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RESEARCH ARTICLE

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Yew matriarchies of the *Sierra de Francia.* Dynamics and ecology of recently identified Yew populations in the Central Iberian Mountain Range (*Sistema Central*)

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Abstract

Aim of study: Our study design presents two main objectives: 1) to create a census that details the number of yew individuals and their geographic distribution, and 2) to attempt to unravel possible reproductive relationships and their connection between true population nuclei and meta-population models.

Area of study: Recently identified yew populations (*Taxus baccata* L.) were studied in the western sector of the Sistema Central mountain range of the Iberian Peninsula, known as the Sierra de Francia. The study was carried out in five watersheds within Las Batuecas-Sierra de Francia Natural Park.

Material and Methods: All yew specimens were counted and assigned to age groups. The notable differences observed in regeneration aof these communities propitiates population analysis aimed at explaining the landscape connectivity relationships between the different population nuclei and the possibility of defining the meta-population set. Ecological niche models were also created to define the main ecological characteristics of the different subpopulations studied, and to compare them.

Main results: Yew in the Sierra de Francia live in an array of different Mediterranean forests, indicative of species dynamics in the Iberian Peninsula. 2,450 specimens were recorded and classified into the three types of yew forest population dynamics: regressional-, naturally regenerating-, and incipient- (i.e. colonizing new territories).

Research highlights: The essential role of connectivity between populations was recognized and confirmed in this study, specifically among the large female trees located at the headwaters. Based on the role of these female trees, we have created a model called "yew matriarchies", which serves to express the relevance of large female yew trees in population dynamics.

Keywords: *Taxus baccata*; census; connectivity; seed dispersal.

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Introduction

The initial visit to the yew trees in our study proved to be purely anecdotal. As the study progressed, however, observing the flora and vegetation of the *Sierra de Francia* has elucidated the remarkable presence of yew in the area. They form several population nuclei that are embedded in markedly diverse environments and exhibit population dynamics which are both different and divergent.

Our study design presents two main objectives: 1) to create a census that details the number of yew individuals and their geographic distribution, and 2) to attempt to unravel possible reproductive relationships and their connection between true population nuclei and meta-population models.

The natural assemblage described in this paper is compromised of many individual trees and groups of yew groves which are dispersed throughout a wide and rugged territory devoid of paths or other means of easy access to the nuclei. Their beauty and interest resides in the simple fact of knowing that the groves and elders exist. As a whole, this hitherto unknown group of trees in the Iberian Peninsula exhibits perfect adaptation to all the climatic belts with exquisite gradation in which they coexist with other species present in a small space, thus demonstrating their ecological originality and differential dynamics.

Materials and methods

The study was carried out over four years (2010-2014) and has materialized as 22 field tours along the main valleys and streams of *Las Batuecas-Sierra de Francia* Natural Park. The yew specimens that were detected and characterized have been counted and assigned to age groups. The perimeter and gender of representative yew trees have been also recorded. Dead trees have been inventoried and their most probable causes of death have been inferred.

Age classifications are as follows:

- Regenerating saplings: plants more than one year old (lignified) between 5 and 150cm tall.
- Juveniles (recruiting stage): Young trees taller than 150cm and with a trunk perimeter up to 50cm.
- Adults: Trees with trunk perimeters above 50 and less than 300cm.
- Old growth: Trees with trunk perimeters near or above 300cm.

Year-old seedlings or plants shorter than 5cm have not been included given their high mortality rates.

Recruitment rate was the key interval used to define the current dynamics of the populations studied. Recruits (juveniles) are considered to be young poles taller than one and half meters which have their main branches safe from herbivore predation. These parameters assume that the trees have a low mortality rate and are thus able to ensure the renewal of the yew grove in the medium to long term. The following formula is used to calculate this rate (I_r):

$$I_r = \text{nº Recruits} / (\text{nº Regenerating saplings} + \text{nº Recruits} + \text{nº Adults and Old growth trees})$$

The dataset was analyzed using GIS to obtain dynamic analysis products. In particular, gaussian kernel density estimation techniques were utilized to get population density maps.

Ecological niche models were also created using the MaxEnt software (Phillips *et al.,* 2006), enabling us to define the main ecological characteristics in which the populations under study are developing (Phillips *et al.,* 2006; Phillips & Dudik, 2008).

We have run a joint analysis of a relevant number of environmental, topographic, hydrological, climatic and bioclimatic variables. Biotic variables have not been included given the challenges posed to obtain them in the field, the low precision level of the information source (Second National Forest Inventory 1:50.000 (MIMAM 1996); Atlas of breeding birds of Spain, UTM10K (Martí, R. i del Moral, J.C. (Eds.) 2003), and the complexity of the cartographic legend (Spanish Soil Occupation Information System (SIOSE), IGN, 2011). All climatic variables were modified from Ninyerola *et al*., 2005.

