



Trait similarity among dominant highly-competitive species rather than diversity increases productivity in semi-arid Mediterranean forests

Ariel Isaías Ayma-Romay^{a,b,*}, Horacio E. Bown^b, Natalia Pérez-Harguindeguy^c, Lucas Enrico^c

^a Programa de Doctorado en Ciencias Silvoagropecuarias y Veterinarias, Campus Sur, Universidad de Chile, Santa Rosa 11315, La Pintana, Santiago CP 8820808, Chile

^b Facultad de Ciencias Forestales y de la Conservación de la Naturaleza, Universidad de Chile, Avenida Santa Rosa, 11315 Santiago, Chile

^c Instituto Multidisciplinario de Biología Vegetal (CONICET-UNC) and FCEfyN, Universidad Nacional de Córdoba, Vélez Sarsfield 299, Córdoba, Argentina

ARTICLE INFO

Keywords:

Productivity
Mass-ratio
Niche complementarity
Traits
Root
Phenology
Isotopes

ABSTRACT

Biodiversity plays a pivotal role in forest productivity and, through it, on the provision of ecosystem services. Consequently, understanding the mechanisms by which biodiversity drives productivity is a challenge for sustainable forest management. It has been proposed that functional dissimilarity can increase forest productivity, particularly in water-limited ecosystems (as Mediterranean forests), where water stress might increase complementarity resource use among species (hypothesis of niche complementarity). Alternatively, strongly water-limited forests may favor the dominance of woody species with slow-growth and conservative resource-use trait values, which in turn, might increase plant community productivity proportionally to their biomass (hypothesis of mass-ratio). The effects of such mechanisms on productivity is yet understudied in water-limited forests. We assessed the effect of both previously described mechanisms on productivity in a semi-arid Mediterranean-type climate matorral of Chile through a trait-based approach. We hypothesized that: (1) higher dissimilarity of functional trait values of crowns, roots and phenology among woody species increases community productivity. Alternatively, (2) higher dominance of woody species of conservative trait values increases forest productivity. We installed twenty-three 25 × 25 m plots in the matorral of the National Reserve of “Roblería de Los Cobres de Loncha” located in the Coastal Range. Forest productivity was estimated as above-ground biomass changes between 2010 and 2017. The mean species pairwise dissimilarity (MPD) and the community-weighted mean trait values (CWM) were calculated for each single trait as surrogates of the hypotheses of niche complementarity and mass-ratio, respectively. Environmental variables (e.g. altitude, slope, precipitation) were included as potential drivers influencing productivity. We performed a selection procedure of multiple linear regression models based on the Akaike Information Criterion. Our findings show that higher forest productivity was related with higher trait similarity of plant maximum height and onset of growth among species. Besides, productivity increased with CWM values that reflect greater dominance of species exhibiting acquisitive traits (i.e. greater maximum plant height, lower wood density and earlier onset of growth) rather than conservative traits. Moreover, forest productivity increased with increasing altitude, precipitation and decreasing temperatures from 300 to 900 m. Therefore, in contrast with our hypotheses, productivity increased by greater trait similarity among dominant highly-competitive species - which might be favored by mesic conditions at middle altitudes of the Coastal Range. The sustainable management of semi-arid Mediterranean forests with the main focus on productivity should promote higher dominance of highly-competitive species with similar functional trait values in mesic conditions, and conservative species with greater trait functional dissimilarity to increase drought resistance in stressful environments.

* Corresponding author at: Programa de Doctorado en Ciencias Silvoagropecuarias y Veterinarias, Campus Sur, Universidad de Chile, Santa Rosa 11315, La Pintana, Santiago CP 8820808, Chile.

E-mail addresses: ariel.isaias.aymar@gmail.com (A.I. Ayma-Romay), hborn@uchile.cl (H.E. Bown), natalia.perez.h@unc.edu.ar (N. Pérez-Harguindeguy), lenrico@unc.edu.ar (L. Enrico).

<https://doi.org/10.1016/j.foreco.2021.118969>

Received 4 October 2020; Received in revised form 20 January 2021; Accepted 21 January 2021

Available online 13 February 2021

0378-1127/© 2021 Elsevier B.V. All rights reserved.

1. Introduction

Forest productivity, defined as the rate at which woody species convert CO₂ and water into organic matter, is a key driver of ecological processes and ecosystem services, ranging from wood production to climate regulation (Chapin et al., 2002). Forest productivity is considered to be highly dependent on biodiversity components (e.g. woody species richness and composition) (Liang et al., 2016; Vilà et al., 2005). However, the ecological mechanisms by which forest biodiversity drives productivity are still debated, mainly under the hypotheses of niche complementarity (Tilman, 1997) and mass-ratio (Grime, 1998). If niche complementarity is the mechanism driving productivity, then in order to increase productivity, forest management efforts should aim at promoting both species richness and functional diversity, since both increase productivity and stability promoting multiple benefits for society (Liang et al., 2016; Paquette and Messier, 2011; Ruiz-Benito et al., 2014; Williams et al., 2017). In contrast, if mass-ratio is the key mechanism driving forest productivity through functional identity (trait values of dominant species), then in order to increase productivity, forest management should promote high dominance of species with particular trait values adapted to environmental conditions (Finegan et al., 2015; Prado-Junior et al., 2016; Tobner et al., 2016). Understanding the relative effect of these mechanisms on forest productivity is relevant for sustainable forest management in general, but also for management in the context of climate change (Mori et al., 2017). A trait-based plant functional approach might be a key tool to test the effects of niche complementarity and mass-ratio on forest productivity (Díaz et al., 2007).

The niche complementarity hypothesis predicts that higher species richness, particularly if leading to high functional trait dissimilarity among species, can increase the rates of ecological processes, by means of complementarity in the use of resources among species and, hence, spatial and/or temporal niche partitioning (Tilman, 1997). In support of this hypothesis, it has been shown that forest productivity may increase with increasing morphological dissimilarity of crowns (Williams et al., 2017), as may increase canopy vertical stratification and light efficiency interception in the understory (Ammer, 2019). Moreover, it has been suggested (but it is still untested) that forest productivity might also increase with increasing morphological dissimilarity of roots and phenology among species, since these contribute to more efficient water and nutrient use by spatial and temporal niche partitioning (Ammer, 2019; Ishii and Asano, 2010). In addition, some studies in semi-arid Mediterranean forests suggested that these expected positive effects of species richness and functional dissimilarity might tend to increase forest productivity with increasing water stress (Jucker et al., 2014; Paquette et al., 2018; Ratcliffe et al., 2016; Rita and Borghetti, 2019), since niche differentiation and facilitation among species may increase under dry conditions (Madrigal-González et al., 2016; Subedi et al., 2019).

Alternatively, the mass-ratio hypothesis proposes that each species contributes to ecosystem properties proportionally to their biomass. Thus, trait values of dominant species (species with greater relative biomass) in a plant community should be closely related to productivity (Grime, 1998). It has been shown that under water-unlimited conditions, forest productivity might increase with the abundance of dominant fast-growing tree species, exhibiting mostly acquisitive resource-use trait values - which confer higher competitive ability for resource acquisition (Grime et al., 1997), such as greater plant height (Finegan et al., 2015; Lohbeck et al., 2015; Shovon et al., 2019), higher specific leaf area (SLA), lower wood density, shallower roots (Fotis et al., 2018) and longer growth periods (Chuine, 2010). In contrast, under drier conditions forest productivity might increase with increases in the dominance of slow-growing species exhibiting mostly conservative resource-use trait values - which promote retention of resources and resistance to environmental stressors (Maracahipes et al., 2018), such as lower SLA, higher wood density (Prado-Junior et al., 2016; van der

Sande et al., 2018) and possibly deeper rooting (Jucker et al., 2014). These conservative traits would allow species improved access and conservation of soil water and nutrients, protect tissues and organs against abiotic and biotic hazards and reduce mitochondrial respiration, while enhancing carbon gain and plant survival in the longer term (Reich, 2014).

