Cork oak Regeneration: an approach based on species interactions at landscape scale

Memòria presentada per Josep Pons i Portolés per optar al títol de Doctor en Ciències Biològiques al Departament d'Ecologia, Facultat de Biologia, Universitat d'Alacant, sota la direcció del Doctor Juli G. Pausas.

Josep Pons i Portolés

Cortes de Arenoso (Castelló)

Maig 2009

ViP
El Director de la tesis
Dr. Juli G. Pausas
CSIC

Cork oak Regeneration: an approach based on species intertactions at landscape scale.

introducció

La mediterrània és una terra poblada més o menys intensivament des d'abans de l'Imperi Romà. Com a resultat d'aquesta llarga història d'ús del territori, el paisatge està típicament fragmentat en zones amb distints usos. El podríem definir com a un paisatge en mosaic que comprèn conreus, pastures, matollars, pinars, alzinars, suredes,.... etc. L'ocupació rural i l'explotació de les terres d'aquest mosaic va tenir possiblement el seu màxim històric durant el primer terç del segle XX .

Tradicionalment, els arbres del gènere *Quercus* (carrasques, suredes, roures i coscoll) han estat molt apreciats per l'alta energia calòrica continguda en la seva fusta, especialment en les carrasques (*Q.ilex*). Açò va donar peu a una explotació d'aquestes espècies sense mesura per a llenyes i per a carbó vegetal. Fins i tot moltes vegades se n'extreien les arrels, especialment quan s'havia de a canviar l'ús del sòl (per exemple per a fer conreus). Cap als anys seixanta del segle passat, la migració a les ciutats i el canvi energètic cap a combustibles fòssils (gas i benzines principalment) va ser decisiu perquè es deixés d'emprar les llenyes i els carbons de manera generalitzada. Mentrestant, es va empendre la reforestació de terres abandonades amb pins (Pausas et al. 2008). Pels anys vuitanta, alguns autors van assenyalar que els *Quercus* no regeneraven bé (p.e. Laguna and Reyna 1990, Montero et al. 1994). La major part de les terres abandonades en anys anteriors van ser ocupades per matollars i pinedes, la qual cosa va contribuir de manera decisiva a l'augment de la freqüència i dimensions dels incendis forestals (Pausas 2004). La causa de la falta de regeneració dels *Quercus* es va atribuir sovint a la necessitat d'intervals de temps llargs perquè la vegetació evolucionés des dels matollars i pinars (comunitats prèvies) cap als carrascars, suredes i rouredes (comunitats clímax). Aquesta visió era hereva directa de les teoria de la successió de les comunitats vegetals exposada per Clemence a principis de segle (Folch 1986, Margalef 1998, Retana et al 1999).

Als darrers anys, aquesta visió de l'evolució del bosc mediterrani ha estat parcialment desestimada i s'ha passat (en no poques vegades) a abandonar els pins en favor de l'ús directe dels *Quercus* en les reforestacions forestals (Pausas et al. 2004, Vallejo et al. 2006). Però, prompte hom es va adonar que la supervivència a la sequera dels plançons de *Quercus* era molt variable, i en conseqüència van aparèixer dubtes sobre la viabilitat del l'ús d'aquestes varietats en les repoblacions forestals. Per a millorar la implantació i desenvolupament dels plançons al camp s'han obert distintes línies d'investigació com són la millora dels plançons en el viver, les tècniques de plantació o l'ús d'hidratants i esmenes (Vallejo i Alloza 2004, Aronson et al. 2009). La sembra directa de glans no ha estat una tècnica de reforestació massa acceptada per la incertesa que es deriva de la depredació que en fa la fauna i les variabilitats en les taxes de supervivència en funció del lloc i l'any (Madsen i Löf 2005).

El present estudi esta concebut sota la hipòtesi que la regeneració natural dels *Quercus* es pot millorar emprant o simulant els dispersors naturals. Aquestes tècniques podrien ser més econòmiques i menys agressives pel medi ambient que les tècniques de restauració tradicionals. Aleshores, el nostre objectiu principal és el desenvolupament de la base científica per augmentar o reproduir la regeneració natural dels *Quercus*. Al llarg de l'estudi utilitzem principalment la surera (*Quercus suber*) com a espècie bàsica perquè: 1) té processos de regeneració semblants a d'altres *Quercus* (generalitat), 2) té una gran importància socioeconòmica (transferibilitat a la societat) (Aronson et al. 2009), i 3) és una espècie protegida amb una distribució fragmentada a la Península Ibèrica oriental on la seva viabilitat ha estat qüestionada (respon a un problema específic).

El reclutament vegetal és un procés que comença amb la producció de llavors i finalitza amb la incorporació de nous adults a la població (Harper 1977). Aquest procés es compon de diverses fases que poden o no entrar en conflicte entre elles: floració, producció de glans, predació de glans abans de la dispersió, dispersió del glans, predació de glans posterior a la dispersió, germinació, establiment dels plançons i creixement dels arbrets (Schupp 1995). L'interés per aprofundir en el coneixement de cadascuna de les fases del reclutament dels *Quercus* ha augmentat significativament els últims anys (fig.1). Per tal de comprendre els factors que limiten la regeneració dels *Quercus* cal parar atenció a totes i cadascuna de les seves fases. Dit d'un altra manera, la regeneració dels *Quercus* pot estar limitada per una o diverses de les seves fases a la vegada, cosa que es coneix amb el terme de 'colls d'ampolla'.

En qualsevol cas, el que cal saber per a identificar un 'coll d'ampolla' és la proporció de la collita de glans que es perd en cadascuna de les fases del reclutament i el balanç final. Tot i això, estudis del cicle complet de regeneració són més bé escassos (veure, però, Pulido i Diaz 2005, Acacio et al. 2007). Aproximacions alternatives al problema com pogués ser la integració d'estudis parcials de la regeneració, no són de molta utilitat perquè és complicada la interpretació de dades de diversos llocs i períodes (Clark 1999), cosa que fa que es reduïsca la possibilitat d'obtenir conclusions fiables que reflectisquen situacions reals.

Pel que fa referència a la producció de glans, el gènere *Quercus* són espècies anyívoles, o dit d'altra manera, amb alternança d'anys amb grans quantitats de glans i anys sense producció o molt escassa. La periodicitat de les grans collites és específica de cada espècie, amb períodes de recurrència de 2, 3 i més anys (p.e. Koening i Knops 2003). En algunes espècies, com en la surera, desconeixem encara la recurrència de les grans collites o és dubtosa perquè en disposem de poques dades. Montoya (1988) suggereix períodes de producció de glans d'entre 2 i 4 anys per a la surera, però les nostres dades apunten cap a períodes més llargs (veure el *Capítol 2*). Aquestes discrepàncies entre autors no són sorprenents puix que hi manquen sèries llargues (probablement >15 anys) de dades de producció de glans per a les sureres necessàries per tal d'extraure patrons de producció fiables.

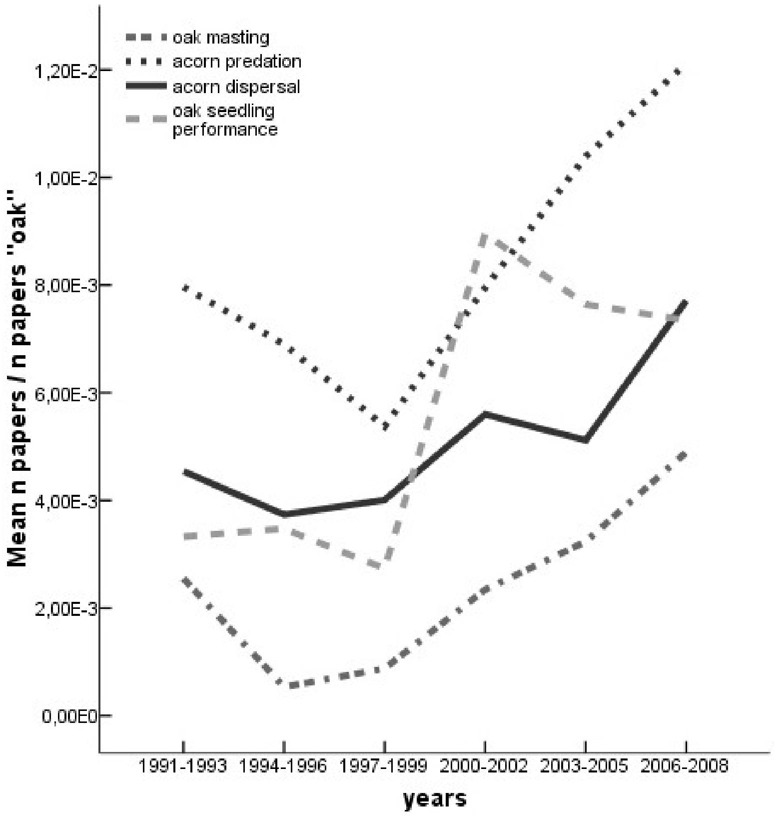


Fig.1. Nombre d'articles publicats des de 1991 fins a 2008 que contenen les paraules clau (veure la llegenda) relacionats amb les quatre fases principals del reclutament als *Quercus*, normalitzat amb el nombre d'articles amb la paraula 'oak'. Dades obtingudes de la Web of Knowledge (ISI).

Les causes de la vecería són confuses i estan encara en debat; fins i tot alguns autors defensen que el concepte mateix no és de gaire utilitat (Herrera et al. 1998). Actualment les hipòtesis més acceptades són a) adequació als recursos disponibles b) sacietat dels predadors de glans, i c) la dispersió per animals (veure la revisió de Kelly i Sork 2002). En general, els períodes curts s'associen a espècies en què la maduració de les glans es produeix el mateix any que van ser pol·linitzades (espècies anuals), mentre què el fet contrari resulta cert per a espècies que tarden 2 anys a madurar des de la pol·linització (espècies biennals)(Koenig i Knops 2003). Entre els *Quercus* mediterranis, la carrasca (anuals) sembla produir glans en anys alterns (Espelta et al. 2008). En el cas de la surera el patró de producció de glans es complica pel fet que pot produir glans d'1 i de 2 anys d'edat al mateix arbre (Elena-Roselló et al. 1993). Com a conseqüència la vecería en la surera sembla variable segons la proporció de cada tipus de gla en la població. Sobre el roure valencià, (anual, *Q.faginea*) i el coscoll (biennal, *Q.coccifera*) disposem també de poques dades. Al *Capítol 2* el nostre objectiu és descriure el patró de producció de glans en la sureda i validar: 1) la importància relativa dels factors meteorològics (precipitació i temperatura) en els patrons espacials i temporals de la producció de glans, tant en el nombre com en la mida de les glans; 2) la importància de la duració del període vegetatiu en el patró de producció anual-biannual de glans i les seves conseqüències a nivell de població.; i 3) si les densitats de predadors predispersió són depenents de la producció de glans.

La dispersió de glans va ser atribuïda tradicionalment a la barocòria (dispersió per gravetat) i a un moviment difús per animals que s'alimenten de glans. Per exemple, era freqüent sentir coses com que a conseqüència que les glans no són llavors recalcitrants, la germinació massiva només es dóna els anys especialment humits que eviten la dessecació de les glans (Laguna i Reyna 1990). Aquesta ambigüitat és deu bàsicament a la dificultat de seguir físicament la dispersió de les glans, especialment a distàncies de dispersió mitjanes i llargues (Cain et al. 2000). La barocòria, encara que juga un cert paper als boscos de *Quercus* (Pardos et al. 2005), ha estat rarament validada. Probablement es necessita clarificar dos conceptes per tal d'avançar en l'ecologia de la dispersió: què entenem per dispersió? i quina és la implicació del terme 'quantitatiu' intrínseca en el concepte mateix de dispersió? Tot al llarg del present estudi entenem per dispersió el desplaçament de la llavor des del seu origen a la planta mare fins a un lloc amb algunes probabilitats que el plançó s'hi establisca, i amb el temps, esdevinga un nou adult. A més a més, el concepte de dispersió té un component quantitatiu puix que el que és dispersat és una collita o una quantitat (producció) determinada de llavors. Aquesta part quantitativa del concepte implica que quan p.e. hom diu que la barocòria és un mecanisme de dispersió en els *Quercus*, és necessari afegir quina proporció de la dispersió total és a causa de la barocòria. L'evidència indica que la barocòria no és la norma al clima mediterrani: la majoria de glans que cauen de l'arbre mare per gravetat es queden a la superfície del sòl i a) se sequen (Gómez 2004) o b) són consumides per diferents animals atrets per grans acumulacions de glans (p.e. rosegadors, ungulats i porcs senglars; predació densodepenent, Rouset i Lepart 1999, Pulido 2002). Encara més, si les glans aconsegueixen sobreviure i germinar, la coberta forestal les suprimeix per competència directa, cosa que es veu reflectit en creixements molt baixos o fins i tot negatius. En aquestes circumstàncies molts plançons perden la part aèria i tornen a rebrotar després de l'estiu de forma recurrent. En conclusió, quan hom diu que la barocòria és un mode de dispersió en els *Quercus*, cal afegir quina proporció de la collita de glans està incrementant la població d'adults per aquesta via (p.e. 0.001% de la collita anual; deixem per al debat si un mecanisme amb molt baixes proporcions de dispersió de la collita val la pena mantenir-lo com un mètode de dispersió).

La majoria dels animals que s'alimenten de glans són considerats només consumidors i no dispersadors puix que les glans no sobreviuen a la ingesta. Atès que la major part de les glans que queden a la superfície del sòl es sequen o són predades, els veritables dispersadors són aquells que escampen glans soterrant-les, és a dir, els gaigs (*Garrulus glandarius*), els esquirols (*Sciurus vulgaris*) i els ratolins (bàsicament el ratolí de bosc *Apodemus sylvaticus* i el ratolí mediterrani *Mus spretus*). El gaig sembla haver desenvolupat una relació simbiòtica especial amb els *Quercus*, i se li ha dedicat una atenció especial (Bossema 1979, Darley-hill i Johnson 1981, Gómez 2003). Com que una reducció en una de les fases del procés de regeneració pot portar a l'absència total de regeneració, per tal de comprendre el reclutament en els *Quercus* hom necessita conèixer l'existència i les densitats dels dispersadors de glans. Al *Capítol 3* ens preguntem fins a quin punt la presència, densitat i distribució espacial del gaig està relacionada i es pot predir a partir de les característiques del territori. L'anàlisi està feta a dues escales espacials: 1) a l'escala de territori per validar la relació entre els atributs del territori (composició i configuració) i l'abundància de gaigs; i 2) a l'escala del territori de nidificació del gaig per validar quines parts del paisatge són seleccionades per les parelles de gaigs. L'objectiu final (pràctic) és l'obtenció d'un model predictiu de la distribució dels gaigs aplicable posteriorment a grans extensions de terreny (com podria ser la totalitat d'un parc natural).

Freqüentment hi trobem distintes espècies de *Quercus* juntes en el mateix bosc (boscos mixts de *Quercus*) o en boscos adjacents (paisatges mixts de *Quercus*) a causa que la major part dels territoris de la Mediterrània tenen una llarga història d'ús pels humans, amb el resultat d'un paisatge característic en mosaic (Pausas i Vallejo 1999). Tots els *Quercus* comparteixen els dispersors, cosa que dóna peu a la possibilitat d'una competència inter i intraespecífica per tal de dispersar les llavors pròpies. Aleshores, la qüestió de si els dispersadors són o no igualment atrets per glans de distintes espècies, formes o mides no és trivial per tal d'entendre la dinàmica demogràfica dels *Quercus*. Al *Capítol 4*, ens preguntem fins a quin punt el gaig mostra una preferència per les glans d'uns *Quercus* determinats, per les glans d'una mida determinada o, si ambdues preferències hi existeixen, quina de les dues (espècie o grandària) és dominant.

L'eficàcia del dispersant depèn també dels llocs on soterra les glans. Per exemple, el picot americà transporta grans quantitats de glans a troncs prèviament foradats on són acumulades com si fos un graner (Grivet et al. 2005). Clarament per als glans un tronc no és un lloc òptim per a germinar. En el cas del gaig, els llocs on les glans són soterrades solen ser òptims per a la germinació: sòls aclarits bons per a l'establiment, i a distàncies d'entre pocs metres a alguns quilòmetres de l'arbre mare (Bossema 1979, Darley-Hill i Johnson 1981). Aquesta dispersió a microllocs 'bons' per a la germinació suggereix que el gaig es pot considerar com un dispersant òptim de glans. Però, com de 'bons' per a la germinació i el creixement són els llocs que selecciona el gaig per a soterrar les glans és encara una incògnita a causa de les dificultats de seguir els vols del gaig al lloc exacte on amaga les glans (Gómez 2003). Aquesta qüestió és encara més rellevant als hàbitats en mosaic, ja que una gran varietat de rodals amb diferent vegetació són a l'abast del gaig. Al *Capítol 5* hem emprat radiotransmissors col·locats a dins del gla per a localitzar-ne amb precisió el lloc de soterrament, i per a: (a) conèixer la distribució de distàncies de dispersió dels glans; (b) determinar la forma del l'ombra de dispersió (p.e., ens demanem fins a quin punt les glans amagades pel gaig són agregades o distribuïdes a l'atzar); (c) determinar quins tipus de vegetació prefereix el gaig per amagar els glans; i finalment, (d) corroborar la idoneïtat d'aquesta metodologia per a l'estudi de les ombres de llavors i les característiques de dispersió del gaig.

Els rosegadors, especialment el ratolí de bosc a la zona mediterrània, consumeix grans quantitats de glans, però se sap també que dispersa glans a distàncies d'entre pocs a algunes dotzenes de metres. La seva eficiència sembla ser més baixa que la dels gaigs, atès que la major part de les glans són consumides i els llocs de soterrament són de més baixa qualitat per al reclutament dels plançons. Tot i això, cal dir que rarament aquesta eficiència ha estat validada (Gómez et al. 2008). En qualsevol cas, les altes densitats de població dels ratolins probablement fan de contrapès a aquesta baixa eficàcia i sembla ser un dispersor adient i suficient per tal de regenerar els clars als boscos de *Quercus*. Les preferències del ratolí per una espècie de gla sobre d'altres, o les diferències de les taxes d'activitat en diferents tipus de vegetació són encara desconegudes en hàbitats mediterranis. Al *Capítol 6* els nostres objectius són: (a) determinar si els ratolins tenen preferències per distintes glans (en concret per a distintes espècies o mides), i (b) quantificar variacions en les taxes de remoció i distàncies de transport de glans en funció del tipus de vegetació. La nostra hipòtesi de treball és que els rosegadors són els màxims depredadors de glans i seleccionen les glans més nutritives. Aquestes glans seleccionades es deuen transportar més lluny pels avantatges energètics. Tot i això, aquest patró podria variar en les distintes unitats de vegetació degut a diferents densitats de rosegadors, diferències en el risc de predació per als rosegadors, fonts d'aliment alternatives presents i/o diferent disponibilitat dels llocs segurs per a soterrar les glans.

En la pràctica, com a resultat de la variabilitat en les fases de regeneració (producció, predació, dispersió, germinació, i supervivència) el que veiem al camp són diferents densitats de plançons i arbrets amb diferents dinàmiques de creixement. Quines zones són colonitzades pels *Quercus*? Sobreviuen i creixen els plançons igual de bé a totes les unitats del territori? En el cas de la surera, com que les poblacions orientals de la Península Ibèrica són relativament menudes (de desenes a milers d'hectàrees) una altra qüestió rellevant és si els boscos menuts estan patint una falta de regeneració. Al *Capítol 7* (a) es mostrem els resultats de les prospeccions de camp fetes per quantificar les densitats de plançons i arbrets, i (b) es validen 3 hipòtesis de treball: en primer lloc ens demanem si la regeneració de sureres en les poblacions orientals és superior a la de les deveses (formacions sabanoides de l'oest de la Península Ibèrica, anomenades 'montados' en portuguès). En les deveses la regeneració de carrasques i sureres sembla molt més baixa que als ecosistemes forestals (Pulido i Díaz 2005), probablement a causa d'un impacte acusat de les activitats cinegètiques i ramaderes (Plieninger et al. 2004) que han derivat en una mancança de dispersió de glans i una pressió a causa del pasturatge excessiva a sobre els plançons (Pulido i Díaz 2005). A l'orient ibèric, la pressió per pasturatge i les activitats humanes s'ha reduït els últims anys a causa de l'èxode rural i dels processos d'abandonament de la terra en concordança amb la resta de zones costeres mediterrànies europees (veure més amunt, Pausas 2004).

La nostra segona hipòtesi al *Capítol 7* és que la regeneració decreixerà amb la reducció de la mida del bosc de sureres i açò podria ser conseqüència de diferents factors: és ben conegut que les poblacions menudes poden presentar efectes negatius a causa de l'endogàmia i l'erosió genètica, que podrien repercutir en una reducció en la producció i qualitat de les llavors, reduint la viabilitat de la població i augmentant el risc d'extinció (Lawton 1993, Vucetich i Waite 2003), i reflectint-se tot plegat en el procés de regeneració. En aquest context, s'ha demostrat que les poblacions marginals de sureres tenen una diversitat genètica menor comparades amb les poblacions centrals (Jiménez et al. 1999). Aleshores, podríem esperar un patró de regeneració decreixent paral·lel a la mida de la població, i en especial pel que fa a la població més menuda estudiada (Pinet), a la qual es pot considerar menuda per a una població d'arbres (aprox. 70 ha de baixa densitat d'arbres). Més encara, el fet que els boscos són l'hàbitat principal del gaig fa que una reducció de la seua mida repercutisca en una reducció de la densitat de gaigs, i que a la vegada repercutisca en una reducció de la regeneració de les sureres. Finalment, cal assenyalar també que les poblacions menudes presenten un major 'efecte vora' que pot suposar una major predació dels glans (Santos i Telleria 1997) i sensibilitat a les alteracions. Tots aquest processos plegats suggereixen que la regeneració de sureres podria reduir-se amb la mida del bosc en les poblacions ibèriques orientals.

La nostra tercera hipòtesi al *Capítol 7* és que, a l'escala de territori, la regeneració no es distribueix a l'atzar per què les condicions ambientals i els factors biòtics diferents (dispersió, predació i competència) afecten de manera distinta a les distintes unitats del paisatge (Grime i Hillier 2000, Gómez et al. 2004). Aleshores, a causa de l'actual heterogeneïtat del territori per a les diferents unitats espacials esperem diferents processos de regeneració i densitats de reclutament.

Al *Capítol 8*, s'integren totes les dades, pròpies i la informació disponible a la bibliografia, en un model demogràfic de regeneració, i intentem mantenir tant com siga possible la variabilitat existent. L'objectiu del model és analitzar dades reals per tal d'entendre la dinàmica actual de la regeneració dels *Quercus* a escala de territori. El model està basat en la surera perquè és l'espècie de la qual disposem de més dades, però probablement és transferible a d'altres *Quercus*. Com a novetats pel que fa a uns altres models basats en transicions recentment apareguts, hi ha la integració de tots els *Quercus* simpàtrics i tots els dispersors (per desgràcia amb l'excepció de l'esquirol, ja que no en tenim dades), i l'ús d'un índex de selecció/disponibilitat de glans per part del gaig. A partir del model es van simular diversos escenaris per validar les implicacions relatives del gaig i dels ratolins en la dispersió de la surera. Altres escenaris intenten esbrinar si la selecció de glans pels gaigs contribueix a la falta de correlació entre la producció de glans i les densitats de plançons. Per tal d'avaluar l'efecte relatiu de cada dispersor sobre la demografia de la surera, es va calcular també la contribució total de cada dispersor al nombre total de reclutaments i l'efectivitat de cadascun a nivell de territori, entenent per efectivitat la proporció entre arbrets atribuïbles a cada dispersor i la proporció de la collita emprada per cada dispersor (Janzen 1971, Schupp, 1993).

Per acabar, al *Capítol 9* s'exposen algunes consideracions generals i les principals conclusions.

Referències

Acacio,V., Holmgren,M., Jansen,P.A. and Schrotter,O. 2007. Multiple recruitment limitation causes arrested succession in mediterranean cork oak systems. Ecosystems 10: 1220-1230.

Aronson,J., Pereira,J.S., Pausas,J.G. (eds). 2009. Cork Oak Woodlands on the Edge: conservation, adaptive management, and restoration. Island Press, Washington DC. 315 pp.

Bossema,I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. Behaviour 70: 1-117.

Cain,M.L., Milligan,B.G. and Strand,A.E. 2000. Long-distance seed dispersal in plant populations. American Journal of Botany 87: 1217-1227.

Clark,J.S., Beckage,B., Camill,P., Cleveland,B., HilleRisLambers,J., Lichter,J., McLachlan,J., Mohan,J. and Wyckoff,P. 1999. Interpreting recruitment limitation in forests. American Journal of Botany 86: 1-16.

Crawley,M.J. and Long,C.R. 1995. Alternate Bearing, Predator Satiation and Seedling Recruitment in *Quercus Robur* L. Journal of Ecology 83: 683-696.

Darley-hill,S. and Johnson,W.C. 1981. Acorn dispersal by blue jays (*Cyanocitta cristata*). Oecol. 50: 231-232.

Elena-Roselló,J.A. 1993. Ecological aspects of the floral phenology of the cork-oak (*Q.suber* L.): why annual and biennial biotypes appear? Ann. For. Sci. 50: 114s-121s.

Espelta,J.M., Cortes,P., Molowny-Horas,R., Sanchez-Humanes,B. and Retana,J. 2008. Masting mediated by summer drought reduces acorn predation in mediterranean oak forests. Ecology 89: 805-817.

Folch,R. 1986. La vegetació dels Països Catalans. Second edition. Ketres.

Gomez,J.M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26: 573-584.

Gomez,J.M. 2004. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. Plant Ecology 172: 287-297.

Gomez,J.M., Valladares,F. and Puerta-Pinero,C. 2004. Differences between structural and functional environmental heterogeneity caused by seed dispersal. Functional Ecology 18: 787-792.

Gomez,J.M., Puerta-Pinero,C. and Schupp,E.W. 2008. Effectiveness of rodents as local seed dispersers of Holm oaks. Oecologia 155: 529-537.

Grime,J.P. and Hillier,S.H. 2000. The contribution of seedling regeneration to the structure and dynamics of plant communities, ecosystems and larger units of the landscape. In: Fenner, M. (ed.) Seeds - the ecology of regeneration in plant communities, pp. 361–374. 2nd ed. CABI, Wallingford, UK.

Grivet,D., Smouse,P.E. and Sork,V.L. 2005. A novel approach to an old problem: tracking dispersed seeds. Molecular Ecology 14: 3585-3595.

Harper, J.L 1977. Population biology of plants. Academic Press, London.

Herrera,C.M., Jordano,P., Guitian,J. and Traveset,A. 1998. Annual variability in seed production by woody plants and the masting concept: Reassessment of principles and relationship to pollination and seed dispersal. American Naturalist 152: 576-594.

Janzen,D.H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2: 465-492.

Jiménez, P. , D. Agundez , R. Alia , and L. Gil . 1999. Genetic variation in central and marginal populations of *Quercus suber* L. Silvae Gen 48:278–284.

Kelly,D. and Sork,V.L. 2002. Mast seeding in perennial plants: Why, how, where? Annual Review of Ecology and Systematics 33: 427-447.

Koenig,W.D. and Knops,J.M.H. 2003. the behavioural ecology of masting in oaks. In: Mcshea,W.J. and Healy,W.M. (eds.), Oak Forest Ecosystems, pp. 129-148. John Hopkins Univ.Press, Baltimore, Mariland.

Laguna,E. and Reyna,S. 1990. Diferencias entre los optimos natural y forestal de las vegetaciones valencianas y alternativas futuras de gestion. Ecologia. Fuera de serie 1: 321-330.

Lawton,J.H. 1993. Range, population abundance and conservation.TREE8:409–413.

Madsen,P. and Lof,M. 2005. Reforestation in southern Scandinavia using direct seeding of oak (*Quercus robur* L.). Forestry 78: 55-64.

Margalef,R. 1998. Ecologia. Omega. ISBN: 978-84-282-0405-7

Montero,G., Torres, E., Canellas, I., Ortega, C., 1994. Aspectos silvicolas economicos y sociales del alcornocal. Agricultura y sociedad, 73: 137-193.

Montoya,J.M., 1988. Los alcornocales. MAPA. Serie Manuales Técnicos, 2ª Edición, 267 pp.

Pardos,M. et al. 2005. Ecophysiology of natural regeneration of forest stands in Spain. Invest Agrar: Sist Recur For (2005) 14(3), 434-445

Pausas,J.G. and Vallejo,V.R. 1999. The role of fire in European Mediterranean ecosystems. In: Chuvieco, E. (ed.). Remote sensing of large wildfires in the European Mediterranean basin. pp. 3-16. Springer, Berlin

Pausas,J.G. 2004. Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). Climatic Change 63: 337-350.

Pausas,J.G., Bladé,C., Valdecantos,A., Seva,J.P., Fuentes,D., Alloza,J.A., Vilagrosa,A., Bautista,S., Cortina,J. and Vallejo,R. 2004. Pines and oaks in the restoration of Mediterranean landscapes in Spain: New perspectives for an old practice - a review. *Plant Ecology* 171: 209-220.

Plieninger,T., Pulido,F.J. and Schaich,H. 2004. Effects of land-use and landscape structure on holm oak recruitment and regeneration at farm level in Quercus ilex L. dehesas. Journal of Arid Environments 57: 345-364.

Pulido,F.J. 2002. Biologia reproductiva y conservación: el caso de la regeneración de bosques templados y subtropicales de robles (*Quercus* spp.). Revista Chilena de Historia Natural 75: 5-15.

Pulido,F.J. and Diaz,M. 2005. Regeneration of a Mediterranean oak: A whole-cycle approach. Ecoscience 12: 92-102.

Rousset,O. and Lepart,J. 1999. Shrub facilitation of *Quercus humilis* regeneration in succession on calcareous grassland. Journal of Vegetation Science. 10: 493-502.

Retana,J., Espelta,J.M., Gracia,M., Riba,M. 1999. Seedling recruitment. Chapter 7 *in* Ecology of Mediterranean evergreen oak forests. Ferran Rodà ed. Edition: Springer, 1999. ISBN 3540650199.

Santos,T. and Telleria,J.L. 1997. Vertebrate predation on holm oak *Quercus ilex* acorns in a fragmented habitat - effects on seedling recruitment. Forest Ecology and Management 98: 181-187.

Schupp,E.W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107/108: 15-29.

Schupp,E.W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany 82: 399-409.

Vallejo,R.and Alloza,J.A. (eds) 2004. La gestion del monte mediterraneo. CEAM. València.

Vallejo,R., Aronson,J., Pausas,J.G. and Cortina,J. 2006. Mediterranean Woodlands. In: van Andel,J., Aronson,J. (eds.). Restoration ecology: The New Frontier. Blackwell Science. Oxford, UK . Pages 193-207.

Vucetich,J.A. and Waite,T.A. 2003. Spatial patterns of demography and genetic processes across the species' range: Null hypotheses for landscape conservation genetics. Conservation genetics 4(5):639-645.

Acorn production in Quercus suber [1]

Abstract

Understanding seed production patterns and variability is essential for predicting plant regeneration. Both non-adaptive (e.g., resource-tracking) and adaptive (e.g., predator-satiation) hypotheses have been deemed responsible for variation in seed production. Here we aim to test the role of these two types of hypotheses on acorn production (i.e., number and size of acorns, and annual/biennial production pattern) of cork oak (*Quercus suber*) in the eastern Iberian peninsula (Spain). Specifically, we tested the following predictions: 1) the number of acorns depends on climatic and weather factors; 2) environmentally-stressed populations have a higher proportion of biennial acorns than non-stressed populations; 3) acorn size is also dependent on resource factors (weather); and 4) monospecific oak patches satiate pre-dispersal predators better than multi-oak species patches. The results suggest that weather variables accounted for approx. 20% of the variability. Models increased the explained variance to 55.4 % if the previous-year production of the tree was introduced. Temporal autocorrelations were related to the number of frost days and droughts suggesting that in northern populations there is a dominance of annual acorns, while in southern ones biennial acorns are more common. Acorn size correlated positively with available water and with spring days below freezing during the current year. Infestation proportion increased in years with low acorn production for both *Curculio* and *Cydia*, but only the former correlated positively with the area and proportion of cover by cork oak. We concluded that cork oak populations are highly diverse in all the acorn production parameters studied and that both the resource-matching and the predator-satiation hypotheses seem to be operating.

Introduction

Understanding variability in seed production is a central question in ecology because it is a key component determining offspring success in plants (Venable and Brown 1988). Indeed, seed production provides valuable insights on the potential regeneration capacity of plant populations, as well as on changes in wildlife populations (Wolff 1996, Boutin et al. 2006).

The number of seeds produced by individuals of a given plant species may be determined by different processes (see reviews by Kelly 1994, Kelly and Sork 2002). Non-adaptive hypotheses suggest that annual seed productions may vary in relation to resources, climate and weather factors (e.g., droughts, cold; also called resource matching or weather tracking hypothesis; e.g., Koenig et al 1996, Selàs et al 2002, Abrahamson and Layne 2003).

---

[1] Pons, J. and Pausas, J. submitted. Acorn production in *Quercus suber* is explained by both adaptive and non-adaptive hypotheses.

Alternatively, adaptive hypotheses suggest that occasional large seed crops are more efficient than regular smaller ones ("economy of scale"; Janzen 1978, Norton and Kelly 1988), and thus variability may be related to endogenous dynamics driven to enhance some of the regeneration processes (e.g., reduction of seed predation, enhancement of wind-pollination or dispersal; e.g., Koenig and Knops 2000, Vander Wall 2002).

Oaks are a very important part of many landscapes worldwide (Rodà et al. 1999, McShea and Healy 2002, Logan 2005, Aronson et al. 2009); they are considered typical foundation species, that is, any changes in these species will have significant consequences on ecosystem functioning (Ellison et al. 2005). Indeed, acorns are crucial in many food webs, and studies on wildlife population changes often track fluctuations in acorn production (Wolff 1996, Ostfeld et al. 1996, McShea and Healy 2002, Schmidt and Ostfeld 2003, Boutin et al. 2006, Clotfelter et al. 2007, Saitoh et al. 2007). Consequently, considerable attention has been given to understanding oak regeneration processes and acorn production patterns in North America (Koenig and Knops 2002, Kelly and Sork 2002, Liebhold et al. 2004); however, little is known in this respect about European Mediterranean oaks (e.g., García-Mozo et al 2007, Espelta et al. 2008). In this paper our specific aim is to understand acorn production patterns in small and fragmented *Quercus suber* (cork oak) populations of the eastern Iberian Peninsula (Mediterranean Basin; Fig. 1). This mediterranean oak is important in terms of conservation (species protected by the European Union Habitat Directive) and also for its cultural and socio-economic value (sustainable cork production; Aronson et al. 2009). Furthermore, there is increasing evidence of the conservation and biodiversity value of fragmented peripheral populations (Lesica and Allendorf 1995; Hampe and Petit 2005, Bridle and Vines 2007), and specifically of *Q.suber*, due to the distinct genetic pools between central and peripheral populations (Jimenez et al. 1999, Magri et al. 2007). Thus, understanding the regeneration capacity and variability of these populations is crucial for inferring their evolutionary potential, and could provide key insights on both the causes (Kelly 1994) and consequences (Ostfeld and Keesing 2000) of reproductive variability.