The variables used are as follows:

- Topographic: Elevation (ELEV); Orientation (OR360_rclss); Slope (PEND_Rclss) and Topographical position (POS_TOPO).
- Hydrological: Topographic humidity index (ITpH); Distance to a stream (Dist_rio); Hydric flow density (Flow_Dns); Hydric flow accumulation (FlowAccsRcls).
- Climatic and bioclimatic: Springtime pluviometry (Pluvio_03); summertime pluviometry (Pluvio_07-08); Maximum temperature (TMax); Minimum temperature (Tmin); Martonne aridity index (ARIDEZ); Thermicity index (Ind_Trmcd); Emberger's ombrothembric index (IoEmbgr); Wintertime solar radiation (RadInv); Summertime solar radiation (RadVer).

All variables have been correlated with the location of each individual as well as with the assigned age group. This allowed us to compare differences between the environmental conditions most representative of the whole set and/or of the different age groups.

Additionally, populations have been analyzed using ArcHydroTools (ESRI) to model seed dispersal by water, and Conefor Sensinode software (Saura & Torné 2009), using resistance surfaces developed for frugivorous birds to determine aspects related to zoochory, connectivity between spots, and their relative significance in preserving the entire habitat.

We have conducted bibliographical research not only on botanical aspects, but also to amplify knowledge relating to complementary subjects such as geology and geomorphology, anthropology, history, ethnography, etc. Furthermore, we contacted environmental agents and interviewed naturalists, hunters and residents in the area to locate and study new spots not referenced in the current bibliography.

Study area characteristics

Located at the south end of the Salamanca province, the Sierra de Francia is one the westernmost foothills of the Central System mountain range in the Iberian Peninsula (Figure 1). The range is included in the National Inventory of Outstanding Landscapes (*Inventario Nacional de Paisajes Sobresalientes, 1975*), and is part of the Las Batuecas Regional Game Reserve (*Reserva Nacional de Caza de Las Batuecas 1970*) in the Las Batuecas-Sierra de Francia Natural Park (*Parque Natural de Las Batuecas-Sierra de Francia 2000*). What's more, it is a Site of Community Importance and SPA (special protection area for birds as part of the NATURA 2000 NETWORK) and was declared Biosphere Reserve in 2006. In the Sierra de Francia, the Las Batuecas Valley is classified as a Cultural Interest Heritage and Historical Site.

The terrains in the Sierra de Francia are Paleozoic: Cambric quartzites in the Maillo Creek, Silurian slates and Armorican quartzites in the Peña de Francia mountains and the Las Batuecas valley, or spots of granite in the Nava de Francia and La Alberca. There is also granitic debris at the bottom of valleys and ravines (Ortuño & de la Peña, 1978).

The tallest peaks are over 1,700m. (La Hastiala 1,735m., Peña de Francia 1,728m.), while the lowest elevation is where the Alagón river exits the natural space (386m.). Hydrologically, the waters feed two watersheds, the Duero river basin through the Morasverdes and Agadón rivers and the Tajo river basin through the Francia, Batuecas and Arroyo Belén rivers, all tributaries of the Alagón river, and the main current of the area. The significant gradient differential between the headwaters of the Batuecas (1,100m) and Francia river (1,200m.) together with the elevation at the mouth of the Alagón river (386m) marks the distinctive physiognomy of this watershed, characterized by steep slopes and a predominantly erosive dynamic that tends to confine river channels to fissures that have been excavated deep below the grade of the hill slope (Martínez-Graña, *et al.*, 2006).

This area is also of biogeographical interest since two altitudinal vegetation belts, the Supramediterranean and Mesomediterranean, come into contact, resulting in a wide variety of vegetation types and species. Oromediterranean belt can be found in the tallest peaks, thus further increasing the floristic and ecological diversity of the area (Figure 1). Precipitation is abundant in the higher regions, where the annual rainfall average is 1700mm y^{-1}; and in the lower, driest areas of the region, will be as low as 490mm y^{-1} (Ninyerola *et al.*, 2005).

