The sign and magnitude of tree–grass interaction along a global environmental gradient

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ABSTRACT

Aim The ecological literature posits that positive interactions are preponderant in stressful environments; however, the net balance between positive and negative interactions at the community level is still under debate. This study analysed the effect of trees on grass biomass in natural and cultivated woody systems distributed along a global aridity index (AI) gradient.

Location Global.

Methods We conducted a meta-analysis including eight natural biomes and tree plantations distributed in five continents. The final database consisted of 93 data pairs across 65 locations spanning a gradient from AI = 0.1 to AI = 2.1, which covered annual precipitation ranging from 70 to 3500 mm. Effect size was calculated as the difference between above-ground grass biomass beneath and outside the tree canopy. We built linear models to evaluate the importance of different biotic and abiotic variables as potential drivers of the effect size. Multimodel inference, based on the Akaike information criterion (AICc) was used to select the best models.

Results The whole data set shows a shift from net facilitation to net competition along an increasing AI gradient. AI had the highest relative importance in explaining the sign and magnitude of the effect size. Tree characteristics (deciduous–evergreen and leguminous–non-leguminous) were the other predictive variables consistently included in almost all the 10 best models. Deciduous and leguminous trees enhanced grass biomass growing beneath them. Increasing soil sand content, C4 grasses and tropical and natural systems all increased the biomass of grasses growing beneath trees, but their relative importance was substantially lower than that of the AI and tree characteristics.

Main conclusions The results of our global meta-analysis showed that climatic context and the characteristics of benefactor trees both represent the main drivers of the sign and magnitude of tree–grass interactions. These findings may contribute to advancing knowledge of the mechanisms behind the global patterns.

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INTRODUCTION

Coexistence of trees and grass occurs from arid scrublands to moist tropical forests. Across such a broad environmental gradient the net balance of this interaction can range from positive to negative or even neutral, although a general pattern has remained elusive. Several factors have been suggested to shape the sign of this interaction, such as climate and soil conditions, human activities, disturbance regimes, characteristics of the interacting species and also tree height, among others (Scholes & Archer, 1997; House *et al.*, 2003; Bucini & Hanan, 2007; Bond & Midgley, 2012; Moustakas *et al.*, 2013; Rivest *et al.*, 2013; Soliveres & Maestre, 2014). Most studies focusing on this topic have been conducted in savannas (Belsky, 1994; Mordelet & Menaut, 1995; Sankaran *et al.*, 2005; Bond, 2008). Some recent works have reported a shift from competitive to facilitative tree–grass interactions along a decreasing gradient of precipitation and between N-fixing and non-N-fixing trees (Blaser *et al.*, 2013; Dohn *et al.*, 2013; Moustakas *et al.*, 2013). However, in order to build a general model of tree–grass interactions it is necessary to incorporate other natural and cultivated woody ecosystems with different structure and functioning. For this reason, in this study we include different natural biomes distributed along a broad gradient of water availability and also tree plantations. This agroecosystem was included because the cultivated area is increasing world-wide to provide fibre and wood. As a consequence, it would be important to know to what extent tree–grass interactions in cultivated and natural systems may differ from each other.

Ecological communities are structured by interactions among organisms. The final outcome between positive and negative interactions allows us to quantify the preponderance of facilitation or competition at the community scale (Brooker & Callaghan, 1998; Brooker *et al.*, 2005). Classical ecological literature posits that positive interactions (net facilitation) tend to increase in stressful environments (Bertness & Callaway, 1994; Brooker & Callaghan, 1998; He & Bertness, 2014). It has also been suggested that positive interactions could expand the range of conditions in which an organism might survive, although not grow and reproduce. Therefore, facilitation would be the dominant interaction when abiotic stress is not extreme (Holmgren & Scheffer, 2010). While it is recognized that positive interactions play an important role in ecological communities (Stachowicz, 2001; Bruno *et al.*, 2003), no consensus has yet been reached about the net balance of positive and negative interactions along wide gradients of environmental stress. This reflects the difficulty in scaling up to the community level, mainly because each species has a particular response to abiotic conditions and also to the local conditions imposed by the presence of different neighbours (Soliveres & Maestre, 2014).