In oaks, fluctuations in acorn production have been related to both the resource-matching hypothesis (Sork et al. 1993, Koening et al. 1996, Cecich and Sullivan 1999, Shibata et al 2002, Masaka and Sato 2002, Guariguata and Saenz 2002, Abrahamson and Layne 2003) and the endogenous dynamics hypothesis (Koenig and Knops 2000, Liebhold et al. 2004). These two general hypotheses are not exclusive and may act simultaneously (Kelly 1994). In this paper we aim to test 4 predictions, 3 under the general hypothesis of resource-matching and one under the endogenous adaptive hypothesis, in cork oak (*Q.suber*) woodlands of the eastern Iberian peninsula.

In their review, Kelly and Sork (2002) suggest that in dry conditions (e.g., Mediterranean ecosystems), fluctuations in seed production should be better explained by resource (water) availability (i.e., non-adaptive hypothesis) than by the benefits of increased pollination or dispersal (i.e., adaptive hypothesis). Indeed, there is evidence that under mediterranean conditions, summer drought reduces crops by abortion of immature acorns (Espelta et al. 2008). Furthermore, *Q.suber* is considered a cold-sensitive species and there is evidence that cold may reduce flower and fruit production (García-Mozo et al. 2001). Thus, our first prediction (Prediction 1) is that the spatial and temporal variability of acorn production in *Q.suber* can be explained by the spatial variability of climatic factors and the temporal variability of weather parameters. We specifically predict that rainfall (especially in summer) and late frost (in spring) should be positively and negatively related to acorn production, respectively.

In contrast to most oaks, the acorn maturation pattern in *Q.suber* is not constant. Populations in good conditions tend to display an annual pattern, that is, acorns ripen the same year as they were pollinated, while stressed populations with short vegetative periods extend acorn development to 2 years (biennial type, i.e., acorns ripen the year after pollination; Elena-Roselló et al. 1993, Díaz-Fernández et al. 2004). Koenig et al. (2003) has shown that oak species producing annual crops have larger 1-year autocorrelations (ACF1) than biennial species. Thus, under the non-adaptive hypothesis, we predict (Prediction 2) that cork oak populations under stressed conditions (strong drought or frequent spring frosts) should have a lower temporal 1-year autocorrelation in acorn production number than populations under less severe conditions.

Seed production varies not only in seed number but also in seed size (Moles and Westoby 2004). Acorn size varies greatly between parent trees (Merouani et al. 2001) and seems to be genetically fixed (García-Monzo et al. 2007). There are many evolutionary forces proposed to act upon acorn size, including selection by dispersers (Pons and Pausas 2007b) and/or post-dispersal predators (Gómez 2004, Xiao et al 2005, Pons and Pausas 2007a), and differences in seedling establishment and performance (Merouani et al. 2001, Gómez 2004, Quero et al. 2007). These studies suggest that acorn size variations have important implications for fitness. However, a reduction in acorn size below a given tree's inherent potential may also be related to weather parameters, that is, to the amount of resources; if so, seed size would provide another indicator of the climatic control on seed production and regeneration potential. Thus, we predict (Prediction 3) that acorn size should be related to resource availability and weather parameters, and that it will be reduced in years with low resources (low precipitation).

The predator satiation hypothesis states that irregular crops could be a mechanism to reduce acorn loss to predators, that is, the irregular or alternate bearing of crops would starves predators (Crawley and Long 1995, Kelly and Sork 2002). A measurable consequence is that the year after a mast the proportion of infested acorns will increase. However, given that pre-dispersal predators attack acorns of any species, this relative increase in infestation could be masked if an alternative food source exists (Shibata et al. 2002), i.e., coexisting oak species that produce acorns during the low production year of the target tree (out-of-phase acorn production among oak species). To test this hypothesis, we measure the infestation of acorns in mixed and pure cork patches and predict that a stronger positive correlation between previous-year acorn production and acorn infestation in a decreased-production year will exist in monospecific *Q.suber* patches than in mixed oak patches (Prediction 4).

In summary, we aim to describe the acorn production of cork oak populations and to test: 1) the relative importance of weather factors (precipitation and temperature) in explaining the spatial and temporal patterns of acorn production, both in number and size of acorns; 2) the importance of the duration of the vegetative period in the annual/biennial acorn production pattern of the population and its consequences for population-level acorn production pattern; and 3) whether predispersal predators are actually controlled by the acorn production pattern.

Methods

Study species

Quercus suber L. (cork oak) is a sclerophyllous evergreen oak that occurs in non-carbonated soils in the western part of the Mediterranean Basin (Fig.1a). Its main distinctive feature is its thick bark which evolved as a fire protection mechanism (Pausas 1997, Pausas et al. 2009) and regrowths after extraction (i.e., for cork production; Aronson et al. 2009). Cork oaks produce both annual and biennial acorns. Annual acorns mature the same year as the flowers which produced them, while biennial acorns grow and mature in the autumn of the following year.

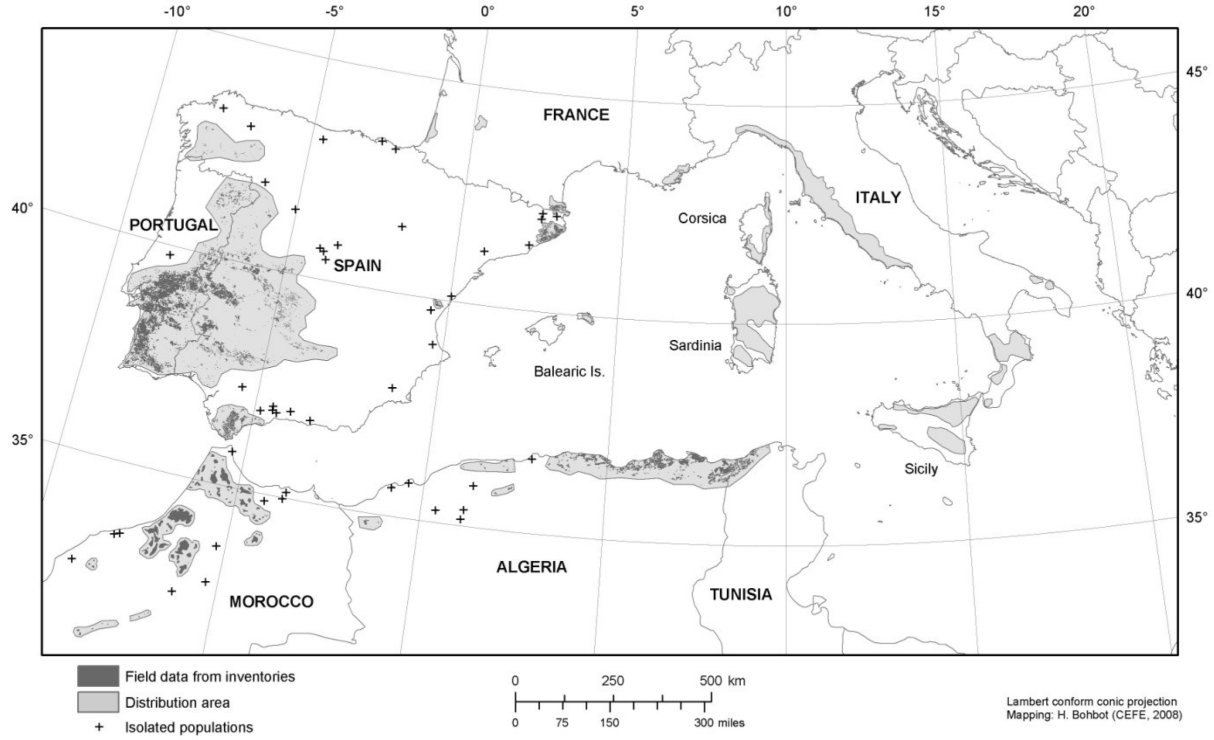
Study areas

The study was conducted in three mountain ranges located in the Valencia region (Eastern Spain), which borders the Mediterranean coast to the east and the central Iberian Plateau to the west (inland). As a consequence, *Q.suber* populations are confined in mesic conditions between the xeric lowlands to the east (close to the Mediterranean sea) and the more continental and higher altitudes to the west (Fig.1b; for *Q.suber* climatic requirements see Montero and Cañellas 2003, Aronson et al. 2009). Because the distance between these two extremes is only about 80 km and non-carbonated soils are rare in the region, *Q.suber* patches are relatively small. In this region there are 3 main *Q.suber* patches, from north to south: Espadà (Castelló, lat = 39° 52', ca. 10000 ha), Calderona (València, lat = 39° 44', ca. 1000 ha) and Pinet (València, lat = 38° 59', ca. 100 ha). We selected five 3 x 3 km areas (hereafter quadrats) distributed on the three main patches: two quadrats in Espadà (Q1, Q2), two in Calderona (Q3, Q4)and one in Pinet (Q5) (Fig. 1b; see Pons and Pausas 2006, 2008 for further details). Soils in Calderona and Espadà are mainly acidic on sandstones (Bundsanstein, which is a Triassic bedrock) with soil pH ranging from 4.9 to 6.4 (mean 5.7). In Pinet, cork oak occurs in non-carbonated soils on dolomites, with pH ranging from 5.5 to 7.5 (mean: 6.5; Cretaceous bedrock, Pausas et al. 2006). Currently, the three sites are protected either as Natural Parks (Espadà and Calderona) or as a regional plant micro-reserve (Pinet). Cork extraction is still ongoing in Espadà and Calderona. The climate in these patches is typically mediterranean, with dry and hot summers and mild winters, and an annual rainfall ranging from 500 to 800 mm distributed in two peaks, spring and autumn (Pérez-Cueva 1994, Millán et al. 2005).

Sampling

Visual counts

We randomly selected 172 cork oak trees ≥ 20cm DBH (diameter at breast height) distributed in the five quadrats as follows (from Q1 to Q5): 33, 37, 46, 25 and 31 trees. Two observers using binoculars and standing on opposite sides of each tree estimated the acorn production by counting the total number of acorns in the crown. Acorn production was monitored during a 5-year period (2003-2007). The counting (September-October) were performed immediately prior to acorn fall (October-November) when acorns were large enough to be detected easily. For each sampled tree we measured the DBH, computed the basal area, and recorded the UTM position.



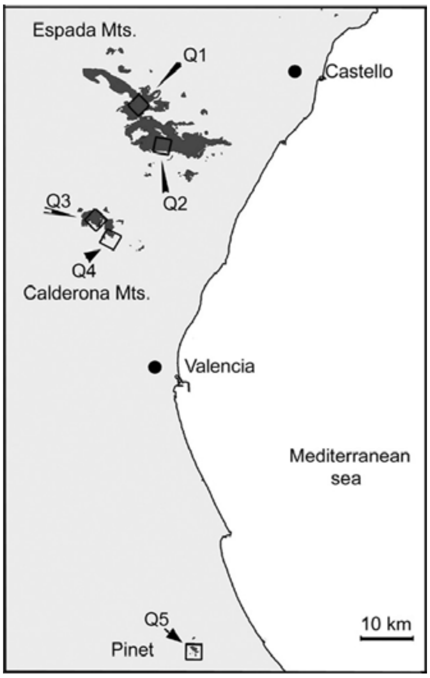


Fig.1. (up) Cork oak (*Quercus suber*) distribution (from Pausas et al. 2009, with permission from Island Press) indicating the study area in the eastern Iberian Peninsula (squared); and (left) localisation of the five sampled Quadrats: from north (top) to south (bottom), two quadrats in the Espadà mountains (Q1, Q2), two in the Calderona mountains (Q3, Q3) and one quadrat in Pinet (Q5); dark gray indicates Q.suber distribution (own data).

To test the validity of our acorn estimations, we also determined the real acorn production per tree on a total of 25 additional trees with a range of DBH similar to the studied trees by means of the traditional method of climbing the tree and using a pole to beat down all the acorns. The relation between the visual estimation and the real acorn production was highly significant ($F_{1,23}$= 731, R^2= 0.9695, p<0.0001, Fig. 2), and thus we are confident about our methodology.

Seed traps

To study acorn size and insect infestation, acorns were collected by means of seed traps in a subsample of 52 trees (8 to 13 trees per quadrat). Between 2 and 7 traps per tree, depending on tree size, were distributed halfway between the trunk and the crown edge. Each trap consisted of three round (30 cm in diameter) plastic baskets tied to the top of a pole (0.85 m^2 per trap). The poles raised the baskets 1.5 m off the ground in order to avoid terrestrial predators such as the wild pig, very common on the study sites. To control for squirrels and avian predators, several types of nuts were added to the traps, but removal of these nuts was never observed.

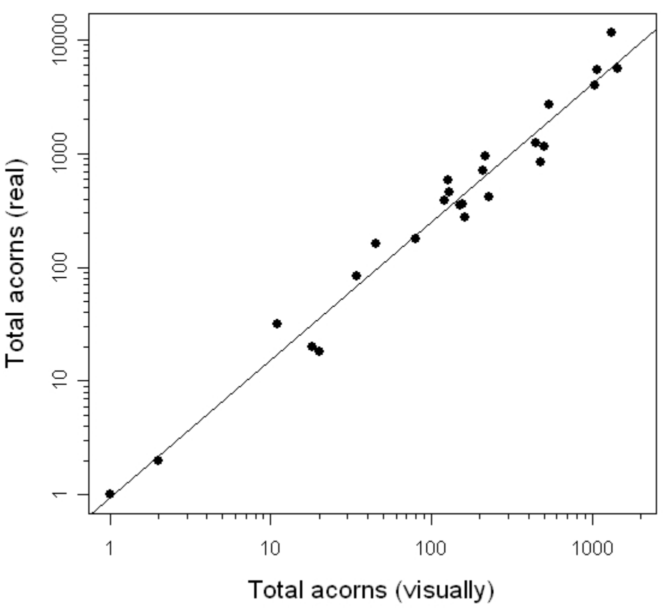


Fig. 2. Relation between the number of acorns estimated visually (by counting acorns with binoculars) and the number of acorns counted by climbing the tree and beating down all the acorns (real). The fitted line represents the following function: $\log_{10}$(real #acorns + 1) = -0.02536 + 1.21336 · $\log_{10}$(visual #acorns + 1); n= 25, $F_{1,23}$= 731, R^2= 0.9695, p<0.0001.

Traps were visited every 2 weeks during three acorn-fall seasons (2003, 2004 and 2005). The collected acorns were counted and their external appearance was classified visually as sound, infested (with exit hole present) or in bad condition. A digital picture of the sound acorns (maximum 20 acorns per sampling date and tree; total n=11649 acorns) was recorded and acorn dimensions (length and width) were computed by means of a commercial image software (Matrox Inspector 4.0). Dimensions were further transformed to fresh weight using a regression obtained from Pascual (2003): acorn weight= 0.67596 x (acorn width x acorn length) + 0.08636 x (acorn width x acorn length)^2 [weight in g, width and length in cm; r^2= 0.994, n=315, p<0.001]. Finally, the sound acorns were opened to check for the presence of still developing larvae; if found, the acorns were reclassified and pooled with the infested acorns. In the 2004 and 2005 campaigns, the larvae genera was also discriminated (*Curculio* or *Cydia*).

Data analysis

Because tree size plays an important role in determining seed production (Goodrum et al. 1971; Greene and Johnson 1994; Greene et al. 2004), we standardised the yearly acorn production of each tree by dividing the number of acorns by the tree basal area (ABA, in acorns/cm^2; Greenberg 2000).

Climatic data was obtained from available meteorological stations in the region (n = 81). Monthly number of frost days and monthly precipitation were interpolated to the center of each sampled quadrat using the spatial module of ArcView 3.3; mean monthly temperature was obtained for each site by regressing the altitude, latitude and distance to the coast (continentality). The number of frost days was considered for March (FDmar), April (FDapr) and the spring total (FDspr = FDmar+FDapr+FDmay). Precipitation data was computed yearly (P) as hydrological years (from September to August) and for three hydrological seasons considered relevant for acorn development: from September to February (Pwinter), from March to May (Pspring), and from June to August (Psummer). Potential and actual evapotranspiration (PET and AET) was computed following Thornthwaite and Mather (1957) from monthly climatic data. For AET, we used a bucket model with soil holding capacity inferred from available soil analysis (i.e., textures) of the studied area (for Pinet: Pausas et al. 2006; for Espadà: Serrasolsas et al. 2009; for Calderona: Rubio et al. 2005). Then, a drought index (DI) was computed as DI= 1 – AET/PET. Mean values (for 2001-2007) of site, weather and water balance variables for each quadrat are shown in Table 1.

To test the effect of weather factors on ABA variability (prediction 1), we used repeated measures ANOVA considering the tree as the subject. Thus we partitioned the variability into within- and between-subject, reflecting the temporal and spatial variability of acorn production, respectively. ABA showed a strong skewed frequency distribution, and so it was log-transformed previous to analysis. Because of the large number of weather variables, many of which were correlated, we first extracted the principal components of the weather variables, including 1-year lagged variables. The first three principal components were then correlated with the original variables (Table 2, Appendix 1) and used as dependent variables in the repeated measures ANOVA. In addition, Quadrat and Year were also tested, and entered if significant, in order to evaluate whether any of these (spatial and temporal) variables accounted for any additional variability not reflected by our weather-based principal components.

We evaluated acorn synchrony and temporal autocorrelation parameters following Koenig et al. (2003; see also Herrera 1998). We calculated correlations of acorn production (ABA) between individual trees (mean individual synchrony, r_p; Buonaccorsi et al. 2001), acorn production Coefficient of Variation for individual trees (Cvi) and population (Cvp) and partial autocorrelation for each tree at 1-yr time lags (ACF1i, data 2004-2007). We used a stepwise procedure to test for weather variables determining our indicator of annual versus biennial acorn production, i.e. ACF1i.

Acorn weight was transformed to Relative Acorn Weight (RAW), that is, the ratio of actual acorn weight to the maximum acorn weight observed during the study for a particular tree. We made this transformation to be able to pool trees together for population assessment. To test the effect of weather on RAW (prediction 3), we used a procedure similar to the acorn number analysis (repeated measures ANOVA on weather-based principal components). However, because the number of measured acorns varied greatly, we used only the trees that in a given year had 5 or more measured acorns, and the regression was weighted by the number of acorns measured in each tree and year. To test for differences of RAW between quadrats a pairwise comparison with a Bonferroni correction was applied.

Table 1. Mean values of the site and weather variables studied for each quadrat and site (total counts= 172 trees). Weather and drought variables refer to the mean of 6 hydrological years (September 2001 to August 2007). The production variable (ABA: # acorn/basal area in cm²) for the mean of 2003-2007 is also included.

Site:	Espadà		Calderona		Pinet
Quadrat:	Q1	Q2	Q3	Q4	Q5
Site variables					
Basal area (cm²)	968	1783	1432	860	1006
Distance to coast (km)	26.9	18.8	25.8	21.7	12.1
Altitude (m.a.s.l.)	687	555	639	761	600
Slope (%)	19.0	19.3	11.5	10.6	13.7
Weather variables					
P Spring (mm)	204	219	192	183	217
P Summer (mm)	52	43	50	49	32
P Winter (mm)	299	341	275	281	456
P Annual (mm)	555	603	518	516	704
FDmar (days)	2.5	1.7	2.0	2.2	1.6
FDapr (days)	0.9	0.3	0.3	0.7	0.2
FD spring (days)	3.3	1.5	1.9	2.1	2.2
Mean Temp (ºC)	14.5	15.2	14.7	14.2	15.2
Drought variables					
AET (mm)	535.3	523.7	443.4	437.4	467.9
PET (mm)	771.1	797.5	781.2	762.0	800.2
DI	0.303	0.341	0.431	0.426	0.414
Production variables					
mean ABA	0.184	0.088	0.037	0.066	0.163

For each tree, insect infestation (pre-dispersal predation) was calculated as the number of infected acorns / total number of acorns. The amount of area covered by different oak species around each cork oak was obtained with conventional GIS tools (ArcView 3.3). The proportion of each oak species was calculated by dividing the area of each oak species in the reference area by the total area of all *Quercus* species. These two parameters (area and relative proportion) were calculated for a total of 40 cork oak trees with available spatial data; we used three reference areas: 100 and 200 m buffer area around the tree, and the entire quadrat (9 km^2). We tested the significance of these two factors determining the proportion of infested acorns by using a stepwise linear regression. The regression was weighted by the number of acorns analysed per tree and year. The proportion data (infested acorns/total acorns, and proportion of *Quercus suber*/total *Quercus*) were arcsine-root-transformed. In order to discriminate the years with a reduced acorn production (in number) in comparison with the previous year, we computed for each tree, ABA_{2004}/ABA_{2003} and ABA_{2005}/ABA_{2004} and obtained a mean ratio for each quadrat. Then, we selected the lower of these two ratios for each quadrat to test the effect of the oaks species occupied area and composition on the mean infestation by *Curculio* and *Cydia*. For this analysis, quadrats 3 and 4 (nearby quadrats on the Calderona site) were pooled together because of the very low number of acorns observed in low production years.

Table 2. Correlations between each principal component (PCA1, PCA2 and PCA3) and the weather variables used. For each principal component, variables are sorted by the correlation coefficient, and only the 10 most correlated variables are shown (for all variables see Appendix 2). All correlations are significant at p< 0.0001. P Annual: total annual precipitation; P Spring: precipitation of March, April and May; P Summer: precipitation of June, July and August; P Winter: precipitation of September to February; FD: sum of number of frost days in March, April and May; FD March: number of frost days in March; FD April: number of frost days in April. DI: annual drought index; WD: annual water deficit . AET: actual annual evapotranspiration; N Drought: annual number of months with water deficit; PET: potential evapotranspiration; mean T: annual mean temperature. "(-1)" refers to previous-year climatic data.

PCA1		PCA2		PCA3	
P annual (-1)	0.789	FD March	0.856	PET	0.517
AET (-1)	0.775	FD (-1)	0.816	P Summer (-1)	0.461
P Spring (-1)	0.770	DI	0.759	N drought	0.341
PET	0.670	WD	0.686	PET (-1)	0.258
N drought	0.642	mean T	0.686	P Spring (-1)	0.231
PET (-1)	-0.658	P annual	-0.456	FD March (-1)	-0.155
P annual	-0.713	AET (-1)	-0.502	P summer	-0.287
DI (-1)	-0.847	P Summer	-0.568	FD April	-0.762
WD (-1)	-0.885	P Spring	-0.665	FD March	-0.941
mean T (-1)	-0.885	AET	-0.827	FD Spring	-0.955

Results

a) Acorn production pattern

The mean acorn production per tree ranged between 0.00 and 8.09 ABA (mean 0.10, see appendix 2 for raw data). Most of the production was supplied by a few trees, e.g., 5.1% of the trees accounted for 54.6% of the ABA (Fig. 3). Three (1.7%) trees did not produce any acorns, and 14 (8.1%) produced ≤ 5 acorns during the five year period. There was no clear pattern in temporal acorn production at individual level and very different production patterns occurred even in trees in the same quadrat (Fig. 4).

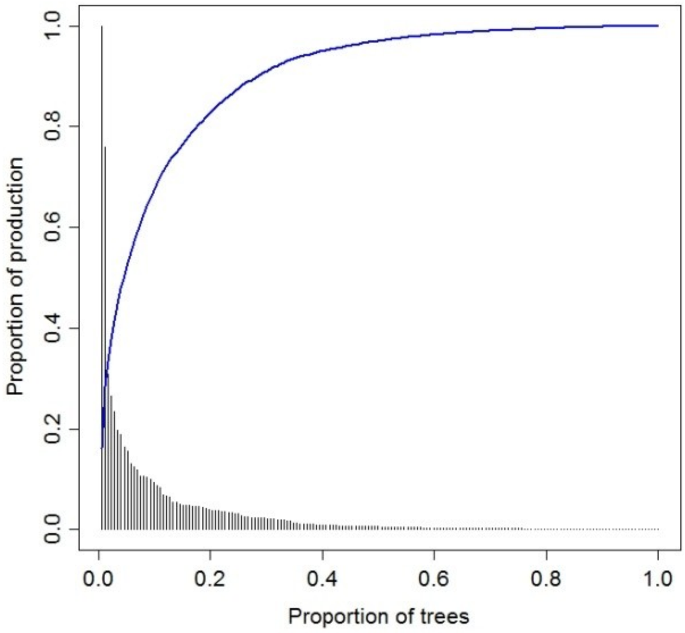


Fig.3. Trees (n= 172) arranged by mean acorn production (vertical lines, relative to the tree with highest production), and cumulative production (curve, relative to the total cumulative production). Individual acorn production estimated as number of total acorns / basal area.

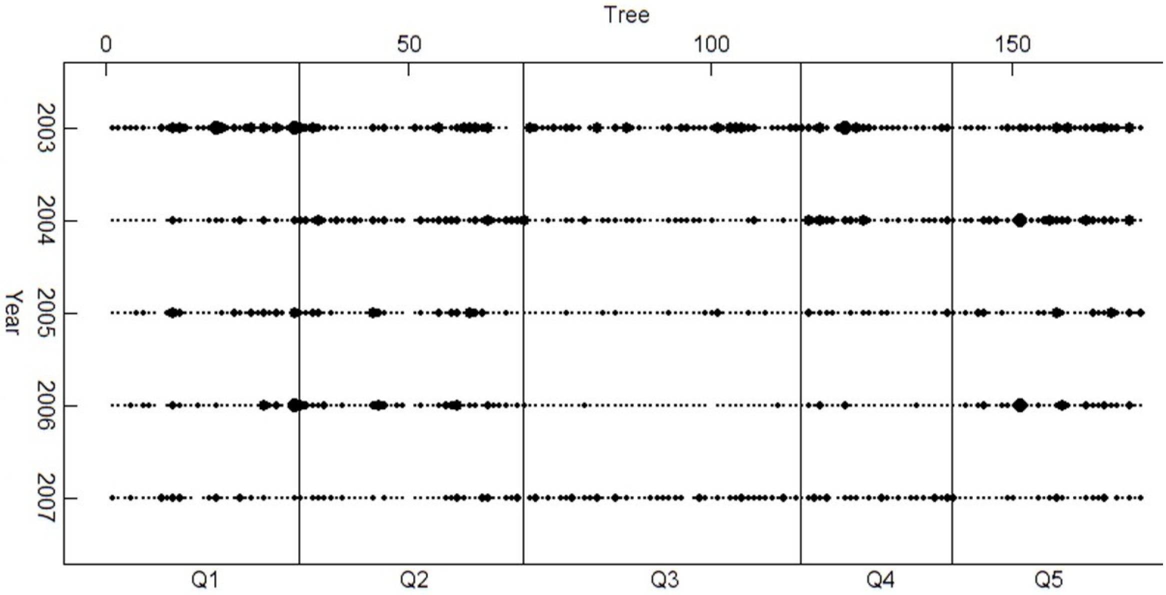


Fig. 4. Acorn production per basal area unit, per year and quadrat. Dot size is proportional to tree crop.

By populations, the lowest acorn production was recorded in quadrat 3 in 2006 (mean ABA= 0.0009) and the highest in quadrat 1 in 2003 (mean ABA= 0.4835). The most productive quadrats were 1 and 5 (mean 5 years ABA= 0.188 and 0.164, respectively), while the quadrat with the lowest production was 3 (mean 5 years ABA= 0.037). The most productive year was 2003 (mean ABA= 0.216), and the year with the poorest production was 2007 (mean ABA = 0.047, Fig. 5). Quadrats 2 and 5 had low population variability (CVp, 72.0 and 88.0, respectively) when compared with the other quadrats (>135.6, see Table 3). Synchrony in acorn production between trees was low in all populations (Rp < 0.4; Table 3; see discussion for the comparison with other oaks). In general ABA varied greatly between trees, years and quadrats.

Table 3. Indicators of acorn production variability in the five populations (Q1 to Q5), in the populations aggregated by mountain (Q1+Q2 = Espadà, Q3+Q4 = Calderona; see Fig. 1) and considering all populations together (Total), for the period 2004-2007 (both included). Indicators used are (Koenig et al. 2003): individual (Cvi) and population (CVp) coefficient of variation, mean pairwise correlation between trees (Rp; mean individual synchrony), and individual (ACF1i: year-1) and population (ACF1p: year-1) partial temporal autocorrelation.

	Q1	Q2	Q3	Q4	Q5	Q1+Q2	Q3+Q4	Total
CVi	229.32	172.51	162.71	222.944	340.64	211.87	178.75	276.95
CVp	141.60	71.99	175.77	135.61	88.02	104.86	164.04	92.16
Rp	0.3573	0.1507	0.3835	0.3181	0.2557	0.1788	0.3382	0.21
ACF1i	-0.1968	-0.2372	-0.1133	-0.1025	-0.1221	-0.2184	-0.1094	-0.15
ACF1p	-0.2650	0.1018	-0.0360	0.1924	-0.7805	-0.1893	0.0165	-0.11

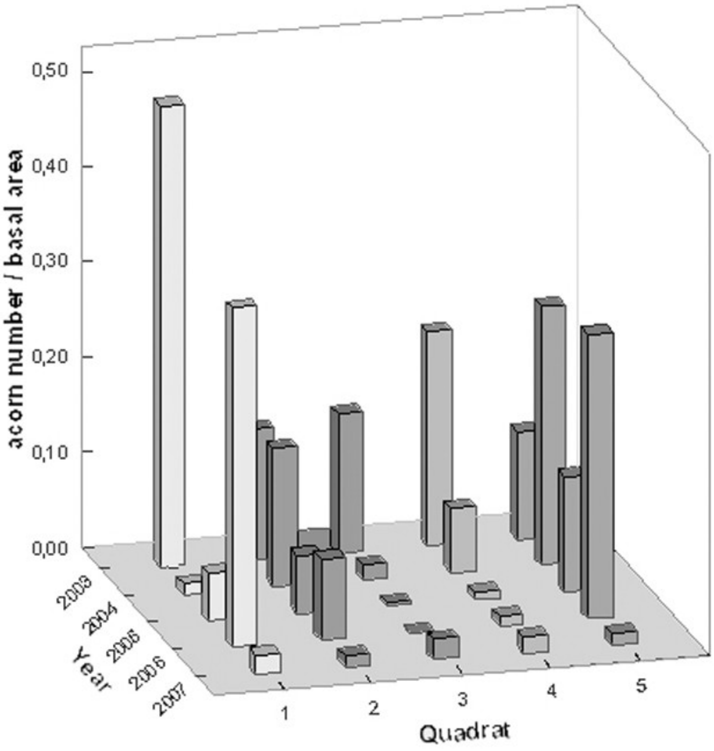


Fig. 5. Mean annual acorn production in each quadrat between 2003 and 2007, expressed as total number of acorns per tree basal area (in cm^2).

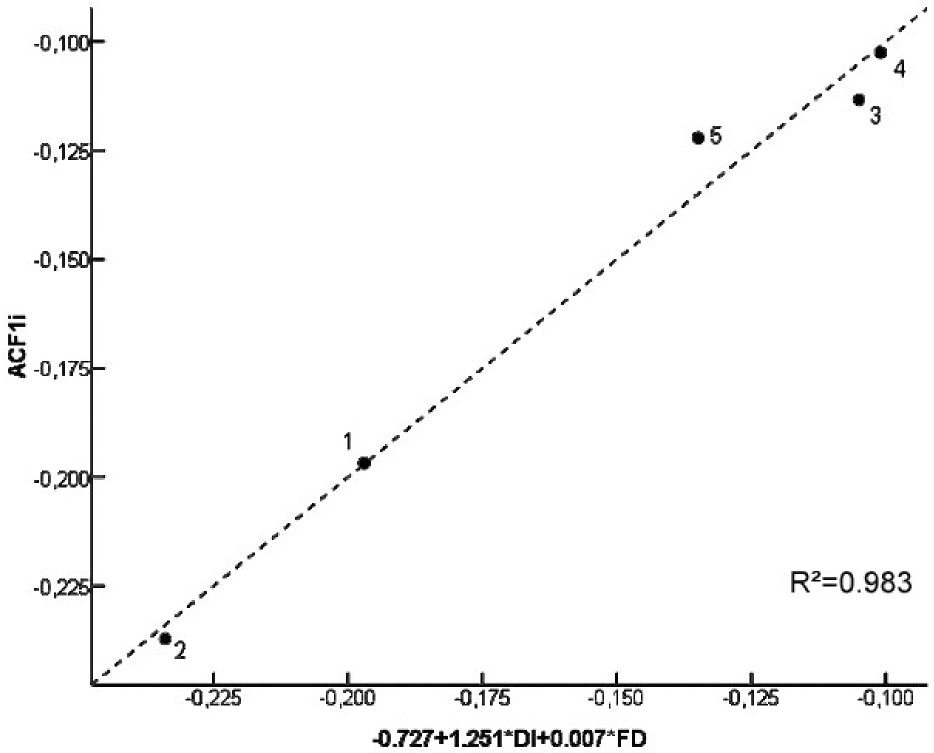


Fig. 6. Relationship between the observed ACF1 and the one predicted by the regression with weather variables (R^2 = 0.986, p = 0.014). Only the Drought index (DI) and the sum of 7 years of spring Frost Days (FD) were significant when tested using a stepwise procedure. Number labels correspond to population (quadrat number)

b) Variability in acorn number

Factor analysis of the weather variables revealed that the first 3 principal components (PC1, PC2, PC3) accounted for 71.38 of the variance. PC1 was mainly positively related to previous year water availability; PC2 was positively related to the previous-year number of spring frost days and negatively to current-year water availability; and PC3 was negatively related to the number of current-year spring frost days (Table 2, Appendix 1). Repeated measures ANOVA of ABA with the three factors showed a significant correlation between acorn production and weather variables. Spatially (between quadrats), the number of acorns was negatively correlated with previous-year water availability and the current-year number of spring frost days. Temporally, more acorns were produced in years with good water status, high number of frost days in the previous year, and low number of current-year frost days; some of the remaining variability was explained by the year factor. The three weather-based principal components explained more temporal than spatial variability, with an overall explained variance of 16.7% (Table 4).

If the previous-year ABA is introduced in the model, the explained variance on ABA improves considerably due to mainly an increase in explained spatial variance (from 18.5 to 86.6%, Table 5). This increase is not only due to the previous-year ABA but also to the fact that PC3 and Quadrat becomes significant. The remaining components are still present in the model although with lower explained variance and with different signs, reflecting the possible role of temporal autocorrelation (see Discussion). However, caution must be taken when comparing the two models as the latter includes a lower number of cases (ABA for 2003 is not included as the previous-year data was not available).

Table 4. Summary of the repeated measures analysis for acorn production (ABA), indicating the explained variance (%), the sign of the coefficient (Coeff) and the significance of each variable (p), for the spatial (between trees) and the temporal (within tree) variability. Only significant variables (i.e., those that are spatially or temporally significant) were included (ns p>0.1, . p< 0.1, * p< 0.05, ** p< 0.01, *** p< 0.001, **** p<0.0001).