In Mediterranean-type forests, it has been proposed that niche complementarity might be a pivotal mechanism explaining productivity, as drought-stressing conditions may lead to high functional trait dissimilarity among woody species (Forrester and Bauhus, 2016; Jucker et al., 2014). In support of these ideas, previous studies show that woody species co-occurring in these ecosystems exhibit high functional dissimilarity, which suggests the existence of spatial and temporal differentiation in light and water use, thus reducing competition by limited resources (Jucker et al., 2014). For example, in Mediterranean ecosystems the differences in functional traits of crowns (e.g. plant height), roots (e.g. rooting depth) and phenology (e.g. onset of vegetative growth) among woody species may lead to greater spatial and temporal complementarity in light and soil water use (at the species level) (Canadell and Zedler, 1994; de la Riva et al., 2016; Filella and Peñuelas, 2003; Fuentes et al., 1995). However, there are still few studies explicitly testing the effects of niche complementarity on productivity in forests at the plant community level (Paquette et al., 2018; Ratcliffe et al., 2016; Ruiz-Benito et al., 2014), and even less using functional trait dissimilarities of crowns, roots and phenology among species to test such hypotheses.

Alternatively, some studies suggest that productivity in Mediterranean forests (e.g. sclerophyllous forests) increases with greater dominance of evergreen species, whose leaf functional attributes reflect a conservative resource-use strategy, while productivity decreases with greater dominance of deciduous species reflecting an acquisitive resource-use strategy (Ayma-Romay and Bown, 2019; Ruiz-Benito et al., 2014). If productivity in Mediterranean forests increases with dominant species exhibiting a conservative-resource-use strategy across different plant organs then productivity might increase in stands exhibiting trait values at the plant community level with higher leaf mass ratio (being the reciprocal of SLA), higher leaf life span (LLS), lower leaf nitrogen content (de la Riva et al., 2016), higher leaf ¹³C- isotopic composition (an indicator of water use efficiency) (Prieto et al., 2018; Querejeta et al., 2018), higher wood density and lower specific root length, smaller plant height (de la Riva et al., 2016), deeper rooting (Mooney and Dunn, 1970) and delayed onset of growth (Ackerly, 2004; Castro-Díez et al., 2003; Montenegro et al., 1979). This trait combination would confer to forests dominated by conservative species higher growth and biomass production as a result of sustaining photosynthesis over longer periods of time, fixing carbon without the energy cost of building new leaves every year and prolonging their growth periods accessing deeper soil water (Canadell and Zedler, 1994; Mooney and Dunn, 1970). In contrast, if productivity in Mediterranean forests decreases with greater dominance of species exhibiting an acquisitive resource-use strategy, then productivity might be reduced in stands with opposite trait values at the plant community level (e.g. greater SLA, lower wood density, shallower roots and earlier onset of growth) since those attributes would allow sustaining high growth but only during relatively short periods of time. However, the effect of trait values of dominant species on community level productivity integrating traits of both multiple plant organs and the whole-plant (e.g. stems and leaves combined with the morphology of crowns, roots and phenology) had been, to the best of our knowledge, scarcely addressed. Particularly, the effects of below-ground and phenology traits of dominant species on forest productivity and other ecological processes are insufficient understood (Ottaviani et al., 2020; Garnier et al., 2016).

This study aimed to assess the effects of both niche complementarity and plant dominance on the productivity of a semi-arid Chilean matorral through a plant functional approach. The effects of functional trait dissimilarity and trait values of dominant species on productivity were assessed at the plant community level integrating functional traits of

crown, stem, leaf, root and phenology. We also considered in the study environmental, soil and topographical variables, as covariates of productivity confounding the effects of niche complementarity and dominance. We tested two alternative hypotheses driving productivity in these Mediterranean forests:

- 1) Higher functional trait dissimilarity of crowns, roots and phenology among woody species increases forest productivity (hypothesis of niche complementarity).
- 2) Higher dominance of woody species with conservative resource-use traits (associated to the crown, root, stem, leaf and phenology) increases forest productivity proportionally to their biomass (hypothesis of mass-ratio).

The Chilean matorral is a typical semi-arid Mediterranean-type forest, which is considered a global biodiversity hotspot and a conservation priority due to its endemism and a high degree of biodiversity loss (Cowling et al., 1996), mainly due to land-use change and degradation of the native vegetation (Rundel et al., 2016). A better understanding of the effects of functional diversity or functional identity (trait values of dominant species) on productivity in the matorral can open opportunities for its sustainable management and ecological restoration linked with biodiversity conservation (Mori et al., 2017). Some studies in the Mediterranean Basin have substantially improved our knowledge about relationships between functional diversity and forest productivity, but using only some key above-ground plant traits of easy measurement such as plant height and SLA (as indicators of the plant resource-use strategies) (Paquette et al., 2018; Ratcliffe et al., 2016; Ruiz-Benito et al., 2014). This study extends this approach by testing explicitly the effects of niche complementarity and mass-ratio mechanisms through multiple functional resource-use-related traits of crown, leaf, stem, root and phenology on productivity. Moreover, the Chilean matorral compared with forests in other Mediterranean regions has longer dry periods and greater interannual variability (Rundel et al., 2016), which might be appropriate for assessing whether either niche complementarity or dominance of species with a conservative strategy increases productivity in water stressed communities.

2. Materials and methods

2.1. Study site

The study was set in the National Reserve “Roblería de Los Cobres de Loncha” (hereafter Loncha) (34°7'36"S, 71°11'18"OE), which is located in Alhué, Chile. Loncha was integrated into the national system of protected areas in 1996. Loncha is located in the Coastal mountain range of the central part of Chile with a prevailing west slope and elevation ranging from 400 to 2000 m. A semi-arid Mediterranean-type climate predominates in the study site with a dry and warm season (October to April) and a humid and cold season (May to September) (Rundel et al., 2016). The mean annual precipitation is 474 mm and the average annual temperature is 14.7 °C. The soils are formed from colluvial materials with soil textures ranging from sandy loam to clay loam (Bown et al., 2014).

The predominant vegetation of Loncha corresponds to the Chilean “matorral” (Rundel et al., 2016). The vegetation ranges from evergreen sclerophyllous woodlands (dominated by *Cryptocarya alba* and *Lithraea caustica*) to deciduous malacophyllous scrubs (dominated by *Acacia caven* and *Trevoa quinquenervia*). These dominant deciduous species are atmospheric nitrogen-fixers (Rundel et al. 2016). Compositional changes in the matorral are generally related to spatial variability in soil water (Bown et al., 2014) and light due to altitude (Orshan et al. 1984) and topographic variability (Armesto et al., 1994) (Table A.1), but also to human disturbances, such as fires, logging and livestock raising (Rundel et al., 2016), which reduce relative abundances of evergreen species and increase abundances of deciduous species (Armesto et al.,

1994).

2.2. Sampling plots

We installed 23 plots of 25 × 25 m distributed in a range of evergreen woodlands to deciduous scrubs (see appendices, list of woody species in Table A.2 and location of plots and species' relative abundances in Table A.3). The identity and the relative abundance of all the trees ≥5 cm of DBH (diameter at breast height) and shrubs ≥1 m of crown diameter were recorded. The plots were distributed from low to middle elevations of the Coastal mountain range in an altitudinal range from 300 to 900 m. The plots have not been disturbed by fire or firewood extraction since the creation of the reserve in 1996 (24 years ago). However, low-intensity cattle grazing is still occurring between May and October each year. The richness of woody species varied from two to seven per plot, the abundance of plants varied from 14 to 262 individuals per plot. The slopes of the plots varied from 6 to 42%. Most of the plots had either a predominant northern or southern aspect. Soil textures ranged from sandy loams to clay loams (Bown et al. 2014).

2.3. Measuring productivity, environmental variables, trait dissimilarity and trait values

We estimated forest productivity as above-ground biomass changes between 2010 and 2017. We calculated also in total 16 abiotic and biotic potential variables explaining forest productivity at the plot level (Table 1). The slope aspect was measured as a categorical variable (it not was included in Table 1), fourteen plots had a predominant northern slope and nine plots a southern slope. The mean species pairwise dissimilarity (MPD) and the community-weighted mean trait values (CWM) were calculated for key traits as surrogates of niche complementarity and mass-ratio, respectively (Table 1).

Table 1

Descriptive statistics of forest productivity, environmental conditions, trait dissimilarity and trait values calculated at the plot level for the Chilean matorral. D = dimensionless variable.