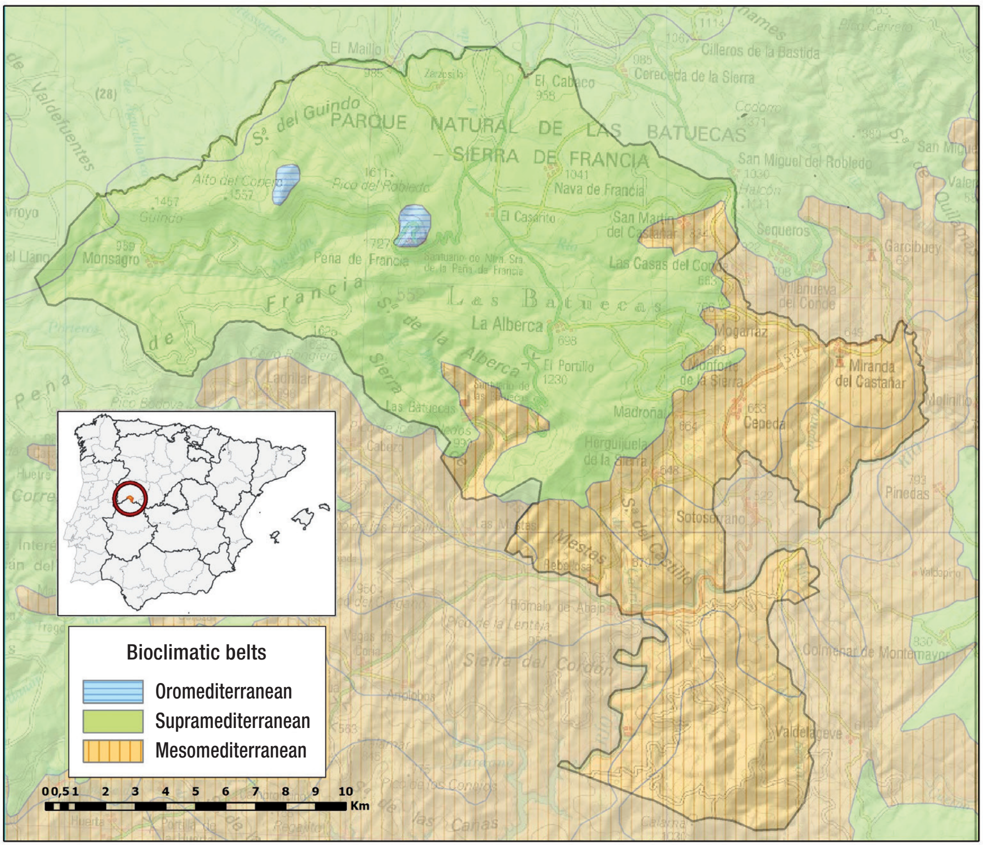

Figure 1. Location and bioclimatic belts: Oromediterranean, Supramediterranean, Mesomediterranean. Modified from Rivas-Martínez (1987).

Previous knowledge

Bibliographical references pertaining to the presence of yew trees in the area have always been scarce and imprecise. The presence of many isolated specimens has been cited in different documents but without precise locations and without mention of groves or even groupings of yews. There were only four bibliographical references with a 1km x 1km precision and references to 4 municipalities.

The presence of yew trees is not mentioned in the Natura 2000 Network framework, nor the existence of a European Priority Habitat of Interest 9580*. *Taxus baccata L*. Mediterranean Forests are, however, contemplated in the official forms for the Las Batuecas-Sierra de Francia Site of Community Importance (ES4150107) (http://rednatura.jcyl.es/natura2000/LIC/Formularios%20oficiales%5CPDF%20LIC%20resumen%5CES4150107.pdf.) (Línea S.L., 2007)

Results and Discussion

Census

The results of yew census in the Sierra de Francia are shown in Table 1 and Suppl. Tables S1 and S2 [online supplements]. Additionally, 127 dead yews have been counted: 71 in the Tajo river basin (22 burned, 34 cut and 15 dried) and 56 in the Duero river basin (6 fallen, 23 burned and 27 cut).

Site relevance depends upon the number of tree specimens counted to date, recorded to be at least 498 in the Tajo river basin and 1954 in the Duero river basin. This is approximately 2,452 specimens in total (not including those in the nearest mountain range, the Sierra de Quilamas). There are also 39 new Universal Transverse Mercator (UTM) 1x1 km grid squares, distributed throughout six municipalities (El Cabaco, El Maillo, Herguijuela de la Sierra, La Alberca, Mogarraz and Monsagro) which have been added to the *Taxus baccata* L. map (Serra & Garcia-Martí, 2008). These figures have increased significantly from those existing prior to this study (450 yews estimated for the entire province of Salamanca (Oria de Rueda J.A, & Díez J, 2011) and four 1x1 km grid square references). 39 grids and 2 municipalities have been added to previous knowledge for this study, resulting in yew presence in 43 squares and 6 municipalities (Figure 2).

Table 1. Census.

River Basin	Total individuals	Juveniles	Ir
TAJO	498	15	0.03
DUERO	1954	637	0.24
Total	2452	652	

In contrast to their scarcity suggested by literature, the reality is that yews are well represented in the area with isolated specimens; some large in size and vestige of the past. The yews are associated with rocky substrates, crests and quartzite stone rivers or runs; and others in relatively important groves comprised of trees of all ages. These trees exhibit abundant regeneration and high recruiting rates in some populations, especially those which are found next to senescent communities and in areas of incipient colonization.

