Forest Systems
24(1), e009, 13 pages (2015)
eISSN: 2171-9845
http://dx.doi.org/10.5424/fs/2015241-05846
Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA)

RESEARCH ARTICLE

Point processes statistics of stable isotopes: analysing water uptake patterns in a mixed stand of Aleppo pine and Holm oak

Carles Comas[1, *], Jorge del Castillo[2], Jordi Voltas[2] and Juan Pedro Ferrio[2]

[1] *Department of Mathematics, AGROTECNIO Center, Universitat de Lleida, Avda. de l'Estudi General 4, E-25001 Spain.*
[2] *Department of Crop and Forest Sciences, AGROTECNIO Center, Universitat de Lleida, Avda. Rovira Roure 191, E-25198 Spain.*

Abstract

Aim of study: Understanding inter- and intra-specific competition for water is crucial in drought-prone environments. However, little is known about the spatial interdependencies for water uptake among individuals in mixed stands. The aim of this work was to compare water uptake patterns during a drought episode in two common Mediterranean tree species, *Quercus ilex* L. and *Pinus halepensis* Mill., using the isotope composition of xylem water ($\delta^{18}O$, $\delta^{2}H$) as hydrological marker.

Area of study: The study was performed in a mixed stand, sampling a total of 33 oaks and 78 pines (plot area= 888 m^2). We tested the hypothesis that both species uptake water differentially along the soil profile, thus showing different levels of tree-to-tree interdependency, depending on whether neighbouring trees belong to one species or the other.

Material and Methods: We used pair-correlation functions to study intra-specific point-tree configurations and the bivariate pair correlation function to analyse the inter-specific spatial configuration. Moreover, the isotopic composition of xylem water was analysed as a mark point pattern.

Main results: Values for *Q. ilex* ($\delta^{18}O = -5.3 \pm 0.2$‰, $\delta^{2}H = -54.3 \pm 0.7$‰) were significantly lower than for *P. halepensis* ($\delta^{18}O = -1.2 \pm 0.2$‰, $\delta^{2}H = -25.1 \pm 0.8$‰), pointing to a greater contribution of deeper soil layers for water uptake by *Q. ilex*.
Research highlights: Point-process analyses revealed spatial intra-specific dependencies among neighbouring pines, showing neither oak-oak nor oak-pine interactions. This supports niche segregation for water uptake between the two species.

Key words: Cross-pair correlation function; Deuterium; Mark correlation function; Oxygen–18; Point patterns; Xylem.

Abbreviations: $\delta^{18}O$, oxygen isotope composition; $\delta^{2}H$, hydrogen isotope composition; BA, basal area.

Citation: Comas C, del Castillo J, Voltas J, Ferrio JP. (2015). Point processes statistics of stable isotopes: analysing water uptake patterns in a mixed stand of Aleppo pine and Holm oak. Forest Systems, Volume 24, Issue 1, e009, Article ID 5846, 13 pages. http://dx.doi.org/10.5424/fs/2015241-05846.

Received: 03 Mar 2014. **Accepted:** 28 Nov 2014
http://dx.doi.org/10.5424/fs/2015241-05846

Funding: This work was funded by the Projects SMARTREES (FP7-PEOPLE-2009-RG-246725, EU) and RESILFOR (AGL 2012-40039-C02-02, MEC, and Spain). JPF and JdC were supported by the Ramon y Cajal programme (MEC, Spain), and a FPI fellowship (MEC, Spain), respectively.

Competing interests: The authors have declared that no competing interests exist.

Correspondence should be addressed to Carles Comas: carles.comas@matematica.udl.cat

Introduction

In Mediterranean climates, the temporal coupling of heat and drought stress, and the existence of nutrient-deficient soils have been major evolutionary forces shaping plant communities (Herrera, 1992; Mooney & Dunn, 1970). Examples of adaptive strategies include extensive root systems, evergreen foliage to compensate for nutrient scarcity and to permit year-round production, or water-saving mechanisms such as leaf sclerophylly or a very sensitive stomatal regulation (Rundel, 1988; Zavala *et al.*, 2000). As a result, dominant tree species in Mediterranean ecosystems are either evergreen sclerophyllous or conifers adapted to the scarcity of water resources. Holm oak (*Quercus ilex* L.) and Aleppo pine (*Pinus halepensis* Mill.) are representative of each one of these functional types, being extensively found in the Mediterranean basin. Although *P. halepensis* and *Q. ilex* are well adapted to seasonally-dry areas, the particular strategies followed by each species differ considerably (Ferrio *et al.*, 2003; Zavala *et al.*, 2000; Baquedano & Castillo, 2006; Del Castillo *et al.*, 2013). On the one hand, *P. halepensis* is a typical drought-avoiding species that relies on water saving mostly through stomatal closure (see e.g. Borghetti *et al.*, 1998; Voltas *et al.*, 2008), but it may also act as an opportunistic species when conditions are favourable (Nicault *et al.*, 2001; Klein *et al.*, 2005). On the other hand, *Q. ilex* is a slow growing species with a considerable stomatal regulation (at least when compared to other species of the same genus, see e.g. Damesin *et al.*, 1998; Infante *et al.*, 1999), but combined with drought-tolerance mechanisms such as osmotic and elastic adjustments (Terradas & Savé 1992; Sala & Tenhunen 1994). The existence of tolerance mechanisms, together with a deeper root system, typical of evergreen schlerophyllous (Canadell *et al.*, 1996), leads to a more effective water uptake of evergreen oaks as compared to pines (Valentini *et al.* 1992; Klein *et al.* 2013). Despite their functional differences, both species often form mixed stands that are widely distributed in the Eastern Iberian Peninsula. In this context, understanding interactions among individuals in pine-oak mixed stands is crucial not only to interpret current species distribution, but also to foresee future vegetation scenarios (Zavala *et al.*, 2007).

A considerable number of studies have shown how inter- and intra-specific competition affects individual growth and stand dynamics under water-limited conditions (Gracia *et al.*, 1996; Moreno-Gutiérrez *et al.*, 2011; Zavala *et al.*, 2007). However, although soil water availability and water uptake patterns are likely to play a major role in shaping the composition of mixed-species stands, information on the use of water resources at inter- and intra-specific levels is still limited (Filella & Peñuelas, 2003a; Moreira *et al.*, 2003; Brooks *et al.*, 2006). In this regard, the analysis of the isotopic compositions of oxygen and hydrogen (δ^{18}O and δ^{2}H) in xylem sap presents a great potential to characterise water movement along the soil-plant-atmosphere continuum, particularly in arid and semiarid environments (Dawson *et al.*, 1993; Dawson & Simonin, 2011; Ferrio *et al.*, 2005). During the dry season, evaporation causes a decreasing trend in soil water δ^{18}O and δ^{2}H with soil depth (Filella & Peñuelas, 2003b; Moreno-Gutiérrez *et al.*, 2012b). Thus, by comparing observed trends along the soil profile with data on xylem water, stable isotopes can reveal differential water uptake patterns in co-existing Mediterranean species (Armas *et al.*, 2010; Máguas *et al.*, 2011; Filella & Peñuelas, 2003a; Filella & Peñuelas, 2003b; Moreno-Gutiérrez *et al.*, 2012b). However, studies so far compared isotopic records averaged over a representative sample of trees per species (Máguas *et al.*, 2011; Filella & Peñuelas, 2003b; Moreno-Gutiérrez *et al.*, 2012b), or focussed on the interaction between selected individuals (Armas *et al.*, 2010; Filella & Peñuelas, 2003a), but a stand-level based study of inter-individual interactions in water uptake is still lacking.