Variable	Units	# plots	Average	Min	Max
Above-ground biomass productivity	kg m ⁻² year ⁻¹	23	0.116	0.009	0.266
Environmental variables					
Altitude	m	23	529	293	910
Slope	%	23	14	6	42
Mean air annual temperature	°C	23	13.4	11.3	15.7
Annual precipitation	mm	23	601	486	804
Soil nitrogen total	%	11	0.19	0.06	0.34
Soil volumetric water content	m ³ m ⁻³	11	0.20	0.14	0.27
Mean species pairwise dissimilarity					
MPD of maximum plant height	D	23	3.6	0.6	9.1
MPD of rooting depth	D	23	2.62	1.3	4.3
MPD of onset of growth	D	23	13.6	40	125
Community-weighted mean trait values					
CWM of maximum plant height	m	23	12.0	6.9	14.9
CWM of rooting depth	m	23	3.12	1.71	5.05
CWM of specific leaf area	cm ² g ⁻¹	23	87.5	56.9	199
CWM of leaf ¹³ C- isotopic composition	‰	23	-27.17	-28.5	-26.8
CWM of wood density	g cm ⁻³	23	0.67	0.64	0.74
CWM of onset of growth*	day	23	94	71	142

* The onset of growth was expressed in days passed since the initiation of the phenological evaluation (1 July 2017).

2.3.1. Estimating forest productivity

Forest productivity was estimated as above-ground biomass changes (AGBP) (Table 1). In 11 plots the forest productivity was calculated from the above-ground biomass (AGB) changes of all trees recorded alive in 2010 (t_0) and the year 2017 (t_f), through the following equation (Prado-Junior et al., 2016):

$$AGBP = \sum_{i=1}^n (AGB_{i-f} - AGB_{i-o}) / (t_f - t_0) \quad (1)$$

where AGBP is the annual above-ground forest productivity expressed in $\text{kg m}^{-2} \text{ year}^{-1}$, AGB_{i-f} and AGB_{i-o} are the above-ground biomass of the i^{th} tree alive at the final time (t_f) and at the initial time (t_0) respectively, expressed in kg. The above-ground plant biomass (AGB_i) for most woody species was estimated with allometric equations (Table A.4). We fitted a linear model of AGBP on above-ground standing biomass (AGB) based on the 11 measured plots ($R^2_{adj} = 0.82$; Fig. A.1) and predicted productivity for the remaining 12 from its AGB (as suggested by Jenkins, 2015).

2.3.2. Environmental, topographical and soil variables

We obtained the altitude above the sea level, terrain slope, slope aspect and climatic variables (mean annual precipitation and mean air annual temperature) for the 23 plots (Table 1). Altitude of each plot was obtained with a GPS receiver (Garmin eTrex 10, USA). Topographical variables were derived from digital elevation models (SRTM -Shuttle Radar Topographic Mission), which were available for the study site with a spatial resolution of $30 \times 30 \text{ m}$ (US Geological Survey, USA, www.earthexplorer.usgs.gov). We used geospatial tools of QGIS 3.2.3 (Free Software Foundation, USA) to obtain these variables. Slope aspect for each plot was obtained in degrees and classified either as a northern or southern aspect. The climatic variables (mean annual precipitation and mean air annual temperature) were obtained from WorldClim version 2.1 with a spatial resolution of 1 km^2 (Fick and Hijmans, 2017) (Table 1). In addition, soil properties, such as volumetric water content and nitrogen content were obtained from previous studies for 11 plots (Bown et al., 2014). The volumetric water content was taken as the average (0–10 cm) in the winter and spring of 2009 and summer and autumn of 2010. The total soil nitrogen was obtained for each plot at 0–30 cm in soil depth in the year 2012 (Table 1).

2.3.3. Functional traits

We measured six key functional traits of crown, leaf, stem, root and phenology related to productivity (Table 2) for twelve plant woody species including dominants, co-dominant and rare species- which accounted for 95–100% of the total abundance of woody plants in the plots (see mean trait values for 12 species in appendix B, Table B1).

Maximum plant height (H_{max}) was the vertical distance between the crown tip and the ground level, expressed in meters. The H_{max} for each species was obtained averaging the plant height of the five tallest individuals (Pérez-Harguindeguy et al., 2013) that were present in the forestry inventory along 15 representative $25 \times 25 \text{ m}$ plots.

Rooting depth (RD) by species was obtained by measuring roots

extracted in agricultural fields, observing roots in road cuts close to Loncha and reviewing previous studies (Giliberto and Estay, 1978; Kraus et al., 2003; Specht, 1988 and references therein). The rooting depth was obtained for the eight most common dominant species, representing at least 80% of the total abundances across the plots. For each species, rooting depth was obtained on two to 17 individuals per species (Appendix B, Table B1).

Functional traits of stem and leaf were measured in neighboring trees to sampling plots according to standardized protocols (Pérez-Harguindeguy et al., 2013) (Appendix B, Table B1). Wood density was obtained as the oven-dry mass divided by the green volume of a stem section. We obtained wood density on 6–21 plants per species. For each plant, one stem section, from 5 to 10 cm in diameter by 10 cm in length was collected. These sections were collected at 30 cm above the ground in shrubs and 1.6 m above ground in trees. The stem sections were stored in plastic bags for 48 h approximately and then immersed in water for 48 h. Then, the fresh volume of the stem section with bark was obtained by water volume displacement. The samples were oven-dried at $70 \text{ }^\circ\text{C}$ for 72 h and their dry mass recorded (Pérez-Harguindeguy et al., 2013).

Specific leaf area (SLA) was obtained as the leaf area of a fresh leaf (soaked from 12 to 48 h), divided by its oven-dry mass (at $70 \text{ }^\circ\text{C}$ for 72 h). SLA was obtained from leaves from 6 to 19 mature plants per species. For each plant, ten fully expanded leaves (without petiole) exposed at the north were collected from three layers of the crown (bottom, middle, top). In the case of plants with composed leaves, the raquis was excluded from the measurements (Pérez-Harguindeguy et al., 2013). The foliar area was obtained through image analyses using ImageJ (version IJ1.46r; National Institutes of Health, Bethesda, MD, USA).

Leaf ^{13}C - isotopic composition ($\delta^{13}\text{C}_{\text{leaf}}$) for each species was obtained averaging the values from ten leaves from six to thirty mature plants per species (Appendix B, Table B1). This trait is related positively to water use efficiency and higher values (less negative) might reflect a conservative water-use strategy of the plant species (Querejeta et al., 2018). Leaves were collected from dominant woody species in the spring of 2014 and spring of 2016. The leaves were oven-dried at $70 \text{ }^\circ\text{C}$ for 72 h, stored and then analyzed by mass spectrometry in the Stable Isotope Laboratory of the University of Idaho in 2014 and the Laboratory of Suelo-Agua-Planta of the Facultad de Agronomía of the Universidad de Chile in 2016 through similar procedures (Pérez-Harguindeguy et al., 2013). Values from both years were averaged for each species.

Onset of growth for each species was obtained by monitoring the elongation of shoots of 78 plants (on two to ten plants per species covering in total twelve species) (Appendix B, Table B1). The monitoring was carried out during one growing season from July 2017 to June 2018, with a frequency between 15 and 30 days, according to methods proposed by Montenegro et al. (1979). We obtained the onset of growth averaging trait values among plants for each species. The onset of growth was expressed in days passed since the date of initiation of phenological evaluation (1 July 2017).

Table 2
Morphological, physiological and phenological functional traits related to forest productivity.

Trait	Acronyms	Units	Plant function	References
Maximum plant height	H_{max}	m	Light interception, competitive ability	Poorter et al. (2012)
Rooting depth	RD	m	Water acquisition.	Canadell and Zedler (1994); Fotis et al. (2018)
Specific leaf area	SLA	$\text{cm}^2 \text{ g}^{-1}$	Light capture efficiency, net assimilation rate, relative growth rate, leaf life span,	Reich (2014)
Leaf ^{13}C - isotopic composition	$\delta^{13}\text{C}_{\text{leaf}}$	‰	photosynthetic capacity.	Farquhar et al. (1989); Querejeta et al. (2018)
Wood density	WD	g cm^{-3}	Intrinsic water use efficiency (WUE _i)	Chave et al. (2009)
Onset of growth	OG	day	Hydraulic conductivity, resistance against cavitation, stem growth rate, light demanding.	Chuine (2010); Montenegro et al. (1979)
			Time for intense water and nutrients acquisition	

2.3.4. Functional diversity

The community-weighted mean (CWM) and the mean species pairwise dissimilarity (MPD) were calculated as surrogates of the mass-ratio and the niche complementarity hypothesis, respectively (Díaz et al., 2007).