	Spatial			Temporal		
	Var. %	Coeff	p	Var. %	Coeff	p
PCA1	3.5	-	*	3.5	+	***
PCA2	2.8	-	*	9.1	-	***
PCA3	0.0		ns	7.0	-	***
Year	4.6	- - - +	.	1.2	- + + -	*
Explained Variance (%)	11.0			20.8		
Total Explained Variance (%) = 16.7						

Table 5. Summary of the repeated measures analysis for acorn production (ABA), including previous-year ABA (log-transformed) as a predictor. (ns p>0.1, . p< 0.1, * p< 0.05, ** p< 0.01, *** p< 0.001, **** p<0.0001).

	Spatial			Temporal		
	Var. %	Coeff	p	Var. %	Coeff	p
PCA1	2.9	-	***	0.9	-	*
PCA2	3.8	+	***	2.6	+	***
PCA3	2.5	+	***	0.8	-	*
Quadrat	7.9	- - - -	***			
Year	0.3		ns	4.9	- + +	***
log(ABA[-1])	68.9	+	***	14.4	-	***
Explained Variance	86.4			23.5		
Total Explained Variance (%) = 55.4						

The regression model of the temporal autocorrelation (ACF1i) with weather variables at quadrat level showed a significant positive relationship with drought and total number of spring frost days (Fig. 6), suggesting that the annual/biennial acorn pattern is climatically controlled.

c) Variability in acorn size

Mean Relative Acorn Weight (RAW) varied between 24.7 ± 2.6 % in quadrat 1 and 39.4 ± 2.1 % in quadrat 5. By year, the lowest mean RAW corresponded to 2005 and the highest to 2003 (Fig. 7a). Pairwise significance differences were found between quadrat 1 and quadrat 5 (p=0.002) when comparing quadrats and between 2003 and 2005 (p=0.016) when comparing years.

The RAW regression model explained 34.8% of the variability in acorn size. Spatially, bigger acorns were positively correlated to the previous and current year number of FDspring; temporally, bigger acorns were negatively correlated to the previous and current number of FDspring, and to water availability in the previous year; the year factor accounted for some of the unknown annual variability (Table 6).

Table 6. Summary of the repeated measures analysis for relative acorn weight (RAW) with respect to spatial and temporal weather variables (3 principal components). (ns p>0.1, . p< 0.1, * p< 0.05, ** p< 0.01, *** p< 0.001, **** p<0.0001).

	Spatial			Temporal		
	Var. %	Coeff	P	Var. %	Coeff	p
PCA1	0.0		ns	16.8	+	***
PCA2	10.3	+	*	15.6	-	***
PCA3	9.7	+	*	4.9	-	*
Year	8.9	+ +	.	6.9	- -	*
Explained Variance	29.0			44.2		
Total Explained Variance (%) = 34.8						

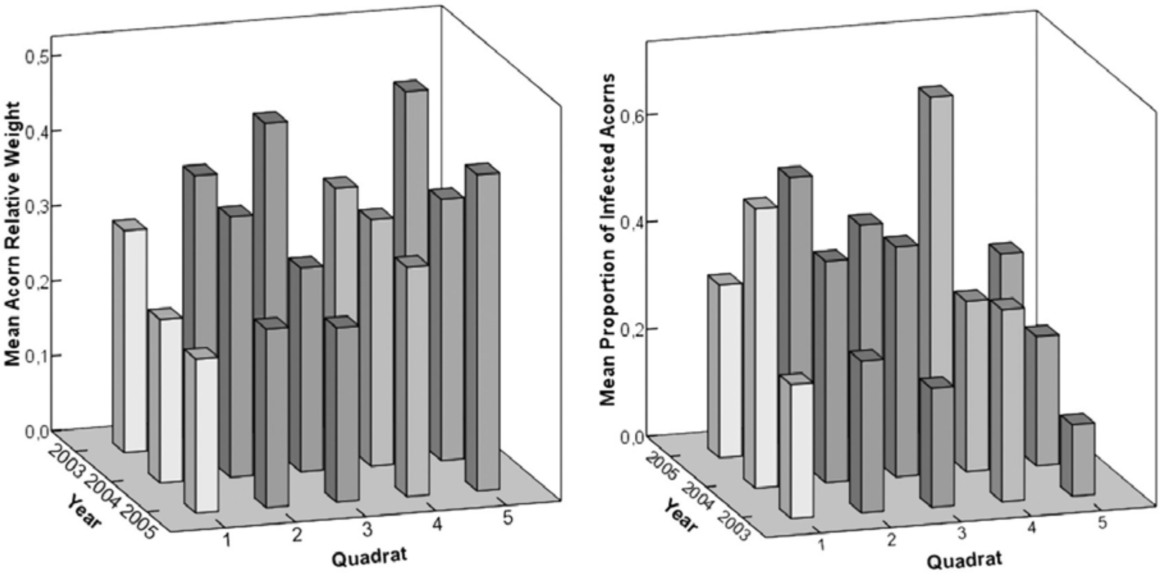


Fig. 7. a) Mean acorn relative weight and b) mean proportion of infected acorns by year and quadrat.

d) Variability in acorn infestation

The proportion of infested acorns varied between 13.4 ±1.7 % in quadrat 5 in 2003 and 54.5 ±7.3 % aggregating quadrat 3 and 4 in 2005 (Fig. 7b). This variable was negatively correlated with tree acorn crop for the total infestation ($r^2 = 0.232$, $p < 0.001$, $n = 106$; Fig. 8), and for the infestation by each species separately (*Curculio*: $r^2 = 0.390$, $p < 0.001$, $n = 67$; *Cydia*: $r^2 = 0.419$, $p < 0.001$, $n = 67$).

The response of infestation to oak abundance and composition in the surroundings of the target cork oak was different for the two predator species: *Curculio* infestation (proportion of infected acorns) was positively correlated with the proportion of cork oak both in the whole quadrat (*QSquadrat*) and in the area within a 100 m radius of the tree (*QS100*) as follows (stepwise regression): $\arcsin(\sqrt{Curculio}) = 0.011 + 0.186 \text{ x } \log(QSquadrat) + 0.154 \text{ x } \arcsin(\sqrt{Qs100})$; ($r^2 = 0.515$, $p<0.001$, n = 25). *Cydia* was not related to any variables.

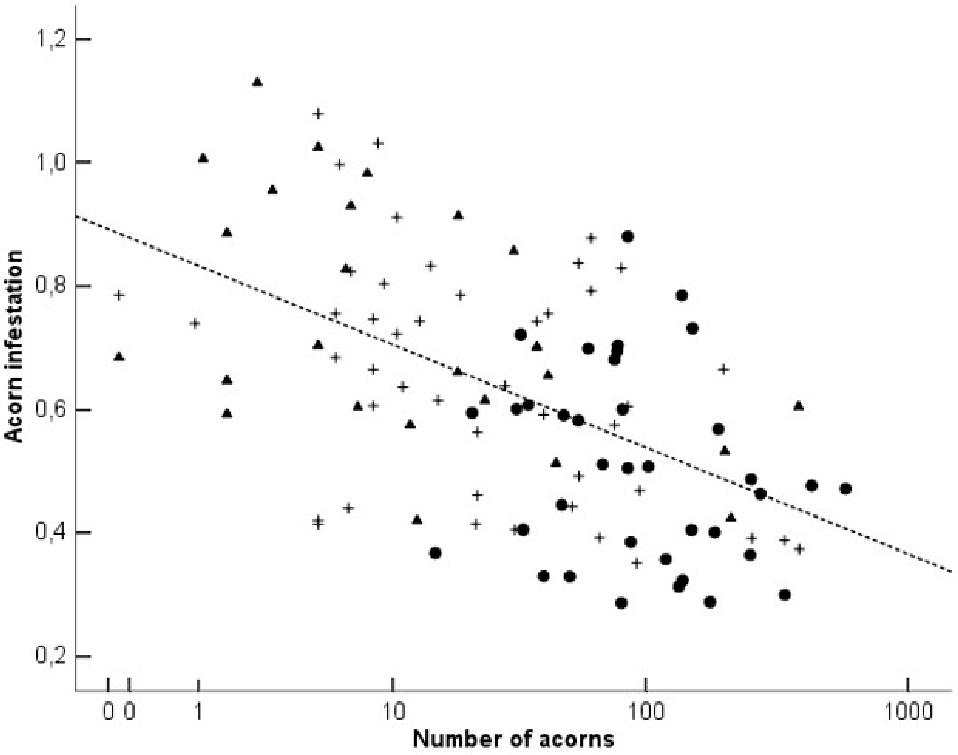


Fig. 8. Relationship between the proportion of infested acorns (arcsine root transformed) and the acorn crop (in acorns trapped /m²) by tree and year (2003= filled circle; 2004= crosses; 2005= filled triangles; n=108, F=43,775; R^2= 0.292; $P < 0.001$).

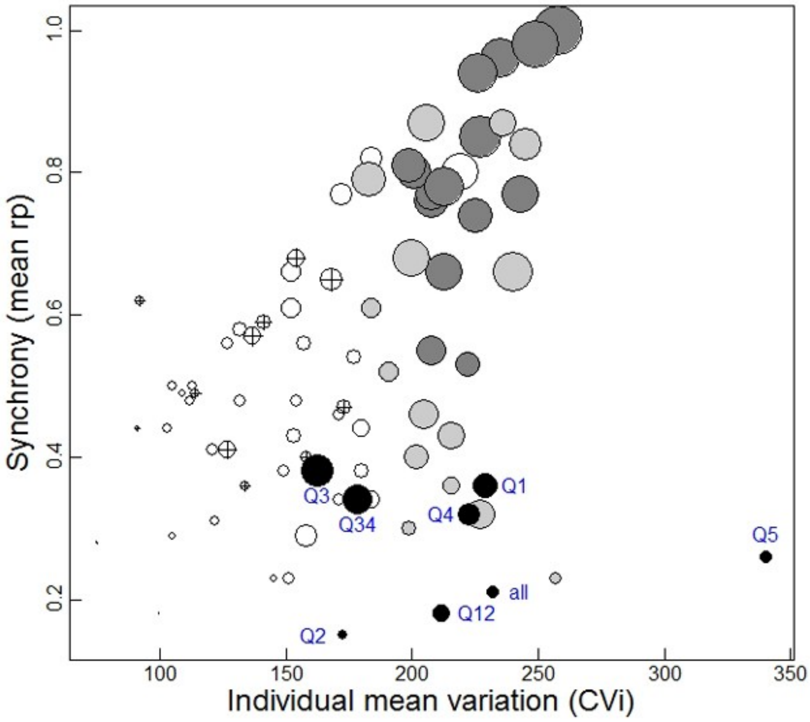


Fig. 9. Interrelation between synchrony (rp), individual mean variation (CVi) and population variation (CVp; proportional to symbol size) in acorn production according to different studies . Data from different species of American oaks with 1-yr and 2-yr acorn maturation (open circle 1 year, crossed circle 2 year, Koenig et al.2003), from Mediterranean oaks (dark-grey filled circles for *Q.ilex* and light- grey filled circles for *Q. humilis*) reported by Espeta et al. (2008) and from the present study (black-filled circles for *Q.suber*). Labelled symbols indicate the plots in the present study individually (Q1 to Q5), aggregated by mountain (Q12 = Espadà, Q34= Calderona; see Figure 1) or all plots together (all).

Discussion

Weather parameters explain a significant proportion of the variability in acorn production in our *Q.suber* populations, and the effect of these parameters is detected on the number (ABA), the size (RAW), and the maturation pattern (annual/biennial; ACF1) of acorns. Thus, the weather tracking (non-adaptive) hypothesis holds for our study system.

ABA increases spatially and temporally with higher available water (precipitation) and lower number of frost days (Table 4, PCA2), thus confirming prediction 1 and supporting the weather tracking hypothesis. April freezing has been demonstrated to reduce acorn production, probably because of frost damage to flowers (stopping the meiosis; García-Mozo et al 2001). In contrast, precipitation enhances production, suggesting that the system is resource-limited.

When the previous year's tree production is added to the model (Table 5) the explained variance increases considerably (to ca. 55.4%), particularly in the spatial analysis: some areas are better producers (quadrats 1 and 5) than others (quadrats 2, 3 and 4); but also in the temporal analysis: trees tend to produce less if the previous year's production was high (negative autocorrelation). In fact, the sign of some weather factors reverses with respect to the analysis with current-year ABA only, which suggests that endogenous dynamics plays a more important role than weather factors in the total number of acorns (Table 5).

As a whole, ABA was poorly correlated among trees. Cork oak acorn production showed high variability and low predictability, not only between populations but also between individuals of the same population (Table 3), as suggested by the low synchrony levels (Rp) and the high individual variability (CVi) when compared with available data from other oak species (Koenig et al. 2003, Martin-Vicente et al 1998, Espelta et al. 2008; Fig. 9). Previous-year production seems to reduce the current crop. However, this character was different between populations: northern populations (Espadà, Q1 and Q2) showed a more negative autocorrelation (ACF1i) than Calderona and Pinet trees (Table 3), which is associated with a gradient from annual to biennial character of acorn production (Koenig et al. 2003). The positive correlation of drought and the number of spring frost days with ACF1i (Fig. 6) confirm prediction 2 and suggest a more biennial type of acorn production in stressed populations (Pinet and Calderona) and a dominance of annual crops in more mesic populations (Espadà). This can be explained by the shorter vegetative period imposed by the intense summer droughts (Díaz et al. 2004) and spring frosts.

Acorn size increases spatially with high and low numbers of frost days during the previous and current year, respectively, suggesting a contribution of biennial acorn type to the current-year crop. This is because biennial acorns tend to be larger due to the longer maturation time (Díaz-Fernández et al. 2004). Temporally, increases in water status and number of frost days also increases acorn size (Table 6), thus reinforcing prediction 3. The number of frost days in the current year reduces the number of acorns per tree but increases their size, which is not surprising as the physiological pattern seems to be very similar to that of the cultivated trees in the area (i.e., almonds and olives trees) and is well-known to local farmers; that is, frost provides higher resources per seed.

The proportion of acorn infestation increases in years with low acorn production. It also increases with cover of *Q.suber* (at quadrat level) and dominance of this species around the target tree (prediction 4). This suggests that at least some predator saturation is working. Nonetheless, differences between *Curculio* and *Cydia* seem to exist as we fail to find a relation of the latter to the tree surroundings. A possible explanation could be the differences in life history and/or mobility between the weevil (*Curculio*) and the moth (*Cydia*).

We can conclude that *Q.suber* is one of the oaks showing most spatial and temporal variability in acorn production. Part of this variability is probably due to different proportions of annual-biennial acorn type in the different populations. As a whole, and with the expectation of longer acorn production series in the future, this oak does not show a marked masting, but rather a very probable trend towards smooth cycles (Caritat et al. 2006). Our results provide evidence that the quantity and size of the acorn production depend on climatic and weather factors, thus supporting the weather tracking (non-adaptive) hypothesis. However, the lower explained variance in the weather-based models and the fact that the previous-year acorn production increases significantly the explained variance suggest that endogenous dynamics may also play an important role in this ecosystem. Indeed, we have likewise found evidence for satiation of pre-dispersal predators suggesting that the satiation hypothesis is also working in the system. When other *Quercus* are present in the area, infected acorn proportions are not quite dependent on past productions; thus, future research in this field should analyse all the acorn producing species in the area along with their pre-dispersal insect predators.

Acknowledgements

We thank Cristina Beseler and Aina Blasco for collaborating in the field sampling and Patricio García-Fayos for insights on an early version of manuscript. This work was funded by the European project CREOAK (QLRT-2001-01594) and the Spanish project VARQUS (CGL2004-04325/BOS). CEAM is supported by *Generalitat Valenciana, Bancaixa*, and the Spanish government (GRACCIE Consolider-Ingenio2010).

References

Abrahamson,W.G. and Layne,J.N. 2003. Long-term patterns of acorn production for five oak species in xeric Florida uplands. Ecology 84: 2476-2492.

Aronson,J., Pereira,J.S., Pausas,J.G. (eds). 2009. Cork oak woodlands on the edge. Island Press.

Buonaccorsi,J.P., Elkinton,J.S., Evans,S.R., Liebhold,A.M. 2001. Measuring and testing for spatial synchrony. Ecology 82: 1668–1679.

Boutin,S., Lucas,A., Wauters,A.G., McAdam,M.M., Humphries,G.T., André,A.D. 2006. Anticipatory reproduction and population growth in seed predators. Science 314: 1928-1930.

Bridle,J.R., Vines,T.H. 2007. Limits to evolution at range margins: when and why does adaptation fail? Trends Ecol. Evol. 22: 140-147.

Caritat,A., Garcia-Berthou,E., Lapena,R., Vilar,L. 2006. Litter production in a *Quercus suber* forest of Montseny (NE Spain) and its relationship to meteorological conditions. Ann. For. Sci. 63: 791-800.

Cecich,R.A., Sullivan,N.H. 1999. Influence of weather at time of pollination on acorn production of *Quercus alba* and *Quercus velutina*. Can. J. For. Res. 29: 1817-1823.

Clotfelter,E.D., Pedersen,A.B., Cranford,J.A., Ram,N., Snajdr,E.A., Nolan,V., Ketterson, E.D. 2007. Acorn mast drives long-term dynamics of rodent and songbird populations. Oecol. 154, 493-503.

Crawley,M.J., Long,C.R. 1995. Alternate bearing, predator satiation and seedling recruitment in *Quercus robur*. J. Ecol. 83: 683-696.

Díaz,M., Pulido,F.J., Moller,A.P. 2004. Herbivore effects on developmental instability and fecundity of holm oaks. Oecol. 139: 224-234.

Díaz-Fernández,P.M., Climent,J., Gil,L. 2004. Biennial acorn maturation and its relationship with flowering phenology in Iberian populations of *Quercus suber*. Trees Structure and Function 18: 615-621.

Elena-Roselló,J.A., Del Rio,J.M., García-Valdecantos,J.L., Santamaría,I.G. 1993. Ecological aspects of the floral phenology of the cork-oak (*Q.suber* L.): why annual and biennial biotypes appear? Ann. For. Sci. 50: 114-121.

Ellison,A.M. et al. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front. Ecol. Environ. 3(9): 479-486.

Espelta,J.M., Corte,P., Molowny-Horas,R., Sanchez-Humanes,B., Retana,J. 2008. Masting mediated by summer drought reduces acorn predation in Mediterranean oak forests. Ecology 89: 805-817.

García-Mozo,H. et al. 2001. Catkin frost damage in Mediterranean cork-oak (*Quercus suber* L.). Israel J. Plant Sci. 49: 41-47.

García-Mozo,H. et al. 2007. Influence of pollen emission and weather-related factors on variations in holm-oak (*Quercus ilex* subsp *ballota*) acorn production. Environ. Experim. Bot. 61: 35-40.

Gomez,J.M. 2004. Bigger is not always better: Conflicting selective pressures on seed size in *Quercus ilex*. Evolution 58: 71-80.

Goodrum,P.D. et al. 1971. Acorn yields, characteristics, and management criteria of oaks for wildlife. J. Wild. Manag. 35: 520-532.

Greenberg,C.H. 2000. Individual variation in acorn production by five species of southern Appalachian oaks. - For. Ecol. Manag. 132: 199-210.

Greene,D.F., Johnson,E.A. 1994. Estimating the mean annual seed production of trees. Ecology 75: 642-647.

Greene,D.F. et al. 2004. An evaluation of alternative dispersal functions for trees. J. Ecol. 92: 758-766.

Guariguata,M.R., Saenz,G.P. 2002. Post-logging acorn production and oak regeneration in a tropical montane forest, Costa Rica. For. Ecol. and Manag. 167: 285-293

Hampe,A., Petit,R.J. 2005. Conserving biodiversity under climate change: the rear edge matters. Ecol. Lett. 8:461-467.

Herrera,C.M. 1998. Population-level estimates of interannual variability in seed production: what do they actually tell us? Oikos 82: 612–616.

Jiménez,P., Agundez,D., Alia,R., Gil,L. 1999. Genetic variation in central and marginal populations of *Quercus suber* L. Silvae Gen. 48: 278-284..

Kelly,D. 1994. The Evolutionary Ecology of Mast Seeding. Trends Ecol. Evol. 9: 465-470.

Kelly,D., Sork,V.L. 2002. Mast seeding in perennial plants: Why, how, where? Ann. Rev. Ecol. Syst. 33: 427-447.

Koenig,W.D. et al. 1996. Acorn production by oaks in central coastal California - influence of weather at three levels. Can. J. For. Res. 26: 1677-1683.

Koenig,W.D., Knops,J.M.H. 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. Am. Nat. 155: 59-69.

Koenig,W.D., Knops,J.M.H. 2002. The behavioral ecology of masting in oaks. In: (eds.). Oak forest ecosystems. pp. 129-148.

Koenig,W.D. et al. 2003. Dissecting components of population-level variation in seed production and the evolution of masting behavior. Oikos 102: 581-591.

Lesica P., Allendorf,F.W. 1995. When peripheral populations are valuable for conservation. Conserv. Biol. 9: 753-760.

Liebhold, A. et al. 2004. Within-population spatial synchrony in mast seeding of North American oaks. Oikos 104: 156-164.

Logan,W.B. 2005. Oak: the frame of civilization. WW Norton and Co.

Martin-Vicente,A. et al. 1998. Producción de bellotas en montes y dehesas del Suroeste Español. Pastos 28: 237-242.

McShea,W.J., Healy,W.M. (editors). 2002. Oak Forest Ecosystems: Ecology and Management for Wildlife. John Hopkins University Press.

Merouani,H. et al. 2001. Effects of acorn storage duration and parental tree on emergence and physiological status of Cork oak (*Quercus suber* L.) seedlings. Ann.For.Sci. 58: 543-554.

Magri,D. et al. 2007. The distribution of *Quercus suber* chloroplast haplotypes matches the palaeogeographical history of the western Mediterranean. - Mol. Ecol. 16: 5259-5266.

Masaka,K., Sato,H. 2002. Acorn production by Kashiwa oak in a coastal forest under fluctuating weather conditions. Can. J. For. Res. 32: 9-15.

Millán,M.M. et al. 2005. Rainfall components: Variability and spatial distribution in a Mediterranean area (València region). J. Climate 18: 2682-2705.

Moles,A.T., Westoby,M. 2004. Seedling survival and seed size: a synthesis of the literature. J. Ecol. 92: 372-383.

Montero,G., Cañellas,I. 2003. El alcornoque. Manual de reforestación y cultivo. Ed. Mundi-Prensa, 2a ed. Madrid.

Ostfeld,R.S. et al. 1996. Of mice and mast: ecological connections in eastern deciduous forests. BioScience 46: 323-330.

Ostfeld,R.S., Keesing,F. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends Ecol. Evol. 15: 232-237.

Pascual,G. 2003. Anàlisi de la capacitat de regeneració en estadis inicials del desenvolupament en divèrses espècies mediterrànies del genere *Quercus*. PhD Dissertation, University of Girona.

Pausas,J.G. 1997. Resprouting of *Quercus suber* in NE Spain after fire. J. Veg. Sci. 8: 703-706.

Pausas,J.G., Ribeiro,E., Dias,S.G., Pons,J., Beseler,C. 2006. Regeneration of a marginal *Quercus suber* forest in the eastern Iberian Peninsula. J. Veg. Sci. 17: 729-738.

Pausas,J.G., Pereira,J.S., Aronson,J. 2009. Chapter 1. The tree. In: Aronson J., Pereira, J.S. and Pausas J.G. (eds). Cork oak woodlands on the edge. Island Press.

Pérez-Cueva,A.J. 1994. Atlas climàtic de la Comunitat Valenciana, 1961–1990. Generalitat Valenciana, València.

Pons,J., Pausas,J.G. 2006. Oak regeneration in heterogeneous landscapes: The case of fragmented *Quercus suber* forests in the eastern Iberian Peninsula. For. Ecol. Manag. 231: 196-204.

Pons,J., Pausas,J.G. 2007a. Rodent acorn selection in a Mediterranean oak landscape. Ecol. Res. 22: 535-541.

Pons,J., Pausas,J.G. 2007b. Not only size matters: Acorn selection by the European jay (*Garrulus glandarius*). Act. Oecol. 31: 353-360.

Pons,J., Pausas,J.G. 2008. Modelling jay (*Garrulus glandarius*) abundance and distribution for oak regeneration assessment in Mediterranean landscapes. For. Ecol. Manag. 256: 578-584.

Quero,J.L. et al. 2007. Seed-mass effects in four Mediterranean *Quercus* species (Fagaceae) growing in contrasting light environments. Am. J. Bot. 94: 1795-1803.

Rodà,F., Retana,J., Gràcia,C.A., Bellot,J. (Eds.), 1999. Ecology of Mediterranean Evergreen Oak Forests. Springer, Berlin.

Rubio,J.L. et al. 1995. Mapa de suelos de la Comunidad Valenciana, Sagunto (668). Proyecto LUCDEME, Generalitat Valenciana.

Saitoh,T. et al. 2007. Effects of acorn masting on population dynamics of three forest-dwelling rodent species in Hokkaido, Japan. Popul. Ecol. 49: 249-256.

Schmidt,K.A., Ostfeld,R.S. 2003. Songbird populations in fluctuating environments: Predator responses to pulsed resources. Ecology 84: 406-415.

Selàs,V. 2002. Climatic factors controlling reproduction and growth of Norway spruce in southern Norway. Can. J. For. Res. 32: 217-225.

Serrasolsa,I., Pérez-Devesa,M., Vilagrosa,A., Pausas,J.G., Sauras,T., Cortina,J., Vallejo,R. 2009. Soil properties constraining cork oak distribution. In: Aronson J., Pereira J.S., Pausas J.G. (eds). 2009. Cork oak woodlands on the edge. Island Press.

Shibata,M. et al. 2002. Synchronized annual seed production by 16 principal tree species in a temperate deciduous forest, Japan. Ecology 83: 1727-1742.

Soria,F.J., Cano,E., Ocete,M.E. 1999. Valoración del ataque de *Curculio elephas* (Gyllenhal) (Coleoptera, Curculionidae) y *Cydia* spp. (Lepidoptera, Tortricidae) en el fruto del alcornoque (*Quercus suber* Linné). Boletin Sanidad Vegetal Plagas, 25: 69-74.

Sork,V.L. et al. 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. Ecology 74: 528-541.

Thornthwaite,C.W., Mather,J.R. 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Laboratory of Climatology, Publication 10, pp. 181-311. Centerton, NY.

Venable,D.L., Brown,J.S. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. Am. Nat. 131: 360–362.

Vander Wall,S.B. 2002. Masting in animal-dispersed pines facilitates seed dispersal. Ecology 83: 3508-3516.

Wolff,J.O. 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. J. Mammal. 77: 850-856.

Xiao,Z.S. et al. 2005. Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species. Act. Oecol. 28: 221-229.

Appendix 1

Correlations between each principal component (PCA1, PCA2 and PCA3) and the weather variables used. For each principal component, variables are sorted by the correlation coefficient.

	PCA1			PCA2			PCA3	
	cor	p		cor	p		cor	p
P Annual (-1)	0.789	0.0000	FD mar	0.856	0.0000	PET	0.517	0.0000
AET (-1)	0.775	0.0000	FD (-1)	0.816	0.0000	P Summer (-1)	0.461	0.0000
P Spring (-1)	0.770	0.0000	DI	0.759	0.0000	N Drought	0.341	0.0000
PET	0.670	0.0000	WD	0.686	0.0000	PET (-1)	0.258	0.0000
N Drought	0.642	0.0000	mean T	0.686	0.0000	P Spring (-1)	0.231	0.0000
WD	0.639	0.0000	FD apr (-1)	0.580	0.0000	N Drought (-1)	0.208	0.0000
mean T	0.639	0.0000	DI (-1)	0.413	0.0000	WD	0.182	0.0000
P Summer (-1)	0.563	0.0000	N Drought	0.365	0.0000	mean T	0.182	0.0000
DI	0.561	0.0000	WD (-1)	0.343	0.0000	FD apr (-1)	0.126	0.0002
FD apr	0.515	0.0000	Mean T (-a1)	0.343	0.0000	DI	0.108	0.0016
P Summer	0.287	0.0000	P Winter	0.158	0.0000	AET (-1)	0.079	0.0200
FD Spring	0.213	0.0000	N Drought (-1)	0.147	0.0000	P annual	0.064	0.0598
P Winter (-1)	0.200	0.0000	P Winter (-1)	0.072	0.0335	P Annual (-1)	0.020	0.5622
FD mar	0.048	0.1615	FD mar	0.071	0.0383	P Winter (-1)	0.010	0.7623
FD mar (-1)	-0.118	0.0005	FD Spring	0.019	0.5854	WD (-1)	0.003	0.9408
FD Spring (-1)	-0.149	0.0000	FD apr	-0.096	0.0047	Mean T (-1)	0.003	0.9408
FD apr (-1)	-0.193	0.0000	PET	-0.214	0.0000	AET	0.000	0.9958
AET	-0.439	0.0000	P Summer (-1)	-0.220	0.0000	DI (-1)	-0.028	0.4134
P Winter	-0.508	0.0000	P Annual (-1)	-0.291	0.0000	FD Spring (-1)	-0.074	0.0309
P Spring	-0.545	0.0000	PET (-1)	-0.380	0.0000	P Winter	-0.093	0.0066
N Drought (-1)	-0.568	0.0000	P Spring (-1)	-0.399	0.0000	P Spring (-1)	-0.111	0.0011
PET (-1)	-0.658	0.0000	P annual	-0.456	0.0000	FD mar (-1)	-0.155	0.0000
P annual	-0.713	0.0000	AET (-1)	-0.502	0.0000	P summer	-0.287	0.0000
DI (-1)	-0.847	0.0000	P Summer	-0.568	0.0000	FD apr	-0.762	0.0000
WD (-1)	-0.885	0.0000	P Spring	-0.665	0.0000	FD mar	-0.941	0.0000
mean T (-1)	-0.885	0.0000	AET	-0.827	0.0000	FD Spring	-0.955	0.0000

P Annual: total annual precipitation; P Spring: precipitation of March, April and May; P Summer: precipitation of June, July and August; P Winter: precipitation of September to February; FD: sum of number of frost days in March, April and May; FD March: number of frost days in March; FD April: number of frost days in April. DI: annual drought index; WD: annual water deficit . AET: actual annual evapotranspiration; N Drought: annual number of months with water deficit; PET: potential evapotranspiration; mean T: annual mean temperature. “(-1)” refers to previous-year climatic data.

Appendix 2

Raw data (basal area and number of acorns) observed for each tree during the studied 5 years.