Forest science has applied numerous statistical methods belonging to point processes (Stoyan & Penttinen, 2000; Diggle, 2003; Illian *et al.*, 2008) to tackle ecological questions (for a review, see Comas & Mateu, 2007). This includes, for instance, the study of the spatial structure of pure and mixed forest stands (Moeur, 1993; Pélissier, 1998; Mateu *et al.*, 1998), the distribution and severity of infected trees (Shaw *et al.*, 2005), and the space-time modelling of forest dynamics (Renshaw *et al.*, 2009; Comas, 2009). Here we propose the use of marked point process tools to analyse the isotopic composition of xylem water as a mark associated to each tree position. The resulting marked point pattern represents the spatial structure of water uptake for each tree species. The analysis of such marked point configurations may be valuable to interpret spatial inter- and intra-specific dependencies (e.g. competition, facilitation) for water uptake dynamics underlying particular tree performances in water-limited environments. As a case-study to show the potential of this method, we analysed the spatial inter- and intra-specific interactions for water uptake under drought for a pine-oak mixed Mediterranean forest based on individual tree δ^{18}O and δ^{2}H records of xylem water. Due to their deeper root system, oaks are likely to extract water from soil layers not accessible for the pines. We hypothesize that, under drought conditions, the two species might not directly compete for the same water pools in the soil, thus showing a functional niche segregation. Accordingly, we would expect different levels of tree-to-tree interdependency, depending on whether neighbouring trees belong to one species or the other.

Materials and methods

Study area

The study area is a forest stand located in the Montsant mountain range (41° 19’ 47.3’’ N, 0° 50’ 2.6’’ E, 750 m a.s.l), in the northeast of the Iberian Peninsula. The climate in the region is Mediterranean temperate with continental tendency, with a mean annual precipitation of 517 mm and mean annual temperature of 12.3 °C. It is characterized by a dry and a relatively warm summer (mean summer precipitation of 89.5 mm, mean average temperature of 20.9 °C; averaged data of the two nearest meteorological stations with a long-term record (period 1970-2000), *El Vilosell* and *Bisbal de Falset*, each located at aprox. 11 km distance from the sampling site (AEMET-IM, 2011)). Year-to-year climate variability at this location is high with extreme drought events occurring every few years, a typical feature of the Mediterranean climate. The forest stand is a dense woodland community co-dominated by two typical Mediterranean trees, Holm oak and Aleppo pine. It is the result of natural regeneration of pine and oak in a former agricultural terrace which, according to the age of some individuals, was abandoned about 80 years ago. Understory vegetation is relatively scarce and current regeneration from both species is rare; thus, only adult pines and oaks with diameter at breast height (dbh) above 10 cm were included in the study. Stand density (dbh>10 cm) was 560 and 863 stems/ha for oak and pine respectively. We considered stem clumps of *Q. ilex* that seemingly derived from the same stool as single individuals. These sprout clumps were relatively common (about 1/3 of individuals), making stool density of *Q. ilex* considerably lower than stem density (370 stools/ha).

The rectangular plot area (24 x 37 m) had a strong slope (15-22%) facing west (X-axis), together with a gentle slope (3-7%) facing south (Y-axis). According to USDA soil taxonomy (Soil Survey Staff, 2010), soil is a loamy-skeletal, carbonatic, termic, active calcic pachic haploxeroll, with soil depths ranging from *ca.* 50 cm in the lower parts of the plot to *ca.* 20 cm in the upper part of the plot.

Sample collection and tree mapping

Field sampling took place on the 9th September 2011, at the end of an exceptionally dry, but moderately warm, summer (summer precipitation of 23 mm, mean summer temperature of 21.5 °C, data from *Ulldemollins*, a recently established automatic meteorological station, only 3.5 km away from the site) (Figure 1). We sampled sun-exposed twigs from the 33 oaks and 78 pines with dbh>10 cm. After removing the bark and phloem, the xylem of the twigs was placed into cap vials, immediately frozen in dry ice and kept until water extraction using a cryogenic vacuum distillation line (Dawson *et al.,* 1993). Six soil samples were also collected from the topsoil layer (2-10 cm, A horizon) and from 5 cm above the maximum soil depth (subsoil, up to 19-33 cm depending on the sample, B horizon), and similarly handled for water extraction. Water isotope ratios of hydrogen and oxygen of the xylem and soil water were determined using a Picarro Water Analizer L2130-*i* (Picarro Inc., Santa Clara, California). They were expressed in delta (δ) notation (‰) relative to V-SMOW (i.e. isotopic composition of oxygen, $\delta^{18}O$, and hydrogen, $\delta^{2}H$). Raw values were calibrated against three internal laboratory references (calibrated against IAEA standards VSMOW2, SLAP2 and GISP). Overall uncertainty (determined as the standard error of repeated analyses (N=20) of a reference sample not included in the calibration) was 0.05‰ and 0.17‰, for $\delta^{18}O$ and $\delta^{2}H$, respectively. The potential presence of organic contaminants was checked using the post-processing software Picarro ChemCorrect 1.2.0, giving in all cases negative results.

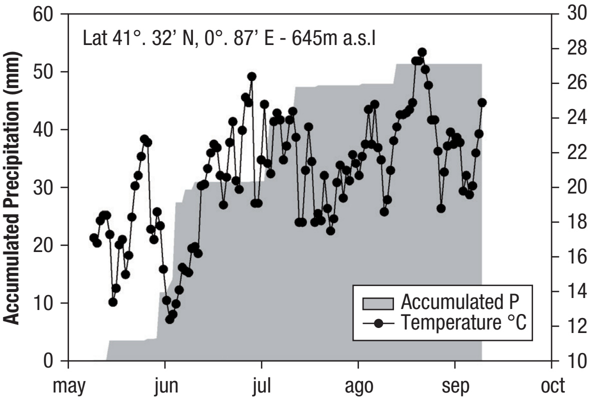

Figure 1. Environmental context. Meteorological data of the four months before sampling, showing mean temperature and accumulated precipitation. The data correspond to the automatic meteorological station of Ulldemolins, located at 3.5 km from the samplig site.

Tree position for spatial analysis was determined using a high resolution GPS technology (GeoExplorer 6000 Series Handheld, Trimble Navigation Limited, California, USA) with spatial error inferior to 20 cm for latitude and longitude and to 40 cm for altitude. Tree coordinates were re-checked in the field with the aid of a measuring tape.