The CWM is a metric closely linked to the mass-ratio, which was calculated through the following equation (Garnier et al., 2004):

$$\text{CWM} = \sum_{i=1}^S r_i^* p_i \quad (2)$$

Where, S = number of species in the community; r_i = value of the functional trait of the i^{th} species; p_i = relative abundance of the i^{th} species, calculated as the relative above-ground biomass of each species in the community.

The MPD measures the expected distance between two randomly chosen species without replacement. Their computation consists in calculating the average distances among all the species pairs according to the values of a single trait (as in this study) or multiple traits, being weighted by the relative abundances of the species in a community (de Bello et al., 2016):

$$\text{MPD} = \sum_{ij} d_{ij}^* p_i^* p_j \quad (3)$$

where S is the species richness in a community, d_{ij} is the trait dissimilarity between each pair of different species i and j ; and p_i and p_j are the relative abundances of species i and j , respectively. The relative abundances for each species were calculated as their relative above-ground dry biomass.

The MPD is a key metric to measure ecological mechanisms related to plant co-existence (Clarke and Warwick, 1999). For example, niche complementarity and facilitation mechanisms can be inferred from patterns of functional trait differences between species. In this case, MPD is conceptually relevant, as it reflects only the differences between species at the community level (de Bello et al., 2016).

The MPD using multiple traits was not considered in this study because the relative weight of each variable was *a priori* unknown (Cadotte et al., 2011). Moreover, differences in single traits might explain different niche axes driving productivity (Butterfield and Suding, 2013; Spasojevic and Suding, 2012), which was relevant in our study.

2.4. Data analysis

We performed a selection procedure of multiple linear regression models based on the Akaike Information Criterion for small samples (AICc) (Burnham et al., 2011). The response variable was above-ground biomass productivity (AGBP). The AGBP was log-transformed in all cases to control for homoscedasticity and normality. The variables were standardized by their mean and standard deviation, thus obtaining standardized regression coefficients (β) in order to evaluate their relative importance in the models. Preliminary, we carried out correlation analyses in order to assess the strength of the linear relationships between pairs of variables. In this analyses, multiple testing computing to adjust the level of significance of p -values was carried-out with Bonferroni's method (Table A.5, Table A.6, Fig. A.2-A.4). Subsequently, a maximum model of multiple linear regression explaining AGBP was performed combining environmental variables (altitude, terrain slope, slope aspect), trait dissimilarity (MPD of H_{max} , MPD of rooting depth and MPD of growth onset) and community-weighted mean traits values (CWM of H_{max} , CWM of $\delta^{13}\text{C}_{\text{leaf}}$, CWM of rooting depth). In this maximum model, independent variables that might be well represented by other potential predictors were excluded, in order to reduce over-parameterization and collinearity (Zuur et al., 2010). Specifically, we excluded climatic variables and soil properties of the maximum model as they were well represented by altitude (all these variables showed high correlation among them, $r > 0.7$) (Table A.6). Besides, we excluded

CWM of wood density, CWM of SLA and CWM of growth onset as were represented by CWM of H_{max} (all these variables had high correlation among them, $r > 0.85$) (Table A.6, Fig. A.4).

This maximum model was used to generate automatically multiple linear regression models with all possible combinations of the nine potential n predictors (in this case $2^n = 512$ models) (Grueber et al., 2011). The strength of evidence for each model explaining AGBP was evaluated and ranked from best to worst with the AICc. The best models had the smallest values of AICc. To deal with uncertainty for selecting the best model explaining AGBP, we obtained a final model following a model averaging approach with the best subset of models having a delta AICc < 4 with respect to the best model as cut-off criterion (Burnham et al., 2011). We verified the collinearity of the predictors in the best subset of models using as criterion the variance inflation factor ($\text{VIF} < 10$) (Dormann et al., 2013). We noted that all VIF values in the models were lower than five, suggesting that collinearity among predictor variables included in the final models did not strongly affect the result. The natural method was used for making a model averaging procedure, which calculates a weighted average for the parameter estimates in each model (Symonds and Moussalli, 2011). The statistical analysis was performed in the R Project program version 3.6.3 (R Core Team, 2020). The MPD variables were computed in the package "vegan" (Oksanen and Guillaume-Blanchet, 2019) using "taxondive" (suggested by de Bello et al., 2016) and the CWM variables in the "FD" package (Laliberte and Legendre, 2010). The multi-inference analysis based on the AICc was performed with the MuMIn package (Bartón, 2020).

3. Results

The above-ground biomass productivity (AGBP) in the Chilean matorral had an average of $0.116 \text{ kg.m}^{-2}.\text{year}^{-1}$ (standard deviation ± 0.08) and ranged from 0.09 to $0.266 \text{ kg.m}^{-2} \text{ year}^{-1}$. Contrary to the hypothesis of niche complementarity, the final averaged model showed that AGBP decreased with increasing MPD of H_{max} ($\beta = -0.31$; $P = 0.004$) and MPD of growth onset ($\beta = -0.43$; $P = 0.003$). Moreover, AGBP was not influenced by the dissimilarity of roots, as the MPD of rooting depth was a poor predictor of AGBP ($\beta = -0.04$; $P = 0.67$) (Fig. 1, Table A.7). Therefore, AGBP decreased with increasing trait dissimilarity of crowns and phenology among species at the plant community level. Besides, the final averaged model showed that AGBP increased with increasing CWM of maximum plant height ($\beta = 0.53$; $P < 0.001$) and with decreasing CWM of rooting depth ($\beta = -0.36$; $P = 0.002$). The CWM of $\delta^{13}\text{C}_{\text{leaf}}$ was included in the averaged final model, but it had no significant effect on AGBP (Table A.7). The CWM of SLA, CWM of wood density and CWM of growth onset were not included in the maximum model and model averaging in order to avoid collinearity and over-parameterization in the model selection procedure. However, as these CWM variables correlated strongly and negatively with CWM of H_{max} (Table A.5–6, Fig. A.4) we suggest that AGBP increased also with lower CWM of SLA, wood density and growth onset. Therefore, AGBP might increase with greater dominance species exhibiting mostly acquisitive-trait values, such as greater plant height, shallower roots, lower wood density and earlier growth onset, combined with conservative leaves. Such trait values might increase their competitive ability for resource use. In contrast, AGBP might decrease with greater dominance of species exhibiting an opposite combination of traits that increase drought resistance. The final averaged model showed also that AGBP increased significantly with increasing altitude ($\beta = 0.23$; $P = 0.005$) from 300 to 910 m (Fig. 1). AGBP was not significantly influenced by the differences in slope aspects (north or south) ($P = 0.08$) or the terrain slopes ($P = 0.26$). This suggests that AGBP increased with higher altitude, and with associated climatic conditions, such as greater annual precipitation and lower air temperature (see Table A.5-A.6, Fig. A.2). The size of the effects of the environmental variables was smaller than the effect of CWM and MPD variables (Fig. 1).

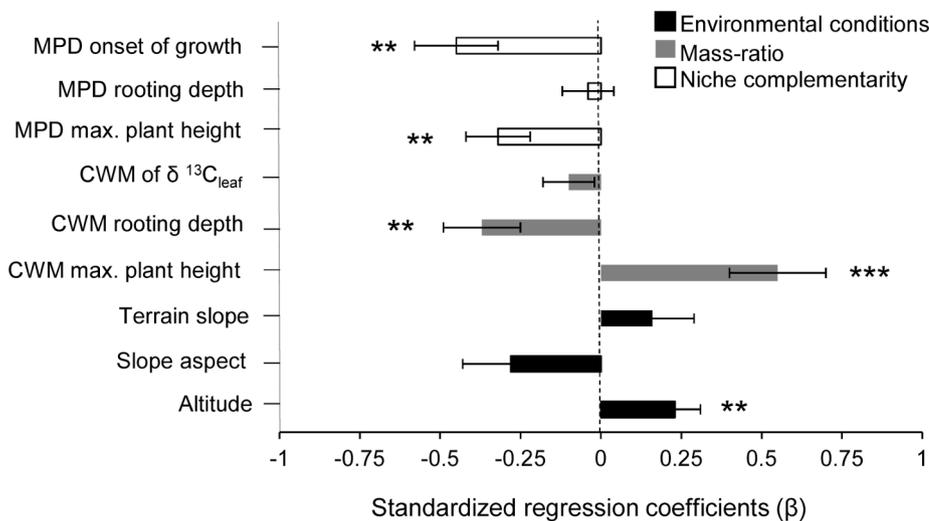


Fig. 1. Effect of trait dissimilarity (MPD parameters), mass-ratio (CWM parameters) and environmental conditions on above-ground biomass productivity in the Chilean matorral. The partial coefficients were standardized (β). Levels of significance are given as: $P < 0.001$ (***); $P < 0.01$ (**), $P < 0.05$ (*). The bars also show the averaged standard error. These variables were selected in the final model through a model averaging procedure using the ten best models of a total of 512 that had a significant effect on AGBP (Table A.7).