Along broad environmental gradients, tree cover ranges from scattered trees in savannas to scarce grasses in closed forests. Such changes in woody–grass proportions are generally associated with changes in mean annual precipitation (MAP) and soil conditions, both setting an upper limit on tree abundance (Scholes & Archer, 1997; Bond, 2008). For example, in African savannas tree cover increases linearly along a gradient of precipitation of up to 650 mm, above which closed woodlands develop (Sankaran *et al.*, 2005). As a consequence, the final balance of woody–grass interaction might shift from positive to negative along a precipitation gradient, which also implies a gradient of tree abundance and/or tree cover (Murphy & Lugo, 1986). In addition, soil texture has also been invoked as a factor influencing the final balance of tree–grass interaction in savannas (Bond, 2008; Dohn *et al.*, 2013). In general, the positive effect of trees could be lower in fine rather than coarse soil textures given the low capacity of coarse soils to retain nutrients, which could be enhanced by adding litter biomass (Jobbágy & Jackson, 2000). In this context, trees could enhance the availability of water for grasses growing beneath them by increasing soil organic matter and reducing evaporative demand.

The structural and functional traits of herbaceous and woody plants may also influence the net balance of tree–grass interaction. In particular, it is not clear what the net effect of trees could be in communities with preponderance of C4 grasses. In one way these communities could be more affected by the shade cast by trees than communities dominated by C3 grasses because of their higher intolerance to light reduction (Long, 1999; Sage *et al.*, 1999; Keeley & Rundel, 2003). Alternatively, in stressful environments, the effect of trees on C4 grass biomass could be positive, due to the amelioration of abiotic conditions (Scholes & Archer, 1997).Tree characteristics may also play a role in shaping the sign and magnitude of tree–grass interaction. Nutrient enrichment under trees has been reported as one of the positive effects of leguminous trees and shrubs on herbaceous biomass in stressful environments (Belsky, 1994; Pugnaire *et al.*, 1996; Scholes & Archer, 1997; Ludwig *et al.*, 2004). In addition it was recently demonstrated that in stressful environments deciduous trees enhanced the absorption of nitrogen by grasses growing beneath them, and also increased mineralization of organic matter (Gargaglione *et al.*, 2014). Other results showed a reduction in grass productivity (Bahamonde *et al.*, 2012) under deciduous trees as well as under an evergreen canopy (Rivest *et al.*, 2013). Overall, a global model of woody–grass interactions should incorporate the main characteristics of both trees and grasses.

To evaluate the net effect (sign and magnitude) of trees on grass biomass growing beneath tree canopies we conducted a global-scale meta-analysis. The study included natural and cultivated woody systems distributed across all continents. Studies were ordered along an axis of aridity index (AI), which is a proxy for water availability (Trabucco *et al.*, 2008). The AI is the ratio between MAP and potential evapotranspiration (PET). This index represents a more sensitive proxy of environmental stress than precipitation since it also includes atmospheric water demand, a better approximation to hydric balance (Knapp & Smith, 2001). The objectives of

this study were: (1) to evaluate the net effect of trees on grass biomass along a gradient of water availability and (2) to quantify how the net effect of trees varies along a gradient of soil sand content, type of woody system (plantation–natural) and characteristic of grasses (C3–C4) and trees (deciduous–evergreen, and leguminous–non-leguminous). By using the net effect, we recognized that positive (facilitation) and negative (competition) interactions are operating simultaneously, and the balance between them will determine the preponderance of positive or negative interaction within a community and the final grass biomass growing beneath trees (Holzapfel & Mahall, 1999).

We postulate the following hypothesis: (1) along a broad gradient of AI, the sign of tree–grass interaction shifts from positive (i.e. net facilitation) to negative (i.e. net competition) as water availability increases; (2) tree characteristics (leaf longevity and N-fixation capacity) both modify grass biomass growing under trees; (3) grass characteristics (C3–C4) are differentially affected by the shade cast by trees because of their differences in tolerance to light reduction; (4) tree plantations have a negative effect on grass biomass because they represent a selected pool of fast-growing and highly competitive trees species, compared to natural systems.