Analysis of covariance

Isotope data ($\delta^{18}O$ and $\delta^{2}H$) and one tree dendrometric characteristic (individual basal area, BA) were subjected to mixed model analysis of covariance (ANCOVA) considering a fixed effect for species (pine, oak) and the variation along the X and Y axes of the two-dimensional space (covariates), allowing for heterogeneity of regression slopes at the species level. This was done to check for (possible) differential systematic variation in the response variables following X and Y directions, i.e. anisotropic effects. We also allowed for heterogeneity of residual variances at the species level, which was checked by means of log likelihood ratio tests. For the difference between two nested models (homocedastic and heterocedastic), minus two times the log likelihood ratio follows, under the null hypothesis, asymptotically a χ^2 distribution with one degree of freedom (difference in the number of variance components; Verbeke & Molenberghs, 2000).

Spatial Statistics

To analyse the spatial structure of *Q. ilex* and *P. halepensis*, we used spatial correlation functions derived from point process theory. A spatial point process is a stochastic mechanism that generates a countable set of events x_i in a bounded region A (see, for instance, Diggle, 2003). Any sequence of events, which can be seen as points on a given region, can be explained by point process theory, and one of the most common applications is the study of point occurrences in the Euclidean plane (e.g. individual trees in a forest stand) (Stoyan & Penttinen, 2000).

Spatial correlation functions

To study the spatial structure of trees (point locations) we used the pair correlation function (Illian *et al.,* 2008), an estimator of which can be obtained as

$$\hat{g}(r) = \frac{1}{2\pi\hat{\lambda}^2 \left|A\right|} \sum_{(x_1,x_2)\in\varphi}^{\neq} \frac{\kappa(\left\|x_1 - x_2\right\| - r)}{e(x_1, \left\|x_1 - x_2\right\|)} \tag{1}$$

for a forest stand A with area $\left|A\right|$, where φ is the observed point pattern, $\hat{\lambda}$ is an estimator of the point intensity, $\kappa(\cdot)$ is the Epanechnikov kernel function, $\sum^{\neq}$ stands for the summation over all pairs such that $x_1 \neq x_2$ and $e(\cdot)$ is the Ripley's factor (Ripley, 1976) to correct for edge effects, for a given inter-distance r between points (trees).

Broadly speaking, this function indicates point inhibition (i.e. repulsion) when $g(r) < 1$, $g(r) = 1$ denotes the Poisson case (i.e. a random point process) with no interaction between points, whilst $g(r) > 1$ implies point clustering, for any $r > 0$.

To analyse the bivariate point pattern of *Q. ilex* and *P. halepensis* we used the partial or cross-pair correlation functions, $g_{12}(r)$ (Illian *et al.,* 2008). This correlation function is a bivariate derivation of the pair correlation function to study the spatial dependencies of point classes for bivariate point patterns. The interpretation of $g_{12}(r)$ is similar to that of $g(r)$. It indicates point-type inhibition when $g_{12}(r) < 1$, $g_{12}(r) = 1$ is the Poisson case (i.e. point types are independently distributed from each other), whilst $g_{12}(r) > 1$ implies point-type clustering. An estimator of this function can be defined as

$$\hat{g}_{12}(r) = \frac{1}{2\pi\hat{\lambda}_1\hat{\lambda}_2 \left|A\right|} \sum_{x_1\in\varphi_1, x_2\in\varphi_2} \frac{\kappa(\left\|x_1 - x_2\right\| - r)}{e(x_1, \left\|x_1 - x_2\right\|)}, \tag{2}$$

where φ_s and $\hat{\lambda}_s$ are the point pattern and the point intensity of the point class s = 1,2, respectively. Note that $\varphi_{12} = \varphi_1 \cup \varphi_2$, i.e. the bivariate point pattern.

To analyse the marked point patterns of oaks and pines, we used the mark correlation function $k_m(r)$ (Stoyan & Stoyan, 1994). This function is a mark counterpart of the pair correlation function that accounts for the spatial correlation of marks (characteristics) associated to each tree. Specifically, this function describes the spatial structure of marks (e.g. tree basal area, stable isotope composition) associated to each tree location, and an estimator of this function can be written via

$$\hat{k}_m(r) = \frac{1}{2\pi\hat{\lambda}^2 \left|A\right|} \sum_{(x_1,m_1),(x_2,m_2)\in\varphi_m}^{\neq} \frac{m_1 m_2 \kappa(\left\|x_1 - x_2\right\| - r)}{e(x_1, \left\|x_1 - x_2\right\|)\hat{g}(r)\mu^2} \tag{3}$$

where φ_m is a marked point pattern, μ^2 is the expectation of $m_1 m_2$ and m_1 is the mark value for tree 1 (say). This function denotes independence between marks when $k_m(r) = 1$, $k_m(r) > 1$ indicates positive mark correlation, whilst $k_m(r) < 1$ implies mark inhibition for all $r > 0$. Because the spatial correlation function is defined for positive marks, we scaled the original stable isotope composition values as to avoid negative values, noting that a change in mark scale does not affect the resulting estimators. In particular, we subtracted the minimum negative values of the resulting isotopic composition to each tree record. Therefore, the new resulting scale is defined for Real positive numbers starting from zero (minimum negative isotopic value of the original dataset). Finally, to study the correlation between species (qualitative mark) with regard to tree quantitative characteristic (basal area, stable isotopic compositions) we adopted a derivation of the mark correlation function initially proposed by Penttinen *et al.* (1992). Here the point pattern consists of two distinct tree species together with a mark associated to each tree position. In fact, two marginal processes are present over the same underlying point configuration, one as a bivariate (qualitative) point process and another as a marked (quantitative) point process. Penttinen *et al.* (1992) defined an estimator of this cross-mark correlation function through

$$\hat{k}_m^{12}(r) = \frac{1}{2\pi\hat{\lambda}_1\ \hat{\lambda}_2 \left|A\right|} \sum_{(x_1,m_1)\in\varphi_{m_1},(x_2,m_2)\in\varphi_{m_2}} \frac{m_1 m_2 \kappa(\left\|x_1 - x_2\right\| - r)}{e(x_1, \left\|x_1 - x_2\right\|)\hat{g}_{12}(r)\hat{\mu}_{12}^2} \tag{4}$$

where φ_{m_1} is the marked point pattern for class 1 (say), and $\hat{\mu}_{12}$ is an estimator of μ_{12}, is the expectation of $m_1 m_2$ (marks from classes 1 and 2). The interpretation of $\hat{k}_m^{12}(r)$ is similar to that of $k_m(r)$ and $g_{12}(r)$. It indicates spatial positive correlations for the spatial pattern when $\hat{k}_m^{12}(r) > 1$, $\hat{k}_m^{12}(r) = 1$ is the Poisson case, whilst $\hat{k}_m^{12}(r) < 1$ implies negative dependencies. For the Epanechnikov kernel function, we chose the bandwidth to be equal to $c/\sqrt{\lambda}$, where typically $c = 0.1 – 0.2$, (here $c = 0.2$) as suggested by Stoyan & Stoyan (1994).