4. Discussion

In contrast with our hypotheses, and with results from studies from the Mediterranean Basin (Madrigal-González et al., 2016; Ruiz-Benito et al., 2014), above-ground biomass productivity (AGBP) in the Chilean matorral was not controlled by niche complementarity (greater trait dissimilarity) or by the dominance of woody species with conservative trait values. We found that AGBP increased with greater trait similarity and dominance of species exhibiting mostly acquisitive resource-use traits that might contribute to a high competitive ability for resource use in less stressful conditions (Maracahipes et al., 2018; Grime, 2001). Moreover, AGBP increased with increasing altitude, and with mesic conditions which are present at middle altitudes of the Coastal Range (Rundel, 1982). However, the size of the effects of environmental variables on AGBP was smaller than those effects of dominance.

4.1. Trait similarity rather than functional trait dissimilarity increases above-ground biomass productivity

Functional trait similarity of dominant species was the mechanism most likely to increase above-ground biomass forest productivity. This finding contrasts with studies conducted in the Mediterranean Basin, where a positive relationship between above-ground functional trait dissimilarity and forest productivity was consistently found (Paquette et al., 2018; Ratcliffe et al., 2016; Ruiz-Benito et al., 2014). However, our results agree with those from other Neotropical forests, where dominant species driving productivity also had high functional similarity (at least for above-ground traits) (Conti and Díaz, 2013; Finegan et al., 2015; Prado-Junior et al., 2016). We believe that the negative relationship between trait dissimilarity and productivity might be explained by the underlying community assembly ecological processes, which depend not only on historical processes but also on environmental conditions (Li et al., 2018). On the one hand, forests with higher productivity might exhibit high trait similarity, as a consequence of high biotic filtering occurring in environments with greater water soil availability and poor light availability in the understory (Zhang et al., 2019). For instance, in the matorral high biotic filtering might occur at middle altitudes of the Coastal Range, where there is greater soil water availability, higher annual precipitation and lower air temperatures in summer (Miller, 1981, and references therein). These environmental conditions might promote greater dominance of highly-competitive species demanding light and soil resources (Holmgren et al., 2000), which exclude shade-intolerant species (Armesto et al., 1994), and reduce functional trait dissimilarity among species (Zhang et al., 2019). On the other hand, forests with lower productivity might be related to

higher trait dissimilarity, as strong niche partitioning and facilitation among species might be occurring in highly stressed environments (Spasojevic and Suding, 2012). For instance, in the Chilean matorral, greater niche partitioning and facilitation can occur at lower altitudes of the Coastal Range, where there are higher air temperatures, lower soil water content and lower precipitation (Miller, 1981, and references therein). Under these environmental conditions, greater phenology niche partitioning might occur under high below-ground competition by soil water availability, while facilitation might be occurring among species with different plant height or crown morphology under high radiative stress (Chesson et al., 2004).

4.2. Above-ground biomass productivity increases by trait values of highly-competitive dominant species

Alternatively, our analysis showed that above-ground biomass forest productivity (AGBP) was driven mainly by mean trait values of dominant species (the mass-ratio mechanism), which means that species contributed to forest productivity proportionally to their biomass (Grime, 1998). Mass-ratio was the key mechanism increasing AGBP since niche complementarity did not increase AGBP (see negative MPD-AGBP relationships) and CWM values explained AGBP better than environmental variables. This result supports and extends the findings in tropical, Mediterranean and temperate forests, where dominant tree species controlled productivity through their functional attributes (Finegan et al., 2015; Hao et al., 2020; Paquette and Messier, 2011; Ruiz-Benito et al., 2014; van der Sande et al., 2018).

However, unlike what we proposed in our second hypothesis and previous studies in the Mediterranean Basin of Spain (Ruiz-Benito et al., 2014) and semi-arid tropical forests (Prado-Junior et al., 2016), these dominant species that increased above-ground biomass productivity (AGBP) exhibited mainly acquisitive trait values that would contribute to higher competitive ability (Grime, 2001) - which allow plants to take advantage in sites or periods of high water availability (Carvajal et al., 2019; Mooney and Dunn, 1970). For instance, AGBP increased with greater CWM of maximum plant height (associated with lower CWM of SLA, wood density and growth onset) and lesser CWM of rooting depth. This combination of CWM trait values, suggests that forest productivity increased by the dominance of species adapted to less stressful conditions (Shovon et al., 2019; Maracahipes et al., 2018) - which in our study are present at middle altitudes of the Coastal Range (Mooney and Dunn, 1970; Rundel, 1982). Such altitudes have mesic conditions with greater annual precipitation and lower temperatures in summer as well as shorter drought period (Miller, 1981). These conditions might promote species with greater above-ground growth and shallower roots to gain

greater ability for light interception (Orshan et al., 1984), as well as to reduce the root production costs and make a more early and efficient exploitation of water and nutrients, mainly available in the topsoil (Fotis et al., 2018; Schulze et al., 1996). Besides, these mesic conditions might promote the dominance of species combining lower wood density to increase their ability to transport water (Ackerly, 2004), as well as sclerophyllous leaves, lower SLA, greater leaf longevity, lower photosynthetic rates (Mooney and Dunn, 1970) and earlier onset of growth to sustain photosynthesis over longer periods and increase the growth period (Montenegro et al., 1979; Rundel, 1982).

Moreover, we found that above-ground biomass productivity (AGBP) decreased with higher dominance of species exhibiting mostly conservative trait values related to resource conservation and stress-tolerance (Castro-Díez et al., 2003; Moreno-Gutiérrez et al., 2012; Poorter et al., 2012). For instance, AGBP decreased with decreasing CWM of maximum plant height (associated with higher CWM of wood density, CWM of SLA and CWM of growth onset), and greater CWM of rooting depth. Such combination of CWM trait values suggests that above-ground biomass productivity in the matorral is reduced by dominant species adapted for sites severely limited by water and higher air temperatures (Armesto et al., 1994) - which in this study are found at low altitudes of the Coastal Range (Rundel, 1982). These drier conditions may promote the dominance of species with greater below-ground growth (smaller plant height and tap-root systems) (Ottaviani et al., 2020) which may help them to better tolerate prolonged droughts in summer and autumn (Ehleringer and Mooney, 1983). These dominant species do not always access groundwater reserves and increase the cost for root production and maintenance and therefore negatively affect the plant above-ground biomass production (Canadell and Zedler, 1994). Besides, these drier conditions might promote the dominance of species combining deciduous leaves to reduce the cost of maintaining leaves for long time periods (Mooney and Dunn, 1970), greater SLA and photosynthetic rates to allow them a fast carbon uptake during shorter favorable growth periods (rainy season) (Carvajal et al., 2019) and higher wood density to avoid embolism in dry season (Chave et al., 2009).

These findings show that productivity changes as a function of trait values of dominant species, which might be filtered through biotic competition and/or environmental stress processes (Grime, 2006) across altitudinal and environmental variations (Orshan et al., 1984). On one hand, middle altitudes of the Coastal Range, with greater soil resource availability and precipitation might favor highly-competitive species, and productivity (Holmgren et al., 2000). On the other hand, lower altitudes may be under conditions of lower soil water availability and higher temperature, which might only allow growing the drought-resistant species (Armesto et al., 1994) of low above-ground productivity, but possibly with high below-growth productivity (Canadell and Zedler, 1994).