Regeneration and threats

The recruiting rate and the kernel density estimation map offer a clear vision of the various dynamics exhibited by the species in the study area. We are able to observe how regeneration concentrates around the rivers and creeks that flow into the Duero River Basin, the highest rate found at the Canalhonda creek, while the rate of regeneration is very low or nonexistent in the creeks that feed the Tajo river Basin (Figure 3). It has been verified that most of the one year seedlings or seedlings shorter than 5cm in height disappear without contributing to regeneration.

Herbivore pressure (by goats and roe deer) creates a burden for yew regeneration (Cortes et al., 2000; García & Obeso, 2003; Thomas & Polwart, 2003; Iszkulo, 2011). In general, the juvenile yew populations are estimated to be younger than 40 years old. There is a lack of middle-aged specimens compared to adults because populations could not properly recuperate until the 1960s and 70s, when forest repopulation efforts and the disappearance of domestic goats permitted yews to have a resurgence in new areas (Ortuño & de la Peña 1978). Nowadays, predation by domestic herbivores is practically nonexistent. Their range has, however, been partially occupied by mountain goats and roe deer, which were reintroduced between 1970-75. These growing populations hence represent an incipient burden on yew regeneration.

Another affliction to yew population regeneration and maintenance is forest fire. Of the 127 dead trees counted, 55 had died on account of fire. It is hypothesized that this number is really even greater, given the great size of many of the burned trees recorded. We suppose that trees of a smaller diameter in fact disappeared upon being completely burnt. We cannot forget how the yew population of the Lera river, one of the

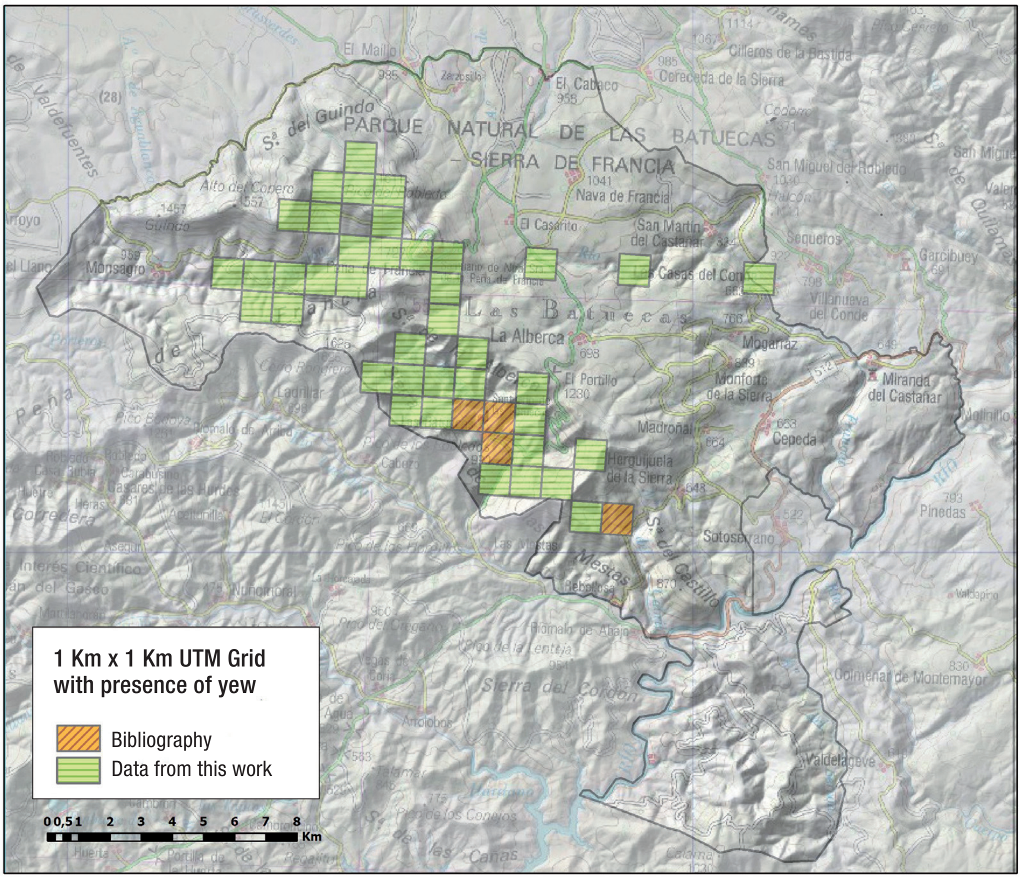

Figure 2. Yew presence in Sierra de Francia.

oldest of the region, was once annihilated by such a fire. The large carbonized trunks of those yews are still standing.