Tree	Quadrat	Basal Area cm^2	Number of acorns				
			2003	2004	2005	2006	2007
1	1	784.24	11	0	0	0	8
2	1	506.69	2	0	0	0	0
3	1	615.73	2	0	0	0	0
4	1	401.14	1	0	0	5	2
5	1	314.15	1	0	1	0	0
6	1	1269.20	16	0	4	28	2
7	1	615.73	1	0	0	13	0
8	1	1170.18	0	0	1	0	1
9	1	876.13	220	No data	No data	No data	59
10	1	688.11	4	0	2	0	2
11	1	589.63	1743	54	305	22	82
12	1	1052.06	1508	5	184	13	51
13	1	366.42	12	0	0	0	0
14	1	415.46	0	0	0	0	0
15	1	598.27	6	0	0	19	No data
16	1	1269.20	6	1	0	0	0
17	1	530.57	5	3	0	0	2
18	1	944.11	460	14	0	28	221
19	1	366.42	195	3	5	0	0
20	1	1625.95	31	2	0	0	0
21	1	506.69	78	2	61	0	0
22	1	706.84	11	26	3	0	58
23	1	4536.33	10506	0	1	0	10
24	1	642.41	707	0	77	0	7
25	1	326.84	0	0	4	0	0
26	1	2789.78	43	No data	No data	No data	No data
27	1	633.45	453	63	22	1557	5
28	1	401.14	2	0	12	3	0
29	1	1425.27	2874	18	85	182	0
30	1	1037.45	12	1	4	0	0
31	1	1839.79	20	4	No data	No data	3
32	1	929.38	2925	36	351	6663	22
33	1	1182.33	788	48	26	868	6
34	2	3018.98	488	111	39	388	0
35	2	642.41	301	13	38	17	4
36	2	1425.27	70	744	52	36	38
37	2	633.45	18	2	1	24	18
38	2	459.95	2	1	3	0	1
39	2	615.73	5	24	1	0	0
40	2	984.20	0	5	1	8	5
41	2	598.27	0	5	0	0	0
42	2	522.78	0	41	0	0	0
43	2	1052.06	0	5	0	0	0
44	2	1411.92	3	0	1	0	3
45	2	2846.23	736	208	2280	117	36
46	2	706.84	22	14	37	980	No data

47	2	5971.87	1720	934	125	382	29
48	2	1052.06	2	0	0	0	0
49	2	437.42	6	9	0	1	0
50	2	995.35	0	32	0	13	0
51	2	7948.28	3	0	No data	No data	No data
52	2	814.31	30	0	0	0	0
53	2	2569.62	15	734	68	26	0
54	2	1516.62	19	5	0	0	0
55	2	1017.85	30	8	2	0	0
56	2	1548.76	1747	110	158	37	1
57	2	4632.33	3	306	10	410	72
58	2	1411.92	18	66	110	184	7
59	2	1346.10	140	354	250	1188	72
60	2	929.38	574	0	0	0	6
61	2	6972.53	3390	106	2800	70	8
62	2	716.29	238	52	196	8	0
63	2	1182.33	207	12	143	0	78
64	2	3608.20	1404	1267	8	451	391
65	2	333.28	0	1	0	7	0
66	2	716.29	0	2	0	3	1
67	2	784.24	1	31	8	13	4
68	2	3018.98	No data	408	1	7	21
69	2	660.50	No data	141	1	9	42
70	2	876.13	No data	2442	0	16	No data
71	3	2715.39	1173	3	0	0	37
72	3	2307.15	566	7	0	0	248
73	3	2189.50	35	0	0	0	1
74	3	794.20	9	3	0	0	6
75	3	359.67	17	0	0	0	0
76	3	2999.54	69	0	0	0	14
77	3	633.45	23	7	9	0	7
78	3	1839.79	125	15	0	0	440
79	3	2042.76	16	1	0	0	1
80	3	660.50	No data	160	0	12	8
81	3	1170.18	25	2	0	0	5
82	3	783.68	1331	0	0	0	47
83	3	1281.86	0	4	24	0	0
84	3	688.11	1	12	0	0	0
85	3	1182.33	49	6	34	0	42
86	3	1562.24	2	1	4	0	0
87	3	506.69	224	2	0	0	11
88	3	452.38	1	4	0	0	0
89	3	929.51	26	13	2	2	0
90	3	1219.18	0	0	0	0	0
91	3	1075.18	0	1	0	0	3
92	3	615.73	0	1	0	0	8
93	3	842.33	18	1	0	0	12
94	3	912.70	80	15	16	0	16
95	3	1086.83	0	4	0	2	7
96	3	547.37	36	6	0	0	10
97	3	824.46	36	13	0	0	No data

98	3	506.69	2	3	0	0	0
99	3	784.24	10	2	0	1	78
100	3	1017.85	21	0	20	0	20
101	3	1604.55	24	12	13	No data	4
102	3	929.38	422	2	32	0	9
103	3	2569.62	21	0	0	0	1
104	3	3379.75	2246	5	0	0	77
105	3	2307.15	1164	1	0	0	53
106	3	940.22	549	0	0	0	102
107	3	1932.15	201	51	38	0	25
108	3	929.38	63	233	0	0	3
109	3	700.30	0	0	0	0	2
110	3	1347.64	0	0	5	0	7
111	3	709.04	4	0	1	0	3
112	3	3237.03	62	6	0	52	0
113	3	2903.25	46	100	9	0	172
114	3	2970.13	541	0	0	0	0
115	3	2226.82	727	0	0	0	9
116	3	2641.56	603	0	5	0	1
117	4	326.84	73	110	21	3	4
118	4	794.20	12	14	0	0	29
119	4	520.12	188	180	0	3	0
120	4	669.64	9	29	2	0	25
121	4	1219.18	No data	131	23	0	No data
122	4	1197.32	48	0	1	0	0
123	4	475.28	1869	78	0	119	4
124	4	929.38	0	67	5	0	24
125	4	962.08	450	28	1	0	4
126	4	876.13	77	310	7	0	0
127	4	1244.07	77	8	6	0	36
128	4	615.73	2	0	0	0	0
129	4	589.63	16	1	2	0	21
130	4	506.69	2	4	5	0	5
131	4	984.20	15	0	0	0	0
132	4	1122.18	17	7	1	0	7
133	4	1182.33	13	3	0	0	1
134	4	929.38	0	3	0	0	6
135	4	995.35	7	1	0	7	3
136	4	1110.33	24	7	2	0	26
137	4	824.46	0	5	1	0	0
138	4	897.24	4	7	6	0	45
139	4	1834.16	93	24	5	0	12
140	4	598.27	23	78	27	0	40
141	4	539.11	0	7	4	0	30
142	5	669.64	1	0	0	0	0
143	5	1690.88	35	36	57	54	0
144	5	660.50	3	9	0	0	0
145	5	782.26	16	0	29	23	0
146	5	1102.07	35	52	304	120	0
147	5	1809.50	0	252	0	5	0
148	5	1750.60	4	150	1	1	0
149	5	498.74	1	0	3	12	0
150	5	366.42	32	5	0	2	8
151	5	615.73	13	0	0	0	2
152	5	984.20	52	5936	0	7958	0
153	5	688.11	24	1	0	7	1
154	5	1052.06	19	6	0	0	1
155	5	940.25	35	14	6	12	8
156	5	598.27	15	39	5	0	1
157	5	764.52	4	279	0	1	4
158	5	1359.14	1586	150	554	24	215
159	5	1474.87	15	258	6	507	20
160	5	1244.07	810	129	0	11	1

161	5	1742.81	17	5	0	0	0
162	5	598.27	4	10	1	1	0
163	5	572.54	117	293	0	114	15
164	5	644.38	36	33	52	6	17
165	5	498.74	41	4	7	2	6
166	5	598.27	236	57	3	37	49
167	5	2498.25	159	116	6400	11	No data
168	5	2358.51	174	49	31	23	14
169	5	633.45	1	0	0	0	0
170	5	642.41	250	313	155	170	8
171	5	547.37	0	0	0	0	0
172	5	784.24	6	0	52	1	8

Jay abundance and distribution.[2]

Abstract

Because natural regeneration of oak is strongly dependent on jay abundance and distribution, we need to understand the determinants of jay abundance and occurrence as a first step to assess oak regeneration. In this paper we modelled the jay population distribution and abundance in a Mediterranean landscape mosaic of the eastern Iberian Peninsula (Valencia, East Spain). The methodology was based on assessing landscape attributes (habitat composition and configuration variables) on seven 9-km^2 sites and registering jay fledgling locations. Using a stepwise regression model we determined the variables that best explained the jay density. The probability of occurrence of jay nests within each site was assessed by comparing the landscape attributes of jay and non-jay areas within each site. Results were validated by predicting each site on the basis of data from the remaining six sites and then calculating the deviation between the predicted and the observed values in the field. The results suggest that jay density correlates positively with forest cover and landscape heterogeneity variables, and negatively with shrubland cover. Validation of the results showed that the model is reasonably effective in predicting both jay abundance and distribution at the extent and resolution used.

1. Introduction

Oaks are frame trees in many ecosystems (McShea and Healy 2002, Logan 2005), including in many Mediterranean ones (Rodà et al. 1999, Aronson et al. in press). However, millennia of land overuse in the Mediterranean Basin has drastically reduced the abundance of oaks, mainly due to the expansion of agriculture and the charcoal and wood production. Currently, with the abandonment of many agricultural areas and the increasing disturbances (Pausas 1994), oaks are target species to be spread in oldfields (Pausas et al. 2004, Vallejo et al. 2006). This is not only because they were native of many landscapes, but also for their high resilience capacity (Pausas 1997, Rodà et al. 1999). However, both poor oak reforestation success (Mesón and Montoya 1993, Vallejo et al. 2006) and reduced natural regeneration (Pulido and Díaz 2005) has been point out as process limiting the spread of oaks in mediterranean conditions.

The regeneration process is a sequence of demographic stages and the collapse of any one of them will impede the overall regeneration (Schupp 1990). For instance, the absence of the dispersal vector will limit regeneration even when other conditions are optimal, and thus

---

[2] Pons,J. and Pausas J.G. 2008. Modelling jay (Garrulus glandarius) abundance and distribution for oak regeneration assessment in Mediterranean landscapes. Forest Ecology and Management 256(4): 578-584.

variables defining the potential regeneration niche may not be sufficiently explicative of the absence of regeneration. Accordingly, the strong heterogeneity observed in oak natural regeneration (Pons and Pausas 2006; Pausas *et al.* 2006) may be due not only to environmental conditions but also to different dispersal vector abundances in the different areas. This means that for predicting oak distribution and spread, we need to be able to predict the presence and abundance of the main oak dispersal vector. This knowledge would allow us to better delimit the factors determining natural regeneration and thus reducing the necessary sampling effort for regeneration assessments of oak communities. Moreover, knowing the dispersal vector distribution is a first step to model the natural regeneration status of animal-dispersed plants in extensive zones (i.e., regional scale).

The European jay (*Garrulus glandarius* L.) is considered a key species in the dispersal and spread of *Quercus* species (Bossema 1979; Mosandl and Kleinert 1998; Pons and Pausas 2007a,b). In autumn (the acorn production period), this corvid cache oak acorns in order to secure a steady food supply throughout the year. This food supply is especially required between May and July due to the high food demand by nestling and fledgling individuals (Bossema 1979; Clayton *et al.* 1996). Acorns are the main food for jays, at least in autumn, spring and winter (Bossema 1979; San Miguel 1983). Oaks benefit from jays because of long-distance dispersal, the good conditions of the hoarding site, and the reduced predation of jay-dispersed acorns (Bossema 1979; Pons and Pausas 2007a,b).

Like other corvidae, jays seem to explore a wide food spectrum (Bossema 1979; San Miguel 1983). As a consequence they seem to prefer diverse and mixed habitats, which are presumed to have more varied and stable resources (Rolando 1995). Because *Quercus* regeneration is strongly dependent on jay densities, it is important to be able to predict these densities from simple landscape units and thus be able to infer potential oak regeneration at landscape scale. However, little has been done to determine the habitat distribution factors of jay populations, especially in Mediterranean landscapes.

In this study we ask to what extent jay occurrence, density and spatial distribution are related to and predictable from landscape attributes. Our approach uses multiple regressions with basic landscape variables obtained from aerial photography and GIS tools (Martinez and Calvo 2000; Sergio et al 2004; Saïd and Servanti 2005). The analysis is performed at two spatial scales: 1) at landscape scale, to assess the relation between landscape attributes (composition and configuration) and jay abundance; and 2) at nesting territory scale, to assess which parts of the landscape are selected by jay-pairs. The ultimate objective is to obtain a tool that can later be applied to larger extensions (e.g., a whole National Park).

Methods

Study area

The study area is located inside the Valencia region, which borders the Mediterranean coast in eastern Spain. The climate is typically Mediterranean. The vegetation is a product of a long history of fire and land use, and many slopes were terraced and cultivated in the past, and then abandoned. In this region there are 4 main *Q.suber* patches (hereafter sites), from north to south: Desert de les Palmes (Castelló, lat = 40° 01', 10 ha), Espadà (Castelló, lat = 39° 52', ca. 70000 ha), Calderona (València, lat = 39° 44', ca. 7000 ha) and Pinet (València, lat = 38° 59', ca. 70 ha) . Soils in Desert de les Palmes, Calderona and Espadà are mainly acidic soils on sandstones. In Espadà soil pH ranges from 4.9 to 6.4 (mean: 5.7). In Pinet, cork oak occurs in non-carbonated soils on dolomites, with pH ranging from 5.5 to 7.5 (mean: 6.5; Pausas et al. 2006). Average annual rainfall in these cork patches ranges from 500 to 800 mm, with a clear seasonal pattern showing two peaks, in spring and autumn. Desert de les Palmes, Espadà and Calderona are currently Natural Parks and Pinet is a microreserve and local Park.

Seven study areas (hereafter sites) of 9 Km^2 each were selected in Mediterranean landscapes in the Valencia region (eastern Iberian Peninsula, Spain; Fig. 1). These site account for the Cork oak landscape variability in the eastern Iberian Peninsula. Sites were squares (3 x 3 km, except site 6 that was irregular in shape but identical in size) selected on four different mountain chains of similar conditions (medium height elevations, 300-1000 m.a.s.l. and rainfall between 600-800 mm) but with different landscape structure and fire histories (see more details of the sites in Pons and Pausas 2006).

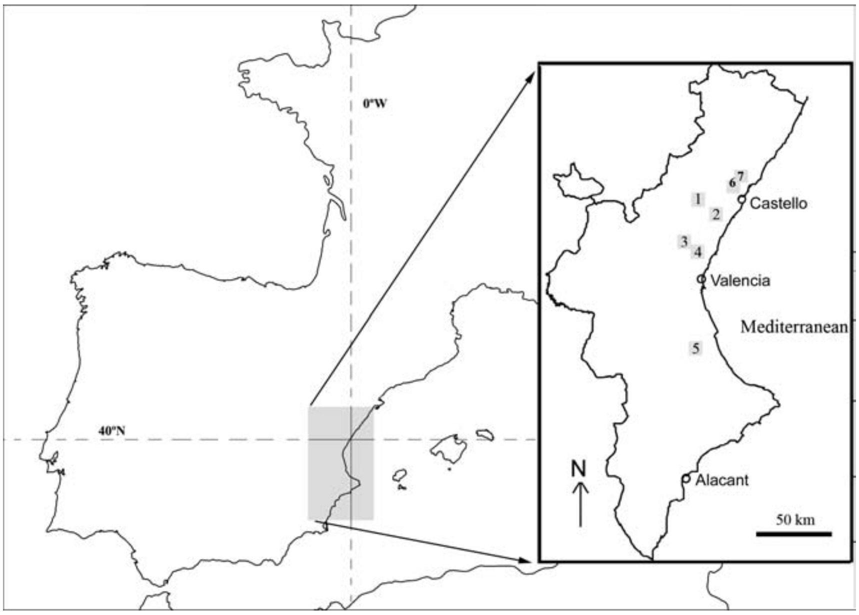


Fig.1. Location of the seven study sites in the eastern Iberian Peninsula. Sites are located in the following areas (from north to south): Desert de les Palmes (sites 6 and 7), Serra Espadà (sites 1 and 2), Serra Calderona (sites 3 and 4), and Pinet (site 5).

Habitat composition

A vegetation map for each of the sites was elaborated on the basis of aerial photography with 1m/pixel resolution and with field validation. Then the vegetation composition was assessed by visiting the zone and setting abundance of the main dominant species. The vegetation types obtained were aggregated according to their possible relevance in jay ecology and the possibility of their identification from available aerial photography. The final six landscape units (vegetation types) considered were: Agricultural fields (in production or very recently abandoned), Old fields (recently abandoned fields with high grass cover or incipient shrublands), Shrublands (also including oldfields abandoned a long time ago with a well-developed shrub layer; tree cover < 20 %), Shrub-Trees (shrublands and oldfields abandoned a long time ago with a well-developed shrub layer; tree cover of ca. 20-50%), Forests (tree cover ca. > 50%), and Others (other vegetation types, urban areas, ponds, etc.). The seven study sites showed different proportions of these vegetation types (Fig. 2). Sites 4 and 5 are dominated by shrublands (>80 % cover), which are mainly the product of recent fires. Forest area on the other sites varies between 25.1% (site 6) and 56.1% (site 1). The main tree species in the area were pines (*Pinus halepensis* and *P. pinaster*) and oaks (*Quercus suber and Q.ilex*).

Jay populations

On each site, jay abundance was quantified by assessing fledgling locations in June 2003. The methodology consisted of locating youngsters through their periodic feeding calls to adults (usually at 20-30 minute intervals) in the few days after nest abandonment by means of a survey of the whole quadrat by car and stopping every 500 m or by walking in the zones without roads. The location obtained is an estimation of nest position because young jays are unable to fly long distances during this period. For habitat selection analysis purposes we assumed jay-nesting territories as circles centred on the fledgling positions, with a radius equal to the mean half-distance of the five closest nest positions. To avoid the overlay of jay nest territory and the subsequent loss of independence, larger areas are not recommended. Jay pair numbers on each site were estimated as the sum of the jay pairs weighted by the proportion of jay nesting territory (as defined above) that falls inside the limits of the site. Otherwise stated, jay density is expressed as the number of jay-pairs/km^2.

Data analysis

Landscape level: On each 3 x 3 km² site, landscape composition (see above) and configuration variables (Table 1) were estimated using Fragstats 3.3 (McGarigal et al 2002). Configuration variables considered were: mean patch size (landscape area divided by the total number of patches, expressed in ha), patch size standard deviation (the root mean square error in patch size), total edge (length of the edge, summed for all patches, expressed in km), mean patch edge (total edge divided by the number of patches, in m/patch), mean shape index (the mean of the shape index of each patch, which is the patch perimeter divided by the square root of patch area) and habitat diversity (computed using the Shannon's index and considering the proportional abundance of each habitat). Pearson bivariant r was used to test for correlations between landscape variables. These attributes were correlated with the jay-pair density on each site. Stepwise linear regression was used to determine the landscape variables that explained most of the variability in jay-pairs density. To assess the predictive error of the model, the regression was repeated seven times, each time excluding one of the sites and then comparing the predicted jay density for the excluded site with the actual jay density observed in the field for this site.

Table 1. Bivariant Pearson correlation coefficient (r) of compositional and configuration variables with the jay pair density found on the 7 study sites. ns: non-significant, !: p = 0.05; *: p<0.05, **: p<0.01.

Variable	r	
a) Landscape composition		
Fields	0.648	ns
Oldfields	0.299	ns
Shrublands	-0.856	*
Tree-shrublands	0.591	ns
Forest	0.772	*
b) Landscape configuration		
Mean Patch Size	-0.896	**
Patch Size Standard Deviation	-0.921	**
Total Edge	0.818	*
Mean Patch Edge	-0.797	*
Mean Shape Index	0.820	*
Habitat Diversity	0.730	!

Nesting territory level: to determine the landscape characteristics of the nesting area selected by jays, we compared vegetation composition and landscape configuration between jay nesting territories and paired randomly generated circles of the same size (JAY versus Non-JAY circles comparison; Martínez and Calvo 2000, Lawler and Edwars 2002). When generating random circles, all partially overlapping circles were discarded to avoid loss of independence. In order to minimise spatial variation, pairwise comparisons were made between the closest JAY/Non-JAY circles using a paired Wilcoxon test. Jay occurrence probability was estimated from the landscape variables in the seven studied sites using a binomial logistic regression, with a forward stepwise method for variable selection. This regression was then repeated seven times, excluding one site each time (i.e., removing a

JAY/Non-JAY circle each time) from the analysis. The resulting regressions were used to predict jay occurrence for the excluded areas (validation exercise). To visually assess the predictive value of the model, significant variables were used to generate a probability-of-jay-occurrence image for one of the sites (site 7) using the moving window option of FRAGSTATS 3.3 (McGarigal et al. 2002), and overlaying the observed nest locations.

Results

Landscape level

A total of 38 nesting positions were registered, but only 24 had more than 50 % of their area inside the study sites. Densities ranged between 0.11 (site 5) and 0.79 (site 1) pairs/km^2, and were correlated positively with forest cover and negatively with shrubland cover (Table 1, Figure 2). Jay densities were also positively correlated with several basic landscape configuration attributes such as the number of patches, the amount and density of edge, and the mean shape index, and they were negatively related to mean patch size and the standard deviation of patch size (Table 1). These relations between different variables is, in part, due to the high correlation between the compositional and configuration parameters (Table 2). All these attributes indicate that jays are more abundant in heterogeneous and diverse forested landscapes (with many small and size-variable patches).

Table 2. Bivariant Pearson correlation coefficient (r) between landscape (composition and configuration) variables. Only significant correlations are shown. * Correlation is significant at the 0.05 level (2-tailed). ** Correlation is significant at the 0.01 level (2-tailed).

Variable pair	r	sig
Fields - Total Edge	0,766	*
Oldfields - Tree-shrublands	0,872	*
Shrublands - Tree-shrublands	-0,860	*
Shrublands - Forest	-0,822	*
Shrublands - Mean Patch Size	0,851	*
Shrublands - Patch Size Standard Deviation	0,910	**
Shrublands - Total Edge	-0,795	*
Shrublands - Habitat Diversity	-0,866	*
Tree-shrublands - Mean Patch Size	-0,759	*
Tree-shrublands - Patch Size Standard Deviation	-0,807	*
Tree-shrublands - Total Edge	0,817	*
Tree-shrublands - Habitat Diversity	0,921	**
Mean Patch Size - Patch Size Standard Deviation	0,985	**
Mean Patch Size - Total Edge	-0,962	**
Mean Patch Size - Mean Patch Edge	0,883	**
Mean Patch Size - Habitat Diversity	-0,822	*
Patch Size Standard Deviation - Total Edge	-0,959	**
Patch Size Standard Deviation - Mean Patch Edge	0,821	*
Patch Size Standard Deviation – Habitat Diversity	-0,865	*
Total Edge - Habitat Diversity	0,898	**

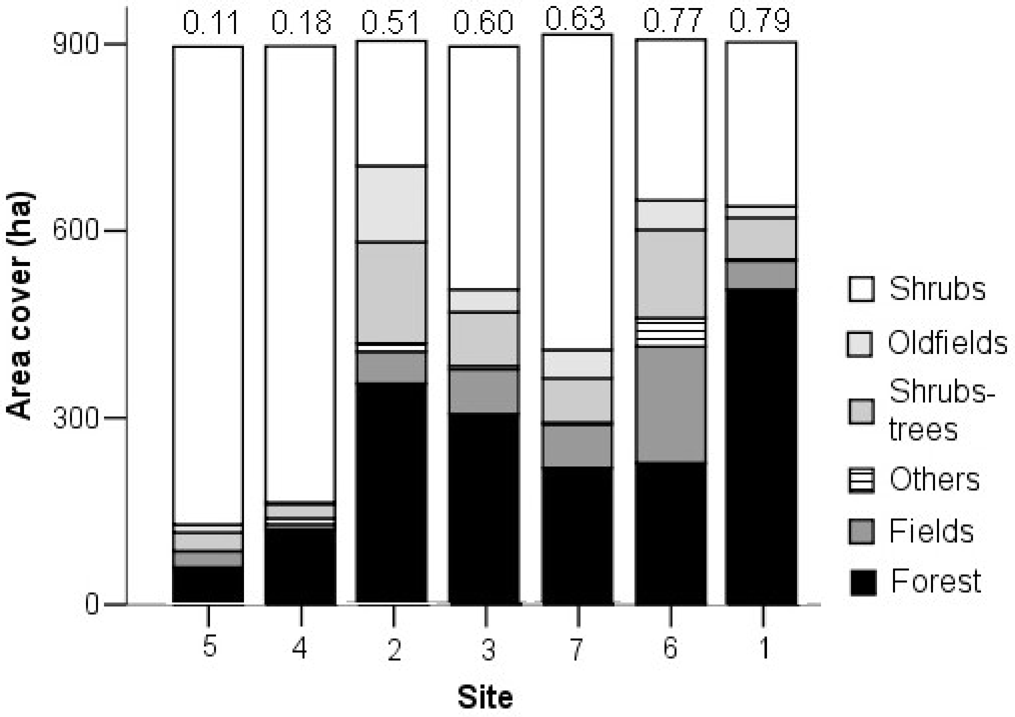


Fig. 2. Area covered by each vegetation type on the seven study sites ordered (from left to right) by increasing jay-pair density (indicated on top of each bar as the number of pairs /Km^2).

Stepwise linear regression of jay density and site composition and configuration parameters for the 7 study areas revealed patch size standard deviation (PSSD) as the best predictor of jay pair density at landscape scale (F= 28.855, Adj R^2 = 0.823, p= 0.003, Jay Density = 0.833 – 0.007 · PSSD); no further variable explained a significant variance when this variable was in the model.

Adjusted R^2 obtained from the seven regressions ranged from 0.674 (for site 5) to 0.941(for site 1) and all were significant at $p<0.03$ (Table 3). The prediction error in jay density from actual (field observed) population density was high for site 2 (+32.6%) but less than 15% for the others (Table 3).

Nesting territory level

Closest inter-nesting position distances varied between 540 and 2841 m (n = 25). Mean half-distance of the five lower inter-nesting positions was 311.4 m (range 270-339 m). Vegetation composition and configuration was different between JAY (n = 38, total area = 1171 ha) and NoJAY circles (n = 38, total area = 1148 ha): Jays selected areas with higher proportion of forest, fields and oldfields and these areas were also more fragmented (i.e., higher number of patches, see Table 4).. As at landscape level, jays preferentially used forested and heterogeneous portions of the area to locate the nesting position.

Table 3. Results of the regressions predicting jay density on each site from the other remaining 6 sites. The first column indicate the site # used as predictors and the site used as validation sites (in brackets). The remaining columns are the regression results (Adj. R^2, p-value, constant, regression coefficients), the Patch Size Standard Deviation (PSSD) value of the site used as dependent, the predicted jay density from the regression, the actual jay density (observed in the field) and the deviation between the predicted and observed values. Jay densities in pairs/km^2. In the analysis using all sites (last row), observed density is computed as the average of all sites. In all cases the predictor variable obtained with a stepwise method was PSSD except for sites 1 and 2 (*) where several other solutions (including PSSD as significant) were obtained; in these cases, and for simplicity, only PSSD was used. [Pred.= predicted; Obs.= observation; dev.= % deviation]

Sites		Regression					Validation		
	Predictor	Adj. R^2	*P*	Const.	Coef.	PSSD	Pred.	Obs.	dev.
123456(7)	PSSD	0.848	0.009	0.830	-0.007	31.46	0.610	0.625	-2.4
12345(6)7	PSSD	0.780	0.012	0.832	-0.007	11.43	0.752	0.758	-0.8
1234(5)67	PSSD	0.674	0.028	0.834	-0.007	102.52	0.116	0.111	4.7
123(4)567	PSSD	0.741	0.017	0.829	-0.007	89.32	0.204	0.179	14.2
12(3)4567	PSSD	0.819	0.008	0.849	-0.007	25.34	0.672	0.608	10.4
1(2)34567	PSSD*	0.890	0.003	0.881	-0.008	25.35	0.678	0.511	32.6
(1)234567	PSSD*	0.941	0.001	0.783	-0.007	34.34	0.543	0.792	6.1
All	PSSD	0.823	0.003	0.835	-0.007	45.68	0.511	0.511	-0.2

Table 4. Mean (and standard error of the mean) of landscape composition (%) and configuration metrics for paired jay (JAY) and non-jay (Non-JAY) circles (n = 38 x 2). Total area analysed was 1171 and 1148 ha respectively. Mean differences were tested with the paired Wilcoxon Signed-Ranks Test. Landscape composition variables (% of area) were arcsine-root transformed prior to analysis.

Variable	No JAY	JAY	*p*
a) Landscape composition			
Fields	5.0 (1.7)	11.6 (1.9)	0.002
Oldfields	3.2 (1.0)	8.0 (1.5)	0.003
Shrublands	54.6 (5.7)	27.4 (3.6)	<0.001
Tree-shrublands	8.6 (2.0)	10.7 (1.8)	ns
Forest	27.1 (4.7)	41.7 (4.0)	0.013
b) Landscape configuration attributes			
Number of Patches	7.8 (0.8)	13.6 (1.1)	<0.001
Mean Patch Size (ha)	6.8 (10.9)	2.9 (0.3)	<0.001
Patch Size Standard Deviation (ha)	7.0 (0.7)	4.5 (0.4)	0.008
Total Edge (km)	6.3 (0.5)	9.2 (0.5)	<0.001
Mean Shape Index	1.5361 (0.0450)	1.5953 (0.0221)	ns
Mean Patch Edge (m/patch)	982.6 (61.5)	758.2 (39.4)	0.002
Habitat Diversity	0.9880 (0.0288)	1.3442(0.0396)	<0.001

Binomial logistic regression of JAY-No JAY with compositional and configuration variables (stepwise regression) reduced jay pair location prediction variables to Total Edge and Forest Cover (Table 5). The overall proportion of correct model predictions was 71.1% (Table 6). Correct predictions of jay occurrence on each site for the seven regressions ranged from 68.8 to 80.6%, and correct predictions of jay absence ranged from 62.5 to 76.7% (Table 6). In the validation exercise, jay absence was correctly predicted in 23 of the 38 jay circles, and its presence was correctly predicted in 30 of the 38 circles (Table 6). As an application exercise, the model was then applied to one of the sites (site 7) to obtain a probability surface of nest positions in the landscape and then compare the predictions with the observed data (Figure 3).

Table 5. Binomial logistic regression of composition and configuration variables of 38 pairs of circles (JAY-No JAY) with a radius of 311 m. Only the best model is shown. * arcsine-root transformed. W= Wald regression statistics.

	Constant	S.E.	W	Sig.
Forest cover *	3.9606	1.1460	11.944	0.001
Total Edge	0.00045	0.00014	10.663	0.001
Constant	-5.9010	1.6164	13.25	<0.001

Table 6. Percent of correct predictions of actual jay nesting positions using binomial regression with forest cover and total edge as independent variables (all models were significant at p<0.005). The first column indicates the site number used as predictors, with the site used for validation in brackets. The two validation columns refer to the number of NoJAY circles and the number of JAY circles correctly predicted in the validation site using the equations from the remaining 6 sites (number of correctly predicted/total number of circles in the validation site). The cut point for Jay/no - Jay validation was at 0.5 probability.

Sites used	N pairs of circles	Correct predictions (%) in the regression			Validation	
		NoJAY	JAY	Overall	NoJAY correctly predicted/total	JAY correctly predicted/total
123456(7)	32	62.5	68.8	65.6	6/6	5/6
12345(6)7	37	64.9	73.0	68.9	1/1	1/1
1234(5)67	34	67.6	76.5	72.1	4/4	1/4
123(4)567	31	67.7	80.6	74.2	2/7	6/7
12(3)4567	33	63.6	75.8	69.7	2/5	5/5
1(2)34567	31	71.0	80.6	75.8	3/7	5/7
(1)234567	30	76.7	76.7	76.7	5/7	7/7
All	38	65.8	76.3	71.1	23/38	30/38

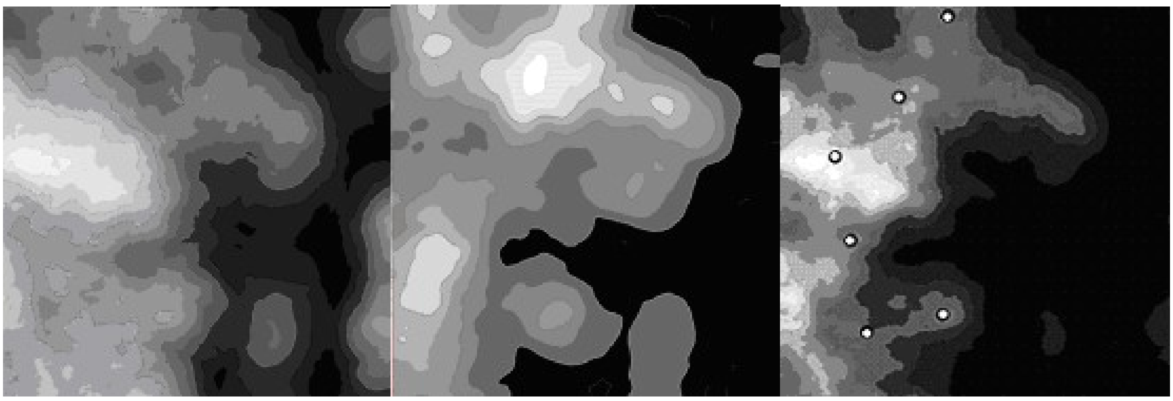


Fig. 3. Example of application of the model at landscape scale. In this example, jay nesting locations on site 7 are predicted from data from sites 1 to site 6 (first case in Table 6). Landscape attributes were obtained from aerial photography. Images were generated assuming a moving window of 311 meters (fledging position buffer zones). A) Total Edge; B) proportion of forests; C) Spring jay nest position probability predicted from A and B; dots are the observed fledgling locations. Grey scale ranges from high (white) to low (black) values. Site dimensions are 3 x 3 km.

Discussion

In our Mediterranean landscape, jay distribution is clearly related to the amount of forested area. Jays select forested landscape and avoid shrublands (Fig. 1, Table 1a); however, jay selection is also related to areas with a high number of patches, i.e., heterogeneous portions of the landscape (Table 1b). The reason for this probably lies in the more diverse food spectrum in these areas (Rollando *et al.* 1995), which would translate into better reproductive success, as seems to be the case of the Steller's jay (Marzluff *et al.* 2004). In the Mediterranean region, the lower number of patches and larger variation in patch sizes (PSSD) are consequences of land abandonment and wildfires (Trabaud and Galtier 1996, Lloret *et al.* 2002, Pausas 2004). This complex landscape distribution might explain previous failures to relate individual breeding pairs with woodland fragment size alone (Hinsley *et al.* 1995). Contrary to our results, Brotons et al (2004) found a tendency for jays to use continuous forest over isolated fragments of forest. We believe that this apparent discrepancy on jay preference is probably due to the fact that in the Brotons *et al.* study: a) the forest fragments were too small to sustain a jay pair (mean size 10 ha); b) the selected forest fragments were surrounded by homogeneous shrublands (avoided jay habitat); and c) tree fruiting fields were not considered. That is, even though the jay requires heterogeneous landscapes, it seems to respond to a fragment suitability threshold.

Our Spring jay densities were lower than those reported for European temperate landscapes (4.4 – 9.8 pairs/km^2, Grahn 1990; Wilzak 2005). This difference may be due to either the reduced forest area or the lower forest quality that jays find in mediterranean landscapes as compared with temperate landscapes. Close examination indicates that both explanations seem to play a role. For example, the observed density on site 7 was 0.63 pairs / km^2, but since all the jays were located in 1/3 of the area (Fig. 3c) the density of the occupied area (minimum successfully reproductive pairs) was about 1.5 pairs / km^2, still lower than in temperate landscapes. Similar conclusions are extracted when analysing the other sites. We suggest that both the lower optimal habitat cover and the reduced capacity of the Mediterranean dry forest as compared with humid temperate counterparts contribute to lower jay densities.

Jay abundance was quantified by assessing fledgling positions. This method produce an underestimation of the real population since non-successful reproduction and floating jays may remain undetected (Grahn 1990). However, it allowed us to optimise fieldwork while prospecting large areas because of the facility in locating fledglings from feeding calls. This contrasts with the difficulties in locating adults during the nesting period. Accuracy of the correspondence between fledgling and nest position depends on the time between location of the fledgling and nest abandonment (i.e., depends on the growth of the fledgling and the improvement in its flying skills). This is true not only because of the progressive separation from the nest but also because of the possibilities of confusion between neighbour pairs. Thus the reduced effort required by this method must be carefully balanced by accurate fieldwork planning to obtain a realistic estimation of nest locations.

Jay-pairs nesting position probabilities maps (Fig. 3c), based on aerial photos, seem to be highly reliable as the configuration factors are easily quantified with standard GIS tools. However, we observed that some a priori suitable areas for jay breeding had no pairs at all (see Fig. 3c). Field observations suggest that competition and predation could be involved. For instance, ravens (in the south-west part of site 2) and magpies (southern part of site 5) seem to prevent jay nesting even in wooded and diverse habitat. A lower competitive ability of the jay with respect to others corvids (Rolando and Giachello 1992), along with heavy nest predation by bigger corvids, squirrels, humans and sparrowhawks, have been reported (Goodwin 1986). As a consequence, the pattern of nest predator distribution can modify jay breeding positions in a way similar to that reported for the red-backed shrike (Ross and Part 2004). The presence of goshawks on the study sites during spring was not observed; however, other predators like owls, hawks and genets may be involved in fine-scale jay-pair breeding positions, although this point needs further research.

At the scale analysed (9 km² extent, 1 m pixel for population density and jay-pair location, and 311-radius circles), both the jay-pairs density and distribution regressions provided reasonably good predictions (Table 3 and 5, Fig. 3). Even with certain grain aggregation (e.g., 5-m pixel) the resolution is sufficiently high to overcome changing grain problems. Moreover, Total Edge present a consistent and robust scaling relation (Wu 2004), thus allowing to apply jay-pair position regression to regional areas.

Oak regeneration are strongly conditioned by jay acorn dispersal, specially at medium to high dispersal distances (Pons and Pausas 2007b). As a consequence, studies analysing sapling densities (i.e. Pons and Pausas 2006) should need to consider jay presence in the sampling design; otherwise seedling densities could be underestimated. As an example, very low densities of oak seedlings in dehesa-type ecosystems has been proposed because of very low jay densities in this systems (Pulido and Díaz 2005). In other words, to correctly separate the implications of each step in the oak regeneration, jay densities and distribution have to be implement in the equation.

In summary, the results of this study suggest that jay-pair breeding locations are (a) related to a mixture of landscape factors, including wooded area, complex landscape (diversity of food supply) and predators and competitors distribution pattern, and (b) can be accurately estimated from basic landscape attributes (woodland cover, fragmentation) using readily available tools (aerial photographs, GIS software). This methodology has also proved to be useful in modelling other vertebrates (Martinez and Calvo 2000; Saïd and Servanti 2005; Sergio *et al.* 2004). The implication for managers is that to favour oak natural regeneration they should take into account that jays populations are highly dependent on forest cover and landscape diversity. For instance, small agricultural fields inside forest areas increases jay populations thus favouring oak natural regeneration and colonization. Inversely, after fire, and specially when burned trees are removed (management activity often performed in the study area), shrub cover and homogenization increase. Our next step is to extend the model over wide areas (i.e., at regional level) and to integrate it in a landscape model for assessing oak regeneration.