5. Conclusions

Higher productivity in semi-arid Mediterranean forests seems to be determined by trait values of highly-competitive dominant species (supporting the hypothesis of mass-ratio), also having high trait similarity among these species (contrary to the hypothesis of niche complementarity), being this pattern promoted by mesic conditions. Matorral productivity increased as a function of mean trait values of highly-competitive dominant species, which exhibit mostly an acquisitive resource-use strategy. This trait combination at the plant community level contrasts with findings in other Mediterranean forests and tropical semi-arid forests of the world where productivity seems to be controlled by dominant species with conservative trait values. These CWM particular trait combinations extend our knowledge about the diversity of plant resource-use strategies related to productivity at the community level in semi-arid ecosystems.

The negative relationships between productivity and trait dissimilarity of crowns and phenology suggest that canopy vertical

stratification and phenology differentiation might occur in stands with low productivity. This would be possibly associated with facilitation among plants to reduce high radiative stress and temporal niche partitioning as strategy for optimizing the use of scarce soil resources in more stressing environments, which results in a greater drought-tolerance and survival in some communities of the matorral.

These highly-competitive dominant species having high functional similarity might increase, in mesic conditions, the provision of ecosystem services related to productivity, such as firewood, carbon sequestration, and climate change mitigation, while dominant conservative species having greater trait functional dissimilarity might increase drought resistance in stressful environments.

Data accessibility

Data for the analysis of dependent and independent variables at the level of the 23 plots for this paper is available in Mendeley Data (<https://doi.org/10.17632/b32rpbv8kw.1>).

CRediT authorship contribution statement

Ariel Isaías Ayma-Romay: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration. **Horacio E. Bown:** Conceptualization, Resources, Writing - review & editing, Supervision, Funding acquisition. **Natalia Pérez-Harguindeguy:** Conceptualization, Writing - review & editing. **Lucas Enrico:** Conceptualization, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank the park rangers of the National Reserve of “Roblería de Los Cobres de Loncha”, administered by CONAF (National Forestry Corporation), for their collaboration. A number of graduate and undergraduate students helped with field data collection, including María Andrea Díaz, Francisca Herrera, Diego Acevedo, Laura Galaz, Diego Peñaranda, Ariel Arzabe and Mariela Baldelomar. The authors thank their valuable assistance with field measurement. The author also wishes to thank Javier Simonetti, Aurora Gaxiola, Edmundo Acevedo, Lohengrin Cavieres, Georgina Conti, Cristián Estades, Alvaro Promis and Álvaro Gutiérrez for their advice. This work was supported by the CONICYT (Comisión Nacional de Investigación Científica y Tecnológica) [Fondecyt No 1150877]; CONICET and SECYT (Universidad Nacional de Córdoba). The authors also greatly appreciate the constructive suggestions of two anonymous reviewers in a previous version of this article.

Appendices A and B. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.118969>.

References

- Ackerly, D., 2004. Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecol. Monogr.* 74, 25–44. <https://doi.org/10.1890/03-4022>.
- Ammer, C., 2019. Diversity and forest productivity in a changing climate. *New Phytol.* 221, 50–66. <https://doi.org/10.1111/nph.15263>.
- Armesto, J., Vidiella, P., Jiménez, H., 1994. Evaluating causes and mechanisms of succession in the mediterranean region in Chile and California. In: Arroyo, M.T., Zedler, P.H., Fox, M. (Eds.), *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia*. Springer - Verlag, New York, USA, pp. 418–434.