Yew ecology in the Sierra de Francia

In the Iberian Peninsula, it is rare to find yew populations above a biogeographical limit as diverse as this one (Blanco Castro *et al.,* 1997; Cortes *et al.,* 2000). Here the environment ranges from wet Mesomediterranean with subtropical madrone, laurustinus, and cork oak vegetation, to Atlantic Supramediterranean, where yews can be found amongst birch forests, holm oaks, Pyrenean oaks, oaks and alders. These yew stands span an altitudinal gradient of 530m above sea level in the Batuecas Creek, to the highest rock slide in the Peña de Francia (also known as Hastiala Peak) at an elevation of 1,580 m.

The general yew distribution follows a NW-SE axis independent of the orientation of the main valleys. It follows the main elevation line of the mountain range in direct relation to the transversal circulation of the prevailing winds which arrive from the Atlantic travelling SSW-NE/ENE, and full of moisture (CENER, 2014), thus bringing frequent and heavy precipitation as well as high ambient humidity.

The distribution of the yew throughout the region appears to be linked to creek and stream locations, which is seemingly logical in a species with more affinity for Atlantic than Mediterranean environments. In-depth analysis based on the use of ecological niche models showed, however, that in many cases this is in fact a residual or shelter position for the species. In terms of its direct relationship to riparian environments, yew trees play two main roles in this biogeographical assembly (companion or dominant) resulting in five, well differentiated, ecological positions that are not always expected.

When in the dominant position, yew determines the vegetation composition. Thus, as the predominant species in the riparian gallery of some creeks, it forms compact groves of varied age and size range, creating a homogenous, single-species nemoral zone. Isolated individuals constitute an important part of the Atlantic-influenced mountain riparian flora where birches grow. This is considered to be one of the most important locations in the entire Sistema Central (Vasco, F., pers. com.). Yews also grow in creeks between steep slopes, over rocky beds, and in Mediterranean environments where

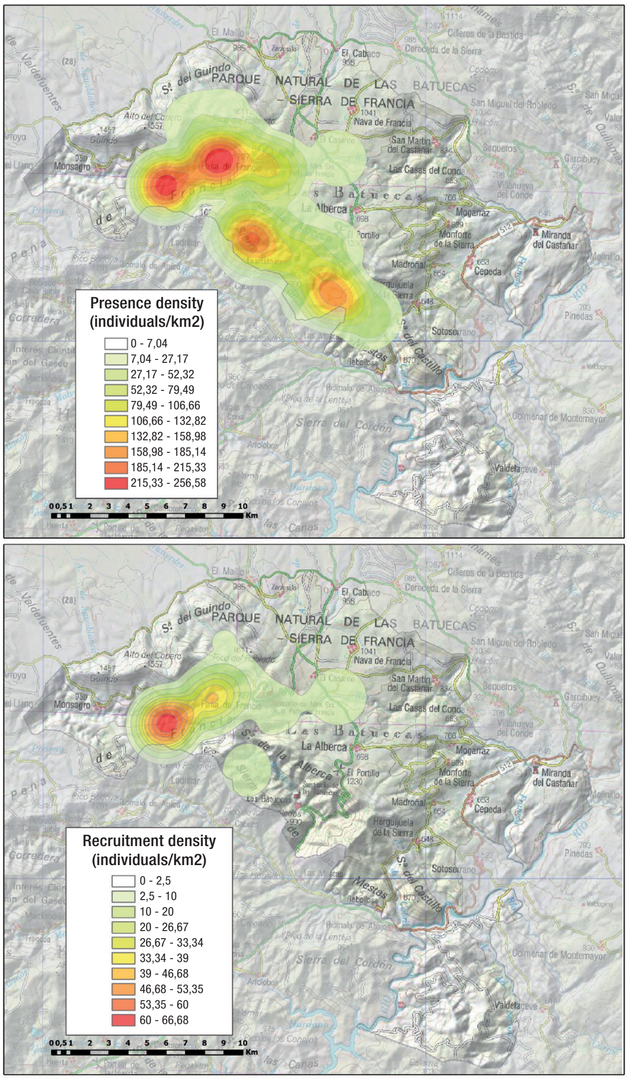

Figure 3. Presence density and recruitment density (individuals km^{-2}).

there is a wide variety of flora, tree, and shrub species such as *Quercus ilex* subsp. *ballota* (Desf.) Samp., *Q. suber* L., *Juniperus oxycedrus* L. , *Q pyrenaica* Willd., *Q robur* L., *Castanea sativa* Miller, *Fraxinus angustifolia* Vahl, *Alnus glutinosa* (L.) Gaertner, *Betula alba* L., *Arbutus unedo* L., *Viburnum tinus* L. etc.. Their growth gradation faithfully reflects the transition from eminently Mediterranean environments, resembling a subtropical rainforest at the south end, to Atlantic forests. Yew often appear sheltered by dense undergrowth of mainly heather or broom mats, but also by other types of low shrubs where, despite the near total absence of adult trees, they grow as a rather dense population of young regenerating trees hidden and protected by the shrub layer (Garcia & Obeso, 2003).