Acknowledgements

We thank L. Brotons for comments and suggestions on an early version of the manuscript, and J. Wu for providing useful insights and references on landscape ecology techniques. This work has been financed by the EU project CREOAK (QLRT-2001-01594) and the Spanish project VARQUS (CGL2004-04325/BOS). CEAM is funded by the *Generalitat Valenciana, Bancaixa* and the Spanish government (GRACCIE Consolider-Ingenio2010).

References

Aronson,J.,Pereira,J.S., Pausas,J.G. (*in press*). Cork oak woodlands in transition. Island Press.

Bossema,I., 1979. Jays and oaks: an eco-ethological study of a symbiosis. Behaviour 70, 1-117.

Brotons,L., Herrando,S., Martin,J.L. 2004. Bird assemblages in forest fragments within Mediterranean mosaics created by wild fires. Landscape Ecol. 19, 663-675.

Clayton,N.S., Mellor,R., Jackson,A. 1996. Seasonal patterns of food storing in the jay *Garrulus glandarius*. Ibis 138, 250-255.

Grahn,M. 1990. Seasonal changes in ranging behaviour and territoriality in the European jay *Garrulus g. glandarius*. Ornis Scand. 21, 195-201.

Hinsley,S.A., Bellamy,P.E., Newton,I., Sparks,T.H. 1995. Habitat and Landscape Factors Influencing the Presence of Individual Breeding Bird Species in Woodland Fragments. J. Avian Biol. 26, 94-104.

Lawler,J.J., Edwards,T.C. 2002. Landscape patterns as habitat predictors: building and testing models for cavity-nesting birds in the Uinta Mountains of Utah, USA. Landscape Ecol. 17, 233-245.

Lloret,F., Calvo,E., Pons,X., Díaz-Delgado,R. 2002. Wildfires and landscape patterns in the Eastern Iberian Peninsula. Landscape Ecol. 17, 745-759.

Logan,W.B. 2005. Oak, the frame of civilization. Norton and Co., pp. 336

Martinez,J.E., Calvo,J.F. 2000. Selección de hábitat de nidificación por el búho real Bubo bubo en ambientes mediterráneos semiáridos. Ardeola 47, 215-220.

Marzluff,J.M., Millspaugh,J.J., Hurvitz,P., Handcock,M.S. 2004. Relating resources to a probabilistic measure of space use: Forest fragments and Steller's Jays. Ecology 85, 1411-1427.

McGarigal,K., Cushman,S.A., Neel,M.C., Ene,E. 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. University of Massachusetts, Amherst. Available at: www.umass.edu / landeco / research / fragstats / fragstats.html

McShea,W.J. Healy,W.M. 2002. Oak forest ecosystems ecology and management for wildlife. Johns Hopkins University Press, pp. 432.

Mesón,M., Montoya,M. 1993. *Selvicultura Mediterránea*. Mundi-Prensa, Madrid, España.

Mosandl,R., Kleinert,A. 1998. Development of oaks (*Quercus petraea* (Matt.) Liebl.) emerged from bird-dispersed seeds under old-growth pine (*Pinus sylvestris* L.) stands. For. Ecol. Manage. 106, 35-44.

Pausas,J.G. 1997. Resprouting of *Quercus suber* in NE Spain after fire. *J. Veg. Sci*. 8: 703-706.

Pausas,J.G. 2004 Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). Climatic Change 63, 337-350.

Pausas,J.G., Bladé,C., Valdecantos,A., Seva,J.P., Fuentes,D., Alloza,J.A., Vilagrosa,A., Bautista,S., Cortina,J., Vallejo,R. 2004. Pines and oaks in the restoration of Mediterranean landscapes in Spain: New perspectives for an old practice - a review. *Plant Ecol.* 171: 209-220.

Pausas,J.G., Ribeiro,E., Dias,S.G., Pons,J., Beseler,C. 2006. Regeneration of a marginal Cork oak (*Quercus suber*) forest in the eastern Iberian Peninsula. J. Veg. Sci. 17, 729-738.

Pons,J., Pausas,J.G. 2006. Oak regeneration in heterogeneous landscapes: the case of fragmented *Quercus suber* forests in the eastern Iberian Peninsula. For. Ecol. Manage. 231, 196-204.

Pons,J., Pausas,J.G. 2007a. Not only size matters: acorn selection by the European jay (*Garrulus glandarius*). Acta Oecol., 31, 353-360.

Pons,J., Pausas,J.G. 2007b. Acorn dispersal estimated by radio-tracking. Oecologia 153, 903-911.

Pulido,F.J., Díaz,M. 2005. Regeneration of a Mediterranean oak: A whole-cycle approach. Ecoscience 12 (1), 92-102.

Rodà,F., Retana,J., Gracia,C.A., Bellot,J. (eds.). 1999. Ecology of Mediterranean Evergreen Oak Forests. Springer, Berlin. 373 pp.

Rolando,A., Giachello,P. 1992. Interspecific Coexistence in Corvids in an Alpine Valley of Northwestern Italy. Bollettino di Zoologia 59, 281-288.

Rolando,A., Calvini,P.,Cursano,B., Olsen,A. 1995. Non territorial behaviour and habitat selection in the jay *Garrulus glandarius* in a mediterranean coastal area during the reproductive period. J. Avian. Biol. 26, 154-161.

Roos,S., Part,T. 2004. Nest predators affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*). J. Animal Ecol. 73, 117-127.

San Miguel,A. 1983. Contribucion al estudio de la alimentacion del arrendajo (*Garrulus glandarius*) en España. Bol. Est. Centr. Ecol. 12, 76-82.

Sergio,F., Marchesi,L., Pedrini,P. 2004. Integrating individual habitat choices and regional distribution of a biodiversity indicator and top predator. J. Biogeogr. 31, 619-628.

Saïd,S., Servanty,S. 2005. The influence of landscape structure on female roe deer home-range size. Landscape Ecol. 20, 1003-1012.

Schupp,E.W., 1990. Annual variation in seedfall, postdispersal predation, and recruitment of a Neotropical tree. Ecology 71, 504–515.

Trabaud,L., Galtie,J.F. 1996. Effects of fire frequency on plant communities and landscape pattern in the Massif des Aspres (southern France). Landscape Ecol. 11, 215-224.

Vallejo,R., Aronson,J., Pausas,J.G., Cortina,J. 2006. Mediterranean Woodlands. In: van Andel, J., Aronson, J. (eds.). *Restoration ecology: The New Frontier*. Blackwell Science. Oxford, UK . pp. 193-207.

Wilzak,T. 2005. Wystepowanie sójki *Garrulus glandarius* w zagospodarowanych lasach sosnowych Wysoczyzny Kaliskiej (central Poland). In: Jerzak L, Kavanagh BP, Tryjanowski P (eds.) Ptaki krukowate Polski. Bogucki Wyd. Nauk., Poznan, 239-250.

Wu,J.G. 2004. Effects of changing scale on landscape pattern analysis: scaling relations. Landscape Ecol. 19, 125-138.

Acorn selection by the European Jay (*Garrulus glandarius*)[3]

Abstract

A strong selection for acorn characteristics is expected to have evolved in the mutualistic relationship between the European jays (*Garrulus glandarius*) and the oaks (*Quercus sspp*). Bossema's pioneer work suggested that jays do not select acorn randomly but they preferentially select some size and species. Preference for some seeds over others may have implications on plant community dynamics by conferring advantages (or disadvantages) on the selected (avoided) seed characteristics. In this paper we test to what extent jays select acorns by species and/or by size and the relation between these two traits in Mediterranean oak species using wild jays. The experiments consist on a set of field tests in which we expose to jays acorns from four different coexisting Mediterranean oak species (*Quercus ilex, Q.faginea, Q.suber, and Q.coccifera*) in artificial feeders. Acorns were previously measured to control individual acorn characteristics. Using video-recording techniques we followed jay activity and the fate of each acorn (sequence of acorn selection and method of transport). *Quercus ilex* acorns were preferred over other acorns, and *Q.coccifera* acorns were avoided when other acorns were available. Preference for acorns of *Q.faginea* and *Q.suber* were intermediate, that is, they were preferred over *Q.coccifera* acorns but not over *Q.ilex* acorns. Large acorns were also preferred although acorn species selection was stronger than size selection. Jays selected species and size by visual means and by using acorn area as an indicator of size. Acorns wider than 17-19 mm were carried in the bill because of throat limitation. Our results confirm Bossema's study on temperate oaks and extend it to Mediterranean oak species revealing implications on mixed oak forest dynamics.

Introduction

Seed size and quality play a vital role in plant life history (Venable and Brown 1988). The dependence of offspring fitness on seed size has been extensively documented: both intra- and inter-specific studies suggest that germination, emergence, and seedling survival is higher in large seeds than in small ones (Rees 1995, Aizen and Woodcock 1996, Bonfil 1998, Jakobsson and Eriksson. 2000, see Moles and Westoby (2004) for a discussion of the seed size-survival conflict). Moreover, predation (Gómez 2004a) and limited dispersal (Hedge et al. 1991, Schupp 1995, Moegenburg 1996,

---

[3] Pons, J. and Pausas, J.G. 2007. Not only size matters: Acorn selection by the European jay (Garrulus glandarius) Acta Oecologica-International Journal of Ecology 31 (3): 353-360.

Moore and Swihart 2006) may also be important for large seeds, suggesting that there could be conflicting phenotypic selection on seed size (Gómez 2004b). Thus, for animal-dispersed seeds, understanding the regeneration process requires the evaluation of seed size selection by the main dispersers.

The European jay is a very efficient acorn disperser (Schuster 1950, Chettleburgh 1952, Bossema 1979) and it is assumed that *Quercus* and jay have evolved a mutualistic relationship in which acorns are shaped by selection exerted by jays and most *Quercus* seeds, especially at medium to large distances, are jay-dispersed (Bossema 1979). Thus to fully understand the phenotypic selection on acorn size, we need to understand direct acorn selection by the jay. Currently, there is little information on acorn size selected by jays, and most interpretations are based on a single study by Bossema (1979).

Furthermore, jay territories may include different *Quercus* species and the preferences by the jay may also have important implication for the regeneration niche of the species. For instances, the North America Blue Jays (*Cyanocitta cristata)* preferentially harvest and disperse oaks with relatively small acorns (Moore and Swihart 2006); however, the preferences for the European jay are unknown. Preferred species may have an evolutionary advantage over avoided species, and these differences may influence oak distribution patterns. To what extent differential *Quercus* occurrence is due to different dispersal capacities (regeneration niche *sensus* Grubb, 1977), that are, in turn, mediated by different jay preferences, remains unknown. Certainly, acorns of different species differ in their nutritional characteristics and tannin levels (Talebbendiab, et al. 1991; Shimada, 2001; Nieto, et al. 2002; Cantos, et al. 2003; Ferreira-Dias, et al. 2003) and have shown differential selection by rodents (Briggs and Smith, 1989; Ivan and Swihart, 2000; Pons and Pausas 2007). Thus, in mixed-oak communities (Pons and Pausas, 2006), we do not expect random selection by jays.

In this context we ask the following questions: a) to what extent do jays show a preference for acorns of a given *Quercus* species; b) to what extent do jays show an acorn size preference; and c) which selection (size or species) is stronger. To answer these questions we placed acorns of different species in artificial feeders located in a Mediterranean landscape and followed their fate using photographs and video recordings. The experiments were performed with three evergreen oak species (*Quercus ilex, Q.suber* and *Q.coccifera*) and a semi-deciduous oak (*Q.faginea*).

Materials and methods

Study area

The study was performed close to the village of La Pobla Tornesa, in the eastern Iberian Peninsula (40º 5' N, 0º 0' W, Castelló province, València, Spain). The climate is typically Mediterranean with summer drought and mild, wet winters. The vegetation is a mosaic of shrublands and pines traditionally used for pasture and wood gathering on steep slopes, together with flat areas and terraces used for agriculture (and now partially abandoned). We used acorns from four *Quercus* species present in the area: Holm oak (*Quercus ilex* subsp. *rotundifolia*), Spanish oak (*Q.faginea*), Cork oak (*Q.suber*) and the kermes oak (*Q.coccifera*) (hereafter abbreviated as Qi, Qf, Qs, and Qc, respectively). Of these, Holm oak and Kermes oak (a shrub) are the most abundant oaks in the study area. Early summer surveys revealed a minimum jay density of 0.77 pairs/km^2, with an inter-nest position of ca. 500 m (authors' unpublished data). In the study area, jays begins the reproductive period about march, and nestlings usually left the nest between mid June and mid July. Familiar groups are seen caching acorns all the autumn. Usually, by January-February few acorns remains available in the wild.

Methods

Acorns were obtained from nearby oak populations or, when necessary, from local seed banks (*Banc de Llavors, Generalitat Valenciana*) and conserved in a refrigerator until use. Only sound acorns were utilised in the trials and these were selected by the floating method (Bonfil 1998) followed by tactile and visual selection. These acorns were used to perform a set of experiments (described below) designed to reveal acorn species (Experiment 1 and 2) and size (Experiment 3) selection by the jay, including an experiment testing the interaction between species and size (Experiment 4).

Comparing initial vs. remaining acorns

Experiment 1. We performed 30 trials in which 10 acorns from each of the four oak species were intermixed in a feeder (i.e., a total of 1200 acorns) during February 2005. Four feeders separated each other at least by 210 m, were used simultaneously. Each feeder consisted of a 40 x 40 cm tray mounted at the top of a 1.7 m pole, in order to avoid non-avian acorn consumers. Feeders were set at places were jays use to be active, i.e. not far from high shrubs or trees in order they feel safe when visiting the poles. After placing the acorns on the trays, we revisited the feeders one to several times a day to recover the acorns not transported by jays. On each visit we counted the number of remaining acorns and considered the trial finished if this number was lower than 30 acorns. On the other hand, if fewer than 10 acorns remained in the feeder, the trial was discarded. The idea was to have as many trials as possible with ca. 50 % of the acorns removed in order to test species selection (removed vs. non-removed).

Tracking individual acorns (videos)

We recorded the exact sequence of acorn removal by jays by means of a video camera hanging vertically 1.5 m over a feeder. Acorns were individually fixed (gently nailed) to the tray and separated by about 3 cm. Previous to providing the acorns to the jays, a digital picture was taken to measure acorn dimensions (length, width and area) using an image processing software (Matrox Inspector 4.0); thus, each acorn was individually identified. A total of 621 acorns were successfully tracked in 22 films. As this method allowed tracking each individual acorn fate, several trials were run for each variable tested and various different designs were used (see below, Experiments 2 to 4). Trials were run in spring (June) 2005 and winter (December) 2005.

Experiment 2 (multi-species trials): ten acorns of each species (Qi, Qc, Qs, Qf) were set intermixed in the feeder. In the winter trials, and to remove any possible size selection, we included only acorns between 1.30 and 1.60 cm in width and between 2.80 and 3.25 cm length. A total of 8 trials were recorded (4 in each season).

Experiment 3 (single-species trials, size selection): only acorns of one species (40 acorns) were used in each trial, with variable size and random distribution in the feeder. Two trials for each species were run (a total of eight films).

Experiment 4 (shape selection): acorns set in the feeder were previously separated into two size and shape groups. Three trials were performed: a) Qi acorns were segregated in narrow (<1.4 cm wide) and wide (>1.4 cm) acorns, all with similar length (ca. 3.4 cm) (20 acorns for each shape); b) Qc acorns were segregated visually in small and large acorns (20 acorns for each size); c) narrow and wide acorns of Qi were placed together with large Qc acorns (12, 13 and 14 acorns, respectively).

Transport

We reviewed all the video tapes of experiments 2, 3 and 4, and for each jay visiting the feeder, and we noted the following information: a) the acorns that were last picked up by the jay in each flight (usually, the last acorn picked was carried out in the bill while the remaining acorns were carried out in the throat); b) the acorns that the jay unsuccessfully tried to swallow (acorns too large); and c) the number of flights and the number of acorns transported in each flight. Because we knew the size of each individual acorn, we were able to compare acorn sizes between the different ways in which the acorns were transported.

Data analysis

The effect of the *Quercus* species on the number of acorns removed for each species (Experiment 1) was tested using the non-parametric Kruskal-Wallis Test (K-W hereafter). Ivlev's Electivity index (Scarlett and Smith 1991) was used to quantify jay preference for a particular acorn species. Electivity was calculated for each acorn species as $E_i = (R_i - P_i) / (R_i + P_i)$, where R_i is the number of selected acorns of the species i and P_i is the number of supplied acorn of the species i. Thus, the index ranges from –1 to 1, with negative values indicating avoidance, positives values indicating selection, and close to 0 values indicing random selection.

The acorn removal observed in the video films (Experiments 2 and 4) was studied using a survival function, with the dependent variable ("survival") being the acorns not removed by the jay and the independent variable being the sequence of removal (from 1 to a maximum of 40 in each video film). Survival analysis was performed for each film and each species. As there were no differences between films in the single species trials (Experiment 3), we finally aggregated the different films of the same species and obtained the mean sequence for each acorn species. Median sequence is the total number of acorns picked by the jay to reach 50% of the given acorn species, and it is an indicator of the acorn species selection by the jay: the lower is the value, the higher is the preference. Survival functions of the different species were statistically compared by Wilcoxon (Gehan) Statistic.

To compare acorn sizes between trials performed in different seasons (Experiment 2) we used the projected area of the acorn (computed from the digital photography) as size indicator. The statistical comparison was performed using the non-parametric Mann-Whitney U test (also called Wilcoxon rank-sum test).

The size selection is evaluated in the single species trials (Experiment 3) by testing the slopes of the relationship between the size of each acorn and the sequence in which the acorn was picked from the feeder by the jay. ANCOVA was used to test the effect of species and films (i.e., differences in the regression slope). The three size measures (length, width and projected area) were tested. A stepwise regression was performed to evaluate the size measure that best explained the selection sequence.

The seasonal differences in the number of acorns transported by jay in each flight were tested using the Kolmogorov-Smirnov (K-S) test, that is, comparing the frequency distribution of the number of acorns transported by flight.

Results

Comparing removed vs. remaining acorns

Experiment 1: Jays removed 77.3% of the total of acorns (n =1200 in a total of 30 trials; Table 1). Of the remaining acorns (i.e. those not removed, n = 272), 70.6 % were Qc acorns, which were also the only acorn species remaining in the feeders in 63.3% of the trials (Table 1). Differences between acorns removed were significant between the four species (n = 30 trials, K-W χ^2 = 64.250, df = 3, $p<0.001$). However, when Qc was removed from the analysis the difference in the number of acorns of each species remaining in the feeders was not significant (n= 11 trials, K-W χ^2= 1.366, df= 2, $p<0.505$). Mean electivity index indicates that Qc was clearly rejected (E = - 0.48) by the jay, but the three other acorn species were randomly selected (E = 0.064, 0.106 and 0.063 for Qi, Qf and Qs, respectively).

Table 1. Proportion between removed and remaining acorns of each species, the number of trials in which acorns of each species remained in the feeder, and mean electivity index, in Experiment 1. A total of 30 trials were performed with 10 acorn of each species. Similar letters denote similar mean electivity based on a multiple comparison test.

	Qc	Qi	Qf	Qs	Total
Total acorns removed	108	274	283	263	928
Total acorn remaining	192	26	17	37	272
% remaining	70.6	9.6	6.3	13.6	22.7
N° of trials remaining	30	7	6	8	30
Mean electivity	-0.482 b	0.064 a	0.106 a	0.063 a	

Tracking individual acorns (videos)

Experiment 2 (multi-species trials): Acorns of Qi were the most preferred (i.e., lower median sequence, Table 2) in both spring (non-controlled-size trials, Cox regression: $p<0.001$) and winter (size-controlled, Cox regression: $p<0.001$) trials. The results were similar in both trials, even though in spring trials Qi acorns were not the largest (Table 2). There was also some preference for Qf over Qc in spring trials even though Qf acorns were much smaller than Qc.

Table. 2. Mean (and SD) size (projected area, cm^2) of acorns used in the spring trials (S, non-controlled acorn size; 4 films, 37 filmed acorns removed) and in the winter trials (W; size controlled acorn; 4 films, 123 filmed acorns removed) in Experiment 2 (multi-species trials). Differences in acorn size are evaluated with the Mann-Whitney U test. The number of acorns used were 40 (spring) and 36 (winter). Median sequence is estimated by a survival function; the lower the value, the faster the removal. The pairwise comparison is shown with letters (from a, the fastest removal, to c, the slowest) and tested using the exact Wilcoxon (Gehan) Statistic for median sequence and the Kolmogorov-Smirnov test for the Electivity index. Different letter (*p*) indicate significantly different mean values (p<0.05).

Acorn	Area (cm^2)		Difference (W-S)	Median sequence				Electivity index			
species	Spring (S)	Winter (W)	*p*	S	*p*	W	*p*	S	*p*	W	*p*
Qi	2.95 (0.56)	4.22 (0.47)	<0.001	13	a	9	a	0.23	a	0.57	a
Qf	2.77 (0.41)	4.02 (0.41)	<0.001	≥20	b	22	b	-0.23	b	-0.10	b
Qs	3.43 (0.86)	3.96 (0.47)	0.005	≥20	bc	30	b	-0.40	c	-0.52	c
Qc	3.55 (0.51)	3.82 (0.44)	0.009	≥20	c	32	b	-0.83	d	-0.53	c

Experiment 3 (single species trials): For each acorn species, there is a clear negative relation between the acorn size and the sequence of removed acorns (Fig. 1, Table 3), suggesting that jays prefer larger acorns. Slopes of these trends were not different between the different films in each species, but there were differences among species (ANCOVA, Table 3). These slopes (and the associated variance) can be considered an indicator of the strength of the size selection by jay. Qi is the species presenting the steepest slopes in all three size measures (Table 3). However, Qi was the smallest acorn set used, and thus, an increased size selection on this species due to their small size cannot be rejected (mean width (cm): Qi: 1.18, Qf: 1.52, Qs: 1.50, Qc: 1.44; mean length (cm): Qi: 2.79, Qf: 2.69, Qs: 2.99, Qc: 2.82; and mean area (cm^2): Qi: 2.40, Qf: 3.09, Qs: 3.51, Qc: 3.01). The size measure that best explained the variability in the acorn selection sequence was the area for Qi, Qf and Qc, and the length for Qs . When these variables were in the model, no additional size variables significantly increased the explained variance. When testing the four acorn species together (overall in Table 3), both area and length together entered in the regression model.

Table 3. Slopes (and SE) of the regression in size (length, width, and area) as a function of the removal sequence for each oak species and for the overall species, in the single-species experiment (Experiment 3). Also included are the adjusted R^2 of the regression, the ANCOVA test considering species and film as factors and sequence as covariable, and the best size variable predictor of the sequence for each species (last column). Significance (p): !<0.1, **<0.01 ***<0.001.

		Length				Width				Area				
Species	N	Slope	SE	Adj. R^2	***p***	Slope	SE	Adj.R^2	***p***	Slope	SE	Adj.R^2	***p***	Best
Qi	70	-0.028	0.004	0.465	***	-0.011	0.002	0.367	***	-0.047	0.006	0.484	***	Area
Qf	64	-0.007	0.002	0.103	**	-0.009	0.002	0.328	***	-0.028	0.005	0.331	***	Area
Qs	58	-0.020	0.007	0.110	**	-0.004	0.003	0.033	!	-0.035	0.014	0.084	*	Length
Qc	74	-0.010	0.003	0.155	***	-0.006	0.002	0.147	***	-0.006	0.002	0.147	***	Area
Overall	266	-0.016	0.002	0.205	***	-0.008	0.001	0.140	***	-0.035	0.004	0.213	***	Area and Length
ANCOVA				0.218				0.468				0.389		
Species					***				***				***	
Film					ns				ns				ns	
Sequence					***				***				***	

Table 4. Mean (and SD) size and median sequence for the shape selection trials (Experiment 4). One film was used for each trial. Size parameter differences were tested with the Mann-Whitney U test. Median sequence removals were tested using Cox regression.

Species	Acorn type	n	Area (cm^2)	Length (cm)	Width (cm)	Med. sequence
Qc	Big	20	3.51 (0.27)	3.00 (0.20)	1.58 (0.10)	11
	Small	20	2.53 (0.25)	2.62 (0.17)	1.33 (0.12)	31
	P		<0.001	<0.001	<0.001	<0.001
Qi	Big	20	4.73 (0.41)	3.64 (0.17)	1.80 (0.10)	11
	Narrow	20	3.02 (0.30)	3.27 (0.19)	1.26 (0.09)	31
	P		<0.001	ns	<0.001	0.007
Qi-Qc	Qi big	13	4.23 (0.47)	3.27 (0.17)	1.74 (0.08)	10
	Qi narrow	12	3.21 (0.22)	3.24 (0.15)	1.29 (0.05)	19
	Qc big	14	3.75 (0.40)	3.04 (0.15)	1.61 (0.12)	33
	P		<0.001	ns	<0.001	0.003

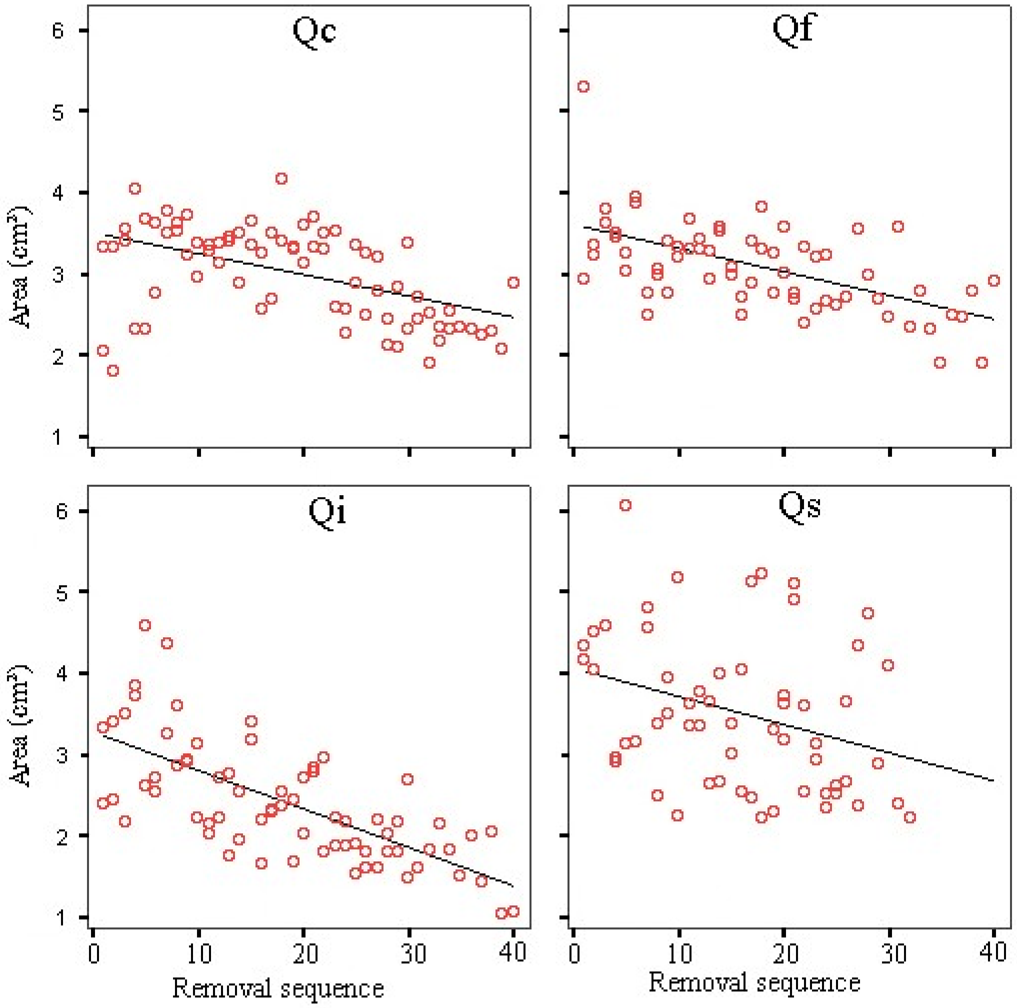


Fig. 1. Relationship between the sequence of jay acorn removal from the feeder and the acorn size (expressed as area in cm^2) for the 4 acorn species studied (Qc= *Q.coccifera*; Qf= *Q.faginea*; Qi= *Q.ilex*; Qs = *Q.suber*). All regression lines are significant ($p<0.01$). See the text and Tables 3 and 4 for more details.

Experiment 4 (shape selection): Jays selected big acorns over small ones for both Qi acorns (preferred species) and Qc acorns (avoided species) (Table 5). In the case of Qi, big and small acorns were different in width but not in length, suggesting that jays preferred wide Qi acorns over narrow ones. When offered big and small Qi and big Qc acorns, all varying in width but not in length, jays selected Qi irrespective of acorn size (Table 4).

Acorn transport characteristics

In a total of 22 films, we recorded 622 acorn removals by jays from our feeders. The mean number of acorns removed at each flight was 1.62 (n = 376 flights). By season, more acorns were transported per flight in winter than in spring-summer (mean Winter = 1.91; n = 232 flights; mean Spring = 1.26, n = 144 flights; K-S z = 3.492,

$p<0.001$). In 61.2% of the flights, jays transported a single acorn, and the maximum number of acorns transported in a single flight was 5 (ca. 2%). Acorns transported in single-acorn or two-acorn flights were larger than acorns transported in multiple-acorn flights (e.g., acorns in 5-acorn flights were 70% the size of those transported in 2-acorn flights, Table 5).

Table 5. For each type of flight (i.e., flights with different number of transported acorns, from 1 to 5), it is shown the number (N) and percentage from the total recorded flights, and the mean values of acorn size (width in cm, length in cm and area in cm^2). Comparisons of size measures between the different flight types were performed with the Kruskal-Wallis Test (χ^2).

N acorns per flight	Flights		Mean acorn size		
	N	%	Width	Length	Area
1	230	61.2	1.53	3.06	3.55
2	81	21.5	1.59	3.11	3.72
3	37	9.8	1.54	2.98	3.48
4	21	5.6	1.44	2.84	3.06
5	7	1.9	1.28	2.80	2.63
Total	376	100.0			
χ^2			18.033	17.788	21.650
p			0.001	0.001	<0.001

Acorns were transported in the bill in all single-acorn transports and when the acorn was the last one picked in multiple-acorn transports. On some occasions (8%), the jay tried to swallow this acorn but could not do so and thus transported it in its bill (Fig. 2). There were significant size differences between the acorns swallowed (transported in the throat; mean width = 1.47 cm, n = 235) and the acorns that could not be swallowed (mean width = 1.72 cm, n = 50; K-S test z (with) = -7.872, $p<0.001$). The last acorn picked by a jay was significantly larger (mean width =1.61 cm, n = 130) than the previously swallowed acorns (mean width =1.47 cm, n = 218; K-S test z = -5.052, $p<0.001$; Table 7).

Discussion

The results suggest that the European Jays select some acorn species over others, as it has been shown for the North American Blue Jay (Scarlett and Smith 1991, Moore and Swiarth 2006). Of the four acorn species used in the trials, Qi was clearly preferred. Moreover, acorn species selection was stronger than acorn size selection, as 1) Qi spring acorns were smaller than Qs and Qc spring acorns (Experiment 2) but were still preferred; 2) small Qi acorns were removed before big Qc acorns (Experiment 4). The lack of Qi selection in Experiment 1 -not acorn size controlled- could be due, in part, to the small size of Qi acorns compared with the other acorn species. In the same way, smaller Qc acorns can be also the cause of the stronger avoidance when comparing with the results in the size-controlled experiment -Experiment 2-. Size differences of the acorn pools used (see Table 2) is probably reflecting some species size gradient in natural acorns populations. The decreasing size from Qs > Qf > Qc > Qi has been found previously (Pascual 2003, but with *Q. humilis* instead of Qf). Altogether this suggests jays' priority of acorn species selection over acorn size selection, with the latter acting as a modulator of the former.

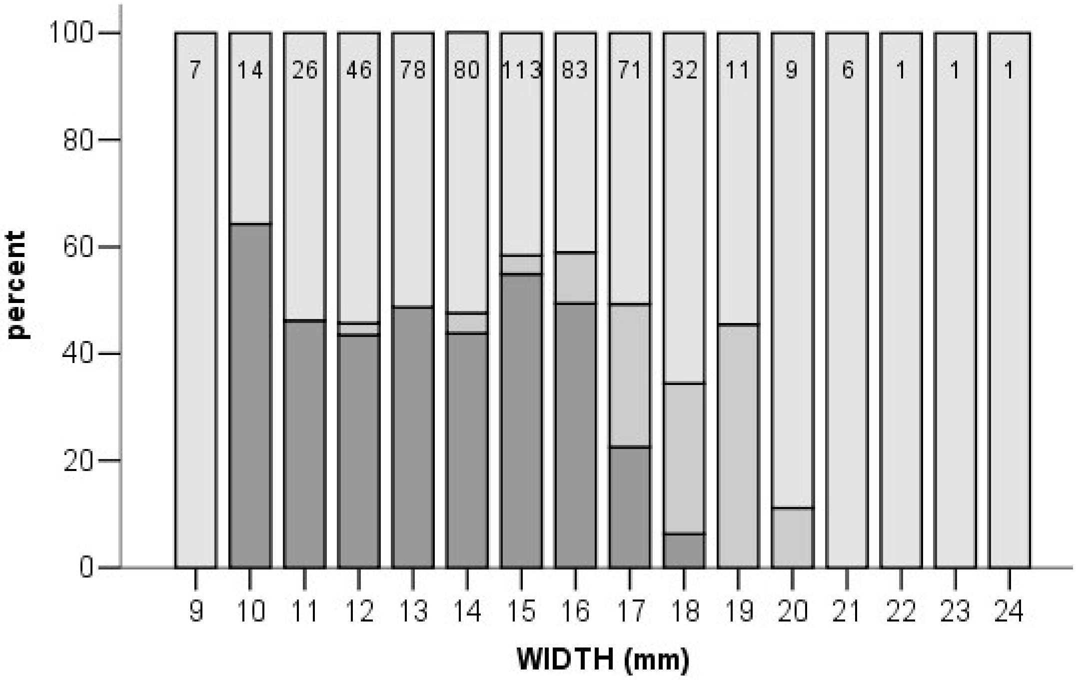


Fig. 2. Proportion of swallowed (dark grey), unsuccessfully swallowed (grey) and bill-transported acorns with no previous attempt of swallowing (light grey) in relation to acorn width (mm). Bars correspond to 1 mm intervals. Numbers at the top of the columns indicate number of acorns observed at each interval.

