



A meta-analysis reveals mostly neutral influence of scattered trees on pasture yield along with some contrasted effects depending on functional groups and rainfall conditions

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ABSTRACT

Scattered trees occurring throughout farmland matrix are prominent features of many human-dominated landscapes around the world, especially in livestock grazing systems. They are keystone structures that may play important roles in maintaining ecosystem functions, services, and farmland biodiversity. However, scattered trees in agricultural landscapes are declining worldwide due to intensive land use. They are often perceived by farmers as having negative impacts on agricultural production. Large-scale assessments in different biomes of agricultural yield in scattered tree ecosystems remain rare. Filling this knowledge gap may help improve decision-making regarding the value of scattered trees in agricultural landscapes. Using meta-analysis, we found that, across four tree functional groups (deciduous, *Eucalyptus*, N₂-fixing, evergreen oak), mature scattered trees do not compromise pasture yield. The sign and magnitude of scattered tree effects on pasture yield did vary, however, among tree functional groups and according to precipitation levels. Our study suggests that, as drought pressure increases abiotic stress, tree facilitation by N₂-fixing trees, and competition by *Eucalyptus*, will become the more common interactions between scattered trees and pasture. Management options exist to conserve and restore scattered trees in agricultural landscapes, but new policies are required to support their widespread adoption by farmers.

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1. Introduction

Current and future agricultural systems will shape, perhaps irreversibly, the surface of the Earth, including its biodiversity, biogeochemistry, and the goods and the services that are supplied to society (Tilman et al., 2001). Of the 14 giga hectares of ice-free land on the surface of Earth, about 25% are used for pasture. Consequently, livestock grazing covers the largest geographic extent compared to any other form of land use (Asner et al., 2004). An increasingly important challenge facing livestock grazing systems is the need to maintain or even increase pasture yield while providing other ecosystem services (Tilman et al., 2002).

Scattered trees are a prominent feature of many human-dominated landscapes around the world, especially in livestock grazing systems (Gibbons et al., 2008). In these landscapes, trees occur as legacies of past forests or of woodland clearing or thinning, or they can be maintained incidentally or deliberately as part

of agroforestry systems (Manning et al., 2006; Moreno and Pulido, 2009). In this study, the key defining feature of “scattered tree ecosystems” is the dispersed and open pattern of mature trees in a grazing landscape. Widespread examples of scattered tree ecosystems include Mediterranean oak (*Quercus* spp.) savannas in the Iberian peninsula and those in California (Marañón et al., 2009), grassy box woodlands dominated by *Eucalyptus* spp. in temperate Australia (Fisher et al., 2010) and dry tropical savannas dominated by *Acacia* spp. in Africa (Treydte et al., 2007). Scattered trees have been designated as ‘keystone structures’ due to the disproportionately large ecological functions and ecosystem services they provide relative to the small area they occupy in landscapes (Munzbergova and Ward, 2002; Manning et al., 2006). Scattered trees provide biological legacies that increase vegetation structural complexity and connectivity, facilitating movements of various organisms across landscapes and ecological networks (Manning et al., 2009; Breed et al., 2011). As such, they simultaneously integrate conservation objectives and agricultural activities. Scattered trees in human-modified landscapes are, however, declining worldwide because of intensive land use (Pleninger, 2006; Treydte et al., 2007; Fisher et al., 2010). Although evidence that the ongoing decline of scattered trees deserves urgent attention, large-scale assessments of

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agricultural production in scattered tree ecosystems remain rare in different biomes. Filling this knowledge gap may help improve decision making regarding the overall values of scattered trees in agricultural landscapes.