For each kind of spatial correlation function, we tested for spatial independence following a Monte Carlo approach based on the random simulation of (marked) point patterns from the null hypothesis (Poisson). We simulated 199 (marked) point patterns under the null hypothesis of spatial independence, and for each one, an estimator of one of the correlation functions defined above was obtained. These set of functions were then compared with the resulting estimator of this correlation function for the point pattern under analysis. Under this test, we rejected the null hypothesis (spatial independence) if the resulting estimator of this correlation function lay outside the fifth largest and/or smallest envelope values obtained from the set of simulated functions with an exact significant level of $\alpha = 2 \times 5/(199+1) = 0.05$. Tests for each (marked) point pattern considered here are defined as follows. For the point patterns of oaks and pines analysed separately we tested against spatial point independence based on the random simulation of Poisson point configurations (see for instance, Stoyan & Stoyan, 1994). Under the bivariate point pattern (i.e. the point patterns of both species together) we considered two approaches, *random labelling* and *random superposition* (see Illian *et al.*, 2008). Testing for spatial independence of marked point patterns of oaks and pines, respectively, was based on the *random marking* approach (Illian *et al.,* 2008). Finally, for the point pattern consisting of both tree species together with a mark associated to each tree position we assumed *random labelling* of tree species over the fixed point positions, and then over this new bivariate point pattern, we considered a random marking approach to generate independent bivariate marked point configurations (see, Penttinen *et al.*,1992).

For the statistical analysis of point patterns, we considered the computational implementation in the statistical package Spatstat for the R statistical environment (R Development Core Team, 2007).

Results

$\delta^{18}O$ and $\delta^{2}H$ in soil water and xylem sap

The analysis of isotopic compositions of water extracted from soil samples showed a decreasing trend along the soil profile. In particular, the topsoil was significantly more enriched ($\delta^{18}O$ = 0.2±1.2 ‰; $\delta^{2}H$ = 34.6 ± 3.8 ‰) than the subsoil ($\delta^{18}O$ = -3.0 ± 2.4 ‰; $\delta^{2}H$ = –45.4 ± 8.5 ‰) ($P = 0.019$ and $P = 0.035$ for $\delta^{18}O$ and $\delta^{2}H$, respectively; two-tailed, paired *t*-test). In addition, the variability found among soil samples taken in the subsoil (ranging from 19 to 33 cm depending on digging point) was mostly explained by soil depth ($\delta^{18}O$ = 20.3–2.2 × depth(m), $R^2 = 0.85$, $P = 0.02$; $\delta^{2}H$ = 3.1 – 0.52 × depth(m), $R^2 = 0.67$, $P = 0.07$). Conversely, we did not find any significant correlation between the isotopic composition of soil water and X or Y coordinates, neither for the topsoil nor for the subsoil. The range of values of xylem water for each species ($\delta^{18}O$ = –7.4 to + 3.0‰ and $\delta^{2}H$ = –61.5 to –7.0‰ in pines; $\delta^{18}O$ = –8.1 to –2.6‰ and $\delta^{2}H$ = –67.8 to –41.6‰ in oaks) was comparable, although in some cases exceeded the range observed in soil samples, particularly for $\delta^{2}H$ ($\delta^{18}O$ = –5.7 to + 1.7 ‰; $\delta^{2}H$ = –55.7 to –28.5‰).

ANCOVA of BA, $\delta^{18}O$ and $\delta^{2}H$

ANCOVAs revealed significant differences between pines and oaks (–1.2 ± 0.18‰ and -5.3 ± 0.15‰, respectively, for $\delta^{18}O$; –25.1 ± 0.78‰ and –54.3 ± 0.66‰, respectively, for $\delta^{2}H$), in addition to a progressive increase of both isotopes along the X axis that was significantly higher for *Q. ilex* (0.054‰ m^{-1} and 0.155‰ m^{-1}, for pines and oaks, respectively, for $\delta^{18}O$; 0.248 ‰ m^{-1} and 0.610 ‰ m^{-1}, for pines and oaks, respectively, for $\delta^{2}H$) (test of unequal slopes; Table 1). These results suggest the existence of spatial anisotropic effects for the xylem water isotopic compositions of oxygen and hydrogen.

Spatial distribution of pines and oaks

Figure 2 shows the bivariate point pattern of *Q. ilex* and *P. halepensis* together with the resulting pair correlation functions (Eq. 1) and cross-pair correlation function (Eq. 2), and their respective fifth-largest and smallest envelope values based on 199 point configurations based on the null hypotheses, i.e. random labelling and Poisson point randomizations. Results suggest that both point configurations were at random, i.e. trees from the same species were independently located from each other, and that trees from distinct species were located at random from each other, thereby pointing to spatial independence between these two species in terms of individual tree location.

Spatial analysis of BA, $\delta^{18}O$ and $\delta^{2}H$

The spatial locations of *Q. ilex* and *P. halepensis*, along with individual tree BA in the area of study, are shown in Figure 3a. Visual inspection of bivariate marked point patterns did not provide much information about the spatial dependence of these two species.