The preference for Qi can be attributed to its higher nutritional value. In fact, Qi acorns have higher proportion of fat than the other three tested species (Talebbendiab et al. 1990, 1991,). Similarly, the rejection of Qc by jays could be attributed to high tannins levels (Cañellas and San Miguel 2003). Unfortunately, studies on chemical caracterization of mediterranean acorns are scarce, despite its relevance found in other ecosystems (Johnson et al. 1993, Fleck and Woolfenden 1997). Interestingly, Qi acorns were also preferred by small rodents (*Apodemus sylvaticus*) in a similar (and nearby) study area (Pons and Pausas 2007), suggesting that Qi acorns are preferred over the other acorns by the most important vertebrates interacting with *Quercus* in the study area (predators and dispersers). However, caution should be taken when extrapolating these results, as acorns are morphometrically highly variable (Natividade 1950), and, thus large intra-specific variation is expected (Aizen and Woodcok 1992). Jays also preferentially select large acorns (Fig. 1); consequently, large acorns likely have a higher chance of being dispersed than smaller acorns. Similarly, longer dispersal distance for larger acorns has also been reported for rodents (Xiao et al. 2005). Furthermore, large acorns have increased germination rates, seedling survival, accelerated germination timing and enhanced seedling growth (Tripathi and Khan 1990, Sonessson 1994, Bonfil 1998, Gómez 2004b). Thus our results have implications for understanding the evolution of acorn size as, the jay selected and dispersed acorns are the most likely to become established, and thus there may be a positive phenotypic selection on acorn size (Gómez 2004b). Nevertheless, the positive selection pressure by the jay should not be understood strictly in terms of a linear acorn size increase as jay physical limitations for acorn handling and transport may limit the selection of very large acorns. This could lead to a stabilising or at least non-linear selection (Gómez 2004b).

Our results on jay transport characteristics confirm many of the results by Bossema (1979). Jays transported 1 to 5 acorns per flight, with a decreasing frequency of flights as the numbers of acorns transported increases (Table 6). It is clearly seen in the videos that most times the jays discriminate visually which acorn to carry, and after making their decision, they swallow or carry the acorn in their bill without hesitation. However, when picking up the acorn, the jay uses tactile means (pressure probably) to discard rooted or infected acorns. By these means, the jay selects the species (probably by colour and shape), the size and the quality of the acorn. In multiple-acorn flights, lower-than-throat-limit acorns are swallowed and bigger acorns are taken last and carried in the bill. In three of the 4 acorn species considered, the area of the acorn was the best predictor of the acorn-size removal sequence, and this agrees with Bossema´s (1979, p. 30) suggestion that jays use this parameter to estimate acorn size. However, jays suffer some size estimation error regarding their throat limit. In our trials, for the total of 4 acorn species considered, the acorn swallow capacity was around 17-19 mm in width, 31-32 mm in length and 3.6 cm^2 in area. At this limit, the jay just stopped picking acorns and carried the unsuccessfully swallowed one in its bill. The number of acorns per trip is probably the consequence of the jay´s previously planned acorn transport distance (Bossema 1979). The lower number of acorns per trip in the spring-summer trials than in the winter ones supports this idea, as the purpose of the acorns was probably different: nestling feeding in the former and scatter hoarding in the second.

Table 6. Comparison of mean size values (length, width and area) between the acorns last picked and the others in multiple-transport flights, and between acorns swallowed and acorns not swallowed (including single flights). Significance of the mean differences is performed with the K-S test.

	Last			Swallowed		
	Yes	No	*p*	Yes	No	*p*

Length (cm)	3.10	2.94	***	2.93	3.08	***
Width (cm)	1.61	1.47	***	1.47	1.58	***
Area (cm^2)	3.78	3.25	***	3.25	3.69	***
n	144	236		235	344	

Our results have applications in forest management. It is often suggested that large acorns should be selected for afforestation projects because of their better germination and growth in the establishment phase (Montero and Cañellas 2003). As acorn size is supposed to be genetically determined, it is probable that these planted trees would also produce big acorns. This artificial selection of large-seeded trees may be detrimental for further population expansion as the dispersal capacity via jays of these planted trees would be deficient if acorn dimensions exceed jay throat limitations. Thus, in afforestation and restoration projects we suggest to avoid using acorns exceeding jay throat dimensions. We suggest that the size limit may be about 1.72 cm width, which for *Q.suber*, corresponds to acorns of about 6 grams (Pascual 2003).

In conclusion, jays select big acorns, although the size of most dispersed acorns is limited by jay physical limitations (e.g., the throat). Furthermore, jays also make a species selection (e.g., Qi acorns are the most preferred and Qc the most avoided), and this selection is both stronger and prior to that of size. Altogether, this study supports the idea of the necessity of a multi-species approach to oak regeneration studies in order to understand oak woodland dynamics in mixed oak landscapes.

Acknowledgements

We thank Aina Blasco for collaborating in the field sampling and acorn size measurements. This work was funded by the CREOAK European project (QLRT-2001-01594) and the VARQUS Spanish project (CGL2004-04325/BOS). CEAM is supported by *Generalitat Valenciana* and *Bancaixa*.

References

Afzalrafii,Z., Dodd,R.S., Pelleau,Y., 1992. Mediterranean evergreen oak diversity - morphological and chemical variation of acorns. Can. J. Bot. 70, 1459-1466.

Aizen,M.A., Woodcock,H. 1992. Latitudinal trends in acorn size in eastern North American species of *Quercus*. Can. J. Bot. 70: 1218-1222.

Aizen,M.A., Woodcock H. 1996. Effects of acorn size on seedling survival and growth in *Quercus rubra* following simulated spring freeze. Can. J. Bot. 74, 308-314.

Bonfil,C. 1998. The effects of seed size, cotyledon reserves, and herbivory on seedling survival and growth in *Quercus rugosa* and *Q.laurina* (Fagaceae). Am. J. Bot. 85, 79-87.

Bossema,I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. Behaviour 70, 1-117.

Briggs,J.M., Smith,K.G. 1989. Influence of habitat on acorn selection by *Peromyscus leucopus*. J. Mamm. 70, 35-43.

Cantos,E., Espin,J.C., Lopez-Bote,C., De la Hoz,L., Ordonez,J.A., Tomas-Barberan,F.A. 2003. Phenolic compounds and fatty acids from acorns (*Quercus* spp.), the main dietary constituent of free-ranged Iberian pigs. J. Agric. Food Chem. 51, 6248-6255.

Cañellas,I., San Miguel,A. 2003. La coscoja (*Quercus coccifera* L.), Ecología, características y usos. Monografías. INIA, Madrid.

Chettleburgh,M.R. 1952. Observations on the collection and burial of acorns by jays in Hinault Forest. Br. Birds 45, 359-364

Fleck,D.C., Woolfenden,G.E. 1997. Can Acorn Tannin Predict Scrub-Jay Caching Behavior? J. Chem. Ecol. 23 (3): 793-806.

Ferreira-Dias,S., Valente,D.G., Abreu,J.M.F. 2003. Pattern recognition of acorns from different *Quercus* species based on oil content and fatty acid profile. Grasas Aceites 54, 384-391.

Gómez,J.M. 2004a. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. Plant Ecol. 172, 287-297.

Gómez,J.M. 2004b. Bigger is not always better: Conflicting selective pressures on seed size in *Quercus ilex*. Evolution 58, 71-80.

Grubb,P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52, 107-145.

Hedge,S.G., Shaanker,R.U., Ganeshaiah,K.N. 1991. Evolution of seed size in the bird-dispersed tree Santalum album L.: a trade-off between seedling establishment and dispersal efficiency. Evol. Trends Plants 5,131–135.

Ivan,J.S., Swihart,R.K. 2000. Selection of mast by granivorous rodents of the central hardwood forest region. J. Mammal. 81, 549-562.

Jakobsson,A., Eriksson,O. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. Oikos 88, 494–502.

Johnson,W.C., Thomas,L., Adkisson,C.S. 1993. Dietary circumvention of acorn tannins by blue jays. Oecologia 94 (2): 159-164.

Moegenburg,S.M. 1996. Sabal palmetto seed size: causes of variation, choice of predators, and consequences for seedlings. Oecologia 106, 539–543.

Montero,G., Cañellas,I. 2003. El alcornoque. Manual de reforestación y cultivo. INIA, Ministerio de Ciencia y Tencnología, Ediciones Mundi-Prensa. 2nd edition.

Moles,A.T., Westoby,M. 2004. Seedling survival and seed size: a synthesis of the literature. J. Ecol. 92, 372-383.

Moore,J.E., Swiarth,R.K. 2006. Nut selection by captive Blue jays: importance of availability and implications ofr seed dispersal. Condor 108: 377-388.

Natividade,J.V. 1950. *Subericultura*. Ministério da Economia. Direcção Geral dos Serviços Florestais e Aquícolas. Lisboa, 387 pp.

Nieto R., Rivera M., Garcia M.A., Aguilera J.F., 2002. Amino acid availability and energy value of acorn in the Iberian pig. Livest. Prod. Sci. 77, 227-239.

Pascual,G. 2003. Anàlisi de la capacitat de regeneració en estadis inicials del desenvolupament en divèrses espècies mediterrànies del genere *Quercus*. PhD. Thesis. Universitat de Girona.

Pons,J., Pausas,J.G. 2006. Oak regeneration in heterogeneous landscapes: the case of fragmented *Quercus suber* forests in the eastern Iberian Peninsula. For. Ecol. Manage. 231, 196-204.

Pons,J., Pausas,J.G. 2007. Rodent acorn selection in a Mediterranean oak landscape. Ecological Research 22: 535-541.

Rees,M. 1995. Community structure in sand dune annuals: Is seed weight a key quantity? J. Ecol. 83, 857–863.

Scarlett,T.L., Smith,G. 1991. Acorn preference of urban Blue Jays (*Cyanocitta cristata*) during fall and spring in north-eastern Arkansas. Condor 93, 438-442.

Schupp,E.W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. Am. J. Bot. 82, 399-409.

Shimada,T. 2001. Nutrient compositions of acorns and horse chestnuts in relation to seed-hoarding. Ecol. Res. 16, 803-808.

Schuster,L. 1950. Über den Sammeltrieb des Eichelhähers (*Garrulus glandarius*). Vogelwelt 71, 9–17.

Sonensson,L.K. 1994. Growth and survival after cotyledon removal in *Quercus robur* seedlings, grown in different natural soil types. Oikos 69, 65–70.

Talebbendiab,S.A., Benmahdi,M., Mashev,N.P., Vassilev,G.N. 1990. Contribution to the Investigation of the Chemical-Composition of the Acorn of Various *Quercus* Species in Algeria - Investigating the Acorn of *Quercus Ilex*. Dokl. Bolg. Akad. Nauk. 43, 83-86.

Talebbendiab,S.A., Benmahdi,M., Mashev,N., Vassilev,G.N. 1991. A Tribute to the Study of the Chemical-Composition of the Acorn of Different Species of *Quercus* Spread in Algeria. Dokl. Bolg. Akad. Nauk. 44, 85-88.

Tripathi,R.S., Khan,M.L. 1990. Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet hill forest. Oikos 57, 289–296.

Venable,D.L., Brown,J.S. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. Am. Nat. 131, 360-362.

Xiao,Z.S., Zhang,Z.B., Wang,Y.S. 2005. Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species. Acta Oecol. 28, 221-229.

Jay acorn dispersal[4]

Abstract.

Bird-dispersed seeds are difficult to track, especially in the case of long-distance dispersal events. To estimate the oak dispersal distance and the seed shadow generated by the European jay (*Garrulus glandarius*), we inserted radio-transmitters into 239 acorns, placed them in bird-feeders and then located them by radio-tracking. Using this methodology we located the exact caching site of 94 *Q.ilex* and 54 *Q.suber* acorns and determine caching habitat characteristics (vegetation type, distance, spatial distribution). The results show that 1) there is no differences in the dispersal distance distribution between the different acorn species or sizes; 2) dispersal distances range from ca. 3 m up to ca. 550 m (mean = 68.6; median = 49.2); 3) recently abandoned fields and forest tracks were preferred by jays to cache acorns, whereas fields and shrublands were avoided; and 4) seed shadows showed acorn aggregation zones (i.e., clusters of caches) close to the feeder, as well as isolated caches at longer distances. The results also suggests that radio-transmitters are a cheap and reliable way to determine seed shadows and quantify both seed dispersal and post-dispersal seed predation for medium to large seeds.

Introduction

A long-standing challenge in ecology is the characterisation of plant dispersal, which has implications on plant regeneration, gene flow and evolution (Herrera 1995, Cain et al. 2000, Wilson and Traveset 2000). For animal-dispersed plants, characterizing the dispersal curve is complicated by the difficulty of following dispersers and locating the transported seeds, especially in the case of long-distance dispersal events (Cain et al. 2000, Nathan 2006). Furthermore, seed shadow size and shape may be dependent on the landscape configuration, as animals may show preferences for distinct landscape attributes (Kollmann and Schneider 1997, Russo et al. 2006).

Inferring seed shadows from seedling recruitment has limitations not only because of differential germination and survival but also because of the difficulties involved in unambiguously determining the mother plant (Cain et al. 2000). For fleshy-fruited endozoochorous species, a simple method based on applying a fluorescent dye to the fruits and recovering it in faecal material has been successfully applied (Levey and Sargent 2000, Levey et al. 2005, Reiter et al. 2006). For plants with large seeds that are dispersed by scatter-hoarding animals (e.g., oaks), magnetic locators (Iida 1996),

---

[4] Pons, J. and Pausas, J.G. 2007. Acorn dispersal estimated by radio-tracking. Oecologia 154 (4): 903-911.

plastic tags (Xiao et al 2004, Pons and Pausas 2007a) and radioisotopes (Vander Wall 2002) have been tested to quantify acorn movement by rodents (Forget and Wenny 2001); however, these methods are not appropriate for long-distance dispersal (e.g., by birds) as the search surface increases exponentially with distance and thus it makes very difficulty to locate extreme long-distance dispersal events.

A very important step forward in dispersal ecology has been the use of maternity analysis (Dow and Ashley 1996, Godoy and Jordano 2001, Grivet et al. 2005). This usually involves the genetic analysis of both the dispersed seeds and the potential mother plants. However, besides the difficulty of the genetic analyses in oaks (Ziegenhagen et al. 2003), dispersed acorns are difficult to locate because most are buried by the jays (e.g., the European jay *Garrulus glandarius*, Bossema 1979, Blue jay *Cyanocitta cristata*, Darley-Hill and Johnson 1981) that travel long distances. Alternatively, maternity analysis can be performed from recruits, but then the results not only reflect the dispersal but also the outcome of predation, germination and establishment on the given location (i.e., effective dispersal or realised recruitment, Nathan et al. 2003; Greene et al. 2004; Hardesty et al. 2005). In some oaks, woodpeckers store acorns in tree trunk granaries, where it is easy for researchers to collect them and study acorn movements using genetic markers (Grivet et al. 2005), although the relation between woodpecker acorn movements and dispersal is still poorly understood. In other cases, acorn dispersal has been inferred from observations of jay flights, providing a first estimate of acorn dispersal curves (Gómez 2003). However, the precise location of the acorn caches is subject to visibility conditions.

In this paper we: (a) estimate the distribution of acorn dispersal distances; (b) determine the shape of the dispersal shadow (i.e., we ask to what extent jay-hidden acorns are either aggregated or randomly distributed); (c) determine which vegetation types jays prefer for hiding acorns; and finally, (d) we infer the suitability of the methodology to study acorn seed shadows and jay dispersal characteristics. For these objectives, we follow individual acorns dispersed by the European jay (*Garrulus glandarius*) by inserting a radio-transmitter inside the acorn, leaving the tagged acorn in a bird-feeder, and then locating the acorn by radio-tracking. This method, which has seldom been used previously, allows us to estimate primary dispersal, i.e., distance from feeders (simulated tree) to jay caches. Previous uses of radio tags include acorn dispersal by mice (Sone and Kohno 1996) and gut passage rates and seed dispersal by flightless cassowaries (Mack and Druliner 2003). Using this method, we aim to obtain direct data on the pattern of acorn primary dispersal by the European jay in a Mediterranean landscape.

Materials and methods

Study area

We performed this study close to the village of La Pobla Tornesa, in eastern Iberian Peninsula (40° 5' N, 0° 0' W, Castelló province, València region, Spain). The area has a Mediterranean climate with dry summers and mild and wet winters. Two bedrock types are common, Bundsandstein sandstone (the most common) and Palaeolithic slates. The vegetation is a typical Mediterranean mosaic shrubs, pines, abandoned fields of different ages and fields in use. Pines (*Pinus halepensis* and *P. pinaster*) are the dominant trees in the area. Oaks (Holm oak, *Quercus ilex* subsp. *ballota* and cork oak *Q.suber*) are present at low density (dispersed or in small groups).

Acorn processing and tracking

We used acorns from *Quercus ilex* subsp. *ballota* and *Q.suber* obtained from nearby oak populations and conserved in the fridge. Sound acorns were visually selected, opened, and partially emptied; then, a transmitter (model TW-4, Biotrack Ltd, 2.2g, 3 month of mean life span) was inserted longitudinally in each acorn, with the antenna rolled up inside (tagged acorns). The acorn was then closed again and sealed (superglue 3, Loctite Ltd.). For each tagged acorn, length, diameter (to 0.1 mm) and weight (to 0.5 g) were recorded. Because the jays do not detect 10% weight variations in acorns (Bossema 1979), no better weight estimation was necessary. Due to size limitations, we introduced the transmitter into relatively large (> 5 g) acorns. We did not use smaller transmitters because of their limited battery life-span.

In autumn 2004, we set up three feeders (feeders 1 to 3) to form a triangle with inter-feeder distances between 210 and 225 m. Each feeder consisted of a 40 x 40 cm seed tray mounted at the top of a 1.7 m pole. We performed the acorn tracking experiment on these feeders in early spring (March-April 2005) and early winter (December 2005-January 2006). Two additional feeders (feeders 4-5) were located more that 2 km away from feeders 1 to 3 (i.e., used by different jays) and set in spring 2006 (March-April). All feeders are located in relatively flat areas with gentile slopes. We did not perform the experiments in autumn because jays did not visit our feeders when natural acorns were available. In each feeder we included about one tagged acorn for every 9 untagged acorns in order to reduce the number of tagged acorns rejected by jays. Acorn location was carried out by radio-tracking (Mariner 5, Biotrck Ltd.), and for each retrieved acorn we recorded the GPS position (GPS 76S, Garmin Ltd.) and the surrounding vegetation type (fields, recently abandoned fields, old-fields, shrubland, pine forest, and roads or forest paths). We recorded the status of each recovered acorn as: 1) cached: acorn buried by jays; 2) opened: acorn found open (or only remaining of the tagged acorn found); 3) abandoned: tagged acorn abandoned (probably because jay detected the transmitter) in the soil surface or in a tree branch. Abandoned acorns were not considered further in the analysis.

Data analysis

Differences in retrieval time between eaten and cached acorns were compared by means of the Mann-Whitney U (MWU) test as the data was not normally distributed. Dispersal distance distribution was tested against four models (Normal, log-Normal, Weibull and Exponential), using the maximum likelihood approach implemented in MASS (Venables and Ripley 2002); Akaike Information Criteria (AIC) was used to compare the fits. In addition, the Kolmogorov-Smirnov test (KS) was also used to compare the four fitted distribution with the four theoretical distributions. We compared both distances (using t-test) and the distance distributions (using the KS test) between different acorn fate (cached vs. opened), different dispersal season (spring vs late winter), different acorn species (*Q.ilex* and *Q.suber*) and between the different feeders. For distance comparisons, we use log-transformed as the log-Normal model was the best to fit the data (see results).

We performed a density analysis with the Spatial Analysis module of ArcView 3.2 using a search radius of 17.5 m and a cell unit of 1 m. This allowed us to develop the kernel shadows and, afterwards, to visually identify all clusters of caches, i.e., areas with high cache density. All spatial analyses were performed on each feeder independently, except for feeder 5 which had very few jay visits, thus precluding any analysis.

Vegetation composition 1 km around the feeders was obtained from the 2003 aerial photographs, and the necessary corrections made during fieldwork (2005). Afterwards, the data was transferred to a GIS for analysis. Vegetation categories were aggregated into six vegetation types (the dominant landscape units): 1) fields, 2) recently abandoned fields (abandoned fields with low plant cover), 3) oldfields (abandoned fields with high plant cover), 4) shrublands, 5) pine forest, and 6) forest roads and tracks. We tested whether the number of acorns found in each vegetation type was different than the expected from the proportion of vegetation types available around each feeder by using a Chi-squared test. The test was performed at different distances to the feeders (0-40, 40-80 and 80-120 m). The residuals of this test were used as indicators of preference (positive residuals) or avoidance (negative residuals). For this analysis, we consider the maximum distance of 120 m, which includes most acorns (88.6%) and all clusters of caches in all feeders.

Results

A total of 239 tagged acorns were tracked, of which 158 (64.0%) were cached; the rest were opened by the jay (26.7 %), abandoned close to the feeder (1.6 %) or their radio-tracking signal was lost (4.5 %). Because radio-interference in the study area was high, retrieval time varied from 1 to 93 days (mean = 5.4 days, SD = 9.9, n = 152). Signal detection was lower (usually about tens of meters) than transmitter specifications (hundreds of meters) due to the fact that the transmitter antenna was rolled up inside the acorn. Mean retrieval time, i.e. the time since the acorn was left at the feeder and the time the cache was found, tended to be less for opened than for cached acorns (2.8 vs. 6.6 days; $p = 0.029$; MWU test) because the opening of the acorn allowed the antenna to unfold to some degree (usually to its full length) and thus increase signal detection. No differences in any of the acorn size parameters (length, width or weight) were observed between cached and opened acorns (t-test, $p > 0.8$), and no association between species (*Q.suber* vs. *Q.ilex*) and acorn status (cached vs opened) was found (χ^2 tests, $p = 0.82$). In some cases (8.3%; and only in the spring trials), the jay-cached acorns were pilfered by rodents and the transmitters were located deep underground or inside stone walls of field terraces. Jays tended to open more acorns in spring (34.3%) than in winter (22.1 %; Chi-square = 3.980, $p = 0.046$).

Dispersal distances

The distance distribution of cached acorns is right-skewed and leptokurtic (Fig. 1; Skewness = 3.39, Kurtosis = 15.41). The distance distribution that best fit the data (with the lowest AIC) was the log-Normal distribution (AIC = 1606.0) with a mean of 3.844 (se = 0.068; location parameter) and a standard deviation of 0.851 (se = 0.048; shape parameter) (values in log-scale). The other fitted dispersal distributions performed worst: Normal (AIC= 1791.1), Exponential (AIC= 1637.7) and Weibull (AIC= 1633.3). The distance distribution data was not significantly different from a log-Normal distribution (KS test: $W = 0.992$, $p = 0.516$), but differ from Normal ($p < 0.0001$), Exponential ($p < 0.0001$) and Weibull ($p = 0.0359$) distributions (KS tests). Similar results were obtained when analysing the different feeders separately, that is, for all feeders (feeder 1 to 4) the best fit was the log-Normal distribution, and there was no significant differences ($p>0.3$, KS test) between the observed distance distributions and a log-Normal distribution.

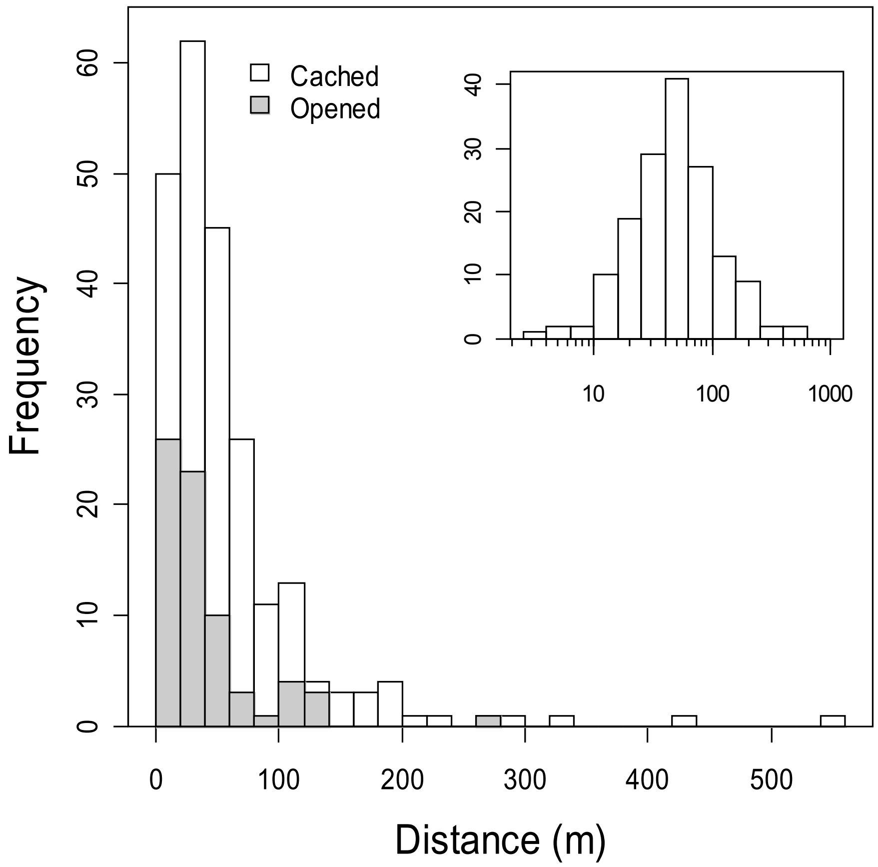


Fig.1. Distance distribution for cached and opened acorns (white and grey bars, respectively). The distribution of cached acorns does not differ from a log-Normal distribution (inset figure; Shapiro-Wilk test, W = 0.99, p-value = 0.55).

The distributions of cached and opened acorns were significantly different (Fig. 1 and 2; Table 1). Mean distances of cached acorns were 68.6 m (SD= 73.57), ranging from 2.8 m up to about 545.4 m (25, 50, 90 and 95 percentiles were 25.87, 49.15, 75.97, 149.60, and 196.71 m, respectively). Opened acorns were moved at much closer distances, from 2.2 up to 137.5 m, with a mean of 37.6 m (SD = 34.1; 25, 50 and 75 percentiles were 11.50, 30.61 and 46.15, respectively; n= 66). No differences in either the mean or the distribution of distances were found between *Q.suber* and *Q.ilex* (Table 1). The mean distance did not differ between spring and winter (89.6 vs 66.0 m; p=0.152), but there were differences in the distance distribution (median = 63.5 vs 48.1 m, respectively; Table 1). There were also differences in mean distance and distribution among feeders, mostly because of shorter distances at feeders 2 and 4 (Table 2). In any of the feeders, there was no positive relation between the order that the acorns were cached and the distance to the caching site. Acorn size (length, diameter or weight) were not correlated with dispersal distance (Person's correlation, n = 220; p > 0.6).

Table 1. Comparison between mean distance movements in several type pairs of marked acorns (data log transformed previous to the analysis). N1 and N2 are the number of cases. Mean diff (m) refers to the difference between the means, in meters.

Pair	N1	N2	Mean diff. (m)	Mean distance P (t-test)	Distance distribution P (KS)
Cached vs. Opened (all)	158	66	31.0	<0.0001 ***	0.0003 ***
Spring vs. Winter (cached)[1]	47	68	23.6	0.152	0.031 *
Spring vs. Winter (opened)[1]	24	19	3.3	0.578	0.97
Q.ilex vs. *Q.suber* (all)[2]	94	54	1.6	0.944	0.965
Q.ilex vs. *Q.suber* (cached)[2]	69	42	5.9	0.544	0.952

[1] only feeders 1, 2 and 3 were considered as data from both seasons was available.

[2] only data from winter 2005 and spring 2006 was used as both species were used simultaneously.

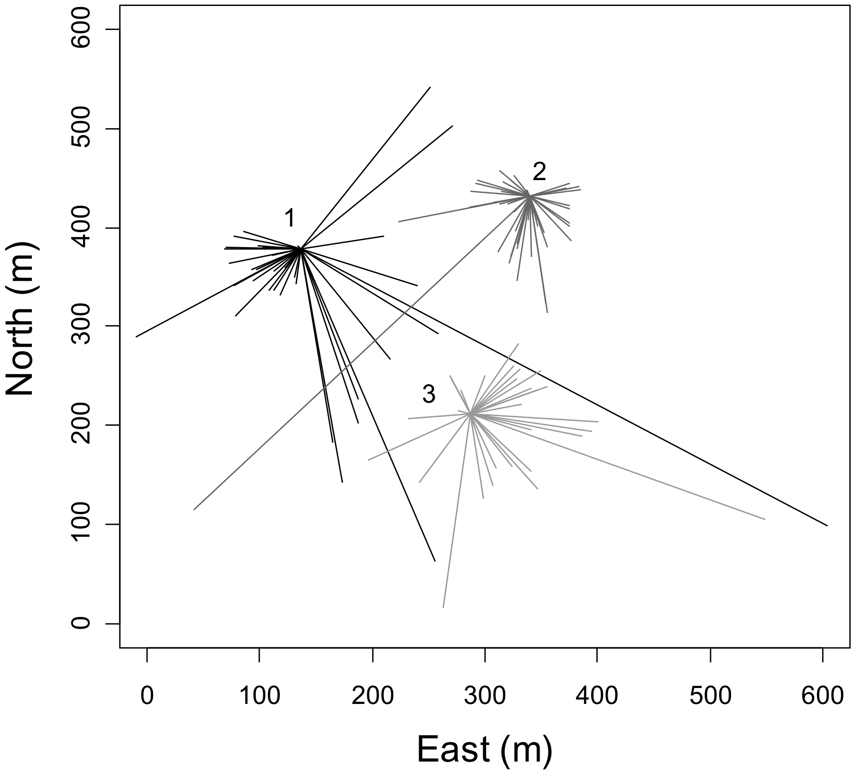


Figure 2. Spatial location of the 3 feeders that are close together, with the strait line from each the cache to the corresponding feeder.

Seed shadow

Feeders 1, 2 and 3 were located close together. Although most (89.4%) acorns were found closer to the source feeder that to the others feeders, 10.6% showed the opposite pattern, evidencing the overlap between seed shadows (Fig. 2).

Density analysis reveals from 1 to 5 high-density areas of cached acorns close to each feeder (Fig. 3), except for feeder 5. These clusters of caches account for 60 % (feeder 1) to 89% (feeder 3) of the total cached acorns, but their areas range from only 3% (feeder 1) to 23% (feeder 3) of the total area covered by all the acorns cached at each feeder (Table 2). Cache density at the cluster ranged between 19.5 and 75.0 (mean 60.9) tagged acorns/ha. Extrapolation of this data to all the acorns left at he feeder (tagged and untagged acorns) suggest that cluster densities raged between 174 and 675 (mean 419.8) acorns/ha (Corrected densities in Table 2). At feeder 5, no such clusters appeared as this feeder had very few visits by jay (no spatial analysis was performed for this feeder). Isolated caches were found farther away than clusters of caches for all the feeders (KS test p < 0.01; Table 2).

Table 2. Summary statistics by feeder for all caches, for caches within clusters and for isolated caches. Included is the comparison of mean distances (ANOVA, log-transformed distances) and distance distribution (KS test), between pairs of feeders (different letters represent significant different between feeders). Minimal polygon area refers to the minimum convex polygon embracing all cached acorns. Corrected densities (*) are estimated on the basis of the proportion of tagged cached acorns to the total acorns in the feeder (1:10). Within cluster analysis was not possible at feeder 5 because of few data (see main text).

	Feeder					
	1	2	3	4	5	mean
All caches						
Total number of cached acorns	37	45	33	27	16	32
Mean distance to feeder (m)	108.4	53.8	68.7	48.4	52.1	68.6
Median distance to feeder (m)	65.9	39.6	60.9	35.4	57.0	51.3
Mean distances (ANOVA test)	A	b	ab	b	ab	
Distance distribution (KS test)	A	b	ad	abc	cd	
Caches within clusters						
Minimal polygon area of caches (ha)	0.47	0.88	1.40	0.28		0.38
% area	2.92	16.77	18.72	14.62		8.77
Number of acorns cached	22	40	27	21		21.5
% number	59.5	88.9	81.8	77.8		68.7
Mean distance from caches to feeder	43.6	38.8	53.9	33.8		38.7
Caching density (acorns/ha)	46.8	45.5	19.3	75.0		60.9
Corrected density* (acorns/ha)	421	410	174	675		419.8

Isolated caches (outside clusters)						
Minimal polygon area of caches (ha)	15.71	4.34	6.07	1.64		6.94
% area	97.08	83.23	81.28	85.38		86.74
Number of acorns cached	15	5	6	6		8
% number	40.5	11.1	18.2	22.2		23
Mean distance from caches to feeder	203.4	174.0	135.4	99.3		153.0
Caching density (acorns/ha)	1.0	1.2	1.0	3.7		1.7
Corrected density* (acorns/ha)	9	10	9	33		15.3

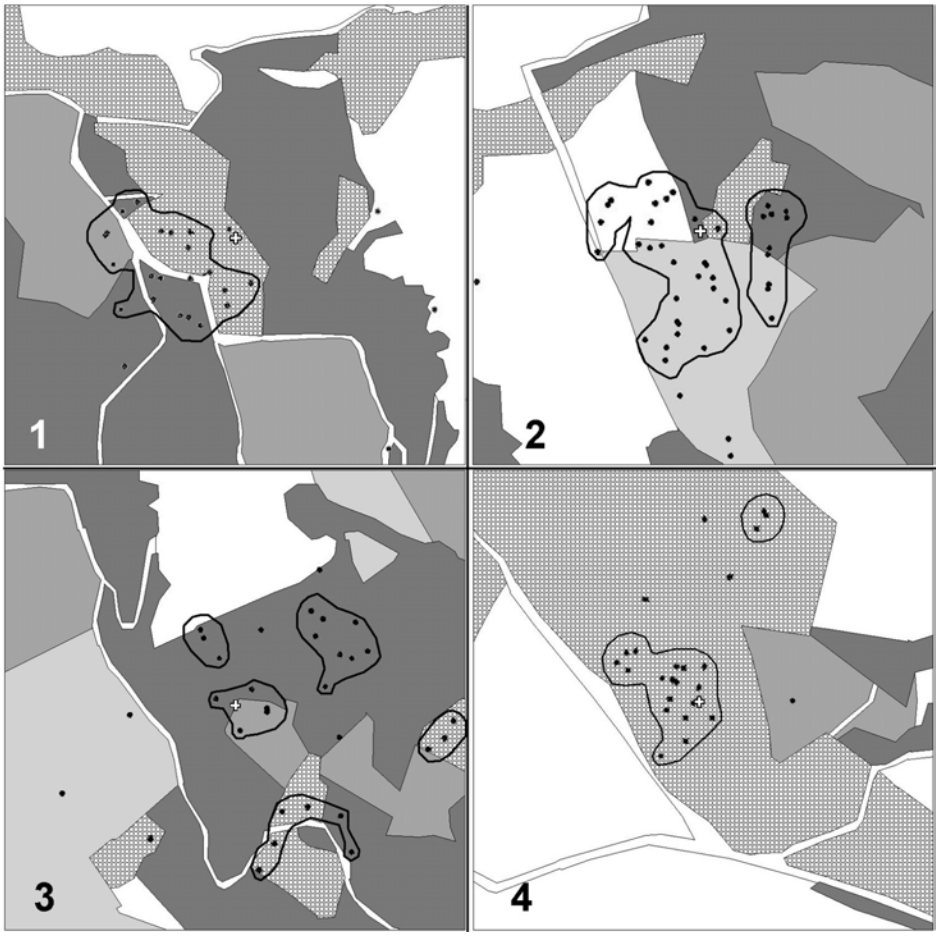


Figure 3. Map of the cached acorns (dots) at feeders 1 to 4. The dimensions of each quadrat are 120x120 m and thus, some isolated caches lay out of the map (see distances in Table 1). Black lines delimit the clusters of caches (i.e., zones of acorn hoarding > 27 tagged acorns / ha); white crosses represent feeder position. Vegetation type legend: white = fields; light grey = recently abandoned fields (i.e., with low plant cover); grey = long-abandoned fields (i.e., with high plant cover); dark grey = shrubland; fine dotted pattern = pine forest; white corridors = field roads and tracks.