An extensive body of literature that has been published in the last few decades shows, however, that there is little consensus regarding the effect of scattered trees on herbaceous production (Mordelet and Menaut, 1995; Scholes and Archer, 1997; Marañón et al., 2009). Trees may enhance pasture yield under their canopies through facilitation processes such as reduced evapotranspiration, soil nutrient enrichment, and hydraulic lift (e.g. Belsky, 1994; Ludwig et al., 2001, 2003). Conversely, the tree overstory may reduce pasture yield through competition for water, nutrients, and light (e.g. Marañón and Bartolome, 1993; Anderson et al., 2001; Ludwig et al., 2004). In fact, both mechanisms probably occur simultaneously and the overall balance of plant-to-plant interactions among different species may change with the ontogeny of the interacting individuals as plant development affects the demand for resources and varies in response to environmental fluctuations (Maestre et al., 2009). While some studies (McClaran and Bartolome, 1989; Belsky et al., 1993b) support the hypothesis that tree facilitation is most likely to occur in water-stressed environments (i.e. stress gradient hypothesis, Bertness and Callaway, 1994), other studies showed that enhancement of pasture production by tree canopies is weakly (Mordelet and Menaut, 1995) or inversely related (Moreno, 2008; Gea-Izquierdo et al., 2009) to increased annual rainfall. Hence, we hypothesized that the relationships between abiotic stress and tree-pasture interactions depends on tree functional group in scattered tree ecosystems.

We addressed the following key questions: (i) What is the overall effect of scattered trees on pasture yield across different biomes and species? (ii) Does the effect of scattered trees on pasture yield differ between different tree functional groups? (iii) Does decreasing annual rainfall influence the effects of scattered trees on pasture yield? (iv) Are the latter interactions mitigated among tree functional groups? We investigated these questions using meta-analysis. This statistical tool is of considerable interest in applied ecology for increasing power, exploring heterogeneity, identifying large-scale patterns, and facilitating evidence-based decision-making (Stewart, 2010). Our meta-analysis included studies that assessed the effects of scattered trees on herbaceous production in grazed landscapes. This meta-analysis was based on field data originating from 27 published studies, all of which included controls (without trees) that allow the comparison of four major tree functional groups (deciduous, *Eucalyptus*, N_2 -fixing, evergreen oak) under contrasting annual precipitations.

2. Methods

The literature published between 1989 and 2011 was investigated using the following electronic databases: CAB Abstracts, Biological Abstract, Scopus and Google Scholar. Titles, abstracts and keywords were searched using these keywords: “agroforestry parkland,” “dehesa,” “grassland production,” “grazed woodlands,” “herbaceous production,” “montado,” “paddock trees,” “pasture understory,” “pasture yield,” “savanna,” “scattered tree,” “silvopastoral system,” “tree-grass.” A total of 73 observations from 27 published studies that covered 10 countries were included in our meta-analysis (Table 1). The meta-analysis focused on field studies where herbaceous aboveground biomass (expressed per unit area) was measured directly beneath the canopy of scattered mature trees (density typically ranged from 15 to 50 trees ha⁻¹) and in an appropriate control (away from tree crowns in open areas).

Data collection was limited to experimental plots that included exclusively an unimproved herbaceous layer (i.e. unfertilized, non-irrigated, not sown with genetically improved varieties) to avoid possible confounding effects of agricultural inputs with that of tree environment. In almost all cases, the herbaceous vegetation studied in our meta-analysis was typically composed of a mixture of spontaneous native species. Some articles reported herbaceous aboveground biomass at different distances from the tree bole beneath the tree canopy. In these cases, only the measurement at the nearest distance from 0.5 times the tree crown radius was used because this is the position most often reported by those studies reporting only one position. If an article reported a pattern of herbaceous biomass accumulation at different times over the course of a growing season, only the result observed at the peak of green biomass was used.

We were specifically interested in how contrasting biological tree trait-based differences influenced the magnitude of herbaceous aboveground biomass responses. Based on previous reviews regarding tree-understorey interactions (Scholes and Archer, 1997; Marañón et al., 2009), four prominent groups of tree species that occurred in scattered tree ecosystems in temperate and tropical climates were selected: *Eucalyptus*, N_2 -fixing (chiefly *Acacia* species), deciduous (chiefly oak species) and evergreen oak. Studies of grazed forest plantations and shrub savanna ecosystems were not considered. We considered different tree species studied in the same experiment as independent observations within the same study (Hawkes and Sullivan, 2001). Likewise, inter-annual results from the same site were considered as independent observations (Maestre et al., 2005). We restricted our data collection to results in which means, variance (standard deviation, standard error, or confidence intervals), and sample size (i.e. total number of repetitions) were reported directly as numerical or graphical data in the paper, or were made available to us through personal communication with the authors. Variance data were not available for several studies. However, four studies (Table 1) could still be included by computing a proxy for variance using inter-annual measurements. We only used data for which pasture yield estimates for a specific year was available together with precipitation (mm) for the same year.