MATERIALS AND METHODS

The database

In order to compare the influence of tree cover on grass productivity, we performed a meta-analysis using the Scopus database. Our search covered a period of 26 years (from 1990 to 2015) and included the following keywords: 'pasture productivity under trees', 'silvopastoral systems', 'grassland tree facilitation', 'herbaceous under trees', 'forest pastures', 'grass–tree interaction', 'grass diversity–productivity trees'. From the 98 studies examined only 47 (see Table S1 in the Supporting Information) met the following requirements: (1) above-ground grass productivity or biomass was measured under tree shade and in open grassland within the same site (data pairs), (2) statistical information (i.e. mean values, measures of error and number of replicates) either in graphs, text or tables was provided. Those articles that did not provide control treatments were not included since comparisons were not possible. Data available in graphs were digitized using GetData Graph Digitizer 2.24. Standard error (SE) values were converted to standard deviation from the product of SE and the square root of the number of replicates. When an article provided more than one data pair we considered only independent data pairs coming from different sites in order to avoid pseudoreplication. The final database obtained (from 47 studies published during the last 26 years) consisted of 93 data pairs distributed across 65 sites (Table S1).

For each data pair we calculated the AI as the ratio between MAP and PET (UNEP 1997), based on data from Trabucco *et al.* (2008). A regression analysis was made between precipitation data reported by Trabucco *et al.* (2008) and those reported in the original papers. This analysis

showed a coefficient of determination of 0.83. There was only one outlier, which was located in a mountainous zone where the interpolation between meteorological stations was not accurate. Data for grass biomass came from eight biomes: tropical and subtropical grasslands savannas and shrublands, temperate grasslands savannas and shrublands, mediterranean forests woodlands and scrub, temperate broadleaf and mixed forests, tropical and subtropical moist broadleaf forests, tropical and subtropical dry broadleaf forests, deserts and xeric shrublands and montane grasslands (Olson *et al.*, 2001). In the case of tree plantations the biomass represents the original vegetation removed.

Effect size was calculated for each data pair and represented the difference between above-ground grass productivity beneath trees (X_b) and outside the tree canopy (X_o). A positive effect size indicates higher grass productivity beneath trees with respect to outside the tree canopy, while a negative effect size means higher productivity outside the tree canopy than under trees. Therefore, when the effect size is positive the dominant interaction is facilitation, whereas if the effect size is negative the dominant interaction is competition.

We built linear models to evaluate the importance of different predictive variables as the potential drivers of effect size. AI, percentage of soil sand and latitude were employed as continuous variables. The characteristics of grasses (C3–C4) and trees (leaf longevity, deciduous–evergreen; N-fixation, leguminous–non-leguminous) and type of system (plantation–natural) were included in the model as categorical variables (Table S1). For the classification into categories of grasses (C3–C4), we considered the dominant form within each community. Soil sand content was obtained from Hengl *et al.* (2014) through ISRIC/WDC-Soils. For each site we extracted the percentage of sand and calculated the weighted average for all the depths in the first 30 cm, where the highest grass root density is found (Jackson *et al.*, 1996). For the other explanatory variables we obtained data from informed values in each publication.

Data analysis

The meta-analysis was carried out using METAWIN 2.0 (Rosenberg *et al.*, 2000). Effect sizes were measured using Hedges' *d* instead of a log-response ratio because it is not biased by small sample sizes (Rosenberg *et al.*, 2000). Hedges' *d* was calculated as

$$d = \frac{X_b - X_o}{S} \times J$$

where X_b and X_o are as defined above, S is the pooled standard deviation and J is a correction factor accounting for a small sample size (Rosenberg *et al.*, 2000) (see Table S3 for an example calculation). Effect sizes were calculated for the whole data set (main effect, $n = 93$) and also for each category previously defined.