Jays did not randomly select vegetation types for hoarding acorns; we detected a trend in their vegetation-type selection (χ^2 test for 0-40 m, p= 0.080; for 40-80 m, p =

0.032; for 80-120 m, p = 0.054). They preferred recent oldfields and forest tracks and avoided shrublands, irrespective of distance (Fig. 4). For fields, oldfields and pine woodlands, we found an interaction with distance in such a way that fields and oldfields were preferred at short distances and avoided at greater distances, while the opposite was true for pine woodlands (avoided at short distances and preferred at greater distances).

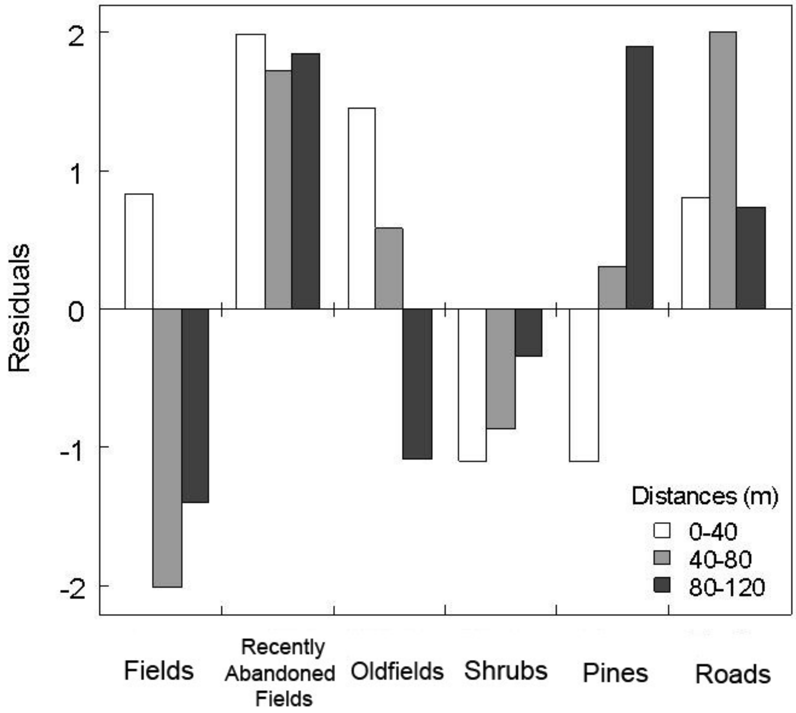


Fig. 4. Residuals of the Chi-squared test for each vegetation type at three distances from the feeder (p-values are 0.080, 0.032 and 0.054 for 0-40, 40-80 and 80-120 m, respectively). Positive values indicate preferred and negative values avoidance.

Discussion

Acorn dispersal by jays

Jay caches were located at distances of ca. 3 m up to ca. 550 m meters from feeders, often aggregated in preferred areas (clusters of caches). These primary dispersal distances are shorter than those previously reported by Gómez (2003) probably because of the different landscape structure. In fact, we found significant differences between our feeders in distance distribution, vegetation selection and number and distribution of preferred areas to cache acorns. Feeder 1 and 4 were in pine woodland patches with no recent oldfields (preferred patches to hoard) nearby. Thus, jays cached the acorns in the same pine woodland, preferentially in paths or forest roads. Selection of recently oldfields can be clearly seen in feeder 2, whereas much of vegetation classes were at the vicinity. In contrast, feeder 3 was located inside non-preferred habitat (oldfields and shrublands) and acorns have been cached in cleared areas of the shrub patch or at medium distance small woodlands (Fig. 3). Thus, we suggest that jay-dispersal distances and seed-shadows are closely related to landscape composition and configuration, and this, in turn, may be because landscape structure determines jay territory composition and use. Altogether, our findings suggest that more attention must be devoted to understanding the role of landscape composition, configuration (Kollmann and Schneider 1997) and structures (Pausas et al. 2006a) in seed dispersal studies.

The dispersal distribution follows a log-Normal distribution, which suggest the importance of the “skip distance” (Greene et al. 2004), i.e., the maximum seed rain is not at the seed source but a few meters away (Fig. 1). Similar results have been observed in many species, including both wind (Greene et al. 2004) and animal (Russo et al. 2006) dispersed seeds. This distance distribution may may represent a generalised dispersal curve for one dimension (distance). However, when considering the two spatial dimensions, we found two clearly defined spatial arrangements of cached acorns (clusters versus isolated scattered caches; Howe 1989, Russo et al. 2006), from which it may be posible to derive important consequences for spatial models of oak regeneration(Ribbens et al. 1994, Pausas 2006, Purves et al. 2007) and for future developments of afforestation techniques based on facilitating natural regeneration (Pausas et al. 2004, Vallejo et al. 2006). The fact that the dispersal distances did not increase with the order that the acorns were cached suggests that at the dispersal densities inferred at the cache clusters , the jays have not reached a hoard saturation; in other words, our results suggest that jays are capable of caching at densities higher than 400 acorn/ha in a season in their preferred habitats (Table 2). This point needs further testing as it is possible that these cluster of catches will be recached further by jays (reallocations after ‘rapid sequestration’, Jenkins et al 1995).

Jays preferred caching acorns in open habitats (recently abandoned fields, forest tracks); this preference progressively decreases as soil cover increases (oldfields, shrublands), which is in agreement with previously reported observations on jay seed caching behaviour (Bosssema 1979, Gómez 2003). This habitat preference also concurs with the seedling regeneration densities in Mediterranean mosaic landscapes (Pons and Pausas 2006, Pausas et al. 2006b). Moreover, in low density oak populations, regeneration by rodent dispersal is often found at a very short distance from the acorn source (Xiao et al 2005, Xiao and Zhang 2006, Pons and Pausas 2007a) . Thus, we suggest that the *Quercus* regeneration pattern is primarily driven by jay dispersal, at least in our mosaic landscape. However, in light of the finding that our jays disperse some acorns to shrublands but we failed to find any significant regeneration in this habitat (Pons and Pausas 2006, Pausas et al. 2006b), some other processes could be affecting seedling densities in this habitat (i.e., high acorn post-dispersal predation by rodents in shrublands; Pons and Pausas 2007a). On the other hand, it is also possible that the regeneration process is not the same in all shrublands, as we have observed some dispersal and reduced predation in *Erica* shrublands but not in *Ulex*-dominated shrublands (unpublished observations). Recently abandoned fields have low plant cover, and are preferred by the jay for catching acorns. In these conditions, the acorn predation risk (by mice) is also low (Torre and Díaz 2004; Pons and Pausas 2007a). Shrublands have very high plant cover and the predation risk by mice is very high; thus, jays avoid caching in such conditions. Oldfields are in an intermediate position with respect to plant cover and are selected at short distances only (Fig. 4), probably because the robbery risk is counteracted by the low cost of catching at short distances. On the other hand, the positive relation between distance and pine woodlands preference (Fig. 4) may be driven by jays using pines as a landmark (Bossema 1979) when flying to a suitable habitat to hoard acorns.

Rodent robbery of the jay-cached acorns was detected only in the spring trials and was lower than expected (8.3% of all cached acorns). Although these data are preliminary, to our knowledge this is the first time that predation on jay-cached acorns has been evaluated, and the proposed methodology should facilitate further research on this topic. Our results suggest that jays might reduce the possibility that rodents will pilfer the acorn by caching preferentially in open habitats where rodent activities are lower (Pons and Pausas 2007a). Moreover, during the jay caching period (autumn-winter), the wood mouse (*Apodemus sylvaticus*, the main post-dispersal acorn predator in the study area; Pons and Pausas 2007a) is at its lowest annual population density (unpublished data). In our study we re-used the tagged acorns very shortly after caching; to obtain more reliable conclusions on post-dispersal predation it would be necessary to monitor jay-cached acorns during the natural dispersal season over longer time periods.

We found no differences in dispersal distance and fate between the two acorn species nor between the different acorn sizes, even though differences in acorn nutrient content determine differential selection by rodents (Pons and Pausas 2006) and jays (Pons and

Pausas 2007b). This suggests that, after selection, jays treated all the acorns in a similarly way.

Methodological issues

Acorn tracking can be used to unambiguously monitor large seeds dispersed by birds over a range of tens to hundreds of meters, thus improving the quantification and delimitation of seed shadows, and (especially) the fate of long-distance dispersal events, which have been underestimated in most previous studies (Cain et al 2000). Seed radio-tracking is relatively easy and cheap, and it does not significantly change acorn weight. Our results indicate that neither acorn species nor acorn weight modify the distance that jays move acorns. Moreover, radio-tracking permits the exact location of the cache site to be determined. Acorn-radiotracking is less time-consuming than surface-searching methods (i.e. magnetic systems), especially in long distance dispersal events. In addition, this technique is not conditioned by vegetation, topography (as in visual flight tracking) or by pilfer and belowground acorn movements by rodents. However, seed-tracking remains limited by the size and life-span of current state-of-the-art transmitter and batteries, respectively, and thus only seeds of intermediate (> 1 g) to large (e.g., acorns) size are feasible for use (Sone and Kohno 1996, Mack and Druliner 2003).

The proportion of opened acorns should be treated with caution as it may not be a good estimation of predation; jays may open the acorn if they detect that it is a ‘false acorn’. Our results also suggest that the season of the experimental set-up may have some effect on dispersal distance. A slight reduction in acorn dispersal distances occurs between acorns cached in December-January (towards the end of the winter period) and acorns cached in February-April (beginning of the reproductive period; Table 1). This may be mediated by a reduction in jay territory size towards the reproductive season (Rolando 1998), which suggest a movement of acorns towards the reproductive core area. Consequently, the dispersal distances obtained in this study especially those corresponding to spring) can be considered to be slight overestimations in comparison with those expected during the natural dispersal period (September-December).

The seed radio-tracking approach has a great potential for providing insights into acorn reallocations by jay and pilfering by rodents. The usual methods for estimating post-dispersal predation are based on artificially sown seeds in the different habitats (Gómez 2004); however, these experiments do not resemble real acorn dispersal shadows. Radio-tracking of the dispersed seeds permits marking the place and following the acorn fate in a “non-invasive” way, thus facilitating a more true assessment of post-dispersal predation. If the tagged seed is left in the field and its position tested periodically, this methodology would also allow us to study seed relocations and secondary dispersal (Van der Wall 2002).

Nonetheless, the seed radio-tracking method has shortcomings; the most important of these is that the experiments need to be performed outside the peak acorn season to force the jay to take acorns from the artificial feeders. However, improvements in the methodology may allow tracking acorns even in autumn, i.e., by inter-mixing the marked acorns with the naturally available acorns. This seems advisable as the size of the jay territory decreases towards the reproductive season (Rolando 1998) and some changes in caching behaviour could occur (Clayton 1996).

Concluding remarks

We report here for the first evidence of a spatially explicit seed shadow for oaks. This application of a seed radio-tracking method allowed us to obtain realistic acorn distributions and densities as well as jay preference forcaching acorns. Because jays selected some vegetation types and the configuration of the vegetation patches was diverse, jays dispersal distances varies greatly with the landscape context. Based on our results, variation in the jay dispersal curve among landscapes deserve future research. The methodology used here may be useful both to evaluate dispersal curves in different conditions and to elucidate some of the open questions in acorn dispersal ecology.

Acknowledgements.

We thank P. Jordano for helpful comments on a draft version of this paper, Aina Blasco for her kind contribution to the fieldwork, and J. Cortina for let us part of the radiotracking material. Comments from the three referees helped to improve the paper. This work has been financed by the EU project CREOAK (QLRT-2001-01594) and the Spanish project VARQUS (CGL2004-04325/BOS). CEAM is funded by *Generalitat Valenciana* and *Bancaixa.*

References

Bossema,I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. Behaviour 70: 1-117

Cain,M.L., Milligan,B.G., Strand,A.E. 2000. Long-distance seed dispersal in plant populations. Amer. J. Bot. 87:1217-1227

Clayton,N.S., Mellor,R., Jackson,A. 1996. Seasonal patterns of food storing in the jay *Garrulus glandarius*. Ibis 138:250-255

Darley-Hill,S., Johnson,W.C. 1981. Acorn dispersal by blue jays (*Cyanocitta cristata*). Oecol. 50:231-232

Dow,B.D., Ashley,M.V. 1996. Microsatellite analysis of seed dispersal and parentage of saplings in bur oak, *Quercus macrocarpa*. Mol. Ecol. 5:615-627

Forget,P.M., Wenny,D.G. 2005. How to elucidate seed fate? A review of methods used to study seed removal and secondary seed dispersal. In Forget,P.M., Lamber,J.E., Hulme,P.E., Vander Wall,S.B., Seed Fate: predation, dispersal and seedling stablishment, Cabi-International, pp. 379-394.

Godoy,J.A., Jordano,P. 2001. Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. Mol. Ecol.10:2275-2283

Gómez,J.M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26:573-584

Gómez,J.M. 2004. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. Plant Ecology 172:287-297

Grivet,D., Smouse,P.E., Sork,V.L. 2005. A novel approach to an old problem: tracking dispersed seeds. Mol. Ecol.14:3585-3595

Greene,D.F., Canham,C.D., Coates,K.D., LePage,P.T. 2004. An evaluation of alternative dispersal functions for trees. J. Ecol. 92: 758-766.

Hardesty,B.D., Dick,C.W., Kremer,A., Hubbell,S., Bermingham,E. 2005. Spatial genetic structure of *Simarouba amara* Aubl. (Simaroubaceae), a dioecious, animal-dispersed Neotropical tree, on Barro Colorado Island, Panama. Heredity 95:290-297

Herrera,C.M. 1995. Plant-Vertebrate Seed Dispersal Systems in the Mediterranean - Ecological, Evolutionary, and Historical Determinants. Ann. Rev. Ecol. Syst. 26:705-727

Howe,H.F. 1989. Scatter- and clump-dispersal and seedling demography: hypothesis and implications. Oecologia 79:417-426

Iida,S. 1996. Quantitative analysis of acorn transportation by rodents using magnetic locator. Vegetatio 124:39-43

Jenkins,S.H., Rothstein,A., Green,W.C.H. 1995. Food Hoarding by Merriams Kangaroo Rats - A Test of Alternative Hypotheses. Ecology 76: 2470-2481.

Kollmann,J., Schneider,B. 1997. Effects of landscape structure on seed dispersal of fleshy-fruited species along forest edges. Bulletin of the Geobotanische Institute ETH 63:77-86

Levey,D.J., Sargent,S. 2000. A simple method for tracking vertebrate-dispersed seeds. Ecology 81:267-274

Levey,D.J., Bolker,B.M., Tewksbury,J.J., Sargent,S., Haddad,N.M. 2005. Effects of landscape corridors on seed dispersal by birds. Science 309:146-148

Mack,A.L., Druliner,G. 2003. A non-intrusive method for measuring movements and seed dispersal in cassowaries. J. Field Ornith. 74:193-196

Nathan,R., Perry,G., Cronin,J.T., Strand,A.E., Cain,M.L. 2003. Methods for estimating long-distance dispersal. Oikos 103:261-273

Nathan,R. 2006. Long-distance dispersal of plants. Science 313:786-788

Pausas,J.G. 2006. Simulating Mediterranean landscape pattern and vegetation dynamics under different fire regimes. Plant Ecol. 187:249 - 259.

Pausas,J.G., Bladé,C., Valdecantos,A., Seva,J.P., Fuentes,D., Alloza,J.A., Vilagrosa,A., Bautista,S., Cortina,J., Vallejo,R. 2004. Pines and oaks in the restoration of Mediterranean landscapes in Spain: New perspectives for an old practice - a review. Plant Ecol. 171:209-220

Pausas,J.G., Bonet,A., Maestre,F.T., Climent,A. (2006a). The role of the perch effect on the nucleation process in Mediterranean semi-arid Oldfields. Acta Oecol. 29:346-352

Pausas,J.G., Ribeiro,E., Dias,S.G., Pons,J., Beseler,C. 2006b. Regeneration of a marginal Cork oak (*Quercus suber*) forest in the eastern Iberian Peninsula. J. Veget. Sci. 17: 729-738

Pons,J., Pausas,J.G. 2006. Oak regeneration in heterogeneous landscapes: the case of fragmented *Quercus suber* forests in the eastern Iberian Peninsula. For. Ecol. Manage 231: 196-204

Pons,J., Pausas,J.G. 2007a. Rodent acorn selection in a Mediterranean oak landscape. Ecological Research 22: 535-541.

Pons,J., Pausas,J.G. 2007b. Not only size matters: acorn selection by the European jay (*Garrulus glandarius*). Acta Oecologica 31: 353-360.

Purves,D.W, Zavala,M.A., Ogle,K., Prieto,F., Rey Benayas,J.M. 2007. Enviromental heterogeneity, bird-mediated directed dispersal, and oak woodland dynamics in mediterranean Spain. Ecol. Monogr. 77:77-97

Reiter,J., Curio,E., Tacud,B., Urbina,H., Geronimo,F. 2006. Tracking bat-dispersed seeds using fluorescent pigment. Biotropica 38:64-68

Ribbens,E., Silander,J.J.A., Pacala,S.W. 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. Ecology 75: 1794-1806.

Rolando,A. 1998. Factors affecting movements and home ranges in the jay (*Garrulus glandarius*). J. Zool. Lond. 246:249-257

Russo,S.E., Portnoy,S., Augspurger,C.K. 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. Ecology 87:3160–3174.

Sone,K., Kohno,A. 1996. Application of radiotelemetry to the survey of acorn dispersal by *Apodemus* mice. Ecol. Res. 11:187-192

Vallejo,R., Aronson,J., Pausas,J.G., Cortina,J. 2006. Mediterranean Woodlands. In: Van Andel,J., Aronson,J. (eds.) Restoration ecology: The New Frontier. Blackwell Science. Oxford, UK, pp 193-207

Vander Wall,S.B. 2002. Secondary dispersal of Jeffrey pine seeds by rodent scatter-hoarders: the roles of pilfering, recaching and a variable environment. Seed dispersal and frugivory: ecology, evolution and conservation. In: Levey DJ, Silva

Venables,W.N., Ripley,B.D. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York.

Wilson,M., Traveset,A. 2000. The ecology of seed dispersal. In: Fenner,M. (ed.) Seeds: The Ecology of Regeneration in Plant Communities. CAB international, pp 85-110

Xiao,Z.S., Zhang,Z.B., Wang,Y.S. 2004. Dispersal and germination of big and small nuts of *Quercus serrata* in a subtropical broad-leaved evergreen forest. For. Ecol. Manage. 195:141-150

Xiao,Z.S., Zhang,Z.B., Wang,Y.S. 2005. Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species. Acta Oecologica-International Journal of Ecology 28:221-229.

Xiao,Z.S., Zhang,Z.B. 2006. Nut predation and dispersal of Harland Tanoak *Lithocarpus harlandii* by scatter-hoarding rodents. Acta Oecologica-International Journal of Ecology 29:205-213.

Ziegenhagen,B., Liepelt,S., Kuhlenkamp,V., Fladung,M. 2003. Molecular identification of individual oak and fir trees from maternal tissues of their fruits or seeds. Trees 17:345-350

Rodent acorn selection[5]

Abstract

Quercus suber, *Quercus ilex* and *Quercus coccifera* (Cork, Holm and Kermes oaks, respectively) are common evergreen oak species that coexist in the landscapes of the western part of the Mediterranean basin. Rodents are the main acorn predators and thus one of the main factors for understanding recruitment patterns in oaks. In this paper we analyse to what extent mice prefer acorns from one oak species over another in three oak species studied using acorn removal experiments and video tape recordings. Twenty labelled acorns from each of the three *Quercus* species (60 acorns) were placed in 40 cm x 40 cm quadrats on each plot. Because selection might vary as a result of the vegetation context, we performed the trials in the five main vegetation types within the study area (four replicates in each vegetation type) in order to control for habitat influences on rodent acorn preferences (a total of 20 plots). The removal of 1,200 acorns occurred within 68 days. Mice removed 98.7% of the acorns. *Q.ilex* acorns were preferred over *Q.suber* and *Q.coccifera* in all vegetation types except in pine forest, where no acorn preferences were detected. Acorn removal rates differed with vegetation type, correlating positively with shrub cover. The distance at which acorns were displaced by rodents (mean = 4.6 m ± 5.1 SD) did not differ between acorn species, but varied among vegetation types. Bigger acorns of *Q.coccifera* were selected only after *Q.ilex* and *Q.suber* acorns were depleted, while no size selection was detected for the latter two species. Thus, we conclude that rodents show preference for some oak acorns and that landscape context contributes significantly to rodent activities and decisions.

Introduction

Many Mediterranean landscapes are dominated by oak (*Quercus*) species, especially evergreen oaks. In the Mediterranean basin, evergreen oaks of different species can coexist, forming mixed forests with pines, appearing in the understory or being dominant in some shrubland communities (garrigue). This oak spatial diversity may be related to different resource requirements, disturbance responses or past uses (Mohler 1990). These different communities with varying oak abundance can be found as mosaics of Mediterranean landscapes (mixed oak landscapes), and thus acorns from different oak species (sympatric acorn-producing species) may be available to predator

---

[5] Pons, J. and Pausas J.G. 2007. Rodent acorn selection in a Mediterranean oak landscape. Ecological Research 22 (4): 535-541.

populations. Furthermore, acorns are a very valuable food source for rodents (Jensen 1985), and rodents are the main acorn predators (Shaw 1968).

It has been suggested that acorn crop variability may affect mouse populations the following spring and summer (Mcshea 2000), but the role of species-specific seed preferences by rodents (Ivan and Swihart 2000, Shimada 2001a, Sone and Kohno 1996) is still unknown. Although the total inter-specific variation in acorn production has been recognised to have a great influence on seed eaters (Liebhold et al. 2004), few studies have dealt with the differential selective pressure by these seed eaters on the producers' actual performance (i.e., mast and regeneration patterns, but see Hoshizaki and Hulme 2002).

It has been suggested that rodents have a preference for large acorns from Holm oak *Quercus ilex* (Gómez 2004a); however, in mixed oak landscapes, acorns of different species may vary not only in size but also in nutritional properties (Ferreira-Dias et al. 2003, Shimada 2001b, Talebbendiab et al. 1991) and tannin levels (Cantos et al. 2003). The question that arises is to what extent rodents show a preference for acorns of a given oak species. Differential acorn selection may produce changes in predation pressure and dispersal rates in different oak species (Shimada 2001a, Stapanian and Smith 1978) and have evolutionary implications on the differential mast seeding dynamics or community oak species composition (Janzen 1971).

Rodents suffer higher predation risk in areas with reduced vegetation cover of low height (Kollmann 1995, Manson and Stiles 1998). Therefore, rodent activity, rodent population densities or rodent species composition may differ between more open habitats and shrubby habitats (Falkenberg and Clarke 1998). As a consequence, if rodents select acorn types (i.e., species or size), the degree of selection and/or other variables in the acorn predation mechanisms could differ as a function of the surrounding vegetation. Rodent differential seed predation has been documented in Fagaceae species for both temperate forests and indoor trials (Briggs and Smith 1989, Shimada 2001a). To our knowledge no such studies have been carried out in Mediterranean landscape mosaics under field conditions.

Thus, our objectives are: 1) to determine if mice prefer any of the acorns tested over the others, and 2) to quantify any variation in acorn removal rates and displacement distances as a function of the vegetation type. Our hypothesis is that rodents are the main predators and that they select for nutritionally superior acorns. These acorns would be transported farther because of the higher nutritional revenue. However, this pattern would vary with respect to the different vegetation types because of different rodent density, predation risk, food availability and/or percent of available places to cache acorns. To test this hypothesis, we performed an experiment in which labelled acorns from three oak species were placed in five different vegetation types and left for depletion by rodents. Video recordings were also used for complementing the analyses.

Materials and methods

Study area

The study was performed in the Espadà mountains, eastern Iberian Peninsula (39° 51' N, 0° 20' W, close to Chovar, Castelló province). The climate is typically Mediterranean with summer drought and mild and wet winters. Two bedrock types are common, Bundsandstein sandstone (the most common) and limestone. The vegetation is the product of a long history of fire and land use, in which many slopes were terraced and cultivated in the past, and then abandoned (Pausas 2004, Bonet and Pausas, in press). Thus, current landscapes are mosaics of five main vegetation types: Holm oak forests (forests dominated by *Quercus ilex* subsp. *rotundifolia*), Cork oak forests (dominated by *Q.suber*), Kermes oak garrigue (shrublands dominated by *Q.coccifera*), pine forests (dominated by *Pinus halepensis* and/or *P. pinaster*) and abandoned fields (at different abandonment ages). The three oaks, Holm oak, Cork oak and Kermes oak, are evergreen species; the first and second are trees and the third is a shrub.

The Wood mouse (*Apodemus sylvaticus*) and Mediterranean mouse (*Mus spretus*) are the dominant rodents in the study area. Previous field trap sessions found that the population of the latter is about a third of the former, and that the black rat (*Rattus rattus*) is present at much lower densities (own unpublished data).

Sampling

Four replicate plots were located in each of the five different vegetation types (therefore, 20 plots): HF, CF, GA, pine woodland (PF) and oldfields (OF, abandoned fields currently covered by shrubs and grasses, without oaks). These vegetation types were selected because they are the dominant landscape units in the study area. For plot characterisation, a plot size of 10 m·10m was considered; however, acorns removed from the centre of the plot (removal experiment, see below) were searched for without considering plot size. Vegetation on each plot was characterised by using four 10-m transects along the main cardinal directions and recording species occurrence and height every 33 cm. Because the objective of the habitat characterisation was to look for variables explaining different acorn predation rates, the cover percentages of structures relevant to rodents were recorded as well (bare soil, fallen branches, stones and terrace walls). Additional plot characteristics (aspect, slope, tree cover, grazing symptoms and bedrock type) were also recorded.

In autumn 2003, acorns of the three oak species were obtained from several trees in the study area or nearby populations and stored in a constant-cold humidity chamber. Nonviable and unripe acorns were discarded by the floating method and visual screening. In spring 2004, 20 acorns from each of the three oak species, *Q.ilex* subsp. *rotundifolia* (Qi), *Q.suber* (Qs) and *Q.coccifera* (Qc), were placed in a 40 cm x 40 cm quadrat in the centre of each plot (therefore, 1,200 acorns). The quadrats were surrounded with coloured powder to be able to identify predator footprints. Acorns were labelled for their identification with a numbered plastic label tied on with a thin iron string (Xiao et al. 2004; mean weight of labels 0.54 ±0.01 g, n=10). To monitor acorn removal, plots were periodically visited: first every 2 days, then every week and finally at 2-week intervals. On each visit, the labels were searched out and mapped; the status of the acorn (unaffected, eaten or partially eaten) was also recorded. Two plots were depleted in just 1 night; although these plots provided information on the total removal rate, they did not offer information on rodent acorn species preferences. Moreover, in order to increase the power of the survival function through ties multiplications, we found it necessary to reduce the time interval to rank cases (Muenchow 1986) as a synchronic approach. Thus, a total of four films (each of 3 h in length) were recorded at two plots (one in an OF and the other in a shrubland). In films 1 and 4, the species of some predated acorns could not be identified and were classified as ‘unknown species’.

To assess whether rodents select acorn sizes, all acorns corresponding to Cork forest habitat (sites 17, 18, 19 and 20) were previously weighed (0.1 mg precision). The mean weight of the acorn plus tag was 4.18 g ± 1.09 SD (n=240, range 2.5–9.0 g). By species, Qi and Qs acorns were similar (4.44 g ±0.98 SD and 4.70 g ±1.17 SD, respectively) and approximately 1 g heavier than Qc acorns (3.46 g ±0.46 SD; ANOVA for species mean weight differences, F=40.621, df=2, P<0.001).

The experiments were performed in spring (that is, outside the peak acorn-drop period) to avoid interference in the selection behaviour by the natural levels of acorn abundance on each site, that is, to avoid the possible differential masting and relative abundance of oak species on each site. This implies that our results may reflect the intrinsic behaviour of the predators (as in a lab experiment) more than their behaviour under natural conditions, which may be too heterogeneous to allow easy interpretation of the results.

Data analysis

Acorn removal

Median removal time, i.e., the time at which 50% of the acorns were removed (hereafter MRT and expressed in days), was used to compare acorn removal rates in both the vegetation type x acorn species experiment and in the films. Survival function analysis (time failure analysis, Pyke 1986) was used to analyse acorn removal rates, taking into account both vegetation type and acorn species. By 'survival', we refer to acorns not removed from the 40 cm x 40 cm quadrat (i.e., remaining in the quadrat). Cox regression was used to control for factor variance and was tested with Gehan's generalised Wilcoxon test (hereafter Wilcoxon).

Video monitoring of acorn removal

Time failure analysis and Cox regression were also used to analyse acorn removal rates by species. However, because of the limited length of the video tapes, in many cases fewer than 50% of the removed acorns were filmed, and thus, MRT was not computed. Alternatively, Ivlev's Electivity Index (Scarlett and Smith 1991) was used to quantify rodent preference for a particular acorn species in the video monitoring. Electivity is calculated for each acorn species as $E_i=(R_i - P_i) / (R_i+P_i)$, where R_i is the number of acorns of the species i selected and P_i is the number of acorns of the species i supplied. This electivity index ranges from -1 to 1, with negative values indicating avoidance and positives values indicating selection.

Acorn size

Acorn weight was tested in the Cork oak vegetation type, and data were grouped between the acorns removed on the day following the beginning of the experiment (early removal) and those removed afterwards (late removal). A univariate ANOVA procedure (GLM module, SPSS 10.5) was used to compare acorn weight and retrieval distances (log-transformed).

Distances of tag retrieval

Tag retrieval distance (TRD) was measured as the distance (straight line) from the quadrat to the place where the label was found, usually a few days after removal, for both eaten and not-eaten acorns. We did not consider cache relocations in this study. To compare the different TRD distribution between vegetation types and between acorn species we used the non-parametric median test. In the cases where it was significant, we performed the pairwise comparisons using the Kolmogorov–Smirnoff test (K–S test); both tests compare the full distribution of distances.

Determinants of removal rates

Stepwise forward multiple regression was used to reveal the significant plot variables that explained most of the variability in MRT (log-transformed prior to the analysis). The initial variables included in the regression model were the parameters obtained from the transects (mean vegetation height, standard deviation in vegetation height, plant cover and a structural diversity index) and aspect. The structural diversity index was computed as the Simpson's diversity index (Simpson's D), including plant species and physical structures relevant to rodents (such as rocks, bare soil and dead branches). For computing Simpson's D, species accounting for less than 5% of total cover or species present on only one site were aggregated into the category 'others'. Plant cover was computed for different strata: ground level (<20 cm), short shrubs (20–50 cm), medium shrubs (50–120 cm), tall shrubs (120–300 cm) and tree layer (>300 cm). Aspect was transformed in an aspect index (AI), which was computed as: $AI=\cos(\alpha-22.5)$, where α is the aspect angle in decimal degrees (Pausas et al. 2004). This transformation is necessary to account for the more mesic conditions of the north–east aspect as most of the humidity in the study region comes from the Mediterranean sea (eastwards).

Results

Acorn removal

Track prints in the quadrats revealed that rodents were the main acorn predators. However, differentiating between the two species in the study area (A. sylvaticus and M. spretus) on the basis of their tracks was extremely difficult, and no attempt was made to quantify them. Only on two plots did other vertebrates (jays and domestic sheep) predate a few acorns (1.6% of total), and these data were omitted from the analysis. Rodents took on average 8.8 nights to discover the acorns (range 1–34 nights) and an additional 11.4 nights (on average) to remove all the acorns (range 1–57 nights). After 68 days, no acorns were left in the quadrats. Acorn removal was higher immediately after the plot was discovered and decreased with time: after 1 week more than 50% of acorns had disappeared (MRT=6.3 days), and after 2 weeks this percentage was about 75%.

The median removal time differs between vegetation types (Wilcoxon statistic= 287.822, df=4, $P<0.001$) and was shortest on OF (MRT=1.6 days), longest on PF

(MRT=18.5 days) and intermediate in the remaining vegetation types (MRT=5–8 days; Table 1). MRT also varied with the acorn species considered (Wilcoxon statistic=9.375, df=2, P=0.009). Qi acorns were removed faster (MRT=5.8 days) than Qs and Qc acorns (MRT=6.5–6.8 days; Table 1). However, acorn species · vegetation type interaction was also significant: Qi acorns were positively selected on HF, CF and GA, but no acorn preferences appear on PF and OF. Very fast removal rates (i.e., removal of all acorns in just 1 night) prevented any acorn species selection evidence in OF. However, the video films revealed a Qi preference over the others (see below) in OF.

Table 1. Median removal time (MRT, in days) values by vegetation type and acorn species. In *P*, letters refer to Bonferroni-corrected pairwise comparisons at p<0.05 significance level, while numbers refer to the significance of the Wilcoxon test.

	Removal time (days)		
	MRT	N	*P*
a) Vegetation types			
HF	5.1	240	b
CF	5.8	240	c
GA	8.0	240	d
PF	18.5	240	e
OF	1.6	240	a
Overall			<0.001
b) Acorn species			
Qi	5.8	400	a
Qs	6.8	400	b
Qc	6.5	400	b
Overall			0.009
c) Overall	6.3	1200	

Video monitoring of acorn removal

Because of limited tape length (3 h), only the first 21.7-58.3% of the removed acorns were filmed (total n= 240) in a total of 4 film sessions. We found differences in removal rates between the different acorn species (Table 2). Qi acorns were preferred in all films, ranging between 47.6 and 61.5 % of the total removed acorns filmed (mean 55%), followed by Qs (24%) and Qc (21%) (Table 2). Qi acorns were removed more than Qc acorns, and more than Qs acorns (Table 2) and no acorn selection seems to occur between the latter two acorns species (Table 2). In accordance, the electivity index was positive for Qi and negative for Qs and Qc, been the lowest in Qc (Table 2).

