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Chapter 21

A framework for analysing spatial patterns and extent of influence by single trees on ecosystem properties in agroforestry

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Abstract

Scattered and isolated trees are a common feature of traditional agroforestry systems, urban landscapes and many other natural and human-modified landscapes. However, they are rarely systematically studied and our understanding of their influence on ecosystem properties is incomplete. The challenge is to provide accurate information on their influences in the landscapes they occur so that evidence-based policies and practices can be formulated for their preservation and management. We undertook a review and analyses with the aim to provide evidence and mechanistic explanation for spatial patterning of ecosystem properties around isolated trees. Using 36 datasets collected from sites across the globe, we show that single-tree effects are monotonically decreasing functions of distance from the trunk. Lateral root density, hydraulic conductivity, soil organic carbon concentrations, nutrient pools, crop yields and biomass of understorey vegetation showed predictable spatial patterns consistent with distance-decay models implicit in Tobler's first law of geography and the neutral theory of biogeography. In 24 out of the 36 cases analysed, the power-law distance-decay model described the patterns better than the exponential decay model. It is concluded that tree effects exceed the crown projection area, and therefore the contribution of isolated tree stands to ecosystem functioning may be disproportionately larger than the area they occupy. The analyses provided a new perspective of pattern formation supporting the notion that isolated trees are keystone structures in the ecosystems where they occur. This provides justification for their protection and prudent management. The patterns elucidated also provide a theoretical justification for a paradigm shift in study design and statistical analysis of tree effects in agroforestry. Since measurements are monotonically decreasing (or increasing) functions of distance from the trunk, we discourage the use of distance as a fixed effect in statistical models when analysing data from agroforestry systems.

Key words: Anisotropy, distance-decay, dehesa, montado, influence circles, keystone structure; oligotrophic

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1. Introduction

Scattered and isolated trees are a common feature of traditional agroforestry systems and many natural, cultural and human-modified landscapes worldwide (Hall and Bunce 2011; Lindenmayer et al. 2012; Manning et al. 2006). Typical examples include dehesas and montados in Mediterranean landscapes (Joffre et al. 1999), savannas and parklands in Africa (Boffa 1999) and India (Batish et al. 2008), Cerrados and Caatinga in Brazil, Trachypogon savannas in Venezuelan, paddocks in the arid rangelands of Australia (Wilson and Lemon 2004), oak savannas in North America, British wood-pastures and the forest-tundra transition zone (Manning et al. 2006). Isolated trees are also a common feature of urban landscapes (Streiling and Matzarakis 2003). Although the role of isolated trees in bio-geochemical processes and biodiversity has recurrently attracted significant researcher attention, they are often poorly managed because their contributions remain underappreciated. Populations of large old trees are also rapidly declining in many parts of the world (Fischer et al. 2010; Lindenmayer et al. 2012) due to urbanization, infrastructure development, agricultural activities and grazing (Lindenmayer et al. 2014; Miguel et al. 2013; Stagoll et al. 2012). The decline in old trees will have serious implications for ecosystem integrity and biodiversity (Fischer et al. 2010; Lindenmayer et al. 2014).

Isolated trees play many ecological roles including the storage of large amounts of carbon, nutrient cycling, improved crop and pasture productivity (Abdallah et al. 2012; Miguel et al. 2013; Vetaas 1992), provision of key habitats for wildlife (Dean et al. 1999; Lindenmayer et al., 2014) and improvement of the urban climate (Streiling and Matzarakis 2003). In systems where scattered trees are associated with crops or pasture, the trees play a vital role not only in crop and forage production, but also soil and water conservation and CO₂ sequestration (Gebrewahid et al., 2018; Nath et al. 2021; Roupsard et al. 2020; Sileshi 2016). For example, the trees create long-term spatial heterogeneity in resources of high interest for adaptation and mitigation of climate change, and the provision of ecosystem services especially in dry areas (Roupsard et al. 2020; Sileshi 2016; Tzuk et al. 2020). At the landscape scale, their roles may include increased tree cover, habitat connectivity for animals, genetic connectivity for tree populations, and ecological continuity through time (Manning et al. 2006). At the local scale, their ecological functions may include modification of the hydrology (Chandler and Chappell, 2008), provision of a distinct microclimate, increased soil fertility, plant species richness and structural complexity (Lindenmayer et al. 2012; Miguel et al. 2013; Manning et al. 2006; Oliver et al. 2006). Soil enrichment by trees has been reported to create islands of fertility supporting distinctive plant assemblages and hotspots of animal activity (Belsky et al. 1989; Dean et al. 1999; Rhoades 1997; Schnabel et al. 2013; Sileshi 2016). Even in arid areas isolated trees have been shown to increase biodiversity by structuring the habitat vertically and horizontally (Dean et al. 1999). However, contradictory reports are common, where some studies reported increased soil fertility and understorey vegetation biomass, while others reported decrease or no effects (e.g., Abrams et al. 1997; Austin-Petersen et al. 2002; Sileshi 2016).

These conflicting results could arise either from context-specific interactions, differences in tree species traits and the environment (Ayres et al. 2009; Burrows 1993; Jetsch et al. 1996). Figure 1 provides a simple conceptual diagram of the possible interactions between the environment, the tree, and understorey vegetation. The growth and performance of a particular tree species largely depends on climate and soil properties, but tree spacing, density, age and tree management (e.g., pruning, lopping, etc.) can also play a determining role on the size of their zones of influence. The leaf lifespan (evergreen vs. deciduous) plays a role in controlling the timing of the litter fall, while litter stoichiometry may control the litter decay rates. These and the distribution of fine roots and their phenology together with soil water content, temperature, soil biota may control accumulation of soil organic matter (SOM), nutrient pools, and finally the productivity of understorey vegetation (Fig. 1).

Since tree species exhibit broad variation in their canopy and root architecture, and the quality and quantity of their inputs to soil, it is likely that these differences will create distinctive soil environments (Ayres et al. 2009). However, most of these effects show broadly similar spatial patterns centred around each tree (Amiotti et al. 2000; Jose and Gillespie 1998; Zinke 1962). These

patterns, called “influence circles” (Fig. 1), have been widely demonstrated by empirical data (Amiotti et al. 2000; Zinke 1962). The younger and closer the trees are, the more their influence circles merge; but a more definite pattern will emerge as the trees grow older and the spacing becomes wider (Zinke 1962). Despite the complex interactions between trees and their growing environment (Fig. 1), certain features remain consistent as they follow first principles. The distance-decay of spatial interactions is one such principle. Distance-decay principles posit that the nearer two locations are, the greater is the expected interaction between the two. This has been formalized as Tobler’s first law of geography (Tobler 1970) and the neutral theory of biogeography and community assembly (Hubble 2000; O’Dwyer et al. 2010).

Distance plays a cardinal role in interactions of various types underpinning a host of empirical regularities (Chen 2015; Hubble 2000; O’Dwyer et al. 2010; Tobler 1970). For example, the similarity among pairs of biological communities typically decays with increasing spatial or environmental distance (Nekola and White 1999). Similarly, tree root profiles often follow a negative exponential pattern of decay (Jackson et al. 1996). Tree root densities and soil fertility also show a sharp decrease with distance from the trunk (e.g., Moreno and Obrador 2007; Moreno et al., 2005; Sileshi 2016). Nevertheless, our knowledge of distance-decay in single-tree effects on soil and understorey crops is limited. A key challenge for good management (i.e., in managed systems) is to understand the spatial patterning in soil functions and crop productivity around isolated trees. This kind of information is relevant for land owners and natural resource managers to enable them to take more informed decisions on whether or not to retain isolated trees in the landscape. The challenge for ecologists lies in accurately modelling and quantifying the impacts of isolated trees so that this information can be quantitatively scaled up to whole farm and landscape levels. In many studies in the past, inferences were based on study designs where distance classes are used as fixed effects. This kind of analysis assumes that measured variables are identically and independently distributed among distance classes, while in reality this is not true. Although distance-decay models can reveal spatial patterns and provide mechanistic insights, they have not been used in modelling effects of isolated trees in ecosystems. Therefore, the objective of this paper was to model and provide mechanistic insights into the spatial patterning of single-tree influences in the ecosystems where they occur. The key hypotheses were: (1) single-tree effects are monotonically decreasing functions of distance from the trunk consistent with distance-decay models of spatial interaction, and (b) the power-law distance-decay model describes single-tree effects better than the exponential distance-decay model.

2. Methods and analytical framework

2.1. Sources of data

We searched the literature focussing on published primary literature and reviews, and identified studies that reported measurements of response variables at a minimum of five distance classes (i.e., sample size $N \geq 5$) from the tree trunk in the target systems. This minimum was set because model parameters and the Akaike information criterion (AIC) used for model comparison cannot be correctly estimated for $N < 5$. In total 36 datasets from 15 peer-reviewed publications qualified for inclusion. The methods used for data collection in those studies are briefly described below organized according to the number of studies and geographic area. A larger number of studies were found in Mediterranean and Europe landscapes and Africa followed by Asia. One study each were found in Australia and the Americas (Table 1).

2.1.1. Parklands in the Mediterranean and Europe

In Mediterranean landscapes, Dehesa (in Spain) and montado (in Portugal) are high nature and cultural value systems forming one of the largest agroforestry land-uses in Europe (den Herder et al. 2017; Moreno et al. 2018; Pinto-Correia et al. 2018). Dehesa is dominated by Mediterranean tree species that are distributed without a regular pattern on pasture land, cropland or fallow land (Joffre et al. 1999; Simón et al. 2012). The trees are originally derived from oak (*Quercus* spp.) forests which were progressively thinned, through time creating an open park-like savannah (Moreno et al.

2013; Simón et al. 2012). The tree species in dehesa can be either evergreen species mainly holm oak (*Quercus ilex*) and cork oak (*Q. suber*) or deciduous species such as Pyrenean oak (*Q. pyrenaica*) and (c) semi-deciduous species such as Lusitanian oak (*Q. faginea*) and Algerian oak (*Q. canariensis*) (Moreno et al. 2013). Montado is mainly characterized by pure or mixed stands of cork oak, holm oak and Pyrenean oak (Pinto-Correia and Mascarenhas 1999). The trees occur at a density of 15–45 per hectare with a canopy cover of 21–40% (Moreno and Pulido 2009).