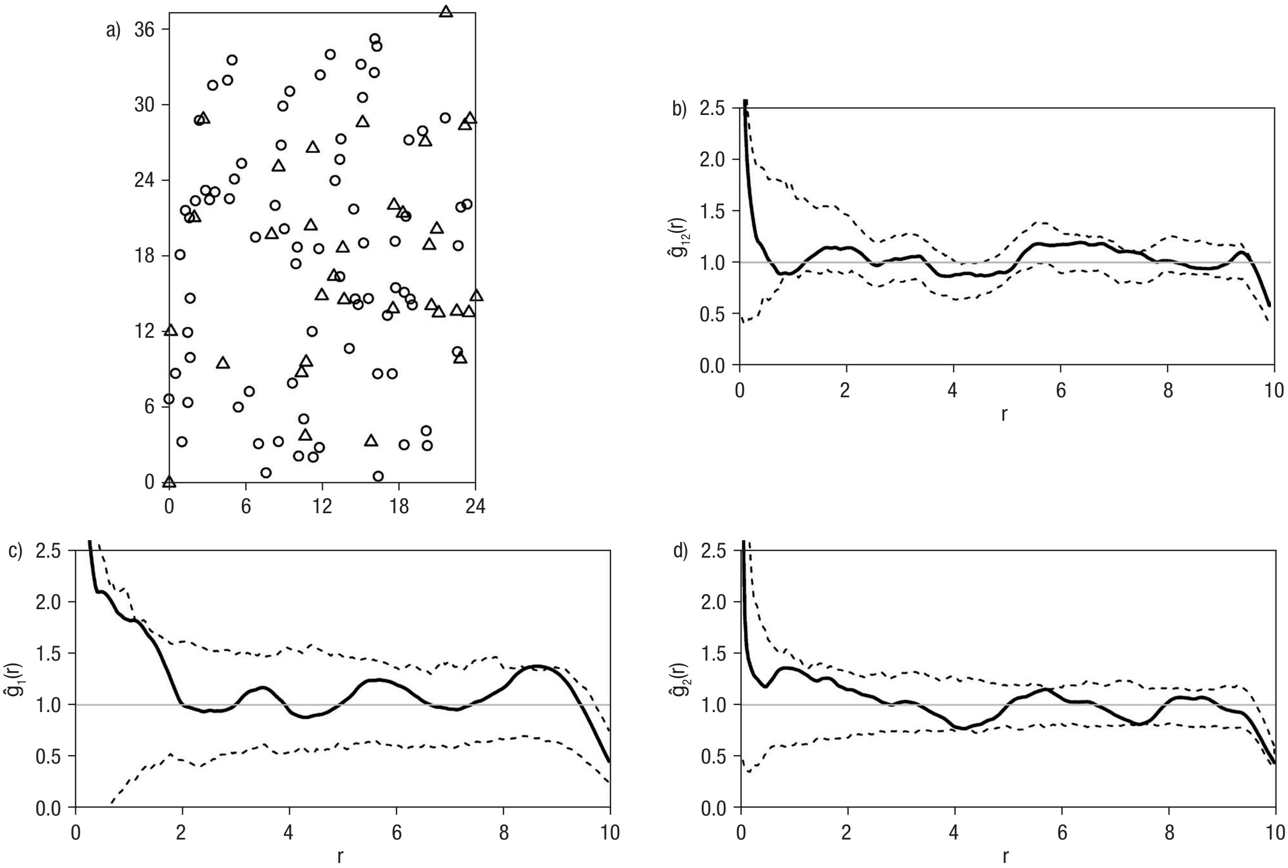

Figure 2. Bivariate point pattern. (a) Bivariate point pattern of *Q. ilex* (triangle) and *P. halepensis* (circle) in a forest stand in Central Catalonia (Spain) together with (b) the resulting cross-pair correlation function (Eq. 2), assuming random labelling, and empirical pair correlation functions (Eq. 1) for (c) *Q. ilex* and (d) *P. halepensis* and their fifth-largest and smallest envelope values (dashed lines) based on 199 random simulations according to these two null hypotheses (random labeling and Poisson point randomizations); inter-tree distance (r) is given in metres.

The resulting estimators of the mark correlation function (Eq. 3) for tree BA (Figure 3c and d) suggested that only the spatial structure of *P. halepensis* showed dependence, whereas no correlation was observed for *Q. ilex*. In particular, tree BA had negative correlation effects for *P. halepensis* as this empirical function lies down the lower envelope. There was evidence that trees at distances of less than two meters had smaller tree sizes than they should have under the hypothesis of random marking. Moreover, the resulting cross-mark correlation function (Eq. 4) for tree BA for both tree species (Figure 3b) suggested no inter-specific BA spatial correlation. Thus, tree size for a given species did not depend on the presence of the other species.

Visual inspection of the mark point pattern of *Q. ilex* and *P. halepensis* for the isotopic compositions of oxygen and hydrogen indicated increasingly higher values along the X-axis, suggesting the presence of anisotropic effects; this result was especially noticeable for *Q. ilex* (figure not included). This is in full agreement with the results obtained in the ANCOVAs. Because we observed directional components in the X-axis, i.e. anisotropic mark effects, and these effects affected the resulting estimated correlation functions, which are defined for isotropic (marked) point patterns, we considered a correction for such effects. Since the related point patterns were isotropic and only the mark component showed anisotropic effects, the use of inhomogeneous (anisotropic) versions of the point correlation functions based on a (non)parametric estimate of the point intensity (see, for instances, Law *et al.,* 2009) were not of applicability. In the case of anisotropy in the marginal distribution of marks, these anisotropic effects should be incorporated in the mark correlation function by allowing this distribution to vary along this directional component. This could be done by assuming the mark expectation (say) to vary along this directional component. However, this approach is not trivial and few studies (if any) have corrected anisotropy for the mark component. Therefore, we adopted an easier procedure to correct mark anisotropic effects by considering the residuals of these variables (marks) after assuming a deterministic, species-dependent linear trend through this X-axis in accordance with the outcome of the ANOVAs. These residuals were

Table 1. Mixed model analysis of variance (ANOVA) for the three variables studied. Covariates accounting for variation along the X and Y axes of the two-dimensional space (alone and interacting with the species factor, i.e. testing for separate slopes) are included in the models. In parentheses, standard errors of variance components.

Source of variation (δ^{18}O)

Fixed effects	**Num DF**	**Den DF**	**Variance ratio**	**Pr > F**
species	1	105	264.7	<.0001
X Coordinate	1	105	21.71	<.0001
Y Coordinate	1	105	1.44	0.2323
X × species	1	105	10.05	0.0020
Y × species	1	105	1.62	0.2055
Random effects			Variance component	
Residual (*Q. ilex*)			0.68 (0.177)	
Residual (*P. halepensis*)			2.40 (0.391)	

Source of variation (δ^{2}H)

Fixed effects	**Num DF**	**Den DF**	**Variance ratio**	**Pr > F**
species	1	105	115.5	<.0001
X Coordinate	1	105	20.9	<.0001
Y Coordinate	1	105	0.1	0.9284
X × species	1	105	4.4	0.0384
Y × species	1	105	2.3	0.1353
Random effects			Variance component	
Residual (*Q. ilex*)			12.43 (3.209)	
Residual (*P. halepensis*)			45.85 (7.487)	

Source of variation (individual basal area)

Fixed effects	**Num DF**	**Den DF**	**Variance ratio**	**Pr > F**
species	1	105	18.54	<.0001
X Coordinate	1	105	0.03	0.8524
Y Coordinate	1	105	0.85	0.3578
X × species	1	105	0.17	0.6776
Y × species	1	105	0.09	0.7685
Random effects			Variance component	
Residual (*Q. ilex*)			22600 (5835.4)	
Residual (*P. halepensis*)			45780 (7475.9)	

also scaled to avoid negative values. The resulting marked point pattern of residuals is not affected by the linear trend and therefore ensures isotropy.

Figure 4 shows the resulting mark point pattern for δ^{18}O residuals and the resulting mark correlation function, highlighting that water uptake strategies for *P. halepensis* were dependent on the spatial tree configuration. Particularly, pine trees had similar water uptake patterns at short inter-trees distances, and neighbouring trees at distances less than 4 meters tended to obtain more superficial (i.e. closer to topsoil values) water. Non-significant spatial dependencies were obtained for *Q. ilex*. In contrast, the cross-mark correlation function for this isotope showed spatial independence between both tree species (see Figure 4b). Thus, species-specific water extraction strategies did not depend on the presence of the other species.

As expected, comparable results to those of δ^{18}O were obtained for the spatial structure of δ^{2}H residuals (Figure 5) since both isotopes were highly correlated. For *P. halepensis*, δ^{2}H residuals had spatial dependencies at short inter-tree distances (<4 meters), while for *Q. ilex* we assumed that the isotopic composition were spatially uncorrelated.

Discussion

Do Aleppo pine and Holm oak occupy different niches for water uptake?