Hedges'g was used as an index of effect size to quantify the difference in the means of herbaceous aboveground biomass yields (g m⁻²) between plots beneath the scattered trees (X_T) and the control (X_C). This effect size is defined as $g = (X_T - X_C)/s$, with s being the pooled standard deviation of X_T and X_C . We also adjusted g with the small-sample correction factor $J(m)$, where $m = N_T + N_C - 2$ and N is the sample size of X . Hedges'g is a unit-free index that estimates the magnitude of the effect and its direction. Positive values for g indicate that pasture yield under scattered trees was higher than in open areas, whereas negative values indicate a negative effect of trees on pasture yield.

The statistical analyses were performed using the MAD and metaphor libraries (Viechtbauer, 2010) in the R software environment (version 2.14.1, R Development Core Team, 2009). We first used a simple random effects model to test the overall effect of trees on pasture yields. A mixed-effects model was then performed by including tree functional group and annual precipitation as moderators. Significant differences between groups were explored using contrasts. We also built mixed-effects models for each group including precipitation as a moderator. Moderators were tested using between-groups heterogeneity (Q_M), which estimates the amount of heterogeneity in effect sizes that is explained by a given moderator while controlling for others. A plot of the effect sizes against sample size (not shown) revealed a funnel-shaped distribution of the data points ($Z = -0.273$, $P = 0.785$), as would be expected in the absence of publication bias (Palmer, 1999).

Table 1
Studies included in the meta-analysis.

Reference	Location	Tree group	Tree crown radius (m)	Tree DBH (cm)	Obs
Akpo et al. (2003)	Senegal	Deciduous	3.2	na	1
Anderson et al. (2001)	TX, USA	N ₂ -fixing	5.3	na	1
Barnes et al. (2011)	New South Wales, Australia	Deciduous	3.8	na	2
		<i>Eucalyptus</i>	6.0–8.6	63–126	4
Belsky et al. (1989)	Kenya	Deciduous	6.6	225	1
		N ₂ -fixing	7	72	1
Belsky et al. (1993a)	Kenya	Deciduous	na	220–400	2
		N ₂ -fixing	na	45–75	2
Belsky et al. (1993b)	Kenya	Deciduous	11.3	301	1
		N ₂ -fixing	8.6	71	1
Belsky (1994)	Kenya	N ₂ -fixing	na	na	4
Cubera et al. (2009)	Portugal	Evergreen oak	7.0	59	2
Durr and Rangel (2002)	Queensland, Australia	N ₂ -fixing	12.3	118	1
Frost and McDougald (1989) ^a	California, USA	Deciduous	na	na	1
		Evergreen oak	na	na	1
Gea-Izquierdo et al. (2009)	Spain	Evergreen oak	4.9	63.5	3
Haworth and McPherson (1994)	Arizona, USA	Evergreen oak	3.2	28.1	2
Harrington and John (1990) ^a	New South Wales, Australia	<i>Eucalyptus</i>	3.6	na	1
Hussain et al. (2009)	Portugal	Evergreen oak	na	na	1
Jackson and Ash (1998)	Queensland, Australia	<i>Eucalyptus</i>	na	30	4
Jackson et al. (1990) ^a	California, USA	Deciduous	na	na	1
Ko and Reich (1993)	Wisconsin, USA	Deciduous	5.5–7.5	50–79	3
Ludwig et al. (2001)	Tanzania	N ₂ -fixing	7.5–10	59	2
Marañón and Bartolome (1994)	California, USA	Evergreen oak	na	na	1
McClaran and Bartolome (1989)	California, USA	Deciduous	na	30–60	10
Mclvor and Gardener (1995) ^a	Queensland, Australia	<i>Eucalyptus</i>	na	30	1
Moreno (2008)	Spain	Evergreen oak	4.8–5.3	43–49	3
Ratliff et al. (1991)	California, USA	Deciduous	na	na	3
		Evergreen oak	na	na	3
Rivest et al. (2011)	Spain	Evergreen oak	5.5	51	4
Sánchez-Jardón et al. (2010)	Chile	Deciduous	na	na	2
Treydte et al. (2007)	South Africa, Kenya, Tanzania	N ₂ -fixing	5.5	44	3
Weltzin and Coughenour (1990)	Kenya	N ₂ -fixing	na	na	1

DBH: diameter at breast height (130 cm).