Table 1. Studies that qualified for inclusion in this analysis

Source	Variable analysed	Location
Chandler and Chappell (2008)	Hydraulic conductivity under <i>Quercus robur</i>	Lancashire, England
Gea-Izquierdo et al. (2010)	Grass yield, soil organic carbon (SOC) and total nitrogen (N) under <i>Quercus ilex</i>	West Central Spain
Moreno and Obrador, 2007	Total N under <i>Quercus ilex</i>	Central West Spain
Montero et al. (2008)	Solar radiation under <i>Quercus ilex</i>	Southwest Spain
Alemie (2009)	Light intensity, soil hydrophobicity; maize yield under <i>Eucalyptus</i>	Northern Ethiopia
Grouzis and Akpo (1997)	Herbaceous vegetation biomass under <i>Balanites</i> and <i>Acacia</i>	Ferlo Zone, Senegal
Weltzin & Coughenour (1990)	Grass biomass under <i>Acacia tortilis</i>	Turkana, Kenya
Tomlinson et al. (1998)	Root number, total N, available phosphorus (P) and potassium (K) under <i>Parkia biglobosa</i>	Burkina Faso
Belsky et al. (1989)	SOC, available P, Ca, K, pH, soil moisture and temperature under <i>Acacia tortilis</i> and <i>Adansonia digitata</i>	Tsavo, Kenya
Hailu et al. (2000)	Litter biomass, SOC and soil nutrients under <i>Milletia ferruginea</i>	Wondogenet, Ethiopia
Yadav et al. (1993)	Mustard yield under <i>Acacia nilotica</i>	Haryana, India
Singh et al. (1998)	Wheat yield under <i>Populus deltoides</i>	Punjab, India
Singh and Kohli (1992)	Phytotoxins in the soil, yield of chickpea, lentil, wheat, cauliflower, toria under <i>Eucalyptus</i>	India
Oliver et al. (2006)	litter biomass, soil SOC and N under <i>Eucalyptus nova-anglica</i>	New South Wales, Australia
Schnabel et al. (2013)	SOC and N under <i>Quercus douglasii</i>	Northern California, USA

From Mediterranean and Europe, studies by Chandler and Chappell (2008), Gea-Izquierdo et al. (2010), Moreno and Obrador (2007) and Montero et al. (2008) qualified for inclusion in this analysis. Chandler and Chappell (2008) studied the influence of English oaks (*Quercus robur*) trees on saturated hydraulic conductivity (K_s) within the 0.10–0.25 m soil depth in parklands in Lancashire, England. K_s was measured at seven distances (1, 3, 5, 7, 9, 11 and 13 m) from the trunk along eight transects. In this analysis the geometric mean and median K_s ($m\ s^{-1} \times 10^{-6}$) data recorded at each distance from the tree were used for modelling. In the study by Gea-Izquierdo et al. (2010) variations in grass yield, soil organic matter (SOM %) and total nitrogen (N %) were quantified under holm oak trees in West Central Spain. For sampling grass, eight points were placed proportionally to the crown radius (R) in North-East (NE) direction representing the lowest exposure to sunlight, and eight in the South-West (SW) representing the highest exposure. The sampling points for grass yield were located at six distances (0.25, 0.5, 0.75, 1.0, 1.25, 1.5, 1.75 and 2.0xR) from each tree in NE and SW directions. Then, herbaceous material was collected in May and April using 50x50 cm frames, and dried for 48 h at 60°C. Similarly, soil samples were collected from the top 20 cm depth at 6 distances proportional to the crown radius (0.375, 0.75, 1.0, 1.5, 2.0 and 2.5xR) in the NE and SW orientations. In the study by Moreno and Obrador (2007), soil nutrients contents were analysed in four Spanish dehesas under three land use types: isolated holm oak with an understorey of native grasses, shrub encroached and crops. Six oak trees were selected randomly per land use, and soil samples were collected at five distances from each tree trunk (i.e., 2, 5, 10, 15, and 20 m) from the 0–30 cm soil depth. Total soil nitrogen (%) contents under the three land use types (i.e., native grasses, shrub encroached and crops) were analysed separately for the present review. In the study by Montero et al. (2008), the radiation transmitted through holm oak tree canopy (radius 3.9 to 4.4 m) to the understorey pasture and crops was quantified in dehesas of

Southwest Spain. The percentage of radiation transmitted was recorded at six distances from the tree trunk (0.5, 1, 5, 10, 20 and 30 m).

2.1.2. Savannas and agroforestry parklands in Africa

Savannas are a vegetation type with a continuous grass layer interspersed with a discontinuous layer of trees, shrubs and forbs (Siebert and Dreber 2019). Small-scale facilitative interaction between the woody and herbaceous components and competitive interaction on larger scales together explain the dynamic coexistence of trees and herbaceous vegetation (Vetaas 1992). Isolated trees are known to structure plant and animal communities and determine patterns and patch dynamics in arid and semi-arid savannas (Belsky et al. 1989; Dean et al. 1999). Most African savanna are a mosaic of savanna habitats and small-scale agriculture (Tripathi et al. 2021). Many African savannas are the new frontier of agricultural expansion (Estes et al. 2016; Tripathi et al. 2021).

Agroforestry parklands are one of the most widespread traditional land use systems in African savannas (Boffa 1999; Teklehaimanot, 2004). They represent traditional land use systems in the semi-arid or subhumid tropics in West Africa, Central Africa, East Africa and to a lesser extent in southern Africa (Boffa 1999). Farmers usually protect naturally regenerating savanna trees during tillage operations thus keeping tree density low so that canopy cover is not continuous. Therefore, isolated tree stands of uneven age, height and canopy are found associated with crops. Although parklands are highly variable, the common species include *Faidherbia albida*, *Parkia biglobosa*, *Vitellaria paradoxa*, *Adansonia digitata*, *Balanites aegyptiaca*, *Tamarindus indica* and *Vachelia* (formerly *Acacia*) species (Boffa 1999; Teklehaimanot 2004).

Six studies from African savannas and agroforestry qualified for inclusion in the analysis. These are studies by Grouzis and Akpo (1997), Weltzin and Coughenour (1990), Tomlinson et al. (1998), Belsky et al. (1989), Alemie (2009) and Hailu et al. (2000). In the study by Grouzis and Akpo (1997), variations in herbaceous vegetation with distance from *Balanites* and *Acacia* trees were determined in a dry Sahelian savanna in Senegal. The understorey vegetation was harvested from 50 x 50 cm plots at distances of 1.25, 2.5, 3.75, 5.0, 6.25, 7.5, 8.75 and 10 m from the trunks in the four cardinal directions. Biomass samples were dried to a constant weight at 85°C.

In Weltzin and Coughenour (1990) grass biomass under 15 isolated *Acacia tortilis* trees was quantified in a savanna in Turkana in Kenya. Grass was harvested from 50 x 50 cm plots placed at nine distances (bole, 25, 50, 75, 100, 125, 150, 175 and 200% of the canopy radius) along each transect, where 100% of the canopy radius represented the drip line. Grassy vegetation was clipped to ground level and dried to constant weight at 85°C.

Tomlinson et al. (1998) determined the root systems of mature *Parkia biglobosa* trees (age 40–60 years, mean diameter at breast height of 49.5 cm and crown radius of 7.02 m) on three savanna locations in Burkina Faso. Roots were excavated using a logarithmic spiral trench to a depth of 60 cm, and the numbers of roots were recorded by placing 50 x 50 cm quadrats positioned along the spiral trench up to a distance of 10 m from the trunk with increments of 1 m. Root counts were expressed as number of roots m⁻². Soil samples were taken at distances of 1, 3, 5, 7 and 9 m measured linearly from the trunk, and total nitrogen, available phosphorus and available potassium were determined.

Belsky et al. (1989) quantified vegetation and soil characteristics around isolated, mature trees of *Acacia tortilis* and *Adansonia digitata* in Tsavo National Park, a semi-arid savanna in Kenya. Soil samples were collected at 5 m intervals along the 50-m vegetation transects from the 0-10 cm depths and SOM, P, Ca, K and soil pH were determined. In addition, soil temperatures were recorded in the 5 and 10 cm depth at 5-m intervals along 40-m transects extending east and west from the bases of target trees. In this analysis, SOM and soil temperatures recorded at 5 cm depth (mean of the east and west transects) were analysed. Since P, Ca and K concentrations followed the same pattern as SOC, these were not presented to avoid cluttering.

Alemie (2009) determined the effect of *Eucalyptus* trees in agroforestry on light intensity, soil hydrophobicity and maize yields at different distances in northern Ethiopia. Light intensity was determined using a light meter at 0.5, 1, 2, 5, 10, 15, 20 and 40 m distances from the tree in maize

fields at different times during a day. For this analysis data collected in the morning (9:00 am) and at noon (12:00) were used. Hydrophobicity was determined using the water drop penetration time (WDPT) test. This test determines how long water repellence persists on the soil surface. The test was done on soil samples collected at 16 distances from the tree (0-300 cm) at 20 cm intervals from three separate plots. The time it took (in seconds) for complete penetration of water drops was recorded. For this analysis, the mean of the data from field dry soil was used. Maize grain yield was recorded in 2 m x 2 m plots at 1, 5, 10, 15, 20 and 40 m distances from the tree trunk, and values were converted to a hectare (kg ha^{-1}). For this analysis, the response ratio was calculated (see below for details) from the mean of three replicate plots.

Hailu et al. (2000) quantified variations in litter biomass, SOC and soil nutrients under *Millettia ferruginea*, a nitrogen fixing tree maintained by farmers in traditional agroforestry practices in southern Ethiopia. The crown diameter of the trees was on average 6.75 m. Sampling plots of 0.5 x 0.5 m were established around four isolated trees in each of four radial transects at distances of 0.75, 2.75, 4.75, 6.75 and 29.5 m from the tree, and litter biomass, SOC, total N, available P, Mg, Na and CEC were determined.

2.1.3. Agroforestry practices in India

Isolated trees are also common elements of various agroforestry practices in India especially in the agrisilvicultural, agrosilvopastoral and silvopastoral systems, covering an estimated area of 8.7, 5.6 and 2.4 million ha (Nath et al. 2021). These are described in detail in Nath et al. (2021). Three studies namely, Yadav et al. (1993), Singh et al. (1998) and Singh and Kohli (1992) qualified for inclusion in this analysis. In the study by Yadav et al. (1993), yields of mustard were measured under *Acacia nilotica* on sample plots of one m^2 laid out in concentric circles around each tree at nine distances (1, 3, 5, 7, 9, 11, 14, 18 and 22 m) from the tree. In the study by Singh et al. (1998), wheat yields were measured at 11 distances up to 20 m from *Populus deltoides* in the Punjab region of India. Singh and Kohli (1992) recorded phytotoxins in the soil at distances of 0.5, 1, 2, 3, 5 and 10 m under *Eucalyptus tereticornis*. They also recorded the economic yield of chickpea (*Cicer arietinum*), lentil (*Lens esculentum*), wheat (*Triticum aestivum*), cauliflower (*Brassica oleracea*), toria (*Brassica campestris*) at distances of 1, 2, 3, 5, 7, 9, 11, 12, 13 and 15 m from *Eucalyptus* shelterbelts.

2.1.4. Paddock trees in Australia

Across much of temperate Australia, isolated trees or small patches of trees locally called paddock trees are a visually defining feature of the agricultural landscape, where they occupy as much as 20 million hectares of farmland (Eldridge and Wong 2005; Wilson and Lemon 2004). These are particularly common in the arid rangelands, where remnant patches of native vegetation and isolated trees of *Eucalyptus* species form an open canopy within a matrix of improved pasture (Eldridge and Wong 2005). A study by Oliver et al. (2006) qualified for inclusion in this analysis. In that study litter biomass as well as soil SOC and N were quantified under *Eucalyptus nova-anglica* in open paddocks in New South Wales. Sampling took place in a star design at 16 distances from the tree every second metre along 30-m transects. Total litter (leaves, twigs, etc.) was collected in a 25x25 cm quadrat at each sampling point and air-dried at room temperature for 1 week before weighing. At the same points, soil samples were taken from the 0-10 cm depth to determine SOC (%) and soil nitrogen (%).