- Ayma-Romay, A.I., Bown, H.E., 2019. Biomass and dominance of conservative species drive above-ground biomass productivity in a mediterranean-type forest of Chile. *For. Ecosyst.* 6, 47. <https://doi.org/10.1186/s40663-019-0205-z>.
- Bartón, K., 2020. MuMIn: multi-model inference.
- Bown, H.E., Fuentes, J.P., Perez-Quezada, J.F., Franck, N., 2014. Soil respiration across a disturbance gradient in sclerophyllous ecosystems in Central Chile. *Cienc. e Investig. Agrar.* 41, 89–106. <https://doi.org/10.4067/S0718-16202014000100009>.
- Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* 65, 23–35. <https://doi.org/10.1007/s00265-010-1029-6>.
- Butterfield, B.J., Suding, K.N., 2013. Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. *J. Ecol.* 101, 9–17. <https://doi.org/10.1111/1365-2745.12013>.
- Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* 48, 1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>.
- Canadell, J., Zedler, P., 1994. Underground structures of woody plants in Mediterranean ecosystems of Australia, California and Chile. In: Arroyo, M.K., Zedler, P., Fox, M. (Eds.), *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia*. Springer - Verlag, New York, pp. 177–210.
- Carvajal, D.E., Loayza, A.P., Rios, R.S., Delpiano, C.A., Squeo, F.A., 2019. A hyper-arid environment shapes an inverse pattern of the fast–slow plant economics spectrum for above-, but not below-ground resource acquisition strategies. *J. Ecol.* 107, 1079–1092. <https://doi.org/10.1111/1365-2745.13092>.
- Castro-Díez, P., Montserrat-Martí, G., Cornelissen, J.H.C., 2003. Trade-Offs between phenology, relative growth rate, life form and seed mass among 22 Mediterranean woody species. *Plant Ecol.* 166, 117–129. <https://doi.org/10.1023/A:1023209230303>.
- Chapin, F.S.I., Matson, P.A., Vitousek, P.M., 2002. *Principles of Terrestrial Ecosystem Ecology*, second ed. Springer - Verlag, New York, USA. doi: 10.1007/b97397.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. *Ecol. Lett.* 12, 351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>.
- Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., Sher, A., Novoplansky, A., Wetzlin, J.F., 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141, 236–253. <https://doi.org/10.1007/s00442-004-1551-1>.
- Chuine, I., 2010. Why does phenology drive species distribution? *Philos. Trans. R. Soc. B Biol. Sci.* 365, 3149–3160. <https://doi.org/10.1098/rstb.2010.0142>.
- Clarke, K.R., Warwick, R.M., 1999. The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. *Mar. Ecol. Prog. Ser.* 184, 21–29.
- Conti, G., Díaz, S., 2013. Plant functional diversity and carbon storage - an empirical test in semi-arid forest ecosystems. *J. Ecol.* 101, 18–28. <https://doi.org/10.1111/1365-2745.12012>.
- Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K., Arianoutsou, M., 1996. Plant diversity in mediterranean-climate regions. *Tree* 11, 362–366.
- de Bello, F., Carmona, C.P., Lepš, J., Szava-Kovats, R., Pärtel, M., 2016. Functional diversity through the mean trait dissimilarity: resolving shortcomings with existing paradigms and algorithms. *Oecologia* 180, 933–940. <https://doi.org/10.1007/s00442-016-3546-0>.
- de la Riva, E.G., Tosto, A., Pérez-Ramos, I.M., Navarro-Fernández, C.M., Olmo, M., Anten, N.P.R., Marañón, T., Villar, R., 2016. A plant economics spectrum in Mediterranean forests along environmental gradients: is there coordination among leaf, stem and root traits? *J. Veg. Sci.* 27, 187–199. <https://doi.org/10.1111/jvs.12341>.
- Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., Robson, T.M., 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proc. Natl. Acad. Sci.* 104, 20684–20689. <https://doi.org/10.1073/pnas.0704716104>.
- Dormann, D., Carsten, F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carr, G., Garc, J.R., Gruber, B., Lafourcade, B., Leit, P., Tamara, M., McClean, C., Osborne, P.E., Der, B.S., Skidmore, A., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>.
- Ehleringer, J., Mooney, H.A., 1983. Productivity of desert and Mediterranean-climate plants. In: Lange, O.L. (Ed.), *Physiological Plant Ecology IV*. Springer - Verlag, New York, pp. 205–226.
- Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 40, 503–537. <https://doi.org/10.1146/annurev.pp.40.060189.002443>.
- Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37, 4302–4315. <https://doi.org/10.1002/joc.5086>.
- Filella, I., Peñuelas, J., 2003. Partitioning of water and nitrogen in co-occurring Mediterranean woody shrub species of different evolutionary history. *Oecologia* 137, 51–61. <https://doi.org/10.1007/s00442-003-1333-1>.
- Finegan, B., Peña-Claros, M., de Oliveira, A., Ascarrunz, N., Bret-Harte, M.S., Carreño-Rocabado, G., Casanoves, F., Díaz, S., Eguiguren-Velepucha, P., Fernandez, F., Licona, J.C., Lorenzo, L., Salgado-Negret, B., Vaz, M., Poorter, L., 2015. Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *J. Ecol.* 103, 191–201. <https://doi.org/10.1111/1365-2745.12346>.
- Forrester, D.I., Bauhus, J., 2016. A Review of Processes Behind Diversity—Productivity Relationships in Forests. *Curr. For. Reports* 2, 45–61. <https://doi.org/10.1007/s40725-016-0031-2>.
- Fotis, A.T., Murphy, S.J., Ricart, R.D., Krishnadas, M., Whitacre, J., Wenzel, J.W., Queenborough, S.A., Comita, L.S., 2018. Above-ground biomass is driven by mass-ratio effects and stand structural attributes in a temperate deciduous forest. *J. Ecol.* 106, 561–570. <https://doi.org/10.1111/1365-2745.12847>.
- Fuentes, E.R., Montenegro, G., Rundel, P.W., Arroyo, M.T.K., Ginocchio, R., Jaksic, F.M., 1995. Functional Approaches to Biodiversity in the Mediterranean-Type Ecosystems of Central Chile. In: Davis, G.W., Richardson, D.M. (Eds.), *Mediterranean-Type Ecosystems: The Function of Biodiversity*. Springer, Berlin Heidelberg, Berlin, Heidelberg, pp. 185–232. https://doi.org/10.1007/978-3-642-78881-9_4.
- Garnier, E., Cortez, J., Billès, G., Navas, M.L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.P., 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85, 2630–2637. <https://doi.org/10.1890/03-0799>.
- Garnier, E., Navas, M.L., Grigulis, K., 2016. *Plant functional diversity*. Oxford University Press, Oxford, UK.
- Gilberto, J., Estay, H., 1978. Water stress in some Chilean shrubs. *Bot. Gaz.* 139, 236–240. <https://doi.org/10.1086/521238>.
- Grime, J.P., 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *J. Veg. Sci.* 17, 255–260. <https://doi.org/10.1111/j.1654-1103.2006.tb02444.x>.
- Grime, J.P., 2001. *Plant strategies, vegetation processes, and ecosystem properties*, second ed. Wiley & Sons, New York, USA.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 902–910. <https://doi.org/10.1046/j.1365-2745.1998.00306.x>.
- Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H., Hendry, G.A.F., Ashenden, T.W., Askew, A.P., Band, S.R., Booth, R.E., Bossard, C.C., Campbell, B.D., Cooper, J.E.L., Davison, A.W., Gupta, P.L., Hall, W., Hand, D.W., Hannah, M.A., Hillier, S.H., Hodgkinson, D.J., Jalili, A., Liu, Z., Mackey, J.M.L., Matthews, N., Mowforth, M.A., Neal, A.M., Reader, R.J., Reiling, K., Ross-Fraser, W., Spencer, R.E., Sutton, F., Tasker, D.E., Thorpe, P.C., Whitehouse, J., 1997. Integrated Screening Validates Primary Axes of Specialisation in Plants. *Oikos* 79, 259. <https://doi.org/10.2307/3546011>.
- Grueter, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* 24, 699–711. <https://doi.org/10.1111/j.1420-9101.2010.02210.x>.
- Hao, M., Messier, C., Geng, Y., Zhang, C., Zhao, X., Gadow, K. Von, 2020. Functional traits influence biomass and productivity through multiple mechanisms in a temperate secondary forest. *Eur. J. For. Res.*
- Holmgren, M., Segura, A.M., Fuentes, E.R., 2000. Limiting mechanisms in the regeneration of the Chilean matorral. Experiments on seedling establishment in burned and cleared mesic sites. *Plant Ecol.* 147, 49–57.
- Ishii, H., Asano, S., 2010. The role of crown architecture, leaf phenology and photosynthetic activity in promoting complementary use of light among coexisting species in temperate forests. *Ecol. Res.* 25, 715–722. <https://doi.org/10.1007/s11284-009-0668-4>.
- Jenkins, D.G., 2015. Estimating ecological production from biomass. *Ecosphere* 6, 1–31. <https://doi.org/10.1890/ES14-00409.1>.
- Jucker, T., Bouriaud, O., Avacaritei, D., Dániel, I., Duduman, G., Valladares, F., Coomes, D.A., 2014. Competition for light and water play contrasting roles in driving diversity-productivity relationships in Iberian forests. *J. Ecol.* 102, 1202–1213. <https://doi.org/10.1111/1365-2745.12276>.
- Kraus, T.A., Bianco, C.A., Weberling, F., 2003. Root system morphology of Fabaceae species from central Argentina. *Wulfenia* 10, 61–72.
- Laliberte, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits A distance-based framework for measuring from multiple traits functional diversity. *Ecology* 91, 299–305. <https://doi.org/10.1890/08-2244.1>.
- Li, Y., Shipley, B., Price, J.N., de Dantas, V.L., Tamme, R., Westoby, M., Siefert, A., Schamp, B.S., Spasojevic, M.J., Jung, V., Laughlin, D.C., Richardson, S.J., Bagousse-Pinguet, Y., Le, Schöb, C., Gazol, A., Prentice, H.C., Gross, N., Overton, J., Cianciaruso, M.V., Louault, F., Kamiyama, C., Nakashizuka, T., Hikosaka, K., Sasaki, T., Katabuchi, M., Frenette Dussault, C., Gaucherand, S., Chen, N., Vandewalle, M., Batalha, M.A., 2018. Habitat filtering determines the functional niche occupancy of plant communities worldwide. *J. Ecol.* 106, 1001–1009. <https://doi.org/10.1111/1365-2745.12802>.
- Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.-D., McGuire, A.D., Bozzato, F., Pretzsch, H., De-Miguel, S., Paquette, A., Herault, B., Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabuurs, G.-J., Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J. V., Chen, H.Y.H., Lei, X., Schelhaas, M.-J., Lu, H., Gianelle, D., Parfenova, E.L., Salas, C., Lee, E., Lee, B., Kim, H.S., Bruehlheide, H., Coomes, D.A., Piotta, D., Sunderland, T., Schmid, B., Gourlet-Flegry, S., Sonke, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto, C., Frizzera, L., Ba azy, R., Oleksyn, J., Zawi a-Nied wiecki, T., Bouriaud, O., Bussotti, F., Finer, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L., Gonmadje, C., Marthy, W., O'Brien, T., Martin, E.H., Marshall, A.R., Rovero, F., Bitariho, R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N.L., Ferreira, L. V., Odeke, D.E., Vasquez, R.M., Lewis, S.L., Reich, P.B., 2016. Positive biodiversity-productivity relationship predominant in global forests. *Science* 80, 354 aaf8957. doi: 10.1126/science.aaf8957.