To quantify the importance of all predictive variables, we used linear models (lm function in R software v.3.1.3)
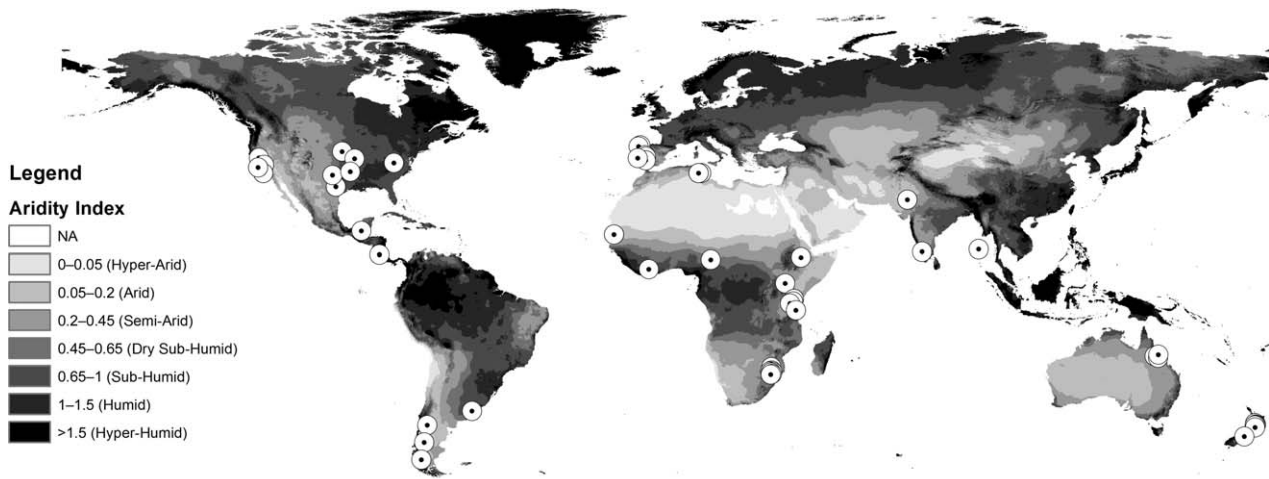
Figure 1 Global distribution of all studies included in the meta-analysis (black circles), the aridity index (mean annual precipitation/potential evapotranspiration) increases from lighter to darker tones of grey, which implies a decreasing level of environmental stress.

(Wilkinson & Rogers, 1973; Chambers & Hastie, 1991; R Development Core Team, 2015). First, we tested the independence of all predictor variables through multicollinearity, based on the variance inflation factor (VIF) (Car package, VIF function) (Fox & Weisberg, 2010). Since none of the variables showed multicollinearity (all VIF values were below 3), we incorporated all of them in the models. Since we were especially concerned to examine to what extent AI might modify the effect of each predictor variable, pair interactions were also incorporated (each predictor variable with the AI). We tested the model for error independence, normal distribution and homoscedasticity. These assumptions were valid in all cases. Then we performed multimodel inference based on the Akaike information criterion (AICc). AICc values were obtained based on maximum-likelihood estimates of regression coefficients (MuMIn package, dredge function). Finally, to quantify the relative importance of the different predictive variables we summed the Akaike weights for each predictor in all the models. According to this criterion, a bigger sum corresponds to a more important variable relative to the other variables that occurred in the same model.

RESULTS

The 93 data pairs distributed across 65 sites encompassed eight biomes in five continents: 24 in America (4 in South America), 6 in Europe, 47 in Africa, 6 in Asia and 10 in Oceania (Fig. 1). There were 74 data pairs in native ecosystems and 19 data pairs in plantations (Table S1). The sites spanned a wide range of environmental conditions, from an annual average temperature of 4.5 to 27.5 °C and MAP from 70 to 3500 mm, which resulted in a range of AI from 0.11 to 2.13 (from arid to hyper-humid). The whole data set shows a shift from net facilitation to net competition (from a positive to a negative effect size) along the increasing gradient of AI (Fig. 2).

From all possible combinations among the predictor variables and the interactions between each one and the AI, we selected the 10 best models. All these models consistently included the AI and tree characteristics as the main predictors of the effect size (Table 1). However, the AI showed the highest relative importance among all predictive variables included in the models (Fig. 5). Leaf longevity and N-fixing trees were included in all and 90% of the best models, respectively (Table 1). Deciduous trees increased grass biomass (positive effect size) growing beneath them, whereas evergreen trees had a neutral effect (Fig. 4). Leguminous trees increased grass biomass across a longer portion of the AI gradient than non-leguminous trees; such interaction was included in 8 out of the best 10 models (Fig. 2, Table 1).