2.1.5. Oak savannas of North America

Oak savannas of North America are characterised by an overstorey dominated by oak species with 10–30% crown cover (Dey et al. 2017). Like the Spanish dehesas, oak savannas are formed of evergreen and deciduous oaks within a grassland matrix dominated by annual grasses and forbs, where livestock production is integrated (Moreno et al., 2013). The common oaks are evergreen species including coast live oak (*Quercus agrifolia*) and interior live oak (*Q. wislizenii*), deciduous species mainly blue oak (*Q. douglasii*) and valley oak (*Q. lobata*), and semi-deciduous species

Englemann oak (*Q. engelmannii*) (Moreno et al., 2013). One study by Schnabel et al. (2013) from this system qualified for inclusion in this analysis. The authors measured SOC (%) and N (%) at 11 equal distances from the tree bole using canopy radius (R) increments of 0.25 (0-2.5 x R) in grazed soils in the Sierra Nevada foothills of northern California. Samples were taken around four blue oak (*Q. douglasii*) trees along the 11 sampling points established in the four directions (i.e., north, east, south and west transects). For each sampling distance, the mean of 16 measurements (4 trees x 4 directions) was used for analysis.

2.2. Theory, models and data analyses

The various factors depicted in Fig. 1 may influence parameters of the distance-decay models. However, for a given tree in a specific location these factors are constant and therefore the distance-decay modelling can be performed without further complications. The modelling in the present analysis is based on existing theory, namely, Tobler's first law (Tobler 1970) and the neutral theory of biogeography and community assembly (Hubble 2000; O'Dwyer et al. 2010). Tobler's first law of geography states that everything is related to everything else, but near things are more related than distant things. In his Neutral Theory, Hubble (2000) proposed the distance-decay of similarity in community composition under ecological drift. Indeed, neutral theory provides a null model for ecologists concerned with the question of how community similarity changes with distance across a landscape (Nekola and White 1999). Distance-decay models are sensitive to key spatial processes and therefore serve as a powerful tool for testing mechanistic ecological theories (Morlon et al. 2008). However, the choice of the functional form can make important difference for predictions.

Distance-decay patterns are normally modelled using the power-law distance-decay model (PDM) and exponential distance-decay model (EDM) (Nekola and White 1999; O'Dwyer et al. 2010; Sileshi and Arshad 2012). However, the performances of the PDM and EDM differ with observational scale (Nekola and McGill 2014). According to a meta-analysis of 26 ecological and four human-system datasets (Nekola and McGill 2014), PDM prevailed at small scale where the species pool remains constant, but EDM prevailed at larger scales over which the species pool varies. The difference between PDM and EDM is significant due to the distributional assumptions inherent in the mathematical functions involved.

The exponential function describes a simple distribution (Chen 2015), whereas the power function describes a scale neutral and complex distribution. As such the power-law function has been widely used in the studies of complexity in physical and biological phenomena (Chen 2015; Marković and Gros 2014). The origin of the power-law behaviour in complex systems is the property of self-organized criticality (Bak et al. 1987; Marković and Gros 2014). According to Chen (2015) a power-law distribution can be deduced from a pair of exponential distributions. This suggests that a power law is based on dual entropy-maximizing processes, which are of unity of opposites in self-organized evolution (Chen 2015). When placed in a spatial context, PDM implies that the strength of relationships between locations decreases as a function of distance at all spatial scales (Palmer 2005).

In this analysis, we applied both the PDM and EDM assuming two scenarios: Scenario 1 represents situations where the tree depresses a measured variable close to the trunk (Fig. 2A), whereas Scenario 2 represents the tree elevates the measured variable near the trunk due to some positive (facilitative) effects (Fig. 2B). In either case, the tree effects are hypothesized to be monotonically decreasing functions of distance from the trunk.

In an unconstrained system, EDM has the following form:

$$Y = \alpha e^{-\beta D} \quad \text{Equation 1}$$

where Y is the dependent variable, D is distance from the origin (here the tree base), e is the base of the natural logarithm, α represents an initial value of Y and β is the exponent.

The PDM has the following form:

$$Y = \alpha D^{-\beta} \quad \text{Equation 2}$$

where α is the normalization constant and β is the exponent often treated as a scale-invariant quantity. In both equations 1 and 2, β represents the rate of decay, i.e., the proportion of similarity lost per unit distance.

In EDM and PDM, β is of great interest because it is key for interpreting scaling relationships, and addressing hypotheses about interactions at different scales. Estimates of β often tend to be scale invariant and therefore may not significantly differ from each other for a given relationship studied in different circumstances (Tables 1-3). If the base of the tree is taken as an invariant point source (i.e., $\alpha = 100\%$ tree effect) for a hypothetical pattern, Y is expected to vary as in Fig. 2C and D in the different directions away from the tree. In that sense, Y may be conceptualized as an interaction strength varying from 0 for no tree influence in the open area to 100 for maximum effect near the trunk. β will be significantly larger than 0 if the tree depresses the measured variable near the trunk with greater intensity, but the tree effect decays with distance (Fig. 2A). Conversely, β will be significantly smaller than 0 if the tree effect is positive or facilitative and the values of the variable are elevated near the trunk relative to locations further away (Fig. 2B).

The tree effect can be partitioned into aboveground (canopy) and belowground (root) effects, which decay with distance as demonstrated by Barbier et al. (2008) and Belsky et al. (1989). Figure 2C and D depicts scenarios for canopy and root effects assuming PDM and EDM. Predictions of EDM (Fig. 2C) decay faster rate than PDM (Fig. 2D). The root effect is hypothesized to decay at a much slower rate than canopy effects (Fig. 2C, D) because lateral roots can extend several meters beyond the crown projection area (Barbier et al. 2008; Belsky et al. 1989), and much of the competition among plants takes place belowground. For simplicity, Fig. 2C and D depicts isotropy in measured variables, i.e., identical properties with values of β being the same in all transects. However, our default model assumes anisotropy (directional variations in β) along different transects. This is because Y may vary with cardinal directions, slope or aspect arising from differences in light and rainfall interception or surface run off. Normally, roots show symmetrical lateral distribution when trees grow on plane soil, but asymmetry is common on steep slopes as a consequence of preferential root elongation to increase the plant's stability (Chiatante et al. 2002).

Any directional variation or deviations from the hypothesized distance-decay may be confirmed using the differences in β , with the caveat that the estimators are considered reasonably close to linearity. This must be confirmed using Hougaard's measure of skewness $|g|$. Skewness is apparent if $|g|$ 0.25-1.0, but a parameter is considerably biased if $|g| > 1.0$ (Ratkowsky 1990). We deemed β estimators biased only if $|g| > 1.0$ (Ratkowsky 1990). When estimators are not biased, we used the β value and its 95% confidence intervals to judge the magnitude and direction of the tree effect on a given variable.

For most analyses we used the response ratio (RR) as the metric to be analysed. The is computed as U_i/C where U_i is the raw value of the measured variable under the canopy at distance i and C is the corresponding value measured in the control plot (Sileshi, 2016). The advantage of RR is that it is related to biologically meaningful indices such as the relative competition intensity ($= 1 - RR$) used in plant ecology (Oksanen et al. 2006). The RR also makes interpretation more straightforward than other metrics especially where measurements of the same variable were given in different units (e.g., yields measured in g m^{-2} vs t ha^{-1}). However, the use of RR may be problematic if the control plot is poorly defined as is the case in the literature reviewed. The majority of studies treated open fields or plots located farthest from the tree trunk as control plots. In some studies, anything beyond the drip line was treated as the control, although such plots can be within the tree root influence (Fig. 1). Therefore, wherever we thought the use of RR is problematic, we analysed the actual measurement.

We compared the performance of the PDM with the EDM using the bias-corrected Akaike information criterion (AIC_c) as well as the predictions and their 95% confidence limits. For studies with less than 5 distance classes ($N < 5$), the AIC_c cannot be estimated because the degrees of freedom are fewer relative to the parameters (p) to be estimated and the denominator ($N-p-1$) in the AIC_c equation becomes zero. As such the AIC_c is undefined for.

$$AIC_c = AIC + \frac{2p(p+1)}{N-p-1}$$

Equation 3

Therefore, we did not present analyses of studies with $N < 5$.

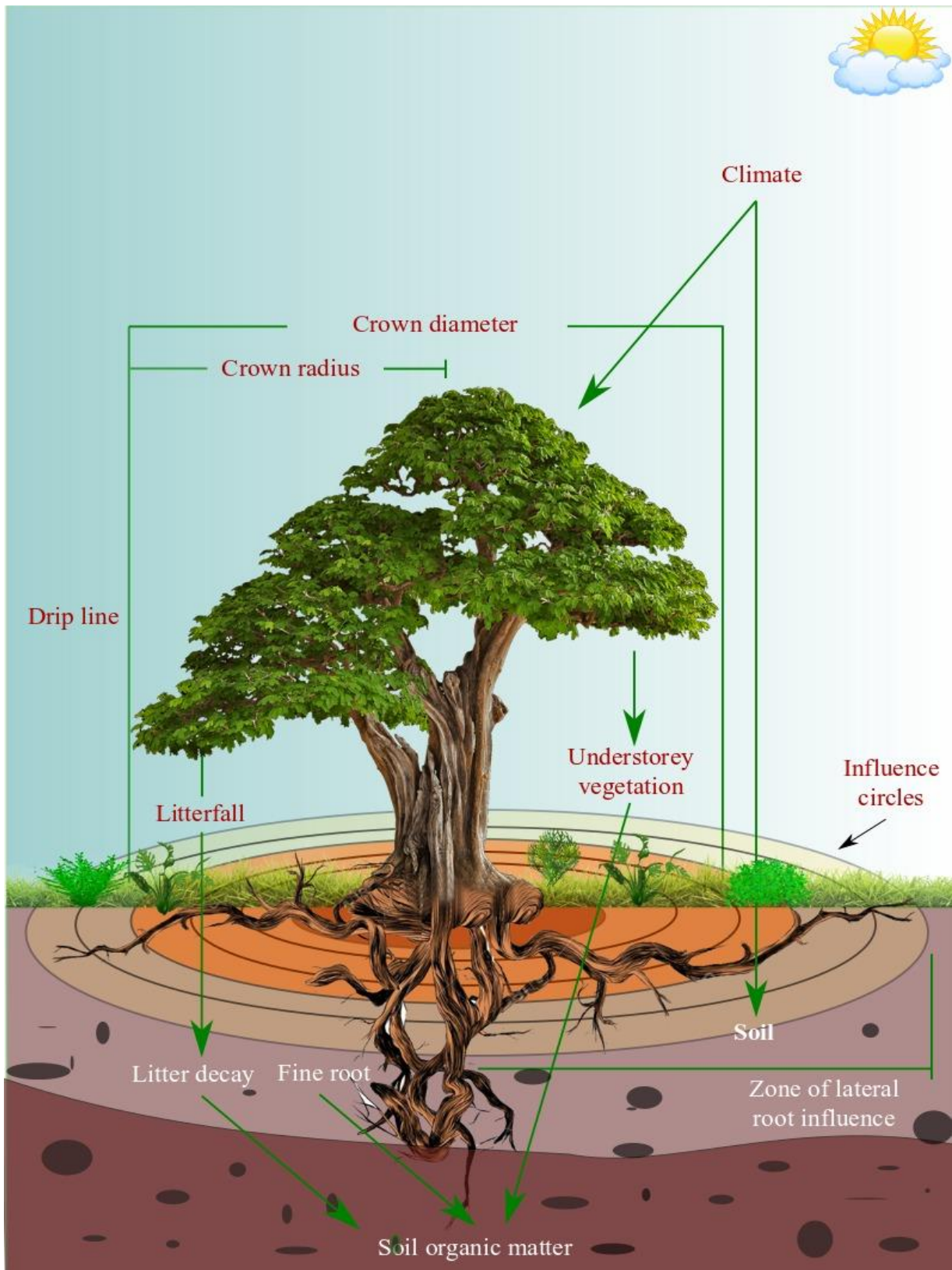


Fig 1. Conceptual representation of the interactions between the environment, single trees and understory vegetation with a schematic representation of the ecological field showing zones of tree crown (canopy) and root influence. The elliptical circles represent influence circles.

