric.online/>), which provides a number of soil variables at a spatial resolution of approximately 1 km² (Batjes, 2016). Among the available soil variables, we extracted soil organic carbon content (C_{soil} , g C kg⁻¹), soil water capacity (W_{soil} , cm m⁻¹), and the carbon to nitrogen ratio (C/N , unitless) in soils. For each soil variable, we computed the average of various soil layers for each pixel of the data set. Geographic coordinates of climatic and soil data were matched with NFI plot coordinates using the ‘raster’ software package available in the R statistical suite v. 3.5.0 (R Development Core Team, 2018).

2.4. Statistical analyses

We applied Generalized Additive Models (GAMs) (Hastie and Tibshirani, 1990) to the entire data set to describe the effects of predictor variables (independent of one another) on stand annual growth increment (I_{cur}) and aboveground biomass of live trees (B_{live}). For

predictor variables, we used the number of live trees (S_{live}), mean annual temperature (T), mean annual precipitation (P), soil organic carbon content (C_{soil}), soil water capacity (W_{soil}), and soil carbon to nitrogen ratio (C/N) (Details on the procedures and applied GAM model are provided in the Appendix). Multivariate relationships between forest productivity, soil factors, climatic factors, and species richness were evaluated sequentially using a structural equation modeling (SEM) approach (Bollen, 1989) [See Grace, 2006 for a review of SEM applications in ecological research.]. We introduced an additional four inferred (latent) variables to our SEM model (defined below): productivity, climate, soil, and species richness, which we used to test our hypothesis that climate, soil, and species richness affect forest productivity and that climate and soil factors affect species richness. In our SEM model, each latent variable was defined by the variables for which we had NFI data (manifest variables): (1) productivity (determined by B_{live} , B_{dead} , I_{cur}), (2) climate (determined by T and P), (3) soil (determined by C_{soil} , W_{soil} , and soil carbon to nitrogen ratio C/N), and (4) species richness (determined by S_{live} , and S_{dead}) (Table 1).

The SEM model, and the causal relationships represented by it, were based on evidence in the literature that identified various factors that might be related to forest growth and productivity [e.g., tree species

richness (Vilà et al., 2007; Liang et al., 2016), local climatic (Jucker et al., 2016), and soil nutrient availability (Huston, 1993; Laughlin et al., 2007; Warren et al., 2009; Goldberg et al., 2017)].

We initially applied structural equation modeling to the entire data set. We estimated model parameters as those that minimized a discrepancy (badness-of-fit) function between the predicted covariance matrix and the observed covariance matrix; we used a robust maximum likelihood estimator (MLR) with Huber-White standard errors and scaled statistics to estimate coefficients (White, 1982). Bias in path coefficients due to deviation from multivariate normality was addressed by estimating standardized coefficients using a nonparametric bootstrap approach (1000 replications), as suggested by Nevitt and Hancock (2001). A full information maximum likelihood (FIML) method was used for missing data (Wothke, 1998). Model fit was tested using different indexes: the root mean square error of approximation index (RMSEA; Steiger, 1990), the standardized root mean square residual (SRMR), and the comparative fit index (CFI, Bentler, 1990). RMSEA is a parsimony-corrected index that tends to favor models with fewer free parameters and greater structural complexity; Browne and Cudeck (1992) suggested RMSEA values ≤ 0.05 mean close fit, values between 0.05 and 0.08 “acceptable” fit, and values ≥ 0.1 poor model fit. SRMR is an absolute measure of fit and is essentially the average difference between the observed correlation and the model predicted correlation; Hu and Bentler (1999) suggest values of SRMR < 0.08 mean good fit. CFI is an incremental fit index that measures the relative improvement in the fit of the model over a baseline (null) model; CFI ranges between 0 and 1, and CFI values > 0.9 suggest “acceptable” model fit (Hu and Bentler, 1999). In addition to model fit testing, the significance of each pathway in the model was evaluated with Wald statistic for $p < 0.05$. Residuals and modification indices were also examined to determine if there were obvious model-data discrepancies (i.e. should a variable be dropped or a path added).

Then we split the data on forest plots into two groups, one consisting of Mediterranean forest plots and the other temperate forest plots (Fig. 1), based on the classification of Pesaresi et al. (2017). Using data from the two groups simultaneously, we performed a Multi-Group SEM analysis (MGSEM) (Kline, 2010) to evaluate the model's invariance, i.e. to assess whether factor means and parameters differed among groups. (Details on model parameters estimates, model fit, and model invariance assessment are provided in the Appendix).