Marked point process statistics are valuable techniques to evaluate and describe forest systems (see,

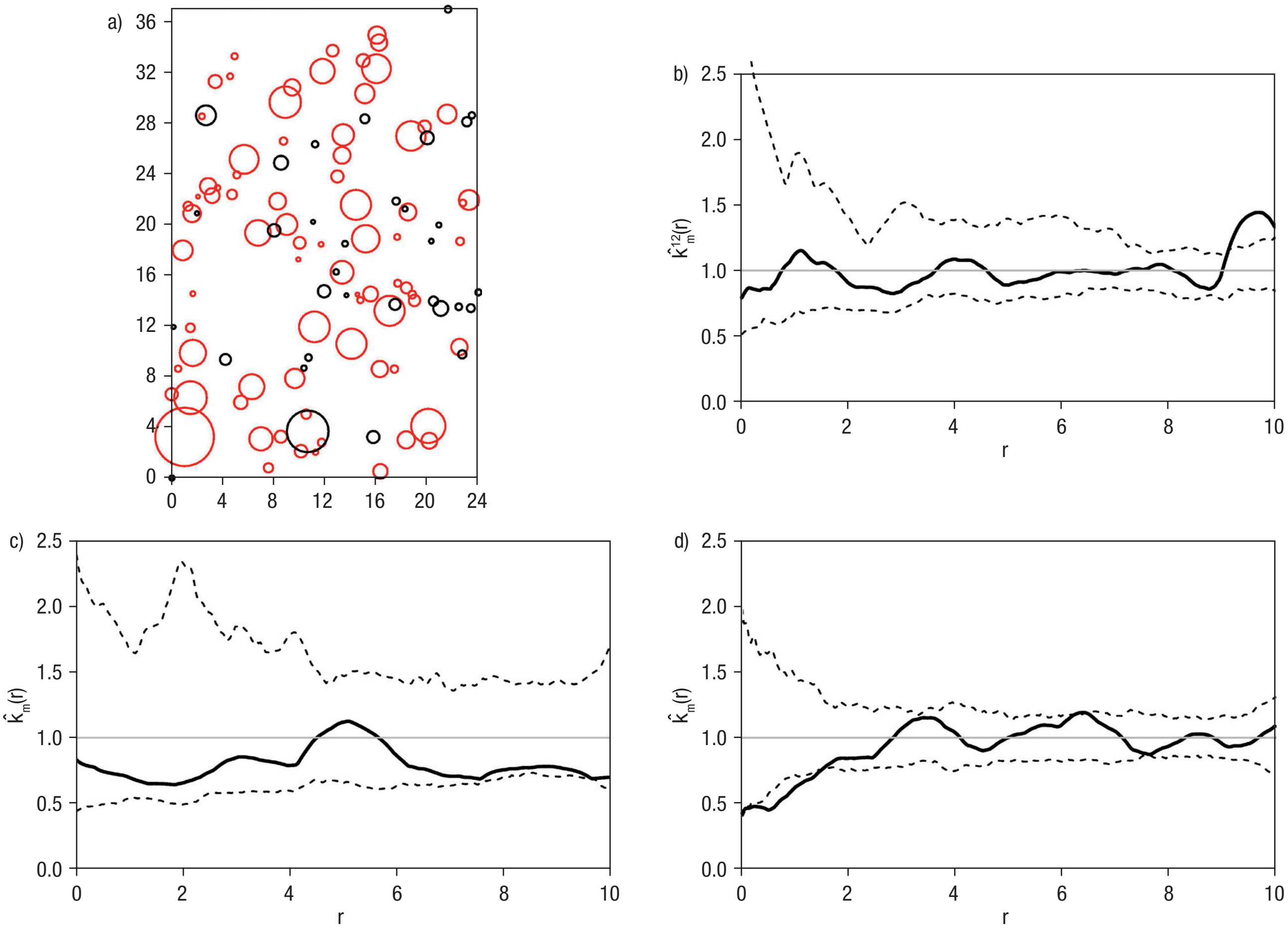

Figure 3. Mark correlation function (basal area). (a) Bivariate marked point pattern for basal area, involving two tree species, *Q. ilex* (black circles) and *P. halepensis* (red circles), together with (b) the estimated cross-mark correlation function (Eq. 4), and resulting mark correlation functions (Eq. 3) for (c) *Q. ilex*, (d) *P. halepensis*. The fifth-largest and smallest envelope values (dashed lines) are based on 199 random labelling and marking (b), and 199 random marking (c and d) over fixed point positions. Circle plot radius is proportional to each mark and inter-tree distance r is given in metres.

amongst others, Stoyan & Penttinen, 2000; Comas & Mateu, 2007). Here, we considered these spatial tools to disentangle competition effects for water at inter- and intra-specific levels in a water-limited environment. Our results highlight the existence of clear niche segregation between the Mediterranean trees *P. halepensis* and *Q. ilex*. Firstly, and using classical analysis of covariance procedures, we found that the stable isotope composition of xylem water (both δ^{18}O and δ^{2}H) was on average significantly higher in Aleppo pine than in Holm oak. Decreasing trends in soil water δ^{18}O and δ^{2}H were also observed with soil depth, confirming the existence of an evaporative gradient in the soil. An increasing trend in xylem water δ^{18}O and δ^{2}H was also observed along the X dimension of the experimental plot, which agrees with decreasing soil depth following this direction, hence favoring higher water evaporation. However, this trend was steeper for *Q. ilex*, suggesting that this species had comparatively better access to deep soil layers than *P. halepensis* with increasing soil depth. Comparing the δ^{18}O and δ^{2}H of xylem water with the soil profile, we may first conclude that Holm oak takes up more water from deeper soil layers than Aleppo pine after a long drought period, as would be expected according to the deeper root system of evergreen schlerophyllous, as compared to pines (Canadell *et al.*, 1996). Besides overall inter-specific differences, the study of tree-tree interactions using mark correlation functions confirmed the existence of two separate niches for water uptake. Firstly, we observed a significant spatial dependencies of neighbouring pines (inter-tree distances of less than 4 m.) to obtain water from upper soil layers (i.e. higher δ^{18}O and δ^{2}H of xylem water), and an uncorrelated spatial configuration for oaks (see Figures 4-5). In contrast, when looking at the inter-specific relationships (i.e. the effect of neighbours from the opposite species), we did not find any clear pattern for either competition or facilitation. Thus, there are interdependencies among neighbour pines, but not among neighbours of different species.