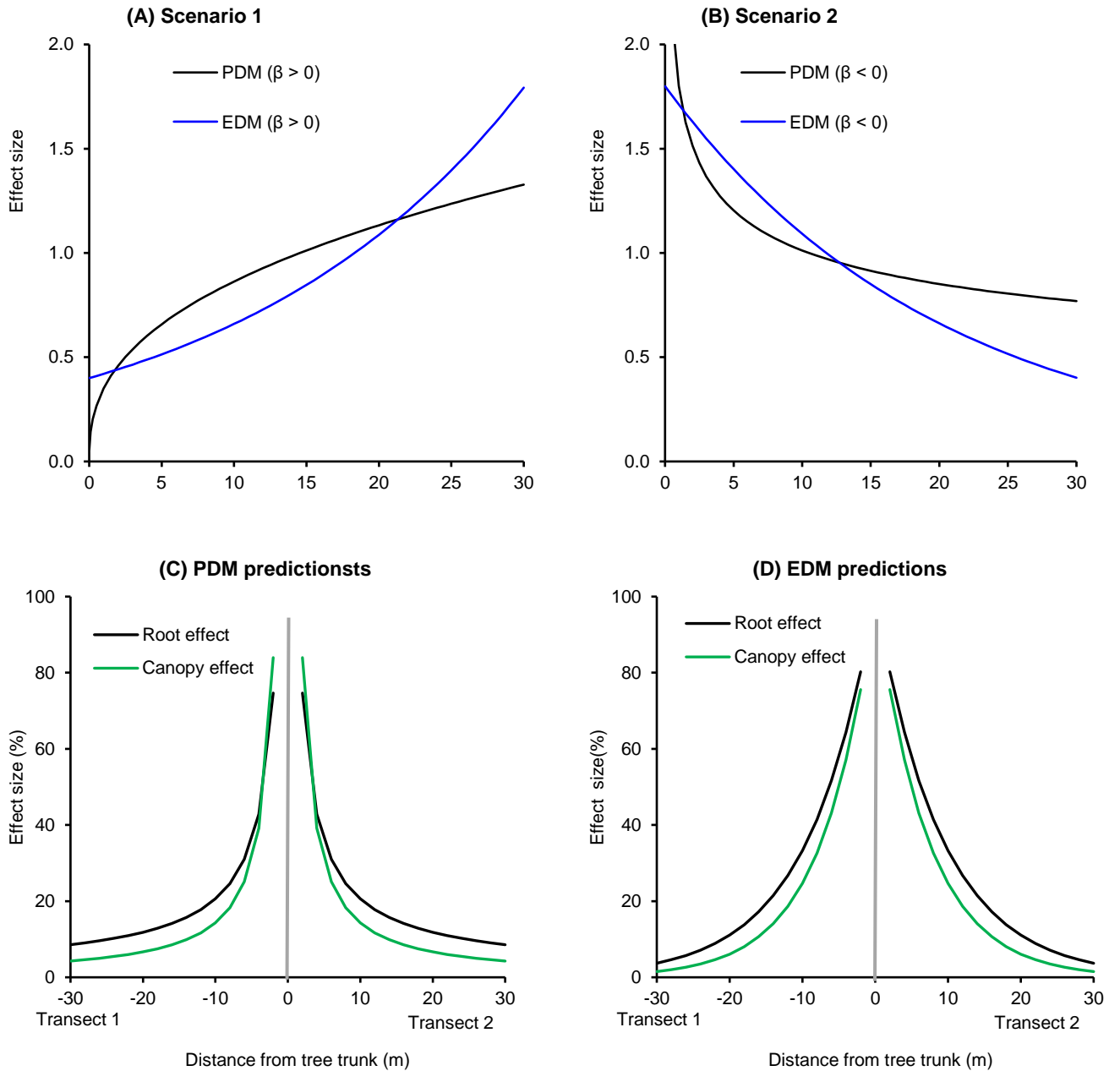


Fig. 2. Conceptual representation of tree effects assuming Scenario 1 (A) and Scenario 2 (B), and hypothesized scenarios of distance-decay in canopy and root effects assuming power-law (C) and exponential (D) distance-decay. The tree is located at distance 0, and its canopy effect is assumed to decay faster than the root effect beyond the drip line.

3. Results and discussion

3.1. Emergent patterns

3.1.1. Light availability and soil temperature,

The two datasets on light availability, namely light transmitted through holm oak canopy (Fig. 3A) and light intensity under *Eucalyptus* (Fig. 3B) followed the same pattern of distance-decay. Similarly, soil temperature at 12:00 hr and 15:00 hr in the canopy of *Acacia* trees increased with increasing distance from the tree trunk (Fig. 3C, D). The AICc indicated that PDM predictions are better than EDM for datasets (Table 1). The models did not fit the soil temperature data smoothly (Fig. 3C, D) due to the sparse sampling between the 0-10 m distance relative to the other distance classes.

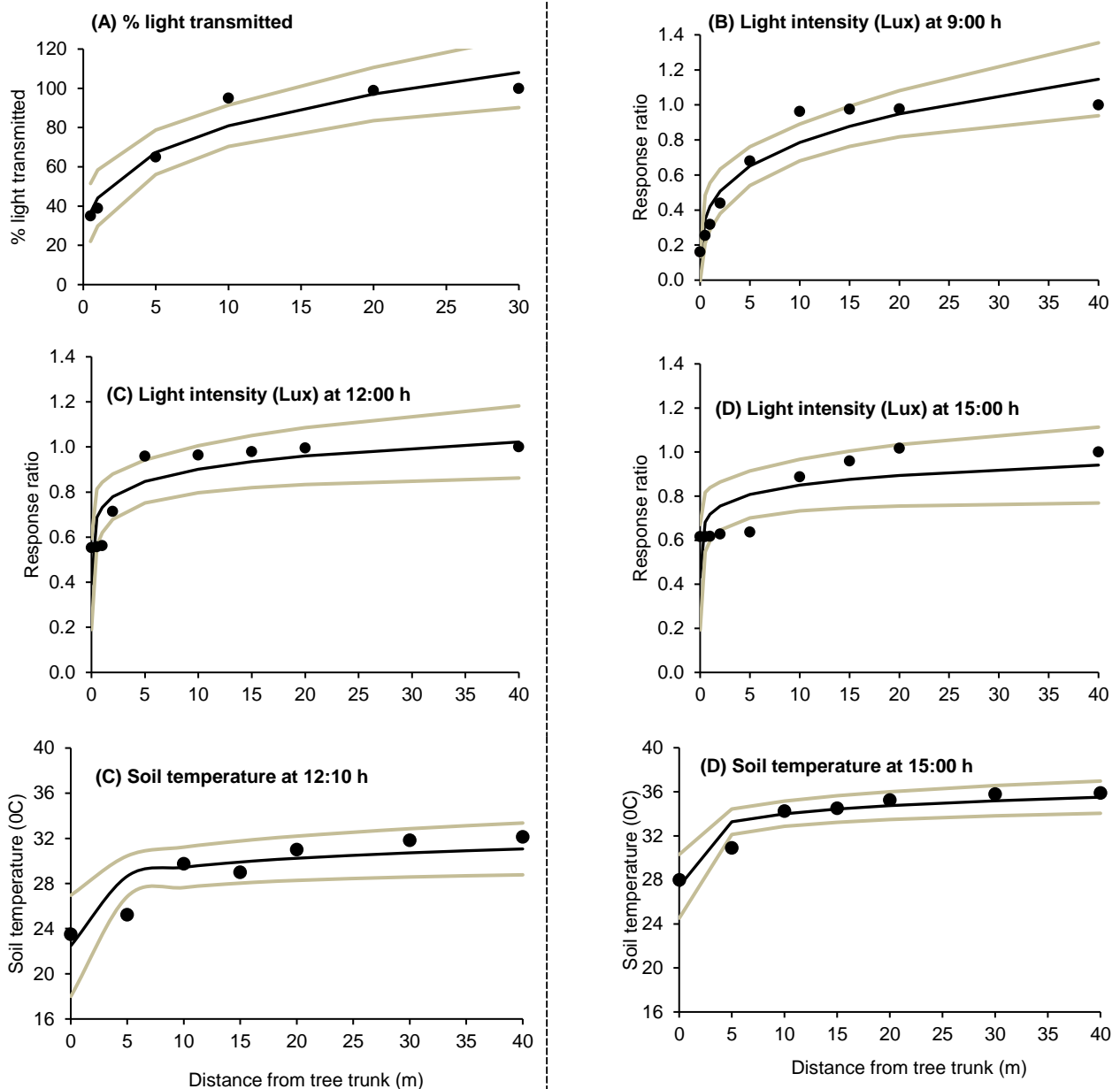


Fig. 3. Distance-decay of light intensity in the morning under *Eucalyptus* (A, B) in Ethiopia (data from Alemie, 2009); soil temperature under *Acacia tortilis* at 12:00 h and 15:00 ha (C, D) in Kenya (data from Belsky et al. 1989). Circles, black lines and grey lines represent measured values, predictions and their 95% confidence limits generated using the power function, respectively.

Table 2. Distance-decay of measured variables assuming Scenario 1 (the variable is depressed closer to tree trunks) and estimates of the exponents (β) and Akaiake information criterion

Variable	Data source	β (95% CL) [†]		AICc	
		PDM	EDM	PDM	EDM
Light transmitted	Alemie	0.60 (0.18; 1.01)	0.03 (0.01; 0.06)	-7.2	-0.4
Light intensity	Montero	0.26 (0.14; 0.38)	0.02 (0.01; 0.05)	41.5	51.7
Soil temperature 12h	Belsky	0.04 (0.01; 0.07)	0.007 (0.002; 0.011)	20.0	20.2
Soil temperature 15h	Belsky	0.03 (0.02; 0.05)	0.005 (0.001; 0.009)	13.8	20.5
Mustard yield	Yadav et al.	0.39 (0.16; 0.62)	0.04 (0.01; 0.08)	-24.1	-16.1
Maize yield	Alemie	0.60 (0.18; 1.01)	0.03 (0.01; 0.06)	-7.2	-0.4
Wheat yield	Singh & Kohli	0.83 (0.54; 1.11)	0.08 (0.03; 0.12)	-39.6	-25.9
Chickpea yield	Singh et al.	0.82 (0.33; 1.30)	0.10 (0.02; 0.17)	-23.7	-16.9
Lentil yield		1.15 (0.81; 1.49)	0.13 (0.07; 0.19)	-36.4	-24.8
Toria yield		1.07 (0.45; 1.69)	0.12 (0.03; 0.20)	-23.3	-16.9
Cauliflower yield		1.41 (0.87; 1.95)	0.14 (0.07; 0.22)	-31.6	-23.7
Available P	Alemie	0.63 (0.13; 1.14)	0.03 (0.02; 0.04)	10.1	-3.5
Exchangeable Ca		0.10 (0.03; 0.18)	0.01 (-0.01; 0.02)	12.1	19.7

^{††}Figures in parentheses are 95% confidence limits of β . All β estimators were unbiased ($|g| < 1.0$) except for PDM in chickpea and toria yields where skewness was apparent.