Soil sand content was included in 4 of the best 10 models, whereas latitude and C3–C4 grasses were included in 2 of the best 10 models (Table 1). These variables had a minor
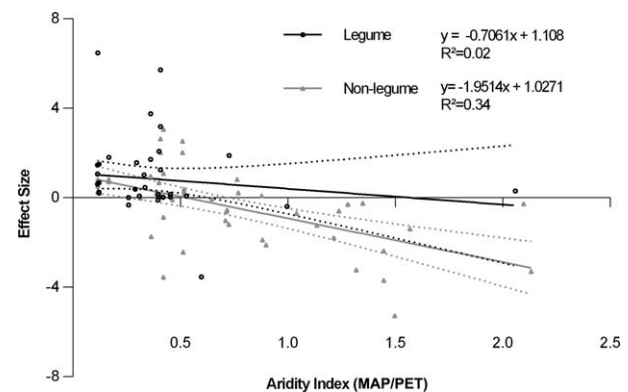

Figure 2 Relationship between effect size (above-ground herbaceous productivity beneath and outside tree canopy) and aridity index (mean annual precipitation/potential evapotranspiration, MAP/PET) for leguminous trees (black circles) and non-leguminous trees (grey triangles). Dashed lines denote the 95% confidence interval.

Table 1 The Akaike information criterion (AIC) of the regression model for the effect size, and partial regression coefficients (standard errors in parenthesis) for all variables included in the 10 best linear models. Predictor variables were aridity index (AI), leaf longevity (evergreen–mixed–deciduous trees), woody N-fixers (leguminous–non-leguminous trees) and sand percentage in soil up to 30 cm depth (sand). The best model was derived from the evaluation of every possible combination of predicting variables and their pair interactions. ΔAIC shows the difference between the model's AIC and that of the best-fitting model.

		Model										
		Best	A	B	C	D	E	F	G	H	I	Null
	AIC	342.1	342.4	343.8	343.9	344.3	344.5	344.6	344.6	344.7	344.9	371.8
	ΔAIC	0	0.3	1.7	1.8	2.2	2.3	2.4	2.5	2.6	2.7	29.6
Environmental variables	AI	−0.49 (0.69)	−0.39 (0.69)	−0.56 (0.70)	−1.97 (1.8)	−0.49 (0.695)	−0.42 (0.74)	−1.8 (0.37)	−3.2 (1.9)	−0.23 (0.75)	−0.39 (0.69)	
	Latitude			−0.0047 (0.0058)						0.0055 (0.010)		
Soil texture	SAND	0.022 (0.016)	0.022 (0.016)		0.0041 (0.024)				−0.0034 (0.028)		0.022 (0.016)	
Tree foliar persistency	Evergreen	0.38 (0.40)	0.38 (0.40)	0.42 (0.41)	0.37 (0.41)	0.35 (0.42)	0.38 (0.41)	0.27 (0.41)	0.091 (0.41)	0.48 (0.41)	0.38 (0.40)	
	Mixed	−1.3 (0.52)	−1.3 (0.52)	−1.3 (0.53)	−1.3 (0.52)	−1.3 (0.53)	−1.3 (0.53)	−1.1 (0.53)	−1.2 (0.53)	−1.3 (0.53)	−1.3 (0.52)	
Leguminous–non-leguminous	Non-legume	0.14 (0.49)	0.16 (0.49)	0.21 (0.50)	0.29 (0.50)	0.22 (0.52)	0.15 (0.50)	−1.64 (0.34)		0.33 (0.51)	0.16 (0.49)	
Grass charact.	C4					0.18 (0.41)	−0.14 (0.54)		0.56 (0.40)			
System origin	Plantation					−1.7 (0.83)	−1.7 (0.83)					
Interactions between variables	AI × non-leg.	−1.8 (0.82)	−1.8 (0.82)	−1.83 (0.83)	−2.033 (0.86)			−1.8 (0.82)		−2.2 (0.89)	−1.8 (0.82)	
	AI × sand				0.035 (0.037)				0.030 (0.039)			
	AI × latitude									−0.015 (0.012)		