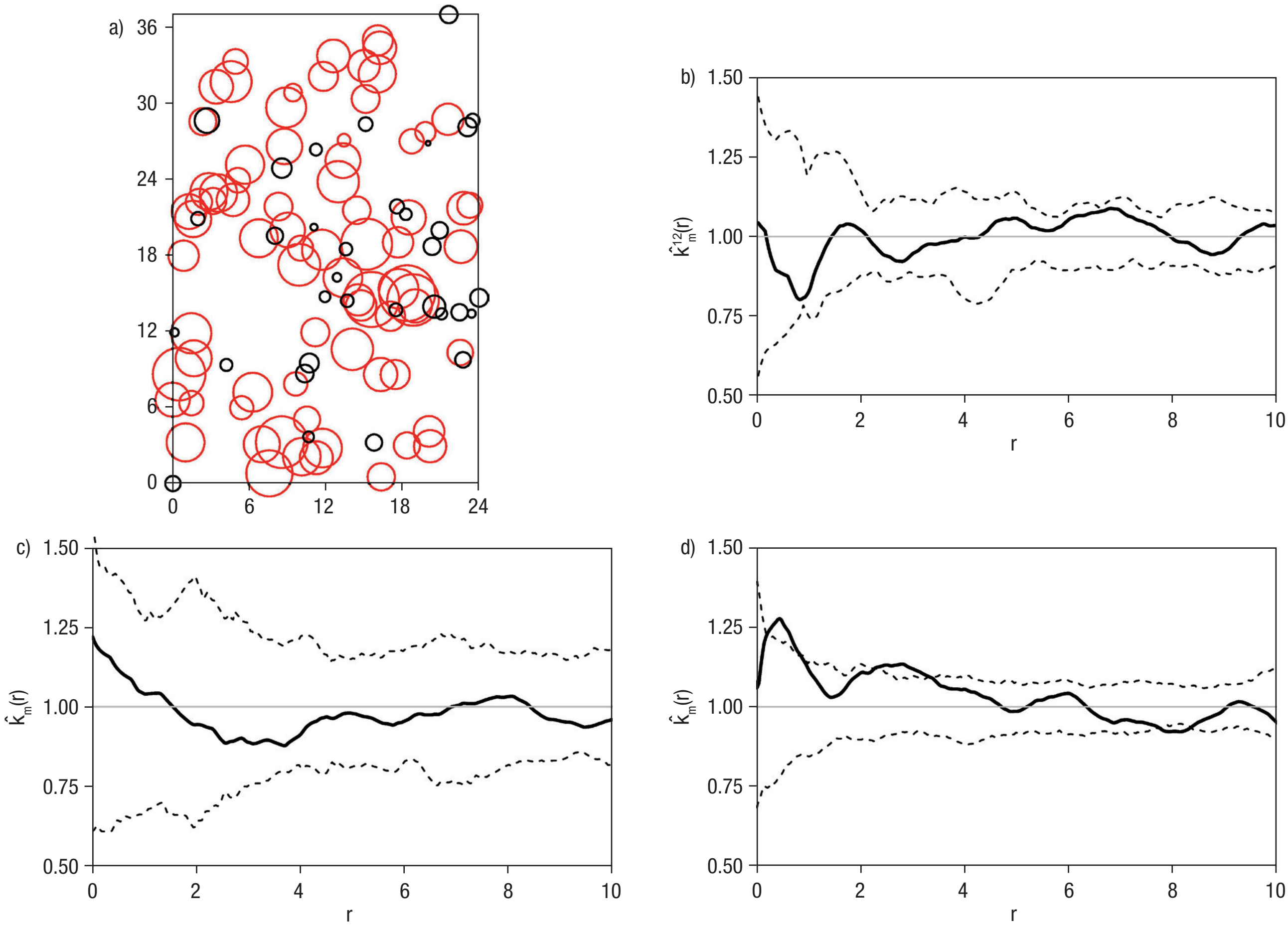

Figure 4. Mark correlation function (oxygen–18). (a) Bivariate marked point pattern for oxygen isotope composition ($\delta^{18}O$) residuals, involving two tree species, *Q. ilex* (black circles) and *P. halepensis* (red circles), together with (b) the corresponding cross-mark correlation function (Eq. 4), and the resulting mark correlation function (Eq. 3) for (c) *Q. ilex*, (d) *P. halepensis*. The fifth-largest and smallest envelope values (dashed lines) are based on 199 random labelling and marking (b), and 199 random marking (c and d) over fixed point positions. Circle plot radius is proportional to each mark and inter-tree distance r is given in metres.

This is in agreement with the niche segregation hypothesis, further supporting the idea that oaks are able to get water from deeper soil layers that may be less accessible for pines. In this regard, the depleted isotopic values observed in the xylem of oaks are typical of deep soil water, showing no signs of evaporative enrichment. The postulated access to non-evaporated deep soil layers, with high water availability, would also explain the lack of spatial interaction among oak individuals: under such conditions, competition for water resources is scarce.

Similarly, the mark correlation function for BA of pines (Figure 3d) suggested the existence of competitive inhibition for growth at distances below 2 m. In direct contrast, tree BA was distributed at random for oaks and oaks-pines spatial structures, respectively. This points out that long-term growth in Aleppo pine is more strongly affected by competition than it is in the case of Holm oak, in agreement with its greater plasticity in radial growth (Ferrio *et al.*, 2003; Zavala *et al.*, 2000). Nevertheless, what remains intriguing is the fact that Aleppo pine, a more sensitive species to competition, does not show a clear response in terms of growth in the presence of Holm oak. In our case, observed BA responses may reflect the shade-intolerant character of Aleppo pine, but also they could be a result of increasing competition for water resources, or (most likely) a combination of both factors (Zavala *et al.*, 2000).

In any case, it is likely that the competitive effect of Holm oak trees on individuals of Aleppo pine was much lower than if neighbor trees were from the same species. Particular reasons for this may be two-fold. On the one hand, and regarding competition for water resources, the observed evidences of distinct water uptake patterns for the two species may explain the lack of interaction, even when water resources are limiting (see e.g. Klein *et al*. 2013). On the other hand, the much faster height growth of pines may ensure them attaining a dominant position in terms of light