Table 3. Distance-decay of variables assuming Scenario 2 (the variable is elevated closer to tree trunks) and estimates of the exponents (β) and Akaiake information

Variable	Data source	β (95% CL) [†]		AICc	
		PDM	EDM	PDM	EDM
Lateral root	Tomlinson	-0.48 (-0.53; -0.44)	-0.14 (-0.18; -0.10)	53.1	72.69
Conductivity	Chandler & Chappell	-0.35 (-0.53; -0.17)	-0.08 (-0.11; -0.05)	-1.5	-9.5
Hydrophobicity	Alemie	-0.13 (-0.21; -0.04)	-0.02 (-0.018; -0.009)	223.5	193.4
Phytotoxins	Singh & Kohli	-0.14 (-0.46; 0.18)	-0.07 (-0.017; 0.022)	70.5	67.0
Grass yield	Gea-Izquierdo (May)	-0.26 (-0.38; -0.14)	-0.07 (-0.09; -0.05)	-18.6	-23.8
	Gea-Izquierdo (April)	-0.48 (-0.64; -0.32)	-0.14 (-0.18; -0.10)	-29.6	-32.9
	Weltzin	-0.14 (-0.23; -0.05)	-0.01 (-0.01; -0.005)	75.0	54.4
Phytomass	Grouzis	-0.43 (-0.49; -0.37)	-0.11 (-0.15; -0.06)	21.9	38.40
Herb. litter	Oliver	-0.31 (-0.60; -0.02)	-0.06 (-0.10; -0.03)	11.7	0.3
Total litter	Oliver	-0.60 (-0.83; -0.37)	-0.14 (-0.17; -0.11)	48.4	26.1
Tree litter	Hailu	-0.44 (-0.95; -0.06)	-0.18 (-0.33; -0.03)	75.9	70.6
	Gea-Izquierdo	-0.45 (-0.56; -0.34)	-0.09 (-0.12; -0.07)	-41.0	-41.1
SOC (%)	Gomez-Reys	-0.21 (-0.31; -0.11)	-0.04 (-0.06; -0.02)	-28.3	-29.4
	Oliver	-0.29 (-0.35; -0.23)	-0.03 (-0.04; -0.01)	-36.5	-15.2
	Schnabel	-0.42 (-0.51; -0.34)	-0.09 (-0.14; -0.04)	-26.0	-4.9
	Belsky	-0.07 (-0.09; -0.06)	-0.01 (-0.02; -0.01)	-52.6	-42.5
	Hailu	-0.06 (-0.10; -0.01)	-0.01 (-0.01; 0.00)	11.2	13.2
N (%)	Gea-Izquierdo	-0.40 (-0.65; -0.16)	-0.07 (-0.13; -0.02)	-94.3	-91.5
	Moreno crop	-0.30 (-0.42; -0.17)	-0.04 (-0.08; 0.00)	1.9	9.8
	Moreno grass	-0.25 (-0.31; -0.18)	-0.03 (-0.06; 0.00)	-6.4	4.4
	Moreno bush	-0.37 (-0.56; -0.19)	-0.06 (-0.08; -0.03)	6.3	5.4
	Schnabel	-0.07 (-0.13; -0.02)	-0.08 (-0.09; -0.06)	-54.9	-78.0
Soil pH	Gea-Izquierdo	-0.10 (-0.13; -0.07)	-0.02 (-0.02; -0.01)	-40.2	-34.2

[†]Values in parenthesis represent 95% confidence limits of β e. All β estimators were unbiased ($|g| < 1.0$)
AICc values in bold represent the better model

3.1.2. Crop and pasture plant productivity

Seven datasets were available on the negative effects of trees on crop yields resulting from allelopathy (Table 1). In all seven datasets, crop yield showed a consistent trend of increase ($\beta > 0$) with distance from the tree (Fig. 4) conforming more to PDM than EDM (Table 1). On the other hand, positive effects ($\beta < 0$) of trees on grass yield and phytomass were found in four datasets, and in all cases distance-decay of the tree effect was confirmed (Table 2, Fig. 6). Based on the AICc values, the EDM described the co-variation between grass yield and distance better than the PDM (Table 2).

Trees can either depress ($\beta > 0$) or increase ($\beta < 0$) crop and grass productivity, but the distance-decay pattern still holds. Our models predict that the negative effects of tree are monotonically decreasing function of distance from the tree. Here we have demonstrated that effects arising from competition for light, nutrients and water resources or allelochemicals fit this distance-decay pattern. Trees such as *Eucalyptus* spp. are known to have negative effect on crops by lowering soil moisture content, by making the soil hydrophobic (water repellent) and reducing light interception by the crop (Alemie 2009). *Eucalyptus*, *Populus* and *Juglans* spp. are well-known to produce allelopathic substances that depress yields of understorey crops due to phytotoxicity (Batish et al. 2008; Jose and Gillespie 1998; Singh and Kohli 1992). Under such situations, an inverse relationship is expected between crop yield and amount of phytotoxins (Singh and Kohli, 1992). As a result, crop yields are lowest around the tree where the amount of allelochemicals are the highest but yields will increase with distance consistent with PDM or EDM. Many other trees, however, increase crop yields through their facilitative effects (Sileshi 2016; Moreno et al. 2007; Marcos et al. 2007).

The effect of trees on forage production may be negative or positive depending on the tree species. For example, Frost and Edinger (1991) reported reduction in total annual herbage production under interior live oak (*Quercus wislizenii*) compared to blue oak (*Quercus douglasii*) canopies in the central Sierra Nevada foothills. This difference occurred regardless of the fact that the same level of soil improvement occurs under both species relative to the open areas. The reduction in herbage production under interior live oak was attributed to the effects of shading by its evergreen canopy (Frost and Edinger, 1991). The improvement in grass production under tree canopies is often attributed to increased nutrient and moisture availability, improved microclimate and reduced evapotranspiration (Abdallah et al. 2012; Frost and Edinger 1991; Grouzis and Akpo 1997; Ludwig et al. 2004; Moreno et al. 2007; Moreno and Pulido 2009). By reducing wind velocity, solar radiation, air and soil temperature, and increased litter inputs on the soil trees can decrease potential evapotranspiration favouring moisture retention in the shaded area (Grouzis and Akpo 1997), which often extends beyond the canopy. For example, the patterns in litter biomass distribution are similar to those observed with grass and herbage yields. The effects of trees on litter inputs can drive patterns in soil organic matter, SOC stocks and biological activity (Howlett et al. 2011; Oliver et al. 2006).

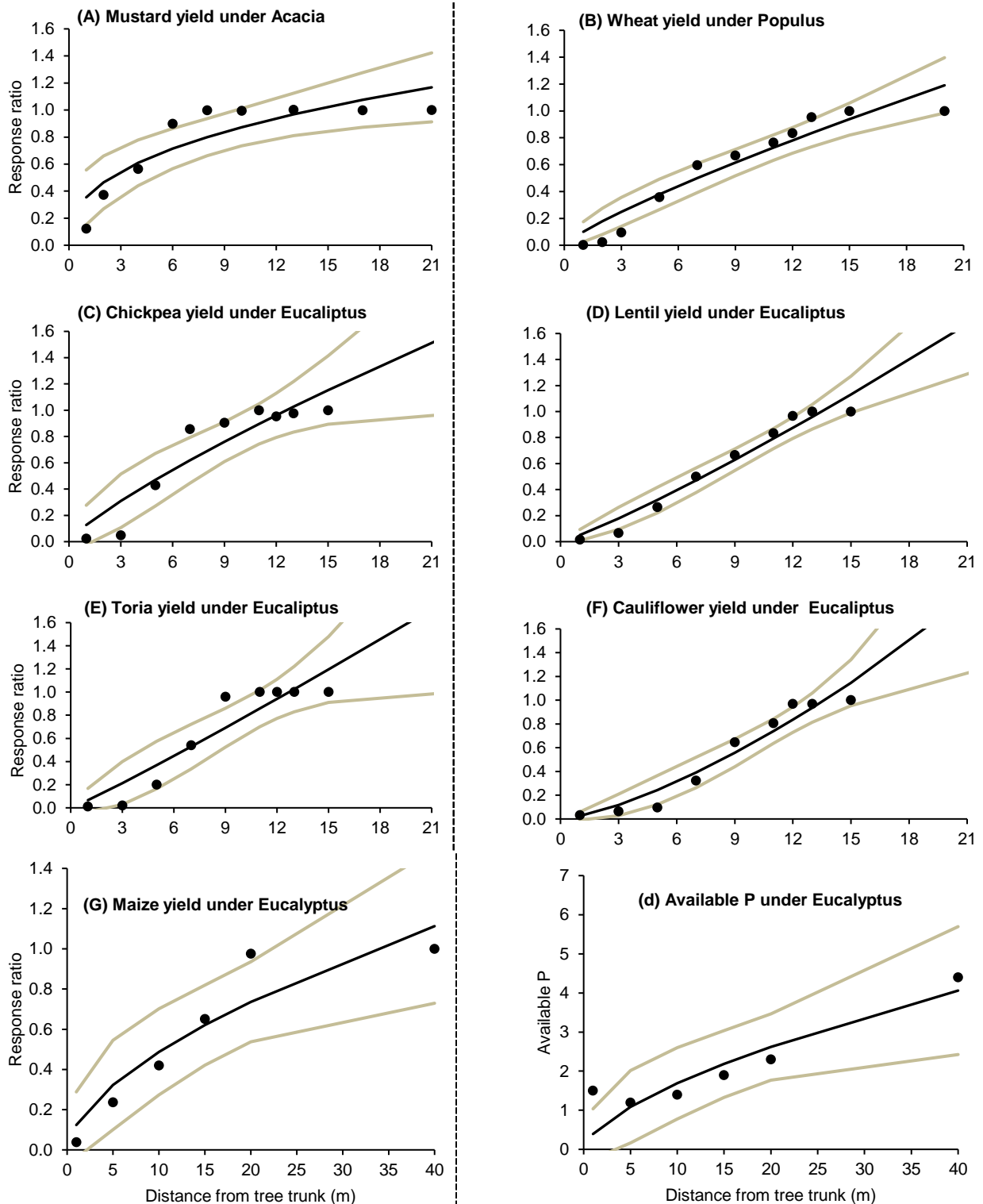


Fig. 4. Distance-decay of (A) mustard yield under *Acacia* in India (data from Yadav et al. 1993); (B) wheat yield under *Populus* in India (data from Singh et al. 1998); (C-F) wheat, chickpea, lentil, toria and cauliflower yields under *Eucalyptus* in India (data from Singh and Kohli 1992); and (G) maize grain yield under *Eucalyptus* in Ethiopia (data from Alemie 2009). Circles, black lines and grey lines represent measured values, predictions and their 95% confidence limits generated using the power function, respectively.