Obs: number of observations extracted per reference.

na: not available.

^a Studies where the variance was determined by computing a proxy using inter-annual measurements.

3. Results

Overall, tree overstorey had a neutral effect on total herbaceous aboveground biomass, with a non-significant ($n = 73$, $Z = -1.268$, $P = 0.205$) mean effect size of -0.39 and 95% CI ranging from -1.00 to 0.21 (Fig. 1). The overall heterogeneity of effect sizes was large ($Q = 1283.39$, d.f. = 72, $P < 0.0001$), indicating that the individual effect sizes in our data did not estimate a common population mean and that other experimental treatments or moderators may have influenced results.

Indeed, the tree functional groups had a significant effect on effect sizes (Fig. 1, $Q_M = 21.44$, d.f. = 3, $P < 0.0001$). The effect size was negative and significant for *Eucalyptus* ($g = -2.49 \pm 1.97$, $P = 0.0135$), positive and near-significant for N₂-fixing ($g = 1.73 \pm 1.91$, $P = 0.076$), and near zero and non-significant for deciduous ($g = 0.16 \pm 0.61$, $P = 0.838$) and evergreen oak ($g = -0.37 \pm 1.66$, $P = 0.666$). Mean effect sizes were ordered among groups as: N₂-fixing > deciduous = evergreen oak > *Eucalyptus* (Fig. 1, contrasts). Annual precipitation had no significant effect on effect size across all tree functional groups when these were taken together ($Q_M = 0.30$, d.f. = 1, $P = 0.584$).

Linear mixed-models within each tree functional group revealed significant effect of annual precipitation for the *Eucalyptus* ($Q_M = 12.16$, d.f. = 1, $P = 0.0005$) and N-fixing ($Q_M = 9.04$, d.f. = 1,

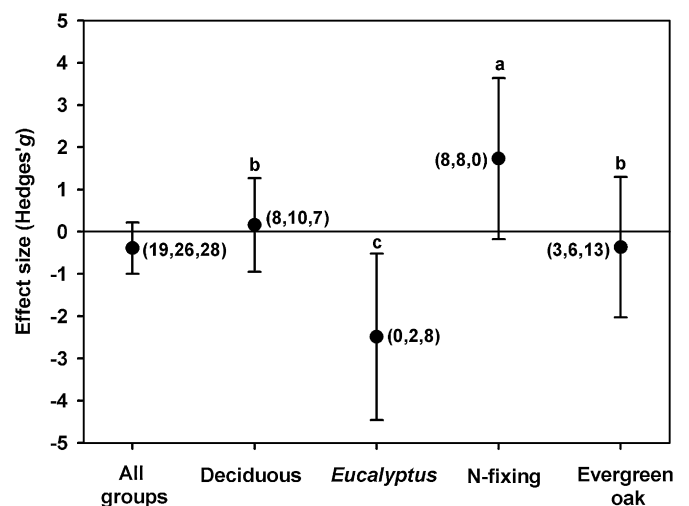


Fig. 1. Mean effect size (Hedges'g) of scattered trees on pasture yield among four functional groups and across all groups (bars = 95% confidence intervals; mean effect size significantly different from 0 for 95% confidence intervals without 0; in () mean number of observations in each group with effect size >0, =0, and <0; means with different letter significantly different at $P < 0.05$ (contrast tests)).