All variables, with the exception of T , were \log_{10} -transformed and centered prior to analysis in order to meet the possible assumption of normality and linearity. We used the “lavaan” (Rosseel, 2012) and “semTools” (Jorgensen et al., 2018) packages to perform SEMs, both available under the R suite.

3. Results

When we examined GAM plots in regions of highest observation densities (i.e., portions of the x -axis with “thicker” lines), we found as

Table 1
Relationships between latent and manifest variables in the SEM model; the operator = ~ means “is manifested by”. B_{live} : biomass of alive trees; B_{dead} : biomass of dead trees; I_{cur} : stand current annual increment; T : mean annual temperature; P : annual precipitation; C_{soil} : soil organic carbon content; W_{soil} : soil water capacity; C/N : carbon to nitrogen ratio; S_{live} : the number of alive tree species; S_{dead} : the number of dead tree species.

Latent variable		Manifest variable
Productivity	=~	I_{cur}
Productivity	=~	B_{live}
Productivity	=~	B_{dead}
Climate	=~	P
Climate	=~	T
Soil	=~	C_{soil}
Soil	=~	C/N
Species richness	=~	S_{live}
Species richness	=~	S_{dead}

most relevant patterns: for I_{cur} and B_{live} , a positive effect by S_{live} (Fig. 2a and g), and an apparent negative effect by T (between 5 °C and 15 °C, considering uncentered data) (Fig. 3b and h). We also found no apparent effect by P (Fig. 2c and i), C_{soil} (Fig. 2d and j), W_{soil} (Fig. 2e and k), and C/N (Fig. 3f and l). (GAM statistics are reported in Table A1 and A2 of the Appendix).

Our specified SEM model for the entire data set converged, with indices indicating relatively good model fit overall (Fig. 3). All paths between productivity and other latent variables (climate, soil, and species richness) were significant, with approximately 60% of the variance in productivity explained (species richness $>$ climate factors $>$ soil factors relative to their contributions to productivity). The association between productivity and climate showed two different pathways, a direct pathway and one involving species richness; however, 18% of the species richness variability was explained by climate. We observed no significant relationship between soil factors and species richness. All manifest variables showed significant factor loading, with standardized coefficients ranging from -0.574 to 0.98 . (Unstandardized coefficients and parameter estimates are shown in Table A3 of the Appendix).

Results of the multi-group structural equation modeling (MGSEM) analysis for the Mediterranean and temperate bioclimatic domains are displayed in Fig. 4 (Unstandardized coefficients and parameter estimates are reported in Tables A5 of the Appendix). The MGSEM model converged with statistics showing a reasonable fit. The model explained 14% of the total variation in productivity for temperate forests and 36% of total variation in productivity for Mediterranean forests. In both cases, climate and species richness were significant in explaining variation in productivity; however, standardized path strengths showed weaker relationships among variables for forest productivity in the temperate climatic region than in the Mediterranean region. Particularly, we observed a dominant effect of climate and species richness on productivity in the Mediterranean region, whereas in temperate region, we observed a modest effect of soil conditions on productivity and climate on species richness (Fig. 4).

4. Discussion

4.1. The link between biodiversity and forest productivity

In this study, we analyzed the information available in the most recent Italian National Forest Inventory (NFI) to assess the relationship between forest biodiversity and productivity and the relevance of this relationship under two different bioclimatic regions relative to climatic and soil conditions.

For the entire data set, species richness showed the strongest relationship with forest productivity, as hypothesized. Climatic factors based on temperature and precipitation was also related strongly to productivity, whereas soil factors showed only a weak relationship. We have also evaluated the relationship between productivity and species richness within different sub-set categories: *i*) conifer-dominated and hardwood-dominated forests; *ii*) shade tolerant, shade intolerant and intermediate, and *iii*) species dominated forests (i.e., evergreen oaks, deciduous oaks, pine, beech and fir, and spruce dominated forests). In most cases (Fig. A3 in the Appendix) a positive productivity - species richness relationship was observed.

Overall, our results support many previous studies that have established a positive relationship between biodiversity and productivity in forests at a variety of spatial scales, ranging from regional to global scales (Vilà et al., 2013; Zhang et al., 2012; Liang et al., 2016; Liu et al., 2018). Indeed, in this study we assumed species richness (the number of live tree species and standing dead tree species) as a proxy of biodiversity. Tree species richness has been found to be positively correlated with forest structure attributes (Hakkenberg et al., 2016), and with functional indices used to describe the effects of biodiversity on ecosystem functions (Paquette and Messier, 2011). However, we are not