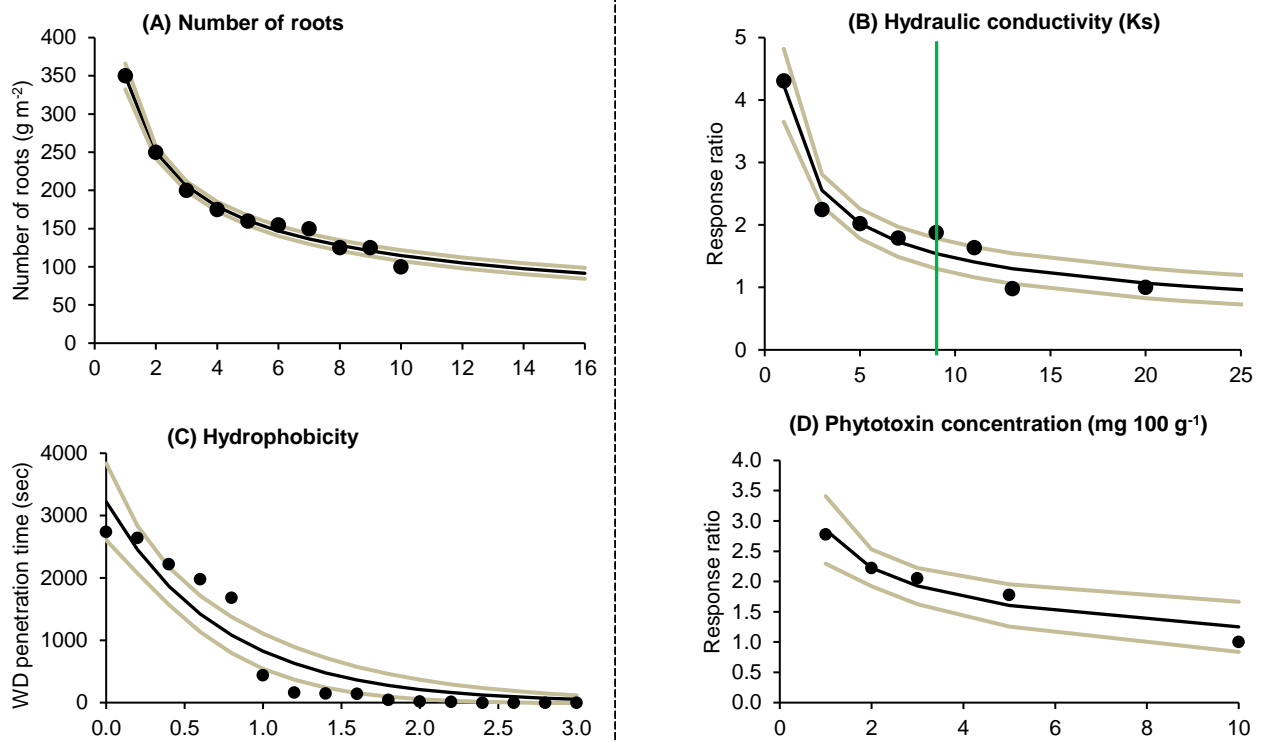


Fig. 5. Distance-decay of (A) *Parkia biglobosa* roots in Burkina Faso (data from Tomlinson et al. 1998); (B) saturated hydraulic conductivity of soils under *Quercus robur* in the UK (data from Chandler and Chappell 2008); (C) hydrophobicity of soils under *Eucalyptus* in Ethiopia (data from Alemie 2009); (D) phytotoxin concentrations under *Eucalyptus* in India (data from Singh and Kohli 1992); (E) light transmitted through *Quercus ilex* canopy in Spain (data from Montero et al. 2008). Circles, black lines and grey lines represent measured values, predictions and their 95% confidence limits generated using the power function, respectively.

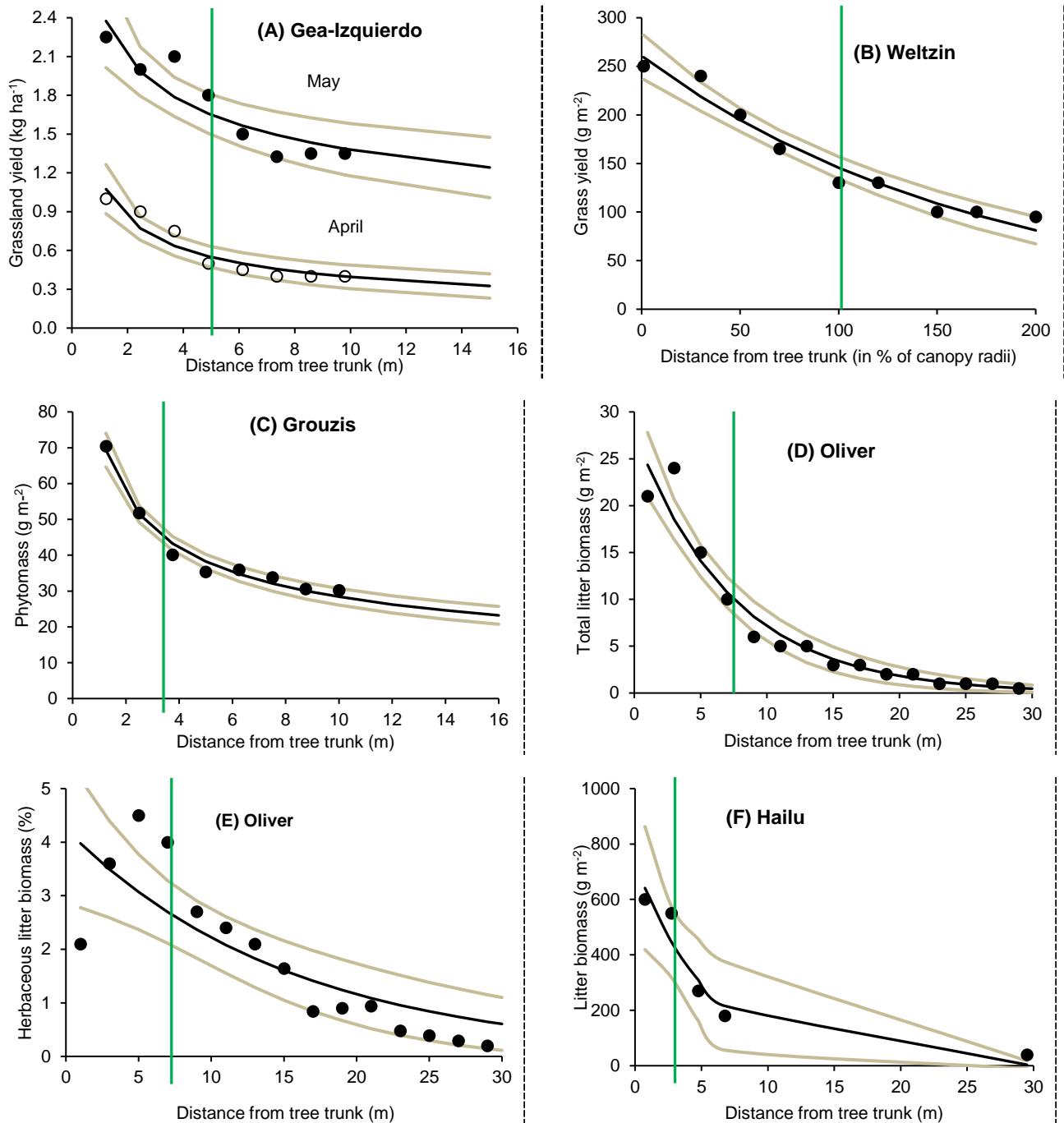


Fig. 6. Distance-decay of (A) grass yield under *Quercus* in Spain (data from Gea-Izquierdo et al. 2010), and (B) grass yield under *Acacia* and *Balanites* in Senegal (data from Grouzis and Akpo 1997); (C) grass yield under *Acacia* in Kenya (data from Weltzin and Coughenour 1990); (D) total litter biomass and (E) herbaceous litter biomass under *Eucalyptus* in Australia (data from Oliver et al. 2006); and (F) litter biomass under *Milletia* in Ethiopia (data from Hailu et al. 2000). Circles, black lines and grey lines represent measured values, predicted lines and their 95% confidence limits generated using the power function, respectively. Predictions between 10 and 16 m are extrapolations. The vertical green line represents the drip line.

3.1.3. Lateral root distribution

The number of lateral roots of *Parkia biglobosa* in the 0-50 cm soil depth was consistent with predictions of PDM but less so with EDM (Fig. 5A; Table 2). The available data show that the tree roots extended to at least 10 m from the trunk, but our predictions show that lateral roots could extend up to 16 m (Fig. 5A). The predicted number of roots at 16 m was 90.6 (95% CL: 82.2-99.0 m⁻²), which was not significantly different from the observed number of 94 roots m⁻² at 10 m from the trunk.

The patterns in lateral root density of *Parkia* (the only species for which adequate data are available so far) are similar to the patterns of fine root distribution of holm oak in Spanish dehesas recorded by Moreno et al. (2005). The data in Moreno et al. (2005) were recorded at only for four distances from the trunk. Therefore, we were unable to establish whether PDM or EDM fits their data. Mechanistic models of agroforestry (e.g., WaNuLCAS) assume a negative exponential decrease (i.e., EDM) in the distribution of lateral root densities (Mulia and Dupraz 2006). Our results provided greater support for PDM than EDM for *Parkia* root distribution. Nevertheless, we do not rule out deviations from PDM as some plasticity in lateral root distribution can occur in response to heterogeneity in the soil environment or management practices. For example, in a Mediterranean climate in France, Mulia and Dupraz (2006) observed patterns similar to those of *Parkia* in the fine root profiles in pure stands of hybrid walnut (*Juglans regia*) and poplars (*Populus euramericana*). However, deviations were noted under intercropped trees.

Our results and the literature reviewed also suggest that the lateral root distribution of trees exceeds two times their crown radius. For example, the lateral roots of *Parkia* could extend beyond 16 m (Fig. 3A) while the crown radius is 7.02 m (Tomilson et al. 1998). Similarly, the root system of holm oak explores a soil volume of >20 m distance and > 4 m depth (Marcos et al., 2007), with maximum distance of 33 m off the trunk for trees with average canopy width of 10.4 m (Moreno et al. 2005). Indeed, the surface of soil explored by holm oak roots exceed 7 times the crown projection area (Moreno et al. 2005). Our analysis of hydraulic conductivity (Ks) also demonstrated that the tree effect extended several meters beyond the canopy. This is attributed to creation of well-connected pores by both living and decayed roots, which increases the flow of water (Chandler and Chappell 2008).

The root length densities of oak trees and herbaceous plants show some overlap in the 0-90 cm soil depth even at 20 m beyond the canopy for trees with canopy radii of 7-12 m (Marcos et al. 2007). Nevertheless, holm-oak trees have a much lower root length density (mean 2.4 km m⁻³) than herbaceous vegetation (23.7 km m⁻³) in the first 10 cm soil depth (Moreno et al. 2005). Thus, competition for soil resources between trees and the herbaceous understorey is probably not as strong as usually assumed (Moreno et al. 2005). However, the tree roots may initiate complex interactions with roots of associated crops or grass as well as mycorrhizae and rhizosphere microflora. This will have implications for uptake of water and nutrients even 20 m beyond the canopy. For example, the roots of trees and associated crops may be interconnected by mycorrhizae thus increasing the likelihood of crop uptake of immobile nutrients (e.g., phosphorus) and availability of moisture.

There is also a growing body of evidence suggesting that trees in savannas can easily avoid competition with grasses for water and nutrients due to niche separation, i.e., due to differences in phenology and rooting systems of trees and grass (Marcos et al., 2007; Scholes and Archer 1997). For example, in Dehesas, crops and grasses take water mostly from the top 40–60 cm of soil, whereas holm-oak can extract water from 3-13 m depths (Moreno and Pulido, 2009). An emergent feature of vegetation in drylands is spatial self-organization (Gilad et al. 2007; Klausmeier 1999; Tzuk et al. 2020) arising from positive feedback loops between local vegetation growth and water transport towards the growth location (Meron 2018). The redistribution of water by patterned vegetation can increase the resilience of the ecosystem to prolonged droughts by providing an extra source of water that vegetation patches draw from their bare-soil surroundings (Meron 2018; Tzuk et al. 2020). Therefore, the root influence of trees is likely to be underestimated when the crown projection area is used to define the trees influence on soil and understorey vegetation.