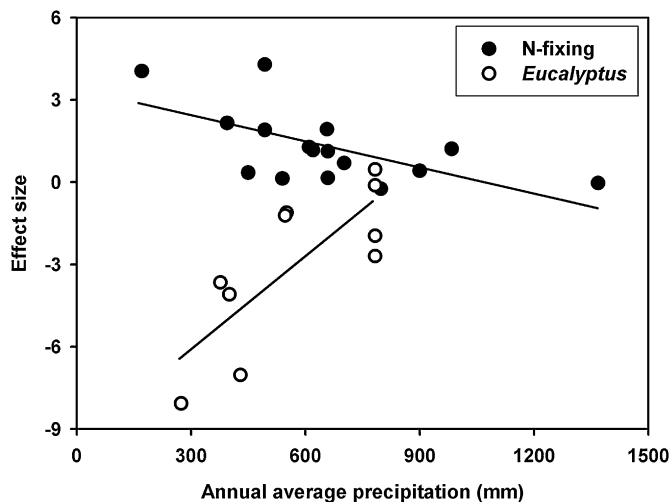


Fig. 2. Linear relationship between annual average precipitation (mm) and the effect size for the *Eucalyptus* ($n = 10$) and N_2 -fixing ($n = 16$) groups.

$P = 0.0026$) groups. A positive linear relationship ($r^2 = 0.35$) between effect size and annual precipitation was found for the *Eucalyptus* group, while a negative linear relationship ($r^2 = 0.61$) was found for the N_2 -fixing group (Fig. 2).

4. Discussion

Our meta-analysis provides evidence that the net effect of trees on pasture yield was nil across the four studied tree functional groups, i.e. pasture yield beneath and outside the canopy of scattered trees did not differ. Considerable efforts have been invested in studying the processes underlying both positive and negative effects of trees on pasture yield (Scholes and Archer, 1997; Sankaran et al., 2004; Marañón et al., 2009). Positive tree canopy effects may involve, for example, microclimatic amelioration through moderate shading (ca. 50% of full sunlight) that may lower soil and air temperatures, reduce pasture evaporative demand and water stress, and enhance plant water-use efficiency (Frost and McDougald, 1989; Belsky, 1994; Moreno, 2008). Tree canopies may also improve soil properties, especially nutrient availability (Belsky et al., 1989; Jackson et al., 1990; Ludwig et al., 2004; Barnes et al., 2009), i.e. the so-called “islands of fertility,” a key pathway through which the nutritional quality of herbaceous understorey may be improved for livestock (Treydte et al., 2007; Cubera et al., 2009; Barnes et al., 2011). Negative tree canopy effects include excessive interception of light and precipitation (Ko and Reich, 1993; Marañón and Bartolome, 1993; Ludwig et al., 2001). Positive belowground tree effects may involve hydraulic lift (Ludwig et al., 2003) and increased water infiltration rates (Joffre and Rambal, 1988). Negative belowground tree effects mainly involve competition for water (Anderson et al., 2001; Ludwig et al., 2004; Xu et al., 2011). Other effects of trees on pasture development include life stage, plant density, herbaceous species composition, species-specific physiological responses, and abiotic stress (Callaway and Walker, 1997). Hence, our results suggest that positive and negative net effects of scattered trees on pasture yield are strongly context-dependent and track the complex interplay between facilitative and competitive effects of tree species.

Given that one of the outstanding positive effects of trees is the increase of soil fertility, one could expect an enhanced positive effect of trees on pasture yield in less fertile soils. In contrast, in fertilized soils the positive effect of trees on soil properties can be outweighed by other factors driving productivity, such as

competition for light and water, which may result in decreases in understorey production beneath the trees (Moreno et al., 2007).

4.1. Tree functional groups induce contrasting effects on pasture yield

Our study clearly showed that the sign and intensity of scattered tree effects on pasture yield vary between tree functional groups. We believe the contrasting effects of *Eucalyptus* vs N_2 -fixing group reflects a lower root niche separation potential for *Eucalyptus* species compared to N_2 -fixing species. The root niche separation model (Walter, 1971) assumes that water is the primary limiting factor and that trees and the herbaceous understorey have differential access to this resource because of spatial differences in their rooting profiles. *Eucalyptus* species typically develop shallow, dense fine root systems that retain water in the upper soil layers where herbaceous species roots are concentrated (Sudmeyer et al., 2002; Zerihun et al., 2006). *Eucalyptus* species also produce phytotoxic compounds (likely allelopathic) that may have inhibitory effects on the pasture understorey (Espinosa-García et al., 2008). Furthermore, *Eucalyptus* litter decomposition and root exudates are likely to increase soil water repellency (Doerr et al., 1998). Although *Eucalyptus* species have an evergreen habit, shading is probably not a determinant of pasture yield because of their low crown densities (Jackson and Ash, 1998).