Perhaps most intriguing is the presence of large and old isolated specimens growing over quartzite screes; both in rock slides denuded of higher vegetation and in rocky grounds semi-fixed by shrubby vegetation and dispersed trees. Another unusual aspect in these locations is the range of trees with N and S (SE and SW) orientation, an arrangement possibly attributed to the prevailing flow of moist winds. The extensive rock slides have been ideal shelter for the species from fire. The dynamics of yew in these geological formations is still not fully understood, particularly in the case of the old isolated specimens, given the apparent difficulty for a species to establish itself in mobile media. Some contemplated possibilities are having survived large rock drifts that would have buried them; or surviving the disappearance of the soil and organic matter matrix by being caught between large blocks of rock deeply excavated by the river. This possibility may explain the existence of old senescent specimens with exposed roots in the Batuecas River basin; while the first hypothesis could attest to the presence of other notable trees isolated in the Agadón and Morasverdes watersheds that appear vital and with suckers, but lack visible roots.

Ecological niche models

The evident divergence between the area currently occupied by yew and the area where regeneration is taking place, together with the variety of environments and orientations the yew occupies in these mountains, have led us to rely on ecological niche models as a means of defining the environmental factors that most influence the presence and dynamics of these populations. The results show differences between the characteristics of the niches populated by established trees (adults and old growth trees) and those of the niches populated by young trees. These differences mean that there are more environmental variables responsible for influencing the juvenile niche and low numbers, at times extremely low, compared with the niche occupied by adults (Table 2).

The juvenile niche is preferably characterized by physiographical variables and to a lesser extent by climatic and bioclimatic variables; while the variables that are significant for the established trees are the bioclimatic (ombrothermic, aridity and thermicity) indexes. The heavy dependency of the adult group on bioclimatic variables, which are also important but not as significant to the juvenile group, together with other variables that depend on the former but have not been quantified, such as soil formation or loss, could explain the divergent population trends observed in the different valleys. The topographic position variable (Pos_Topo) is, for both sets, the most important factor for the characterization of the respective niches, although there is one notable difference in terms of percentage

Table 2. Environmental variables with more influence over niche.

Variable	Percent contribution	
	Adults	Juveniles
POS_TOPO	34.1	25.5
Dist_rio	7.7	21.7
Ind_Trmcd	7.9	15.5
TMax	1.2	13
IoEmbgr	29	12.4
Pluvio_03	0.7	4.8
RadInv	1.1	4.7
ELEV	1	0.5
Pluvio_07-08	0.9	0.3
ARIDEZ	13.6	0.2
RadVer	0.8	0.2

of representativeness. Topographic position represents the difference between the elevation of any given point and the average elevation of the surrounding terrain in a 50m radius. Figure 4 show how the maximum probability for the presence of adults (85%) are in positions located 10 meters or more below the average terrain elevation (strongly boxed-in), and with nearly zero probability of appearing at grade level or higher than its immediate environment. However, most of the juveniles (70%) are between 6 and 8 meters below the average elevation of the terrain, and some (25-30%) are found at grade level, or higher than their immediate surroundings (10%). This implies a trend of juveniles occupying more open ground than adults, thus confirming the generalized idea that fires, herbivory, or adverse climatic events have restricted adult yew distribution to the most sheltered or hardly accessible spots.

Since it can be assumed that there will be greatest rates of regeneration wherever seed rain is more intense, it seems consistent that the greater proportion of regenerated trees is found in tightly boxed-in environments where the reproductive individuals are located. However, the proportion of recruitment existing in the more open areas entails, on the one hand, expansion (migration) of the species towards new territories and on the other, active seed movement, either via water transport (always downhill and within the same drainage) or animal dispersal (upslope or in drainages without reproductive trees). Comparing both curves in Figure 4, leads us to postulate the role of barochory, hydrochory and zoochory processes on the dispersion of yew.

Seed dispersal

The relevance of gravity as a seed dispersal agent in steep slopes, and most particularly, its action combined with that of water, is innovatively documented by the copious accumulation of yew fruit and needles. The run off of heavy rain flows between the boulders and cobble scree, yew groupings are, and drags the fruit and needles. Accumulations were found in the ditch beside the road which interrupts the drainage path from said site (Figure S1 [online supplement]). This finding also shows how human intervention drastically modifies both the natural dynamics of rainfall, and the possibility of yew seed dispersion downhill (Figure S2 [online supplement]). Similar seed-dragging processes during high water events such as freshets or floods occur in all the streams and gullies where yew trees grow, and is considered to be the main agent for seed dispersal in the area for medium-long distances (Nilsson *et al.,* 1991; Nathan *et al.*, 2008).