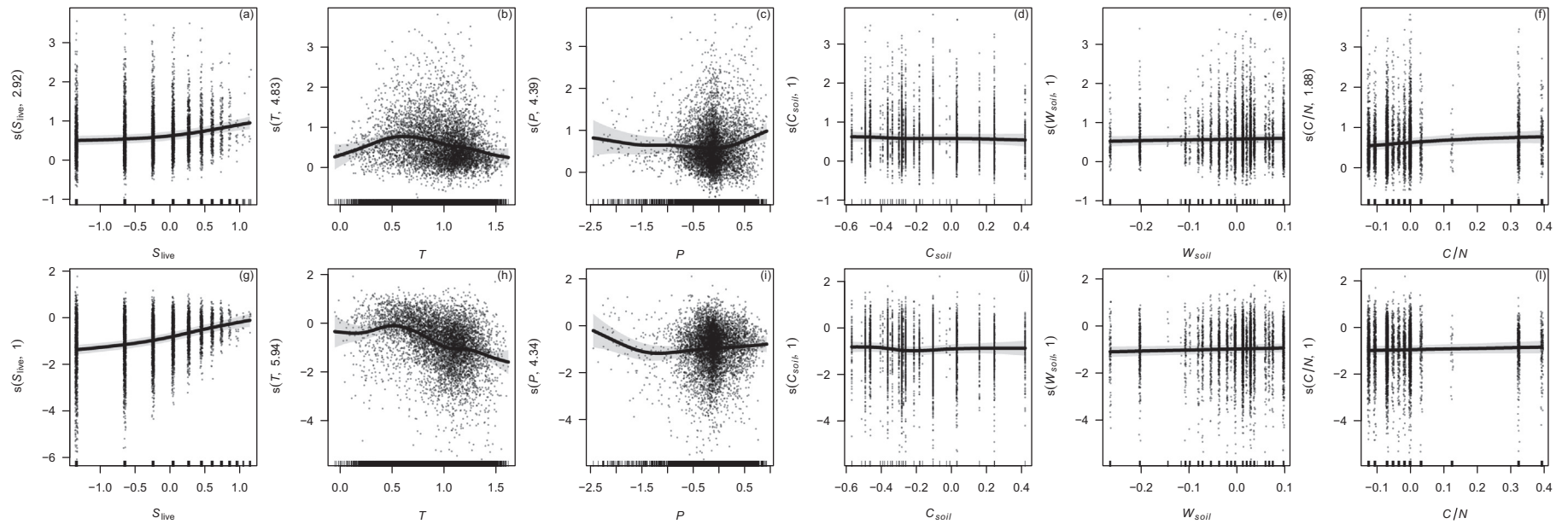


Fig. 2. Generalized Additive Model (GAM) results of predictor variables for stand current annual increment (I_{cur} , upper panels), and above ground biomass of alive trees (B_{live} , lower panels). Predictor variables were: number of alive tree species (S_{live}), mean annual temperature (T), annual precipitation (P), soil organic carbon content (C_{soil}), soil water capacity (W_{soil}), and carbon to nitrogen ratio (C/N). The y-axis values indicate x-axis covariate effects on deviation from the mean predicted by the model (continuous line). The shaded areas indicate the 95% confidence interval. The number on each y-axis caption is the effective degrees of freedom for the term plotted. The small lines along the x-axis are the “rug”, which show the observation density. The continuous line is an estimate of the smooth function of the partial residuals (thus, the y-axis is centered on zero) and indicates the x-axis covariate effects on the measured trait. In these plots, a positive slope of the continuous line shows a positive effect of the x-variable, and a negative slope of the line indicates a negative effect.