3.1.4. Hydraulic conductivity

Analysis of the dataset on saturated hydraulic conductivity of soils under *Quercus robur* revealed distance-decay of tree effects consistent with our hypothesized models (Table 2; Fig. 5B). Comparison of the models in terms of raw data and RRs resulted in similar β values and their 95% CL for each model. In terms of AICc, the EDM outperformed PDM when the geometric means were analysed, but the reverse was true when median values were analysed. Skewness was also apparent ($|g| > 0.25$) for EDM when median values were used. In the case of PDM, there was no significant loss in information (AICc) when either the geometric mean or RR was analysed. Our predictions using PDM show that the tree roots extend 2-3 times the crown radius. For example, the predicted geometric mean Ks at 20 m (1.37; 95% CL: 0.80-1.85) was not significantly different from Ks of 1.42 recorded at the drip line (Fig. 5B).

3.1.5. Hydrophobicity and allelochemicals

Hydrophobicity (water repellence) of field-dried soil followed a clear decay with distance from the trunks of *Eucalyptus* tree (Fig. 5C, Table 2) although the fit of the PDM was poorer than expected. Soils were over 53,000 times more hydrophobic at 20 cm, 440 times more at 1 m and 20 times more at 2 m around the tree than at 3 m from the trunk. The concentration of phytotoxins showed a distance-decay trend similar the one observed with hydrophobicity (Fig. 5D).

3.1.6. Litter biomass, soil organic carbon (SOC) and nutrients

Total litter biomass and herbaceous litter biomass under *Eucalyptus* (Fig. 5D, E) and *Millettia* (Fig. 5F) trees declined with distance from the tree trunk. In both cases the EDM fitted the data better than PDM (Table 3). However, herbaceous litter biomass (Fig. 5E) showed a weaker pattern ($\beta = -0.31$) than total litter biomass ($\beta = -0.60$). In the case of *Millettia* (Fig. 5F), the model did not fit the data smoothly due to the lack of sampling between the 5-30 m distance.

SOC content showed a common trend of distance-decay in all five datasets (Fig. 7). The PDM fitted the data better than EDM in five out of the six datasets analysed (Table 3). The β values of the PDM fell within a narrow range of -0.06 to -0.45 (Table 3). In the case of SOC under *Acacia* (Fig. 7), the model did not fit the data smoothly due to the sparse sampling between the 0-10 m distance relative to the other distance classes. Our models predict distance-decay of SOC, with positive effect of trees on SOC (but negative effect on bulk density) extending several meters into the open area. Earlier reports (e.g., Amiotti et al. 2000; Gallardo et al. 2000; Howlett et al. 2011; Simón et al. 2012; Yadessa et al. 2009) have reported a common pattern of higher SOC concentrations under the trees than in adjacent open areas. Unlike most of these reports, our models predict that spatial heterogeneity in SOC forms a continuum of influence circles around the tree. Similarly, a Universal Kriging model revealed that the correlation peaks around 4 m, indicating the existence of an influence area around trees where higher SOC concentrations are found (Simon et al. 2013). Thus, the spatial patterning in SOC elucidated in this study can help in developing sampling schemes and models for accurate estimation of ecosystem carbon in support of international negotiations regarding climate change.

A general pattern of distance-decay in soil total nutrients similar to that of SOC was also evident in the data we analysed. With β values ranging between -0.07 and -0.40, trees also had significantly positive effects on soil total N content in all five datasets (Table 3). Using geostatistical analysis, Gallardo (2003) established that SOC and mineral-N show very similar ranges (the distance at which samples remain spatially correlated) of 9.5-9.7 m in a dehesa. In terms of the AICc (Table 3) and the 95% CIs of predictions, the PDM fitted the data better than the EDM in three out of the five datasets (Fig. 8). Under *Acacia tortilis* and *Adansonia digitata* trees in Kenya, the concentrations of soil P, Ca and K declined with distance from the tree trunk (data not shown). On the other hand, under *Eucalyptus* in Ethiopia, soil available P and exchangeable calcium concentrations increased with increased distance from the tree trunk (Fig. 8).

Phosphorous and Na concentrations showed higher ranges (13-13.4 m), with the lowest range being 3.8 m for K (Gallardo 2003). A number of other data not analysed here due to the small sample sizes also reveal that soil P, Ca²⁺, K⁺, Mg²⁺ and CEC show the same patterns of distance-decay in dehesas (Gallardo 2003; Moreno and Obrador 2007; Moreno et al. 2007), savannas and agroforestry parklands in Africa (Belsky et al. 1989; Sileshi 2016) and paddocks in Australia (Eldridge and Wong 2005; Wilson 2002). The enhancement of soil nutrients is greatest in the upper 30 cm of the soil, and this extends to approximately two canopy radii from the tree trunk (Schnabel et al. 2013).

3.1.6. Soil pH

As in soil nutrients, pH declined with distance from the trunk consistent with PDM (Table 3; Fig. 8). Eldridge and Wong (2005) and Wilson (2002) found a similar pattern under Eucalypt paddock trees in Australia, but we were unable to fit our models to their data. In an African savanna, Belsky et al. (1989) found more acid soil at the base of Acacia trees. Although acidification of the surface soil occurs below the entire tree canopy, alteration is most severe in proximity to the trunk (Amiotti et al. 2000). This has been mainly attributed to stemflow and bark litter near the trunk (Zinke 1962). The acidity of stemflow is mostly due to the charge of water-soluble phenolic substances leached from bark and their chelating properties (Beniamino et al. 1991). Soils under the inner ring of bark litter also exhibit evidence of acid hydrolysis of primary silicates (Amiotti et al. 2000).

An emergent pattern from all of the datasets analysed (Fig. 3-8) was the ability of the distance-decay models to adequately simulate the measured values. This indicates the predictability of effects of isolated trees in a variety of settings. In 21 out of 33 cases analysed, the PDM described single-tree effects better than the EDM. Thus, the results support our hypotheses that single-tree effects are monotonically decreasing functions of distance from the trunk. However, the explanations for these patterns may differ with the variable under study.

The observed pattern may arise due to above and belowground organic matter inputs from the tree and associated vegetation, nutrient cycling and protection of soil nutrient from erosion loss. Some of the soil nutrients may have been transported to the canopy zone from surrounding soils by the lateral roots or deposited in dung by birds and mammals that utilize the tree (Belsky et al. 1989). Trees can also pump nutrients from deep soil horizons (Scholes and Archer 1997), which are then recycled via leaf litter (Sileshi 2016). This can concentrate nutrients around the tree. Trees are also shown to promote the development of thicker topsoil horizons through addition of organic matter and nutrient cycling (Schnabel et al. 2013). Therefore, it is not surprising that isolated trees create islands of soil fertility and high quality (Belsky et al. 1989; Eldridge and Wong 2005; Rhoades 1997; Schnabel et al. 2013). From an ecological perspective, these islands can serve as keystone structures and important local and regional nutrient reserves that can influence community structure and ecosystem functions (Rhoades 1997).

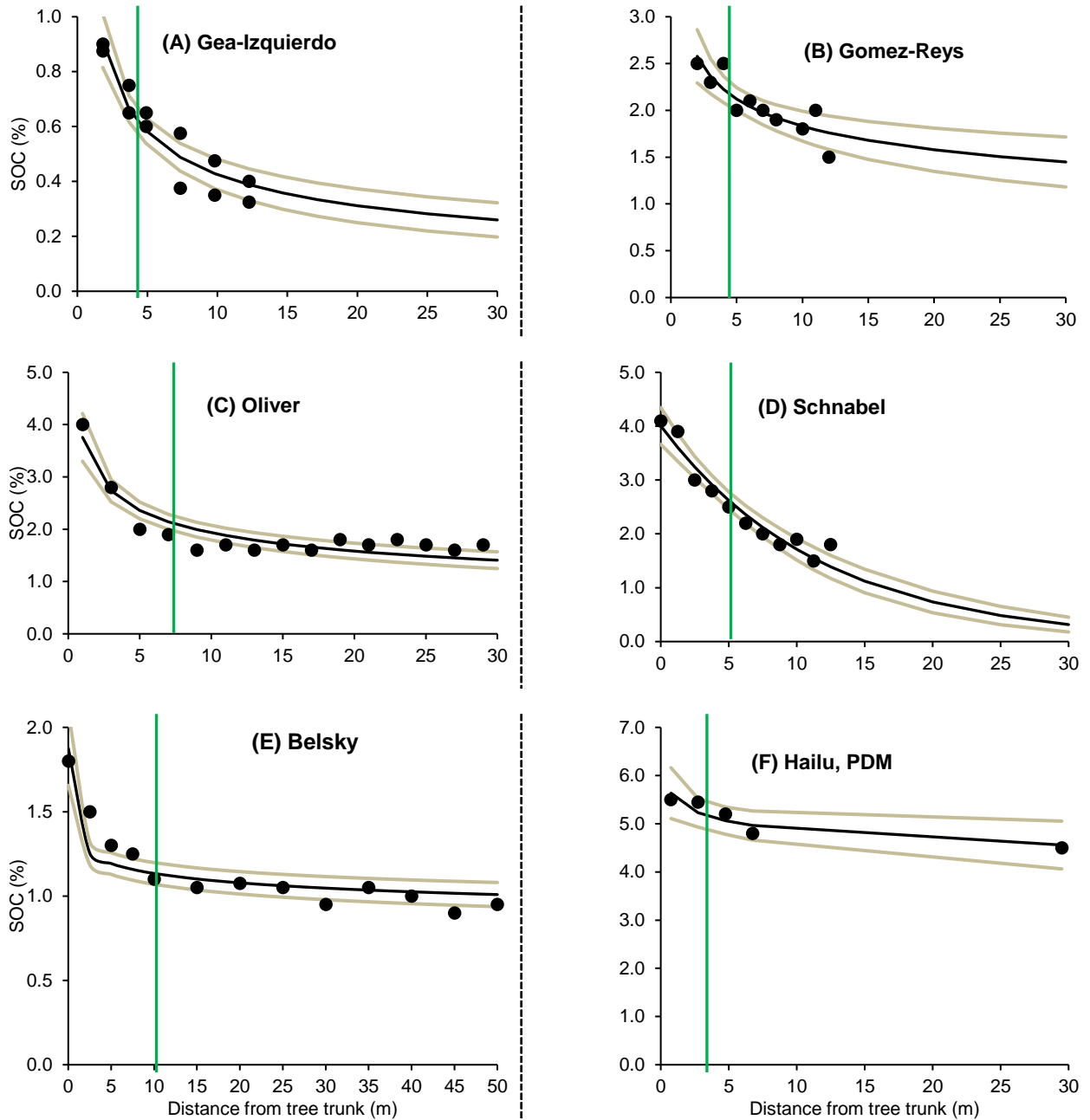


Fig. 7. Distance-decay of soil organic carbon under (A) *Quercus* in Spain (data from Gea-Izquierdo et al. 2010), (B) *Quercus* in Portugal (data from Gomez-Reys et al. 2011); and (C) *Eucalyptus* in Australia (data from Oliver et al. 2006); (D) *Quercus douglasii* in USA (data from Schnabel et al. 2013); (E) *Acacia* in Kenya (data from Belsky et al. 1989); and (F) under *Milletia* in Ethiopia. Solid circles, black lines and grey lines represent measured values, fitted lines and their 95% confidence limits. In A and B predictions between 12 and 30 m are extrapolations. The vertical green line represents the drip line.