The existence of zoochory is verified by the presence of yew seeds in the scat and regurgitation of foxes and small mustelids. They eat the yew arils and leave the remnants in animal paths, old cattle ways, or on top of

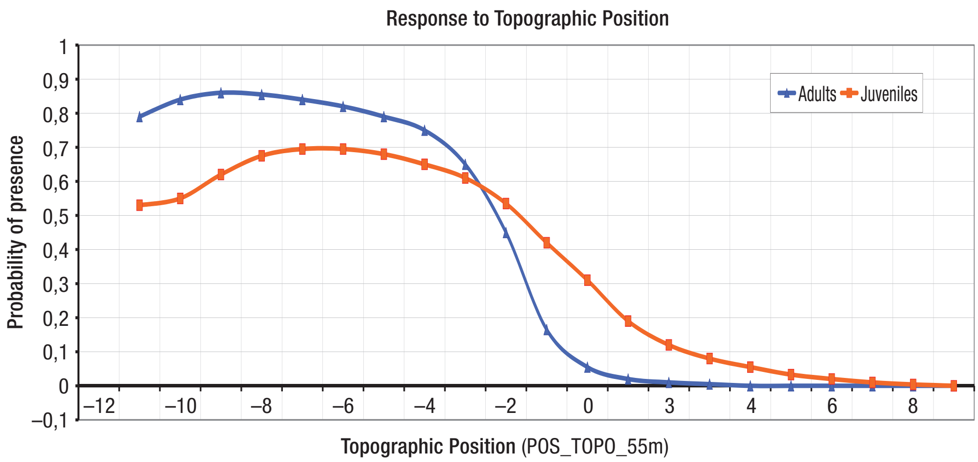

Figure 4. Response of adult and juveniles yew trees to topographic position

stones to mark their territory. This behavioural pattern is directly related to seed dispersal upstream. The relevance of the role of fruit eating birds in seed dispersal at distances up to 1km (García & Obeso, 2003, Cuevas Moreno JA, 2008; Carlo *et al.,* 2013), and oftentimes to habitats similar to the source habitat is also becoming more wholly understood (Carlo *et al.,* 2013), and is practically the only means of communication between populations in different valleys.

Connectivity, population and metapopulation

The set of yew trees and yew groves described herein appears to be splashed onto the landscape in isolated spots. It was for this reason that a study was developed to address the connectivity between these populations, and whether their relationship should be considered as a collection of isolated populations, as a metapopulation, or a simple single population. In the end, the reproductive and regenerative dynamics are what established the difference. For a metapopulation to exist, migration or exchange of propagules between the associated populations must occur and the greater or lesser frequency of this exchange determines whether this is a single population or a metapopulation (Hanski, 2001; Terrer-Moreno, 2007).

The extinction-colonization dynamics verified in the local populations exhibited: 1) patches in active regeneration stages and areas of expansion or new colonization (Agadón), and 2) stabilized areas both with low regeneration (Morasverdes, Francia) and without regeneration or even senescent communities (Batuecas, Belén). This information could be assimilated into a metapopulation set with source and sink populations. Considering the regeneration densities and the seed dispersion flows (mentioned above), along with their power and reach, connectivity analysis between local populations (Figure 5) shows a mixed status in which groups of local populations must be considered as single populations on account of the high possibility of exchange (Agadón, Morasverdes, Francia, Batuecas headwaters, lower Batuecas, Belén). On a larger scale, however, metapopulation behavior appears with the rational possibility of exchange between various headwaters (Agadón- Francia headwaters, Batuecas-Morasverdes headwaters, Batuecas headwaters-lower Batuecas), while there are some isolated local populations due to the scarcity of seed sources within reasonable distance (Belén).