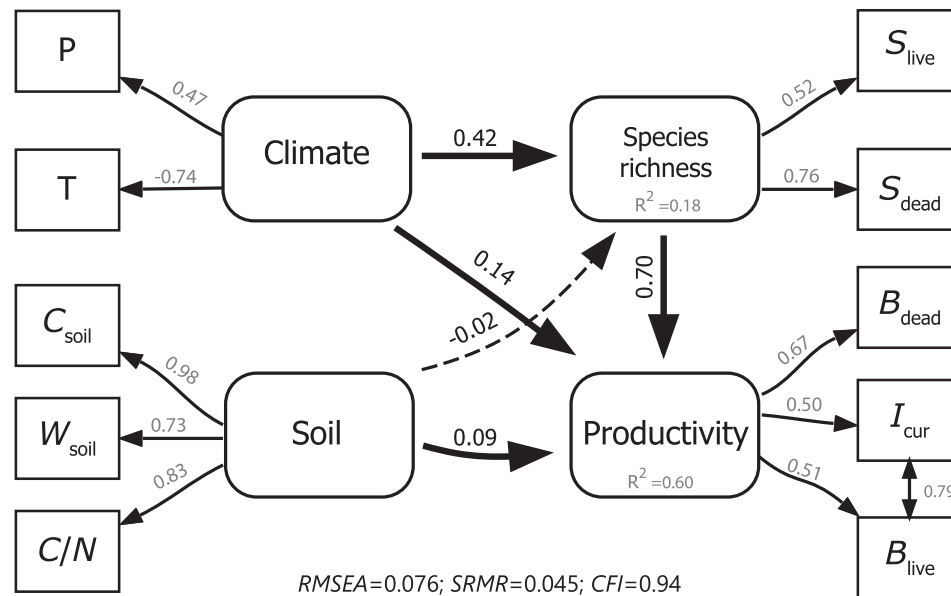


Fig. 3. Results of structural equation modeling (SEM) on the entire data set. Arrowheads lines represent causal paths and bidirectional arrowhead indicates (co)variance, with superimposed standardized partial regression coefficients: solid lines represent significant ($p < 0.05$) paths, dashed lines not significant ones. Squares represent manifest variables and rounded rectangles represent latent variables. Inside rounded rectangles, the amount of variance (R^2) explained for each dependent variable. At the bottom, model's fit indexes: RMSEA, root mean square error of approximation index; SRMR, standardized root mean square residual; CFI, comparative fit index.

certain how this assumption could have affected the relationships we observed. In part, this may depend on the mechanisms responsible for the biodiversity/productivity relationship. For example, tree species richness could reflect the likelihood that the most productive species are the ones that dominate a forest community (selection effect). Alternatively, species richness could be caused by niche partitioning and complementarity effects, wherein the coexistence of a broad variety of functional strategies among species is the main mechanism underlying the correlation between plant diversity and primary production (Cardinale et al., 2012; Morin et al., 2011). Complementary resource use between tree species may be related for instance to below-ground root complementarity or to above-ground crown complementarity allowing higher canopy packing and greater light interception in more diverse forest stands, as observed in the field experiment (Williams et al., 2017). We also argue that high tree species richness is frequently associated with forest structural heterogeneity and the development of a large number of ecological niches, both of which increase forest productivity (Poorter et al., 2017). Indeed, forest stands with high species diversity also tend to have a high stand structural complexity and hence determine aboveground biomass indirectly, indicating that forest stands with a high carbon storage potential also have a high biodiversity conservation potential (e.g., Ali et al., 2019).

Results of structural equation modeling showed that species richness strongly mediates the response of forest productivity to climate. As such, climate exerts a strong control on forests productivity and their functioning either directly, including key aspects such as nutrient and water availability affecting tree carbon storage, or indirectly via species richness, which in turn strongly influence plant communities composition, stand structure, biotic interaction and thus ecosystem functioning (Paquette and Messier, 2011; Jucker et al., 2016; Poorter et al., 2017).

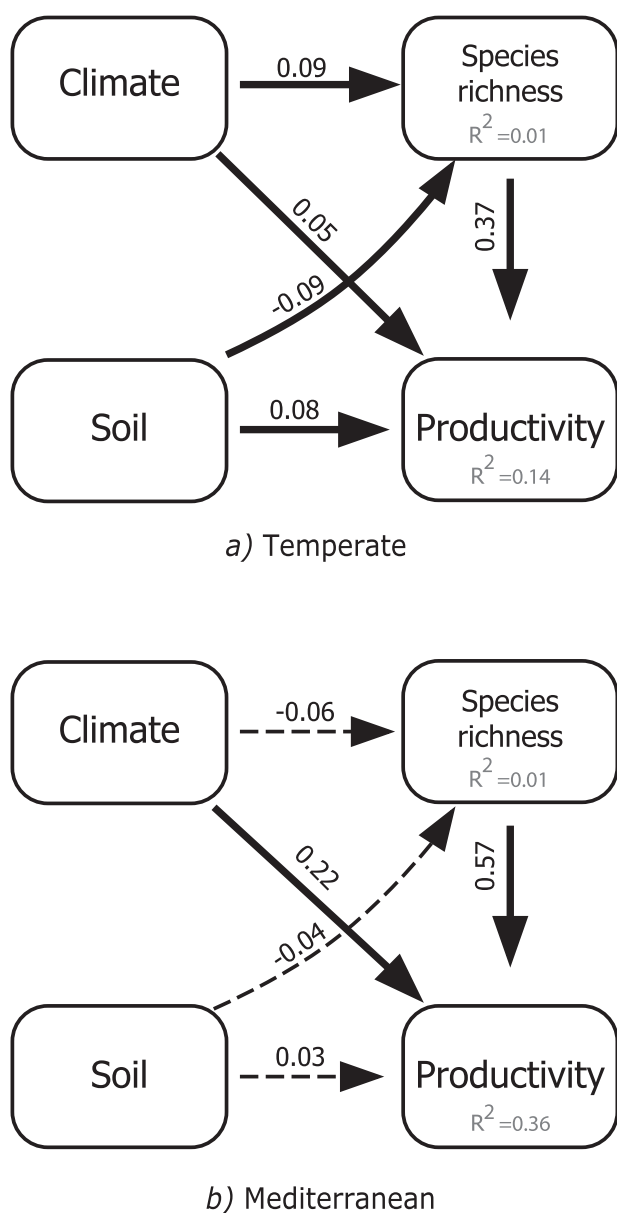
The weak relationship between soil factors and productivity is surprising because soil fertility and soil moisture are widely regarded as important in influencing forest productivity. This weak relationship can be partially explained by the poor spatial resolution (1 km^2) of our soil variable data associated with the fair approximation of the NFI geographical location. This low data resolution means that the soils data likely poorly represent conditions at the plot scale, which likely accounts for the moderate variability of our soils data (Fig. 2) and the weak relationship between soil condition and tree productivity.