In our meta-analysis, species that were included in the N_2 -fixing group were mostly *Acacia* spp. Vinícius da Silva et al. (2009) provided fine root data that suggest a lower belowground competitive ability of *Acacia* species compared to *Eucalyptus* species. *Acacia* species may develop a deep tap root system that allows utilization of deep water sources when it is available and which can facilitate its access by pasture via hydraulic lift (Belsky et al., 1989; Belsky, 1994; Ludwig et al., 2003). Compared to *Eucalyptus* species, *Acacia* species in scattered tree ecosystems can exhibit higher spatial segregation of their root systems with respect to pasture roots. This hypothesis is supported by results from Knoop and Walker (1985), who provided evidence of belowground niche separation between *Acacia* spp. and an herbaceous understorey. Likewise, Xu et al. (2011) provided evidence of belowground niche exclusion with another N_2 -fixing tree species (*Elaeagnus angustifolia*) in a scattered tree ecosystem. As a result, the commonly expected N-enrichment incurred by N_2 -fixing trees to previously N-limited soils can outweigh moisture competition, thereby increasing pasture yield. Indeed, patches where N_2 -fixing trees occur may contain more soil nitrogen than patches with non-fixing trees. For instance, in different agroforestry and forest plantation systems, total soil N and N-mineralization enhancement by trees were found to be significantly higher in *Acacia*-based systems compared to other *Eucalyptus*, deciduous and non-fixing tree systems (Kaur et al., 2000; Jeddi and Chaieb, 2009).

Our results indicate that under deciduous and evergreen oak groups near-neutral net effects of trees on pasture yield may be more frequent. We believe this finding reflects the likely root niche separation between these tree functional groups (Moreno et al., 2005; Mulia and Dupraz, 2006) and the herbaceous layer, without any specific and predominant facilitative mechanism (at least none so direct as for N_2 -fixing tree species).

4.2. *Eucalyptus* competition and N -fixing facilitation increase in the driest conditions

The magnitude of net negative effects by *Eucalyptus* species and the net positive effect by N_2 -fixing species increased in the driest conditions. Our results thus suggest that the relationships between drought pressure and tree-pasture interactions depends on tree functional group in scattered tree ecosystems, which agrees with

the refined stress-gradient hypothesis (Maestre et al., 2009). The latter states that the sign of an interaction depends on the interacting species and predicts that facilitation increases with increased water limitation, when the beneficiary (e.g. pasture plants) and benefactor (e.g. N_2 -fixing tree) species are competitive and stress-tolerant, respectively. In contrast, it predicts that the effect of neighbors can be negative with increased abiotic stress when both interacting groups of species (e.g. *Eucalyptus* spp. and pasture plants) have similar “competitive” life histories. The decreased facilitative effect of N_2 -fixing trees where rainfall is less limiting may be due to increased tree root densities and competition within the tree-crown zone, where trees could take advantage of soils richer in nutrients (Belsky, 1994). The increased competitive effect of *Eucalyptus* species under high water stress conditions are likely to occur because the ratio of belowground biomass to aboveground vegetation biomass in *Eucalyptus* is expected to increase as annual rainfall decreases (Zerihun et al., 2006). This biomass distribution adjustment may facilitate the acquisition of water by *Eucalyptus*. As a result, the level of the most limiting resource (i.e. water) is so low that the potential benefits provided by *Eucalyptus* (e.g. soil nutrient enrichment, Barnes et al., 2011) cannot overcome its own resource uptake demands (Maestre and Cortina, 2004).

Understanding under what environmental conditions and for what tree species scattered tree ecosystems are likely to produce more or less forage is increasingly important in light of global climate change. For example, the IPCC (2007) predicts increased severity and frequency of drought in many regions of the globe over the next several decades. Our results suggest that, as drought pressure increases abiotic stress, facilitation of N_2 -fixing species and competition of *Eucalyptus* species will become the most common interaction between scattered trees and pasture.

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