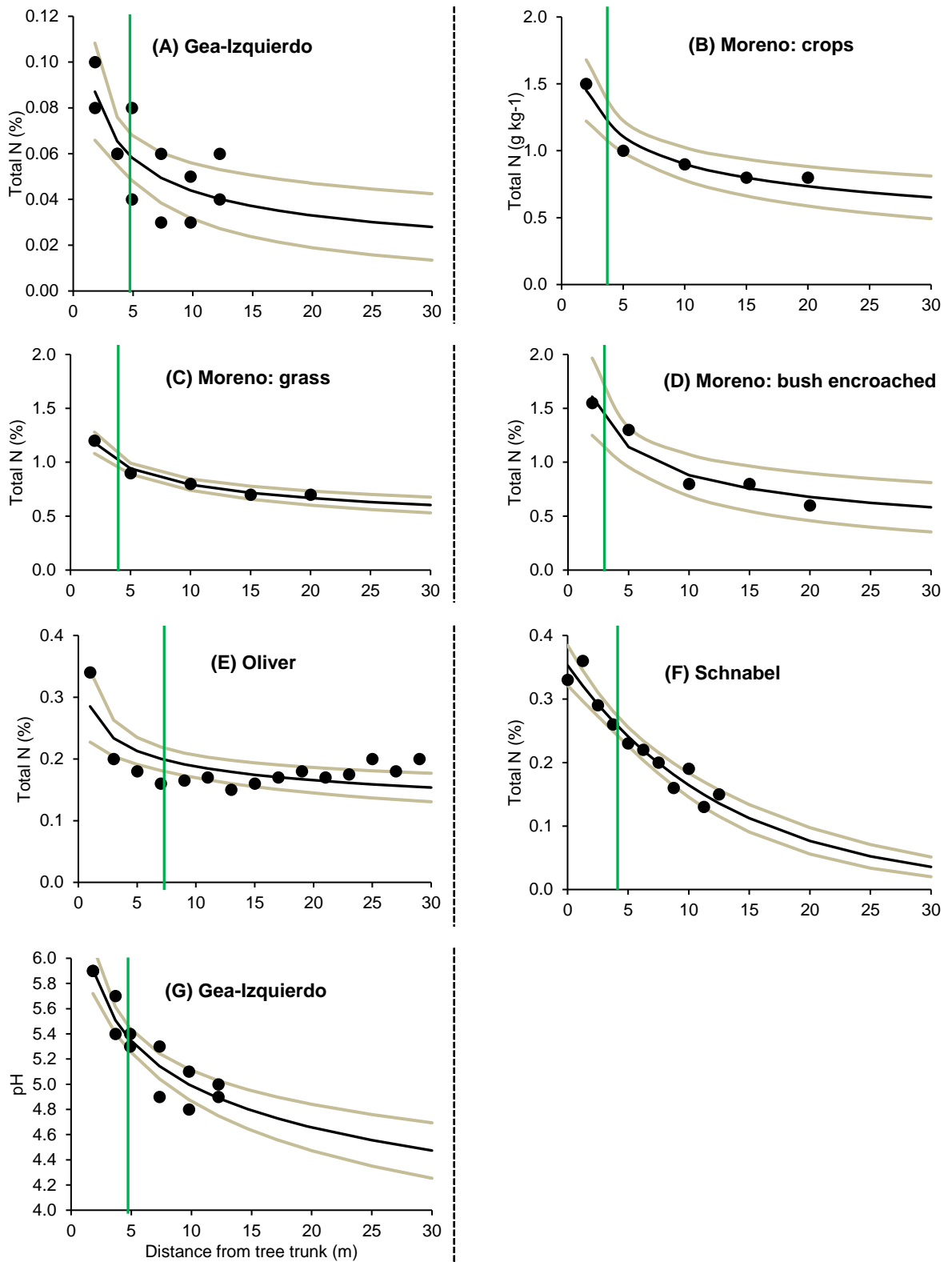


Fig. 8. Distance-decay in soil nitrogen content (%) (A) under *Quercus* in Spain (data from Gea-Izquierdo et al., 2010); (B, C and D) crops, grass and bush encroached plots under *Quercus* in Spain (data from Moreno and Obrador, 2007); (E) under *Eucalyptus* in Australia (data from Oliver et al., 2006); (F) under *Quercus* in USA (data from Schnabel et al., 2013); and (G) soil pH in under *Quercus* in Spain (data from Gea-Izquierdo et al., 2010); Solid circles, black lines and grey lines represent measured values, fitted lines and their 95% confidence limits generated using power (left) and exponential distance-decay functions. In (A-D) predictions between 12 and 30 m are extrapolations from the model. The vertical green line represents the drip line.

3.2. Unifying perspectives and theory

The distance-decay patterns established in this study are consistent with the concepts of “influence circles” (Zinke 1962) and ecological field theory (Li et al. 2000). “Influence circles” defines the predictable variation in soil properties as a function of the distance from the axes of trees often observed in forest stands (Zinke 1962; Boettcher and Kalisz 1990). Zinke (1962) postulated that in the absence of external variables such as wind and steep slope, the properties of the soil under the tree’s influence will develop in a symmetrical pattern around each tree. Thus, each tree has an influence circle roughly proportional to the size of the crown projection area on the soil surface. The tree has a maximum influence under the canopy and the influence decreases outward from the tree (Boettcher and Kalisz 1990). However, Zinke’s (1962) definition oversimplifies the patterns because it limits the tree’s influence to the canopy effects and conceptualizes three concentric circles; bark, litter and outside zones of influence. In reality these circles intergrade due to the movement and mixing of bark, litter and vegetation due to various forces. This concept also does not recognize the facilitative and negative effects of lateral roots that extend several meters beyond the crown projection area. Therefore, we propose that the definition of “influence circles” to be relaxed to include the root zone of influence.

Ecological field theory (EFT) was originally introduced by Wu et al. (1985) as a theoretical framework to account for the effect of competition by forest trees on the growth of a subject tree or neighbouring vegetation. EFT models express the effect of trees on a given point X in the space as an exponential function of individual tree properties and the point’s distance to neighbouring trees (Liu and Halvorsen 2012). The individual tree is considered to be surrounded by a circular field of influence (called ecological field), where the tree affects the availability of resources according to its own characteristics and other environmental factors. As the tree adds or subtracts resources, it either improves or suppresses the growth of other plants in its zone of influence. Predictions of PDM are consistent with EFT, and thus our findings provide a mechanistic explanation for the EFT. If the exponential function is replaced by the power-law function as the default model, the EFT can be a unifying theory for tree influences in various settings.

3.3. Implications for conservation and management

The results of this analyses support the growing realization that large old trees are keystone structures in the landscapes where they occur (Hall and Bunce 2011; Lindenmayer et al. 2012; 2014; Manning et al. 2006; Mouquet et al. 2013; Stagoll et al. 2012). Keystone structures are defined as distinct spatial structures providing resources, shelter or goods and services crucial for other species (Mouquet et al. 2013). According earlier of reviews, large isolated trees play a disproportionately large role in generating habitat diversity, maintaining plant species richness and providing shade, shelter and resting places for wild animals (Dean et al. 1999). This perspective can be useful for instituting policies and practice to guide conservation agencies and land owners to protect and manage single tree stands (Lindenmayer et al. 2014). In natural ecosystems, it is important to maintain the population structure of key tree species especially in the oligotrophic arid savannas and critical habitats. In managed ecosystems, land owners often remove or excessively prune trees, for example in dehesas/montados (Pinto-Correia and Mascarenhas 1999; Plieninger et al. 2003) in the hope of improving grass productivity. They also engage in excessive control of shrub under the trees although shrubs play a key role in the natural regeneration of oaks (Moreno and Obrador 2007). Even if the trees do not increase pasture productivity, the spatial variability they create may play a critical role in maintaining other ecosystem functions by concentrating limiting resources. In the past systematic planting of trees has been widely promoted in agroforestry. The review of the literature and the analyses have highlighted the value of isolated trees in various systems. Recently Tzuk et al. (2020) showed that in contrast to the widespread practice of planting the woody and herbaceous species in alternating rows (or stripe pattern), hexagonal patterns increase the system’s resilience to droughts, while maintaining higher crop yields of annuals.

3.4. Implications for study design and analysis

The results also have implications for study design and analysis. In the past, inferences about single-tree effects were based mainly on study designs where distance classes are used as fixed effects in regression and analysis of variance (ANOVA) models. The distance–decay in measured variables indicates that observations around trees are spatially structured. In the presence of spatial structure and autocorrelation, conventional sampling and statistical methods are inappropriate. However, researchers still use conventional design-based sampling and classical statistics which assume that observations are identically and independently distributed. A common study design involved comparing plots under the tree canopy with those outside the canopy, assuming the crown projection area as the limiting zone for defining the control plots. Another common practice has been comparing plots under the canopy, drip line and the open area. Such comparisons often assume that the area under the canopy is homogeneous, and that measurements under the canopy, drip line and the open area are discrete. They also ignore the effect of distance, direction and the correlation between neighbouring samples. Other studies take measurements at different distances, and then apply correlation analysis or linear regression to establish the relationship between measured variables and the distance from tree bases (e.g., Oliver et al. 2006; Wilson 2002; Yadav et al. 1993). ANOVA and regression assume that measured variables are identically and independently distributed among distance classes. In reality, the measurements in the different distance classes and directions are not independent as observations that are closer together show spatial autocorrelation due to their neighbouring physical locations. Another problem with ANOVA arises because of unequal number of observations in the open area, which are often fewer than under the canopy. The standard *F*-test was originally designed for balanced designs (samples of equal size) and assumes equality of variance. Results from *F*-test can be unreliable when samples of unequal size are combined with unequal variance and spatial dependence. Therefore, ANOVA is inadequate to model single-tree effects, which are often monotonic functions of distance. Another concern is the use of the tree canopy vertical projection as limiting zone in defining the control plots. The majority of studies used open fields or plots located farthest from the tree trunk as controls. As demonstrated here, the tree's influence through canopy light interception may greatly exceed the drip line. Due to root activity, the influence of the tree may extend what is considered outside the canopy. Review of the literature shows that canopy spread is not a good predictor of root spread, or conversely root distribution may not correspond to canopy distribution especially for older trees (Day et al., 2010). Tree roots may extend to treeless zones up to 60 m from tree trunks. Even plots located 5-10 times the crown radius far may not be true controls unless trenching is used. The use of extensive treeless areas as controls may also give rise to dissimilarity in soil conditions. Therefore, we discourage the common practice of establishing sampling plots randomly around the tree and the binary comparisons of measurements under the tree canopy with those in the open areas. We also discourage the use of distance as a fixed effect in statistical models when analysing data from agroforestry systems. We strongly recommend application of model-based geospatial sampling and analyses.

4. Conclusions

Despite the large differences in tree species and their growing environment, their influence on ecosystem properties followed remarkably similar spatial patterns across a wide range of ecosystems. Therefore, it is concluded that single-tree influences follow predictable patterns in measured variables, and that the spatial heterogeneity under trees and the open area is a continuum. It is also concluded that tree effects exceed the crown projection area, and therefore the contribution of isolated tree stands to ecosystem functioning may be disproportionately larger than the area they occupy. The results provide support to the claim that isolated trees can serve as keystone structures in the landscape. This provides a justification for preservation and prudent management of isolated trees in the landscapes where they occur. It also provides a theoretical basis for a paradigm shift in study design and data analysis.

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