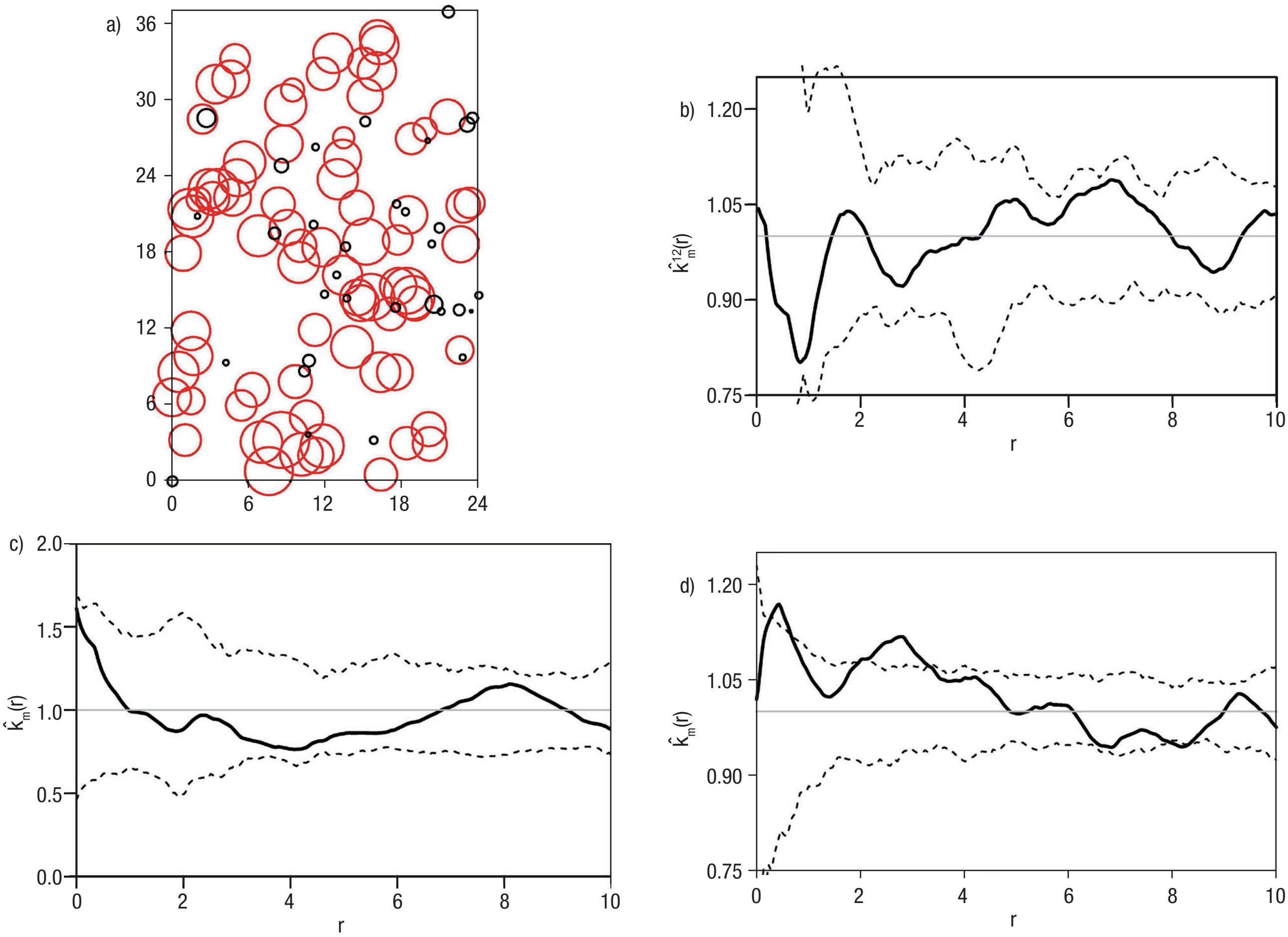

Figure 5. Mark correlation function (hydrogen-2). (a) Bivariate marked point pattern for hydrogen isotope composition (δ^2H) residuals, involving two tree species, *Q. ilex* (black circles) and *P. halepensis* (red circles), together with (b) the corresponding cross-mark correlation function (Eq. 4), and the resulting mark correlation function (Eq. 3) for (c) *Q. ilex*, (d) *P. halepensis*. The fifth-largest and smallest envelope values (dashed lines) are based on 199 random labelling and marking (b), and 199 random marking (c and d) over fixed point positions. Circle plot radius is proportional to each mark and inter-tree distance r is given in metres.

interception, as compared to oaks (Zavala *et al.*, 2000). Conversely, the shade-tolerant nature and conservative growth of the evergreen oak would cause a lack of negative response to this sort of dominance. Nevertheless, due to the existence of a relatively open canopy, it is more likely that growth patterns were dominated by water limitation, at least for the case of the most shade-intolerant species.

Alternative sources of variation for stable isotopes in xylem water

In this study we initially assumed that differences in xylem water would reflect distinct water uptake patterns originating from contrasting contributions of soil layers.

However, whereas interspecific differences can be easily explained by the uptake of water from different depths, the observed increase in δ^{18}O and δ^2H in neighbouring trees, particularly in pines, is less straightforward. The presence of close neighbours can be interpreted as a local increase in stand density, and indeed more positive values in δ^{18}O of xylem water of Aleppo pine have been reported when comparing a densely afforested stand (770 trees ha^{-1}) with an open woodland (20 trees ha^{-1}) (Moreno-Gutiérrez *et al.*, 2012a). The direct interpretation is that closer trees tend to use more water from upper soil layers, although there is no clear physiological reason for this behaviour. As pointed out by Moreno-Gutiérrez *et al.* (2012a), one possibility is that the presence of close neighbours increased shadowing, thus reducing soil evaporation and keeping more water available in upper soil layer, which is generally enriched as compared to deeper soil. Nevertheless, since the enrichment of upper soil water is caused by evaporation, the water available in the upper soil of dense stands is likely to be less enriched than that of a more exposed soil surface, thus having an opposite effect. In addition, a similar effect would have been expected in response to shadowing caused by oaks, and this is not supported by our data. An alternative explanation may come from evaporation processes occurring in the branch (Dawson & Ehleringer, 1993): when transpiration rates are drastically reduced, e.g. during drought periods or in a cold winter, water in the branches has a longer turnover time and may show progressive evaporation, or partially mix with enriched phloem water. In this regard, it is likely that neighbour trees competing for a limited water source would show higher restrictions in transpiration than those trees having fewer neighbours, thus becoming more prone to branch evaporation. Branch evaporation, in turn, would increase the proportion of heavy isotopes in xylem water, due to the faster evaporation of the light isotopes, and thus could explain the higher δ^{18}O and δ^{2}H observed in trees with close neighbours. This would also explain the stronger neighbour effect in pine as compared to oak, since the former is a water-saving species, with a more sensitive stomatal response (Ferrio *et al.*, 2003; Zavala *et al.*, 2000). However, again certain effect of the presence of oaks over pine isotope composition would have been expected, since the effective water uptake of oaks would also decrease water available for the pine, pushing the reduction of transpiration. Nevertheless, although we do not have direct measurements of tree transpiration in our site, previous studies on *P. halepensis* have shown that late-summer transpiration at the leaf level may still account for *ca.* 20% of maximum values (Klein et al. 2005; Baquedano & Castillo 2006; 2007), and a similar proportion has been observed in whole-tree transpiration (Raz Yaseef *et al.* 2010; Klein *et al.* 2013, 2014). Similarly, studies on Ponderosa pine have shown that even during summer drought the trees do not cease transpiration and can still use a significant proportion of water from upper soil layers (Fernández *et al.* 2008). Altogether, both current isotope evidence and previous works on *P. halepensis* suggest that the observed inter- and intra-specific differences could reflect the use of distinct water pools in the soil, although the underlying causes still require further clarification.

Conclusions

Although results from our case study are not totally conclusive, the application of point-process statistical tools has allowed us to go beyond the comparison of inter and intra-specific (non-spatial) differences in water uptake, thereby revealing complex spatial dependencies in the use of water. In particular, our study indicates complementary water uptake patterns between Aleppo pine and Holm oak during the dry season, showing intra-specific competition among neighbour pines, but neither facilitation nor competition between individuals of different species. These results, however, might not be extrapolated to any pine-oak mixed stands, since root development might be affected by the history of the stand (e.g. whether oaks are seedlings or sprouts) and the different degree of dominance of each species. However, it should be noted that competition for water resources can be dynamic, mainly modulated by water availability (see e.g. Bellot *et al.*, 2004; Hentschel *et al.*, 2013). In this regard, assessing the seasonal-course of tree-to-tree interactions might help to explain how pines and evergreen oaks often co-exist in long-term equilibrium in areas with limited water resources (Zavala & Zea, 2004).

Acknowledgements

We gratefully acknowledge the assistance of JR Olarieta in soil taxonomy classification.

The authors acknowledge M.J. Pau and P. Sopeña for technical assistance.

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