- Lohbeck, M.L., Poorter, L., Martínez-Ramos, M., Bongers, F., 2015. Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology* 96, 1242–1252.
- Madrigal-González, J., Ruiz-Benito, P., Ratcliffe, S., Calatayud, J., Kändler, G., Lehtonen, A., Dahlgren, J., Wirth, C., Zavala, M.A., 2016. Complementarity effects on tree growth are contingent on tree size and climatic conditions across Europe. *Sci. Rep.* 6, 32233. <https://doi.org/10.1038/srep32233>.
- Maracahipes, L., Carlucci, M.B., Lenza, E., Marimon, B.S., Marimon, B.H., Guimarães, F. A.G., Cianciaruso, M.V., 2018. How to live in contrasting habitats? Acquisitive and conservative strategies emerge at inter- and intraspecific levels in savanna and forest woody plants. *Perspect. Plant Ecol. Evol. Syst.* 34, 17–25. <https://doi.org/10.1016/j.ppees.2018.07.006>.
- Miller, P.C., 1981. Resource use by chaparral and matorral. Springer-Verlag, New York, USA.
- Montenegro, G., Aljaro, M.E., Kummerow, J., 1979. Growth dynamics of Chilean matorral shrubs. *Bot. Gaz.* 140, 114–119.
- Mooney, H.A., Dunn, E.L., 1970. Convergent evolution of mediterranean-climate evergreen sclerophyllous shrubs. *Evolution (N.Y)* 24, 292–303. <https://doi.org/10.1111/j.1558-5646.1970.tb01762.x>.
- Moreno-Gutiérrez, C., Dawson, T., Nicolás, E., Querejeta, J., 2012. Isotopes reveal contrasting water use strategies among coexisting plant species in a mediterranean ecosystem. *New Phytol.* 196, 489–496. <https://doi.org/10.1111/j.1469-8137.2012.04276.x>.
- Mori, A.S., Lertzman, K.P., Gustafsson, L., 2017. Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. *J. Appl. Ecol.* 54, 12–27. <https://doi.org/10.1111/1365-2664.12669>.
- Oksanen, J., Guillaume-Blanchet, F. Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, H., Szoecs, E., Wagner, H., 2019. *Vegan: Community Ecology Package*.
- Orshan, G., Montenegro, G., Avila, G., Aljaro, M.E., Walckowiak, A., Mujica, A.M., 1984. Plant growth forms of Chilean matorral a monocharacter growth form analysis along an altitudinal transect from sea level to 2000 m a.s.l. *Bull. la Société Bot. Fr. Actual. Bot.* 131, 411–425. <https://doi.org/10.1080/01811789.1984.10826681>.
- Ottaviani, G., Molina-Venegas, R., Charles-Dominique, T., Chelli, S., Campetella, G., Canullo, R., Klimešová, J., 2020. The neglected belowground dimension of plant dominance. *Trends Ecol. Evol.* 35, 763–766. <https://doi.org/10.1016/j.tree.2020.06.006>.
- Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: From temperate to boreal forests. *Glob. Ecol. Biogeogr.* 20, 170–180. <https://doi.org/10.1111/j.1466-8238.2010.00592.x>.
- Paquette, A., Vayreda, J., Coll, L., Messier, C., Retana, J., 2018. Climate change could negate positive tree diversity effects on forest productivity: A study across five climate types in Spain and Canada. *Ecosystems* 21, 960–970. <https://doi.org/10.1007/s10021-017-0196-y>.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P., Poorter, L., Wright, I., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., Sack, L., Bonlder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* 61, 167–234. <https://doi.org/10.1071/BT12225>.
- Poorter, L., Lianes, E., Moreno-de las Heras, M., Zavala, M.A., 2012. Architecture of Iberian canopy tree species in relation to wood density, shade tolerance and climate. *Plant Ecol.* 213, 707–722. <https://doi.org/10.1007/s11258-012-0032-6>.
- Prado-Junior, J.A., Schiavini, I., Vale, V.S., Arantes, C.S., van der Sande, M.T., Lohbeck, M., Poorter, L., 2016. Conservative species drive biomass productivity in tropical dry forests. *J. Ecol.* 104, 817–827. <https://doi.org/10.1111/1365-2745.12543>.
- Prieto, I., Querejeta, J.I., Segrestin, J., Volaire, F., Roumet, C., 2018. Leaf carbon and oxygen isotopes are coordinated with the leaf economics spectrum in Mediterranean rangeland species. *Funct. Ecol.* 32, 612–625. <https://doi.org/10.1111/1365-2435.13025>.
- Querejeta, J.I., Prieto, I., Torres, P., Campoy, M., Alguacil, M.M., Roldán, A., 2018. Water-spender strategy is linked to higher leaf nutrient concentrations across plant species colonizing a dry and nutrient-poor epiphytic habitat. *Environ. Exp. Bot.* 153, 302–310. <https://doi.org/10.1016/j.envexpbot.2018.06.007>.
- R Core Team, 2020. R language and environment for statistical computing version 3. 6. 3.
- Ratcliffe, S., Liebergesell, M., Ruiz-Benito, P., Madrigal González, J., Muñoz Castañeda, J.M., Kändler, G., Lehtonen, A., Dahlgren, J., Kattge, J., Peñuelas, J., Zavala, M.A., Wirth, C., 2016. Modes of functional biodiversity control on tree productivity across the European continent. *Glob. Ecol. Biogeogr.* 25, 251–262. <https://doi.org/10.1111/geb.12406>.
- Reich, P., 2014. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *J. Ecol.* 102, 275–301. <https://doi.org/10.1111/1365-2745.12211>.
- Rita, A., Borghetti, M., 2019. Linkage of forest productivity to tree diversity under two different bioclimatic regimes in Italy. *Sci. Total Environ.* 687, 1065–1072. <https://doi.org/10.1016/j.scitotenv.2019.06.194>.
- Ruiz-Benito, P., Gómez-Aparicio, L., Paquette, A., Messier, C., Kattge, J., Zavala, M.A., 2014. Diversity increases carbon storage and tree productivity in Spanish forests. *Glob. Ecol. Biogeogr.* 23, 311–322. <https://doi.org/10.1111/geb.12126>.
- Rundel, P.W., Arroyo, M.T.K., Cowling, R.M., Keeley, J.E., Lamont, B.B., Vargas, P., 2016. Mediterranean biomes: Evolution of their vegetation, floras, and climate. *Annu. Rev. Ecol. Evol. Syst.* 47, 383–407. <https://doi.org/10.1146/annurev-ecolsys-121415-032330>.
- Rundel, P.W., 1982. Nitrogen utilization efficiencies in Mediterranean-climate shrubs of California and Chile. *Oecologia* 55, 409–413.
- Schulze, E.-D., Mooney, H.A., Sala, O., Jobbágy, E., Buchmann, N., Bauer, G., Canadell, J., Jackson, R.B., Loreti, J., Oesterheld, M., Ehleringer, J., 1996. Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. *Oecologia* 108, 503–511.
- Shovon, T.A., Rozendaal, D.M.A., Gagnon, D., Gendron, F., Vetter, M., Vanderwel, M.C., 2019. Plant communities on nitrogen-rich soil are less sensitive to soil moisture than plant communities on nitrogen-poor soil. *J. Ecol.* 1365–2745 <https://doi.org/10.1111/1365-2745.13251>.
- Spasojevic, M.J., Suding, K.N., 2012. Inferring community assembly mechanisms from functional diversity patterns: The importance of multiple assembly processes. *J. Ecol.* 100, 652–661. <https://doi.org/10.1111/j.1365-2745.2011.01945.x>.
- Specht, R.L., 1988. *Mediterranean-type Ecosystems, Tasks for vegetation science*. Springer Netherlands, Dordrecht, The Netherlands. doi: 10.1007/978-94-009-3099-5.
- Subedi, S., Ross, M.S., Sah, J.P., Redwine, J., 2019. Trait-based community assembly pattern along a forest succession gradient in a seasonally dry tropical forest. *Ecosphere* 10, 1–17. <https://doi.org/10.1002/ecs2.2719>.
- Symonds, M.R.E., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* 65, 13–21. <https://doi.org/10.1007/s00265-010-1037-6>.
- Tilman, D., 1997. *Biodiversity and ecosystem functioning*. In: Daily, G.C. (Ed.), *Nature's Services Societal Dependence on Natural Ecosystem*. Island Press, Washington, USA, pp. 93–112.
- Tobner, C.M., Paquette, A., Gravel, D., Reich, P., Williams, L.J., Messier, C., 2016. Functional identity is the main driver of diversity effects in young tree communities. *Ecol. Lett.* 19, 638–647. <https://doi.org/10.1111/ele.12600>.
- van der Sande, M.T., Arets, E.J.M.M., Peña-Claros, M., Hoosbeek, M.R., Cáceres-Siani, Y., van der Hout, P., Poorter, L., 2018. Soil fertility and species traits, but not diversity, drive productivity and biomass stocks in a Guyanese tropical rainforest. *Funct. Ecol.* 32, 461–474. <https://doi.org/10.1111/1365-2435.12968>.
- Vilà, M., Inchausti, P., Vayreda, J., Valverde-Barrantes, O.J., Gracia, C., Ibañez, J., Mata, T., 2005. Confounding factors in the observed Productivity-Diversity relationship in forests. In: *Forest Diversity and Function: Temperate and Boreal Systems*. Springer - Verlag, Berlin, Germany, pp. 65–86.
- Williams, L.J., Paquette, A., Cavender-Bares, J., Messier, C., Reich, P., 2017. Spatial complementarity in tree crowns explains overyielding in species mixtures. *Nat. Ecol. Evol.* 1, 1–7. <https://doi.org/10.1038/s41559-016-0063>.
- Zhang, H., John, R., Liu, K., Qi, W., Long, W., 2019. Using functional trait diversity patterns to disentangle the processes influencing the recovery of subalpine grasslands following abandonment of agricultural use. *Front. Ecol. Environ.* 7, 1–13. <https://doi.org/10.3389/fevo.2019.00128>.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.