*For categorical variables with two levels (leguminous–non-leguminous trees and natural systems and plantations), the reference level was leguminous and natural systems. For categorical variables with three levels (deciduous–mixed–evergreen), the reference level was deciduous. Mixed denotes a system with the three categories.
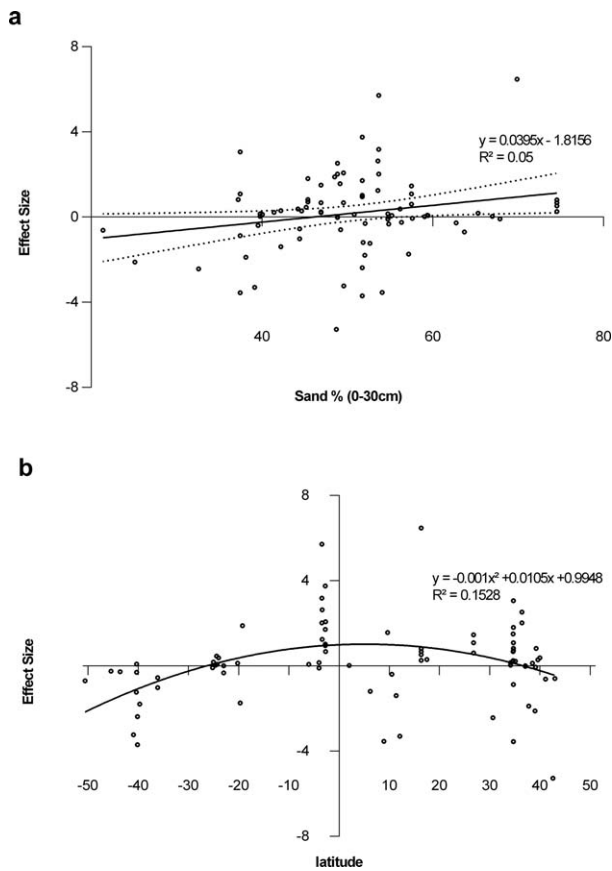
Figure 3 Relationship between effect size (above-ground herbaceous productivity beneath and outside the tree canopy) according to (a) percentage of sand in the soil (0–30 cm depth) (dashed lines denote the 95% confidence interval) and (b) latitude (negative and positive values of latitude correspond to the Southern and Northern Hemisphere, respectively).

relative importance in explaining the variability of the effect size (Fig. 5). We found that along an increasing axis of soil sand content the effect size changed from negative to positive (Fig. 3). In general C3 grasses were negatively affected by trees (net competition) while C4 grasses showed the opposite pattern (net facilitation; Fig. 4). Natural or cultivated systems were included in 1 of the 10 best models, showing a low relative importance (Table 1, Fig. 5). Tree plantations negatively affected grass biomass growing beneath tree canopy (Fig. 4). Latitude showed a quadratic response, which implied that the effect size was positive in tropical systems and tended to be negative above nearly 30° latitude (Fig. 3).

DISCUSSION

We examined the sign and magnitude of tree–grass interaction along a global gradient of AI. Our results showed that AI, as a proxy for water availability, was the main predictor in explaining the impact of trees on grass biomass. Net facilitation occurred from an AI of 0.1 to nearly 1.5, whereas net competition occurred from an AI of 0.5 to 2.0 (Fig. 2). These findings partially agree with recent studies in the savannas of
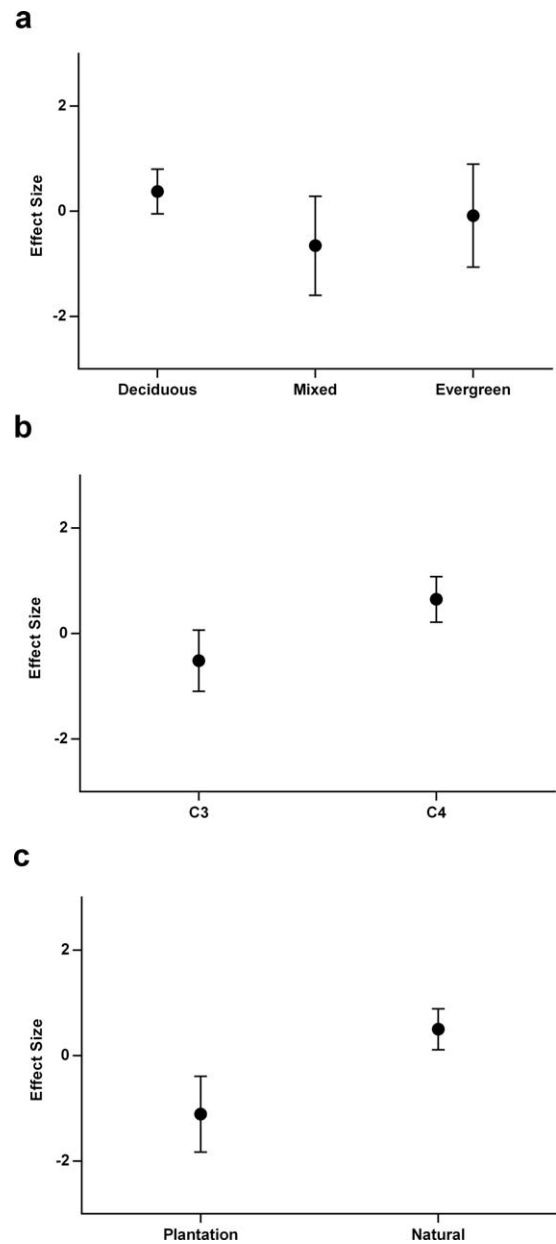
Figure 4 Effect size (above-ground herbaceous productivity beneath and outside the tree canopy) according to (a) evergreen–mixed–deciduous trees, (b) C3–C4 grasses, and (c) plantations–natural systems. Vertical bars for each point denote the standard error for each axis of the graph.