Age is also an important determinant of tree growth and forest productivity (Cienciala et al., 2016; Gentilesca et al., 2018), but the NFI data set does not include data on tree age at the forest plot level. However, we did examine forest age data available at the scale of administrative districts. Based on those data, we did not find any systematic variation in forest age across the study area (Fig. A4 and A5 in the Appendix). Thus, we assumed that forest age did not strongly interact with other variables in driving forest productivity in our data set.

4.2. Differences between bioclimatic domains

In order to assess whether climatic differences modulate the effects of biodiversity on productivity, we split our data set into two groups, one representing temperate climates and the other representing Mediterranean bioclimates. We found substantial differences in the biodiversity/productivity relationship among forests growing under the more stressful Mediterranean climatic conditions than under the more stable temperate conditions. These differences are in agreement with recent studies of forests across Europe using tree ring (age) data, which demonstrate that the relationship between tree diversity and forest productivity is dependent on environmental conditions i.e., with positive relationships in the more stressful Mediterranean climatic conditions and a weaker relationship in the less stressful temperate climates (Jucker et al., 2016). This backs the common theory that the strength and direction of the diversity-productivity relationship is context dependent and affected by conditions and available resources within the encompassing environment. Indeed consistent with the prediction of the stress-gradient hypothesis (sensu Bertness and Callaway, 1994), Paquette and Messier (2011) attributed the higher biodiversity effects on productivity in boreal, compared with temperate, forests to a stronger beneficial species interaction in the more environmentally stressed boreal climates, although such a full generalization at the biome scale would require more evidence.

This result leads to important considerations for biodiversity conservation, carbon storage and forest management. Southern European environments have become harsher in recent decades (Giorgi, 2006), and we may suggest that under warmer and drier conditions, biodiversity will play a major role in driving forest productivity by promoting beneficial interactions between species and complementarity in resource



RMSEA=0.063; SRMR=0.062; CFI= 0.93

Fig. 4. Results of multi group structural equation modeling (MGSEM) for the temperate (a) and Mediterranean (b) bioclimatic domains. Arrowheads lines represent causal paths, with superimposed standardized partial regression coefficients: solid lines represent significant ($p < 0.05$) paths, dashed lines not significant ones. Inside rounded rectangles, the amount of variance (R^2) explained for each dependent variable is reported. At the bottom, model's fit indexes: RMSEA, root mean square error of approximation index; SRMR, standardized root mean square residual; CFI, comparative fit index.

used by forest trees, in accordance also with recent simulation-based studies (e.g. Morin et al., 2018). Species richness may therefore buffer ecosystem productivity against environmental change and enhance the ecosystem's resilience to disturbance particularly in dry, hot, Mediterranean climates, where an increased frequency of more severe droughts is expected to severely impair ecosystem processes (Anderegg et al., 2013; Allen et al., 2010; Gazol et al., 2018).

5. Concluding remarks

The following conclusions can be drawn from this study: (1) there is a positive relationship between biodiversity and productivity for forests

throughout Italy, thus supporting the hypothesis that tree diversity in forests is related to carbon storage, (2) under current climatic conditions, the positive biodiversity-productivity relationship in the climatically more moderate temperate regions was weaker than that observed for the climatically harsh Mediterranean regions, and (3) promoting and increasing tree diversity in forests could help reduce the negative effects of climate warming and enhance the resistance of ecosystem productivity to climate events in the Mediterranean regions.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.06.194>.

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