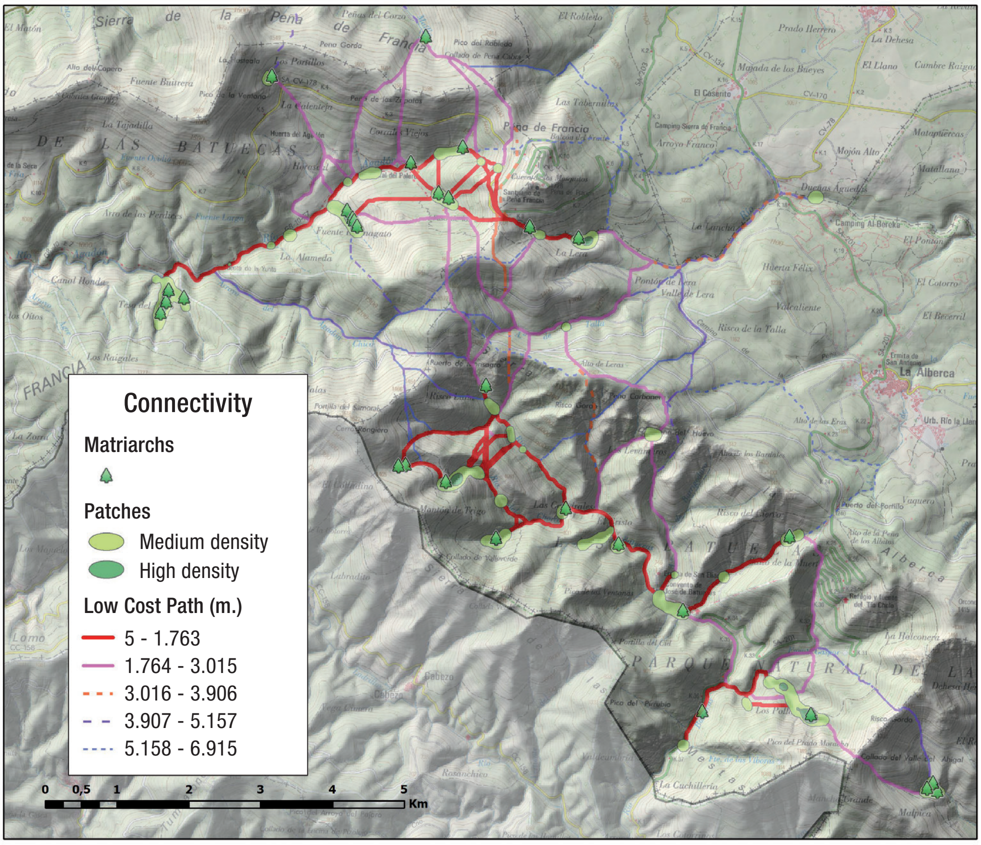

Figure 5. Connectivity relations between local populations and Matriarchs, at short, medium and long distances.

Matriarchs and matriarchies

In combination with aforementioned seed dispersion processes, we have observed large female trees in many of the stream headwaters, gullies and gorges, sometimes hugging the rocky escarpments or isolated on the boulder strewn screes that safeguard them from fires. Their position high in the valleys gives their seeds greater probabilities to travel over hillocks and saddles and reach the neighbouring valleys, thus shortening the distances between populations by acting as stepping stones (Figure 5).

Their high elevation, isolated positions, greater size, and height increases these female yews' exposure to pollen from different populations. Hence, it can be expected that their seeds have greater genetic diversity than seeds from female trees located in more sheltered locations.

If the situation is, as we believe, that these elder trees which have been sending their seeds downstream for centuries are 1) the mothers and grandmothers of most of the trees established below them, 2) have favored the regeneration process after fires, 3) enriched the gene pool of local populations and 4) are the keepers of the link between populations in neighboring valleys, then we should consider these old growth trees as crucial elements in the genetic exchange processes of the entire population set. This would therefore make them the de facto guardians of their own survival in the long term; for they condition demographic trends, genetics and the population dynamics of the habitat. These trees could be essential components of the population, not only to maintain the stability of the yew populations, but to drive diversity, complexity, and ensure the permanence of the entire ecosystem.

The fact that these processes are currently active, and shared with the other females of the group in creating ecosystem functions and potent dispersive flows whilst safeguarding the general process is what makes us consider their role as that of Matriarchs, and the population groups downstream as their matriarchies.

Conclusions

Contrary to the existing bibliography and official information (JCyL – Red Natura 2000), this study shows that the presence of yew trees in the *Las Batuecas-Sierra de Francia* Natural Park is not anecdotal and isolated, as previously documented, but is in fact broadly present; occupying 43 UTM (1 km^2) grid squares that span 6 municipalities, and in some locations forming relatively large groves. Our census included a total of 2,452 trees.

Notable differences have been observed in the regeneration rates in the different populations that are much higher in the valleys of the Agadón river, where colonization processes of new territories have been detected, as opposed to the southernmost populations where regeneration is practically inexistent and some populations are in decline.

The ecological niche analysis showed that the species occupies marginal strongholds, despite appearing in different ecological positions and bioclimatic zones associated with all local vegetation. The new colonized areas tend to recover territories lost due to factors like herbivory or fires. Seed dispersal is then seen as the fundamental factor that connects, conserves and expands these populations. We have verified that hydrochory is the most habitual and important agent for dispersion within the river basin as a whole, but inter-basin dispersion is zoochory dependent. The large female trees at the headwaters of streams and gullies have exhibited a transcendent quality for the role they play in maintaining connectivity and genetic exchange between the populations of different watersheds, thus sustaining local populations and the entire population set over time.

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