North America and Africa in that they found that trees enhanced grass productivity in dry environments (Blaser et al., 2013; Dohn et al., 2013; Moustakas et al., 2013). However, by using the AI as a proxy for abiotic stress, we found that the range of annual precipitation where facilitation occurred was more extended than previously reported. Our results show that facilitation extended from 70 to 1800 mm (cf. Dohn et al. 2013), whereas competition extended from 600 to 3500 mm. Therefore, it seems that to employ AI at a global scale as a signal of abiotic stress could be more
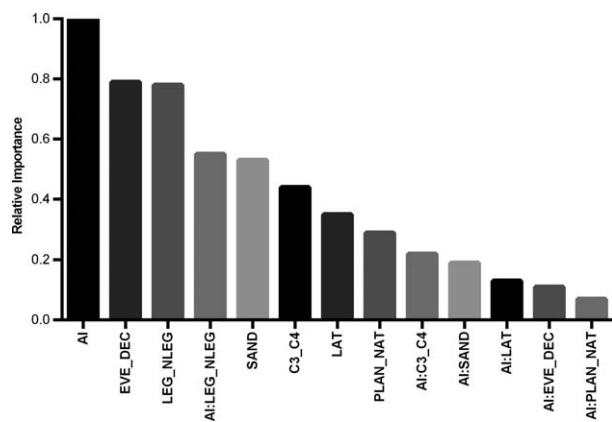
Figure 5 Relative importance of each predictor variable and the interactions between aridity index (AI) and each predictor variable (LEG_NLEG, leguminous–non-leguminous trees; EVE_DEC: evergreen–mixed–deciduous trees; SAND, sand percentage in soil (0–30 cm depth); C3_C4, C3–C4 grasses; LAT, latitude; PLAN_NAT, plantations–natural systems). The height of each bar is the sum of the Akaike weights of all models that included the predictor of interest, taking into account the number of models in which each predictor appears.

appropriate than to employ annual precipitation. Overall, the pattern (facilitation–competition) was consistent at global scale (five continents) even including natural systems (other than savannas) and tree plantations. Interestingly, as was found by Dohn *et al.* (2013) within a narrow geographical context, at a global scale the effect size recorded in tropical systems was positive, whereas such effect in temperate systems in both the Northern and Southern Hemispheres was always negative (Fig. 3b).

Leaf longevity was the second most important variable in modifying the effect size, and it was independent of climatic conditions (AI × leaf longevity was not included in the best models). We found that deciduous trees had a clear positive effect on grass biomass growing beneath trees, whereas the effect of evergreen trees was neutral, mainly due to its high variability (Table 1, Fig. 4a). A somewhat obvious implication regarding the role of deciduous tree cover is the increase in solar radiation during winter, which may relax competition between trees and winter grasses. In this respect, Callaway *et al.* (1991) measured 90% of total radiation under deciduous trees during winter, a value that decreased to 45% by the end of spring. So water stress could be ameliorated during the spring and summer, while light competition could be reduced during the winter when hydric stress is not a limiting factor. Therefore, deciduous trees might represent the best balance between negative and positive effects of trees on grass biomass (Holmgren & Scheffer, 2010).

Leguminous trees were also an important predictor variable in controlling the sign and magnitude of tree–grass interactions, and were included in almost all the best models. Facilitation by leguminous trees extended along a wide range of AI (0.1–1.5), whereas facilitation by non-leguminous trees

occurred within a short range of AI (0.1–0.5; Fig. 2). These results agree with other studies in showing that facilitation was the dominant interaction when the benefactor was a leguminous tree whereas non-leguminous trees had a neutral or negative effect (Blaser *et al.*, 2013; Moustakas *et al.*, 2013). It is recognized that the presence of fertility islands beneath leguminous trees, mainly due to enhanced soil nitrogen availability, represents one of the main mechanisms involved in the positive interaction between leguminous trees and grasses in savannas (Belsky, 1994; Scholes & Archer, 1997; Ludwig *et al.*, 2004). Our results suggest that the extended range of facilitation by leguminous trees may be associated with a double-facilitation mechanism – the amelioration of microclimatic conditions in stressful environments and the addition of nutrients in less stressful environments (Scholes & Archer, 1997). These double-facilitation mechanisms were globally extended and occurred along a broad axis of AI which included a range of annual precipitation from 70 to 1800 mm (cf. Blaser *et al.*, 2013; Dohn *et al.*, 2013; Moustakas *et al.* 2013). Therefore, by focusing on a global scale and also by employing AI as the axis of the environmental gradient, positive tree–grass interaction appears to be a more extended mechanism than has previously been reported.

Sand soil content was a low-ranked predictor variable, and was included in 4 out the best 10 models. We found that effect size increased along with soil sand content, although its effect was weaker than that of AI and tree characteristics (Fig. 5). Such a positive effect of trees might be attributed to their capacity to improve retention of water and soil nutrients in sandy soils. In contrast, Dohn *et al.* (2013) showed that the positive effect of trees was higher in fine than in coarse soil. It could be possible that differences in the spatial scale covered by Dohn's study and our's plays a role in the results. As a consequence, it is difficult to compare the results of both studies because the simplified model of Dohn *et al.* (2013) included fewer variables, possibly due to its narrow geographical context.

Interestingly, we have hypothesized that grass characteristics and the type of system (natural–plantation) could act as the main variables in explaining the effect size. Contrary to our expectation, we found that only a few models included these variables. Although our results revealed that the effect size of C3 was negative whereas that of C4 was positive, their relative importance was weak compared with AI and tree characteristics (Fig. 5). In addition, while we found tree plantation negatively affected grass biomass, the relative importance of the type of system was nearly three times less than that of the AI. Overall, at a global scale, the characteristics of beneficiary plants and type of system were less important than the characteristics of climatic context and benefactor trees.

The results of our study may contribute to the design of sound management decisions related to the implementation of dual-purpose systems (wood and livestock farming) in woody ecosystems. In particular, our analysis highlights the importance of trees in enhancing grass biomass in arid and

semi-arid environments. The degradation of these ecosystems by overgrazing and wood extraction could reduce the positive tree–grass interactions. On the contrary, in less stressful environments the maintenance of a highly productive herbaceous layer could require the opening of gaps through thinning, for example with selective logging, thus reducing tree cover to relax plant competition. Finally, our results could contribute in the design of agroforestry (silvopastoral systems) by aiding the selection of the best combinations of tree and grass traits according to the abiotic conditions.

CONCLUSIONS

Tree–grass coexistence is a major concern in ecology and many studies developed in savannas have shed light on the factors shaping this interaction. However, a general model of coexistence in woody systems remains unresolved. To our knowledge, this study is the first attempt at helping to understand the main drivers in shaping tree–grass interactions world-wide and beyond savannas. Our results highlight that the sign and magnitude of tree–grass interactions are defined by a number of hierarchically ordered factors. At global scale, water availability and the characteristics of benefactor trees are consistently the main controls of the effect size.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Types of biomes and characteristics of trees and grasses included in the analysis.
Table S2 Effect size, variance and aridity index of each study included in the analysis.
Table S3 Example of the calculation procedure to obtain the effect size.

BIOSKETCH

Noemí Mazía is interested in the dynamics of woody–grass interactions in grasslands and savannas, and on plant–herbivore interactions in forest ecosystems, with emphasis on the trophic and environmental controls of insect herbivory.

Author contributions: N.M., L.P. and T.S. developed the ideas and designed the research. N.M., J.M., L.P. and S.A. performed the research. J.M., L.P. and L.A.G. analysed the data. N.M. wrote the first draft, with inputs from J.M., L.P. and T.S.; all the authors contributed substantially to revising the manuscript.

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APPENDIX 1: DATA SOURCES

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