Acorn size

Plots 17, 18 and 19 were depleted after two to three visits to the plot (6-7 nights). We grouped the data as a function of removal time ('Early' acorns were removed on the first visit; 'Late' acorns were removed on the second or third visit) and analysed the three acorn species separately as they differ in weight. Mean acorn plus tag weight did not differ between groups for either Qi (Early = 4.69 ± 0.72 g, n= 14; Late = 4.38 ± 1.10 g, n= 46; Table 3) or Qs (Early = 4.83 ± 1.29 g, n= 28; Late = 4.43 ± 1.17 g, n= 32; Table 3). On average, a significant difference of 0.2 g was detected between Early and Late Qc acorn groups (Early, mean weight = 3.62 ± 0.48 g, n= 20; Late, mean weight = 3.40 ± 0.48, n= 40; Table 3) and marginal significance for the group (Early/Late) x plot interaction (see Table 3). Since acorn size is directly proportional to acorn weight, these results indicate some preference by rodents for bigger Qc acorns but no size discrimination for Qi or Qs acorns.

Table 2. Overall results on acorn removal in the four films, including the number of initial and removed acorns, the electivity index, the pairwise comparisons for differences in the estimated survival functions for each acorn species and the pairwise comparisons for the mean electivity index (only significant differences are shown).

	Number of acorns	Mean electivity (SE)
Initial acorns for each species	80	
Acorns removed by species		
Qi	55	0.424 (0.021)
Qs	24	-0.357 (0.029)
Qc	21	-0.417 (0.031)
Total acorns tracked	100	
Significant pairwise comparisons (Wilcoxon test)		
Qi-Qs	23.07 (p< 0.0001)	9.178 (p<0.001)
Qi-Qc	27.35 (p< 0.0001)	8.928 (p<0.001)

Table 3. ANOVA analysis of acorn weight as dependent factor and plot and removal group (Early or Late) as main factors. Analysis was run independently for each acorn species (see text for further details).

Acorn sp	Source	MS	Df	F	Sig.
Qi	Plot	218.240	2	2.330	0.107
	Group	34.300	1	0.366	0.548
	Plot * Group	54.081	2	0.577	0.565
	Error	93.661			
Qs	Plot	80.578	2	0.516	0.600
	Group	186.150	1	1.191	0.280
	Plot * Group	91.099	2	0.583	0.562
	Error	156.261			
Qc	Plot	16.315	2	0.744	0.480
	Group	98.532	1	4.492	0.039*
	Plot * Group	63.733	2	2.905	0.063!
	Error	21.936			

Distances of tag retrieval

Mean TRD was 4.6 m (SD=5.1), with a maximum of 62 m on an OF. However, these values should be considered underestimations as only 36% of the tags were located. This is probably because the effort involved in locating long-distance tags increases exponentially, and some of the lost tags would correspond to long-distance movements.

No acorn species differences were found in the percent of acorn label retrieval (Qi=33.9%, Qs= 34.1%, Qc=31.5%, n=1,154, F=0.339, P=0.713).

Tag retrieval distance differed between vegetation 2 type (median test, v =23.287, df=4, P<0.001, n=431). Pairwise comparisons (K–S test) indicate that TRD was longer in OF (mean =6.7±7.4 m, maximum=62.0, n=74), shorter in garrigue (mean =3.3±1.8 m, maximum =7.5, n=118), Holm (mean =4.6±3.4 m, maximum =18.4, n=72) and CF (mean =4.0±4.1 m, maximum =16.3, n=119) and intermediate in pine forest (mean =6.3±8.7 m, maximum =40.1, n=48) (Fig.1). All pairwise comparisons between vegetation types were significant at the P<0.03 level (K–S test) except for and GA–PF (P=0.07). When considering acorn species, no significant differences in TRD were found for the whole population (median test, v =2.417, df=2, n=431, P=0.299). The maximum TRD for Qs (62.0 m, n=149) was remarkably larger than for Qc (18.6 m, n=151).

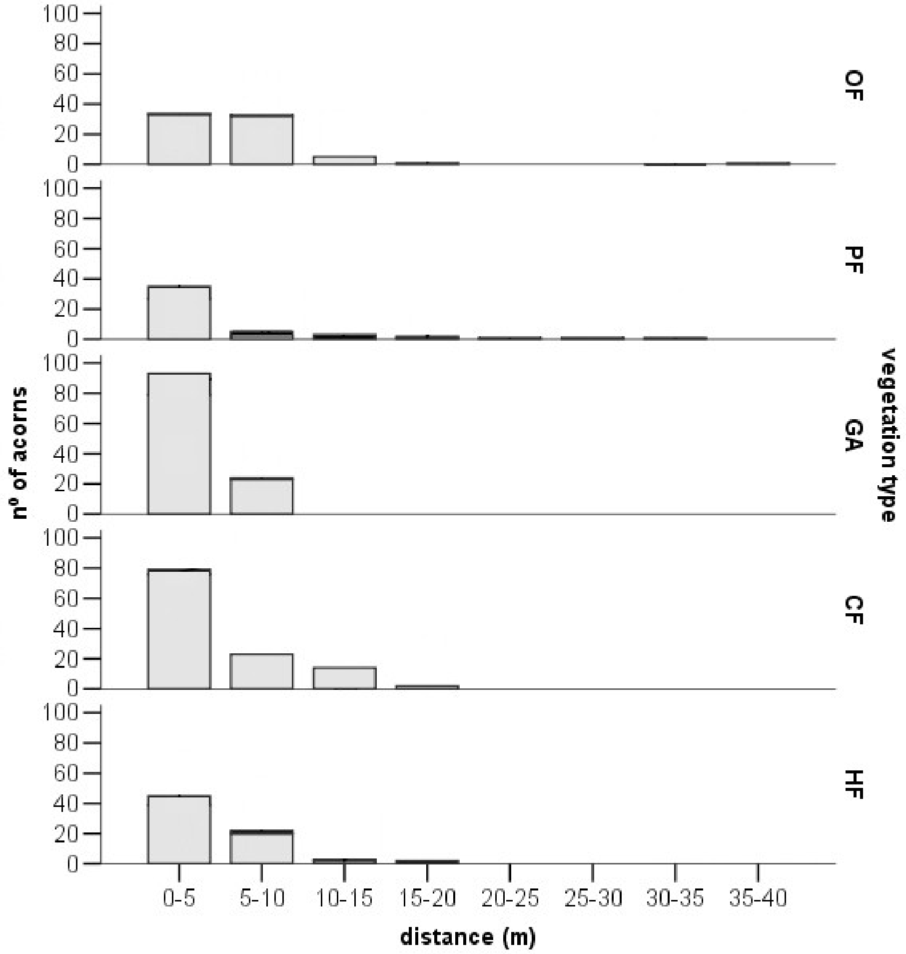


Fig.1. Frequency distributions of tag retrieval distances by Vegetation Type: OF, oldfields; PF, pine forest; GA, garrigue; HF, Holm oak forest; CF, Cork oak forest.

Determinants of removal rates

At plot scale (20 plots), the stepwise regression was selected as the best fit for MRT the model with medium shrub (50–120 cm) and the SD of vegetation height (vertical complexity). MRT shows a negative relation with both parameters (log MRT =2.715 - 1.772 x medium shrub cover - 0.012 x vegetation height SD; cover was arcsine-root transformed, adjusted R^2=0.485, P=0.001). That is, mice remove quicker in sites with greater shrub cover and vertical complexity, which corresponds to shrublands, long abandoned OF and shrubby oak forest. For TRD, a significant, but weak relation was found with short shrub (20–50 cm) cover (log TRD =0.840-0.016· short shrub cover, adjusted =0.19, P=0.032), suggesting greater acorn movements in sites with high short vegetation cover, usually corresponding to recently abandoned OF and pine forest sites.

Discussion

Rodents were the main agents in the acorn removal, as has been reported in other Mediterranean landscapes (Alcantara 2000; Gomez et al. 2003; Borchert 1989), and they clearly selected Qi acorns. Preferences for Qi acorns could be related to their higher nutritional value in terms of oil content (7.3–9.1% relative to Qs= 5.0–5.2%; Talebbendiab et al. 1990, 1991; Afzalrafii et al. 1992; Nieto et al. 2002; Ferreira-Dias et al. 2003) or to their lower content in tannins relative to Qc (Cañellas and San Miguel 2003), or probably to both. Higher tannin content indirectly implies lower nutritional value because energy is needed to neutralise the tannin (Janzen 1971). The selection of Qi over Qs could be partially explained by the high phenolic compound content in the Qs acorn skin (Cantos et al. 2003), but it is still unknown whether this substance acts as a signal cue or has an effect over rodents by itself. Species preferences could not be related to synchronic exposure to different acorn densities because the field experiments were carried out in March when natural acorn production does not occur.

At least in CF, rodents removed Qi and Qs acorns independently of their size, while for Qc, they chose large acorns. The Qc acorns used in our trials were smaller than those of the other species, and this might have contributed, to some extent, to the selection of the larger Qc acorns. The absence of acorn-size selection reported by Xiao et al. (2004) seems to be in conflict with results from other studies (Alcantara 2000; Gómez 2004a). However, our results suggest that size selection could be species-dependent (i.e., seed quality). Differences in acorn location may contribute to the differences between our results (from acorns set at the soil surface) and those from Gómez (2004a; buried acorns), because detectability and time to remove the acorns may be longer in buried acorns.

Rodent preferences for different acorns can be divided into feeding and carrying/hoarding preferences (Shimada 2001a). We have not tested these separately, but the lack of differences in TRDs suggests that Qi preference is set at the experimental depot site. However, the fact that Qc acorns were found attached to the tag more often than expected (data not shown) suggests that Qi and Qs acorns were preferred for feeding and that, afterwards, Qc acorns were moved for storage. Alternatively, the preferred acorns could have been better hidden, thus making it harder for us to locate (i.e., sampling error). To solve this problem, more accurate acorn-tracking methods (Sone and Kohno 1996; Hoshizaki and Hulme 2002) should be used.

Removal rates, acorn species preference and TRD varied with the vegetation type considered. Vegetation structure (mostly shrub cover) accounts for part of these differences in agreement with previous studies (Díaz 1992; Kollmann 1995), but food availability and rodent community composition—species and relative densities—could also be important (Ostfeld et al. 1997). In relation to vegetation type, we have found three clear patterns: (1) mice Qi preference is observed in all the vegetation types except in PF. A probable reason for this pattern is a high mice predation risk in pine forests (i.e., shorter time for acorn discrimination and selection; Willson and Whelan 1990; Hulme 1994, 1997; Alcantara 2000; Torre and Díaz 2004; Díaz et al. 2005). (2) Acorn removal rates are higher in OF and lower in PF (intermediate in HF, CF and GA). This seems to be related to shrub cover and vegetation structure. This pattern is in agreement with higher mice densities deduced from live trapping under increasing shrub cover (unpublished data) and with the *Quercus* recruitment densities (Pons and Pausas 2006). (3) TRDs increase from GA to OF and PF (HF and CF intermediate). An explanation for this pattern is difficult as TRD showed a weak correlation with short shrub cover. The greater acorn movement distances in OF and PF might be the result of different causes such as the lack of safe sites in PF or the high mice densities in OF (e.g., longer distance movements for reducing pilfering by congeners; Vander Wall 2002).

Most of the literature deals with just one acorn species (Shaw 1968; Herrera 1995; Gómez et al. 2003; Gómez 2004a,b; Pulido and Díaz 2005). However, most vertebrates that consume acorns interact with several acorn species at the same time. Our finding of Qi preference over Qs and Qc might have implications for differential recruitment in a mixed oak population. However, prior to extracting the direction of this selection on the population dynamics of the different *Quercus* species, we must deal with the possible variation because of a specific *Quercus* masting pattern and with the relationship between mice populations and the last year's acorn availability (see, i.e., Ostfeld et al. 1996). We suggest that the predator–disperser activity of mice would be different not only because of the vegetation type and the previous year's acorn production, but also because of the preferences of mice for specific acorns. In other words, under specific conditions mice could act as a disperser for some acorns and as a predator for others.

Acorn predation is one of the multi-steps in oak recruitment. Probably extending the multi-species approach to the whole oak regeneration process will yield some promising results.

Acknowledgements.

This work has been financed by the EU projects CREOAK (QLRT-2001-01594) and the Spanish project VARQUS (CGL2004-04325/BOS). T. Rodrigues and P. Azeiteiro helped with the field work under an EU Leonardo da Vinci fellowship. We thank M. Díaz, A. Muñoz and J. Belliure for their kind review of the first draft of this paper. CEAM is funded by *Generalitat Valenciana* and *Bancaixa*.

References

Afzalrafii,Z., Dodd,R.S., Pelleau,Y. 1992. Mediterranean Evergreen Oak Diversity - Morphological and Chemical Variation of Acorns. Can. J. Bot. 70:1459-1466

Alcantara,J.M. 2000. Factors shaping the seedfall pattern of a bird-dispersed plant. Ecology 81:1937-1950

Bonet,A., Pausas,J.G. (*in press*) Old field dynamics on the dry side of the Mediterranean Basin: patterns and processes in semiarid SE Spain In: V.A. Cramer and R.J. Hobbs (eds). Old Fields: Dynamics and Restoration of Abandoned Farmland. Island Press

Borchert,M. 1989. Interaction of factors affecting seedling recruitment of blue oak (*Quercus douglasii*) in California. Ecology 70:389-404

Briggs,J.M., Smith,K.G. 1989. Influence of habitat on acorn selection by *Peromyscus leucopus*. J. Mamm. 70:35-43

Cañellas,I., San Miguel,A. 2003. La coscoja (*Quercus coccifera* L.): Ecología, características y usos. Monografías. INIA, Madrid

Cantos,E., Espin,J.C., Lopez-Bote,C., De la Hoz,L., Ordonez,J.A., Tomas-Barberan,F.A. 2003. Phenolic compounds and fatty acids from acorns (*Quercus* spp.), the main dietary constituent of free-ranged Iberian pigs. J. Agri. Food. Chem. 51:6248-6255

Diaz,M., Torre,I., Peris,A., Tena,L. 2005. Foraging behaviour of wood mice as related to presence and activity of genets. J. Mamm. 86:165–172

Falkenberg,J.C., Clarke,J.A. 1998. Microhabitat use of deer mice: effects of interspecific interaction risk. J. Mamm. 79:558-565

Ferreira-Dias,S., Valente,D.G., Abreu,J.M.F. 2003. Pattern recognition of acorns from different *Quercus* species based on oil content and fatty acid profile. Grasas y Aceites 54:384-391

Gomez JM (2004a) Bigger is not always better: Conflicting selective pressures on seed size in *Quercus ilex*. Evolution 58:71-80.

Gomez,J.M. 2004b. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. Plant. Ecol. 172:287-297

Gomez,J.M., Garcia,D., Zamora,R. 2003. Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. For. Ecol. Manage. 180:125-134

Hoshizaki,K., Hulme,P.E. 2002. Mast seeding and predator-mediated indirect interactions in a forest community: Evidence from post-dispersal fate of rodent-generated caches. In: Seed Dispersal and Frugivory, 227-239. CAB International, UK.

Hulme,P.E. 1994. Post dispersal seed predation in grassland: its magnitude and sources of variation. J. Ecol. 82:645-652

Hulme,P.E. 1997. Post-dispersal seed predation and the establishment of vertebrate dispersed plants in Mediterranean scrublands. Oecologia 111:91-98

Ivan,J.S., Swihart,R.K. 2000. Selection of mast by granivorous rodents of the central hardwood forest region. J. Mamm. 81:549-562

Janzen,D.H. 1971. Seed predation by animals. Ann. Rev. Ecol. Syst., 2:465-492.

Jensen,T.S. 1985. Seed-seed predator interactions of European beech (*Fagus silvatica*) and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. Oikos 44:149-156

Kollmann,J. 1995. Regeneration Window for Fleshy-Fruited Plants During Scrub Development on Abandoned Grassland. Ecoscience 2:213-222

Liebhold,A., Sork,V., Peltonen,M., Koenig,W., Bjornstad,O.N., Westfall,R., Elkinton,J., Knops,J.M.H. 2004. Within-population spatial synchrony in mast seeding of North American oaks. Oikos 104:156-164

Manson,R.H., Stiles,E.W. 1998. Links between microhabitat preferences and seed predation by small mammals in old fields. Oikos 82:37-50

McShea,W.J. 2000. The influence of acorn crops on annual variation in rodent and bird populations. Ecology 81:228-238

Mohler,C.L. 1990. Co-occurrence of oak subgenera: implications for niche differentiation. Bull. Torrey Bot. Club 117:247-255.

Muenchow,G. 1986. Ecological use of time failure analysis. Ecology 67:246-250

Nieto,R., Rivera,M., Garcia,M.A., Aguilera,J.F. 2002. Amino acid availability and energy value of acorn in the Iberian pig. Livestock Prod. Sci. 77:227-239

Ostfeld,R.S., Jones,C.G., Wolff,J.O. 1996. Of mice and mast. Bioscience 46: 323-330.

Ostfeld, R.S., Manson,R.H., Canham,C.D. 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. Ecology 78:1531-1542

Pausas,J.G. 2004. Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). Clim. Change 63:337-350

Pausas,J.G., Blade,C., Valdecantos,A., Seva,J.P., Fuentes,D., Alloza,J.A., Vilagrosa,A., Bautista,S., Cortina,J., Vallejo,R. 2004. Pines and oaks in the restoration of Mediterranean landscapes of Spain: New perspectives for an old practice - a review. Plant Ecol. 171:209-220

Pons,J., Pausas,J.G. 2006. Oak regeneration in heterogeneous landscapes: the case of fragmented *Quercus suber* forests in the eastern Iberian Peninsula. For. Ecol. Manage. 231: 196-204.

Pulido,F.J., Diaz,M. 2005. Regeneration of a Mediterranean oak: A whole-cycle approach. Ecoscience 12:92-102

Pyke,D.A. 1986. Statistical analysis of survival and removal rates experiments. Ecology 67:240-245

Scarlett,T.L., Smith,G. 1991. Acorn preference of urban Blue Jays (*Cyanocitta cristata*) during fall and spring in north-eastern Arkansas. The Condor 93: 438-442

Shaw,M.W. 1968. Factors affecting the natural regeneration of Sessile oak (*Q. petraea*) in North Wales: acorn losses and germination under field conditions. J. Ecol. 56:647-659

Shimada,T. 2001a. Hoarding behaviors of two wood mouse species: different preference for acorns of two Fagaceae species. Ecol. Res. 16:127-133

Shimada,T. 2001b. Nutrient compositions of acorns and horse chestnuts in relation to seed-hoarding. Ecol. Res. 16:803-808

Sone,K., Kohno,A. 1996. Application of radiotelemetry to the survey of acorn dispersal by *Apodemus* mice. Ecol. Res. 11:187-192

Stapanian,M.A., Smith,C.C. 1978. A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. Ecology 59:884-896

Talebbendiab,S.A., Benmahdi,M., Mashev,N.P., Vassilev,G.N. 1990. Contribution to the investigation of the chemical composition of the acorn of various *Quercus* Species in Algeria - Investigating the acorn of *Quercus ilex*. Dokladi Na Bolgarskata Akademiya Na Naukite 43:83-86

Talebbendiab,S.A., Benmahdi,M., Mashev,N., Vassilev,G.N. 1991. A tribute to the study of the chemical composition of the acorn of different species of *Quercus* spread in Algeria. Dokladi Na Bolgarskata Akademiya Na Naukite 44:85-88

Torre,I., Diaz,M. 2004. Small mammal abundance in Mediterranean post-fire habitats: a role for predators? Acta Oecol. 25:137-142

Vander Wall,S.B. 2002. Masting in animal-dispersed pines facilitates seed dispersal. Ecology 83: 3508-3516.

Willson,M.F., Whelan,C.J. 1990. Variation in postdispersal survival of vertebrate dispersed seed: effects of density, habitat, location, season and species. Oikos 57:191-198

Xiao,Z.S, Zhang,Z.B, Wang,Y.S 2004. Dispersal and germination of big and small nuts of *Quercus serrata* in a subtropical broad-leaved evergreen forest. For Ecol Manage 195:141-150

Cork oak regeneration pattern[6]

Abstract

Quercus suber recruitment is quantified at local (in different vegetation types) and landscape level in three marginal populations (sites) located in the eastern Iberian Peninsula and ranging in size from 70-7000 ha. We hypothesised that: (1) recruitment of marginal *Q.suber* populations in eastern Iberia should be higher than in the core area of distribution, western Iberia, (2) within our study area, there should be a trend in the regeneration from north (the largest forest patch) to south (the smallest patch), and (3) within a site, recruitment should not be randomly distributed, but rather some vegetation types should show higher recruitment than other vegetation types. To test these hypotheses, a total of 61 plots measuring 12.5 x 12.5 m were established on 7 vegetation types in 5 previously selected 3 x 3 km^2 quadrats. On each plot all *Quercus* plants shorter than 3 m were labelled and tracked between 2003 and 2005. Results support the first and third hypotheses but not the second one. *Q.suber* recruitment densities ranged from 0 to 7200 plants per hectare. The complete regeneration process (from recruitment to growth) occurred on old fields; well-established seedling banks were abundant under forest canopies; recruitment in shrublands was practically null. To better understand *Q.suber* recruitment, both landscape configuration and interactions with other *Quercus* species should be considered.

Introduction

Natural oak regeneration is the product of complex processes such as acorn production, predation, animal dispersion, germination and establishment in the habitat where the acorns were dispersed, and finally, growth to mature trees (Schupp 1990). The combination of all these processes may determine the success or failure of oak regeneration and the final fitness of this species to a given set of conditions. Thus, evaluating natural regeneration is an integrative way to evaluate fitness and provides a first indication of the future of the populations under study.

Quercus suber (cork oak) is an evergreen tree species from the western part of the Mediterranean Basin (Tutin et al. 1964). In the Iberian Peninsula, most *Q.suber* occur in a highly managed savannah-like agrosystem (called *dehesa* or *montado*) on acidic soils (the core area). Nevertheless, several patches of cork oak (peripheral cork oak patches) also occur in the eastern part of the peninsula, where calcareous soils are

---

[6] Pons,J. and Pausas, J.G. 2006. Oak regeneration in heterogeneous landscapes: The case of fragmented Quercus suber forests in the eastern Iberian Peninsula. Forest Ecology and Management 231 (1-3): 196-204.

dominant. There are some large *Q.suber* forests in the northern part of the eastern Iberian Peninsula (Catalonia, ca. 70,000 ha, Montero et al. 1994); however, patch size decreases towards the south by about three orders of magnitude. Thus, in the Valencia region (eastern Iberia), the main *Q.suber* forest patches range from ca 70 to ca 7000 ha (Pausas et al. 2004) and are considered marginal and fragmented, and their future has been questioned. Even so, there is still some cork industry in the region. In fact, cork oak forests are protected by the European Union (Habitat directive 92/43/EEC), and the cork oak is considered an important species for the socio-economic development of some European regions due to its potential use in sustainable forestry (*Q.suber* products, cork and acorns, do not require the elimination of trees but rather their protection).

Furthermore, *Q.suber* is a very good candidate for reforestation plans in the Mediterranean area due its efficient and rapid post-fire regeneration capacity (Pausas 1997). All these aspects contribute to the importance of amassing knowledge on this species and its natural regeneration capacity in order to focus further restoration plans (Mosandl and Kleinert 1998, Pausas et al. 2004). To date, however, very little research has been performed on the regeneration of *Q.suber* (Montero et al. 1994), and it has been carried out only in the core area of the species distribution. There is increasing evidence of the conservation and biodiversity value of peripheral populations (Lesica and Allendorf 1995, Hampe and Petit 2005), and specifically of *Q.suber*, due to the distinct genetic pools between central and peripheral populations (Jiménez et al. 1999).

Most current landscapes are highly heterogeneous at several spatial scales, and studies on oak dispersal and regeneration should account for this spatial variability in order to understand the future of this species. Thus our initial hypotheses are framed within different spatial scales: between eastern and western Iberian Peninsula, between different sites of the eastern Peninsula, and between different patch types within the landscape.

Regeneration problems have been described for a variety of *Quercus* species (e.g., Shaw 1968, Mellanby 1968, Loftis and McGee 1993, Lorimer et al. 1994), but little is known about regeneration of Mediterranean species. Part of the research on Mediterranean *Quercus* has been performed in the *dehesa* agrosystems of SW Spain (Plieninger et al. 2004, Pulido and Díaz 2005). In such *dehesas*, oak regeneration seems to be much lower than in forest ecosystems (Pulido and Díaz 2005), probably because intense human impacts (Plieninger et al. 2004) have resulted in an unsuccessful acorn dispersal and a heavy grazing pressure (Pulido and Díaz 2005). In eastern Iberia, these pressures (intense human impact and grazing) have decreased in recent last decades due to rural exodus and abandonment processes occurring on European Mediterranean coasts (Pausas 2004). Thus, our first hypothesis is that *Q.suber* regeneration in eastern populations will be higher than *Quercus* regeneration in dehesas.

Our second hypothesis is that regeneration will decrease from northern (larger) to southern (smaller) populations (site-scale analysis) and that this may be due to different processes. It is well known that small populations may face both inbreeding effects and genetic erosion, which result in a reduction in their viable seed production and seed quality and make them more prone to extinction (Lawton 1993, Vucetich and Waite 2003). This would be reflected in the regeneration process. In this context, it has been demonstrated that marginal *Q.suber* populations have lower genetic diversity than central populations (Jiménez et al. 1999). Thus, we could expect a decreasing regeneration pattern that parallels the size of the different populations, especially with respect to the southernmost population (Pinet), which is considered small for a tree population (ca. 70 ha of low-density trees). Furthermore, the fact that forests are the main habitat for the oak-dispersal agent (the European jay *Garrulus glandarius*) and there is a decreasing abundance of forest stands from north to south in our study area could also contribute to reduced *Q.suber* regeneration. Finally, small populations have a higher edge effect, which may imply higher predation (Santos and Telleria 1997) and disturbance sensitivity. All these processes would suggest that regeneration would decrease from northern to southern *Q.suber* populations in eastern Iberia.

Our third hypothesis is that, at landscape scale, regeneration will not be randomly distributed because environmental conditions and biotic factors (dispersal, predation, competition) affecting seed and seedling success vary in different landscape units (Grime and Hillier 2000, Gómez et al. 2004). Thus, given the current heterogeneity of our landscapes we expect differential recruitment and regeneration processes for different spatial units.

To test these hypotheses we quantified the amount and variability of *Q.suber* recruitment and that of all other *Quercus* species appearing within the study area in different landscape units around the three main *Q.suber* patches in the Valencia region. We considered the following non-sequential stages of regeneration: recruitment, development of seedlings, formation of a seedling (sapling) bank and development to mature trees. The final objective was to understand to what extent these fragmented marginal cork oak populations are stable and would persist in the study area. Alternatively, other oak species may preferentially occupy the potential habitat of *Q.suber* and thus displace it.

Methods

Study area

The study area is located inside the Valencia region, which borders the Mediterranean coast in eastern Spain (Fig.1). The climate is typically Mediterranean. The vegetation is a product of a long history of fire and land use, and many slopes were terraced and cultivated in the past, and then abandoned. In this region there are 3 main *Q.suber* patches (hereafter sites), from north to south: Espadà (Castelló, lat = 39° 52’, ca. 70000 ha), Calderona (València, lat = 39° 44’, ca. 7000 ha) and Pinet (València, lat = 38° 59’, ca. 70 ha). Soils in Calderona and Espadà are mainly acidic soils on sandstones. In Espadà soil pH ranges from 4.9 to 6.4 (mean: 5.7). In Pinet, cork oak occurs in non-carbonated soils on dolomites, with pH ranging from 5.5 to 7.5 (mean: 6.5). Average annual rainfall in these cork patches ranges from 500 to 800 mm, with a clear seasonal pattern showing two peaks, in spring and autumn. Espadà and Calderona are currently Natural Parks.

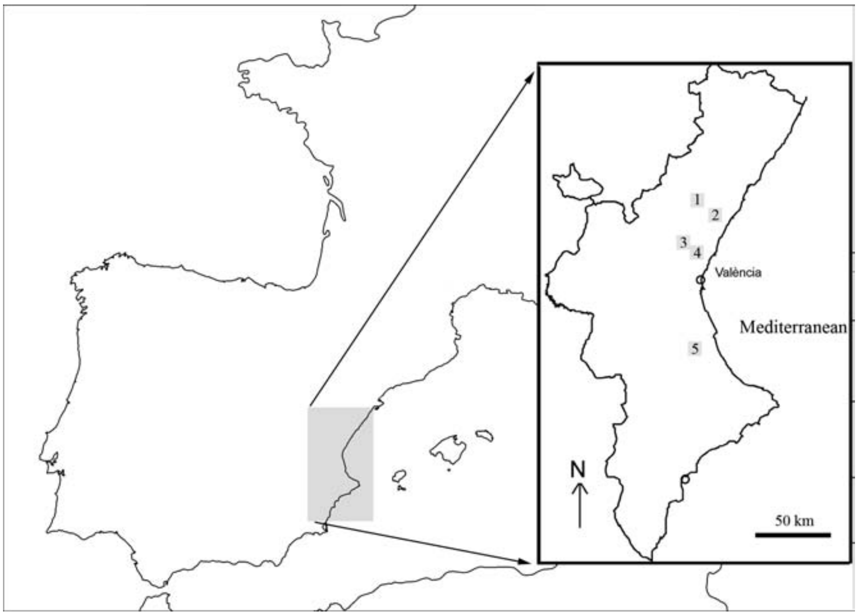


Fig.1. Localisation of the five sampled Quadrats. From north (top) to south (bottom), two quadrats in Espadà (1, 2), two quadrats in Calderona (3, 4) and one quadrat in Pinet (5).

Sampling

In order to study a wide range of cork oak landscape conditions, we selected five 3 x 3 km areas (hereafter quadrats) distributed on the 3 main sites: two quadrats on the Espadà site, two in Calderona and one in Pinet (Fig.1). The quadrats include a variety of both vegetation types and environmental conditions (soils, aspect), but they mostly fall within the range of environmental conditions under which *Q.suber* is observed in the study area. For instance, soils are all non-carbonated, from acidic sandstones (mainly Espadà) to dolomitic soils (in Pinet). We mapped each quadrat into simple vegetation units during an intense field sampling; then the information was translated to digital maps for subsequent landscape analysis. Vegetation units were aggregated into seven vegetation types (hereafter Vtypes) for the regeneration sampling, as follows:

Yaf: Recently abandoned (young) old fields, with grass-dominated vegetation.

Oaf: Old fields abandoned long ago, currently dominated by woody plants.

Maf: Old fields that apparently had an age between Yaf and Oaf due to the combination of grass and young woody plants

Shrub: Shrublands

PineS: Pine forest with shrubby understory

PineC: Pine forest with clear understory, that is, with low shrub cover or grassy understory

Cork: Cork oak forest

In each vegetation unit, we sampled *Quercus* regeneration within 12.5 x 12.5 m plots. In addition to *Q.suber*, other oak species found in the study area are two evergreens (*Q.ilex, Q.coccifera*) and one semi-deciduous (*Q.faginea*) species. The number of plots included in each Site and Vegetation unit varied from 0 to 5 depending on the availability of the VTypes on each Site (Table 1); for instance, the only old fields in the Pinet area were recently abandoned (Yaf), while Oaf and Maf were missing. In June 2003 we counted and tagged all oak individuals regenerating on 36 plots. In June 2004 and 2005 we revisited all plots to quantify both the new recruitment and the aerial stem die-back of the individuals tagged in 2003. Additional plots were set in 2004 and 2005, reaching a total of 61 plots. Recruitment was classified in four categories: Seedlings (with acorn or cotyledon scatters still attached), saplings (< 50 cm without acorn and with a clear main stem), resprouting sapling (< 50 cm with evidence of new shoots after top killing) and small trees (50 - 300 cm).

Table 1. Number of plots sampled in each VType and Site.

	Espadà	Calderona	Pinet	Total
Yaf	3	3	2	8
Maf	2	1	0	3
Oaf	3	3	0	6
Shrub	3	5	3	11
PineS	3	1	3	7
PineC	4	5	3	12
Cork	3	4	3	10
Others	2	1	1	4
Total	23	23	15	61

Data analysis

Landscape analysis was performed for each of the five quadrats using FRAGSTAT (McGarigal and Marks 1994). Regeneration density was expressed as the number of individuals in 100 m^2. Regeneration variability was tested against VType and site using ANOVA with Quadrat as the nested factor within Site. Previous to analysis, regeneration density was square-root transformed. A one-way model with both VType and Site was also performed to check the different amounts of variance explained by each of these two factors.

Results

Landscape analysis

Landscape pattern differs between different Quadrats and Sites (Table 2). The northern quadrats (Espadà) are more forested than the Calderona and Pinet quadrats. However, the type of forest differs between the two Espadà quadrats: Quadrat 1 includes a mixed forest with several oak and pine species, while Quadrat 2 is the result of several recent fires and the only dominant tree species is *Q.suber*. Quadrat 3 (Calderona) is the most patched quadrat, with both forests and shrublands. Quadrat 4 (Calderona) and Quadrat 5 (Pinet) are very homogeneous landscapes dominated by shrubs and result from fires during the 1990s. That is, forests decrease from Espadà to Pinet and from Quadrat 1 to Quadrat 5.

Table 2. Composition and configuration attributes of the five landscape quadrats considered. In bold are relevant figures emphasising differences between Quadrats (see main text and Fig. 1).

	Espadà		Calderona		Pinet
	Q1	Q2	Q3	Q4	Q5
Landscape composition (% area)					
Fields	5.1	5.6	8.0	0.9	2.9
Old fields	2.0	13.6	4.1	0.3	1.4
Shrublands	29.1	22.3	43.7	81.4	85.6
Tree-shrublands	7.4	18.0	9.6	2.5	3.3
Pine forest	31.5	0.7	18.5	9.7	4.0
Oak forest	24.6	38.4	15.4	4.1	2.7
Urban	0.1	1.5	.6	0.1	0.0
Others	0.2	0.0	0.0	0.9	0.0
Landscape configuration					
Number of Polygons	150	173	194	72	58
Mean Polygon Size (ha)	6.0	5.2	4.6	12.5	15.5
Polygon Size SD	23.3	25.2	22.5	85.5	99.0
Total Edge (km)	169	191	209	83	78
Shannon Diversity Index	1.747	1.741	1.757	1.495	1.552

Recruitment

Recruitment of *Q.suber* is highly variable, ranging from 0 to 76.2 individuals/100 m^2 (Table 3), and shows a clearly skewed distribution (Figure 2a). Most of the recruitment

(50.1%) consisted of sprouting saplings, 24.4% were saplings, and the remaining were small trees (14.2%) and seedlings (11.3%). The distribution of each of these recruitment classes follows a similar pattern to the total regeneration. In 2005, 15 of the 55 plots showed no *Q.suber* regeneration. Changes in regeneration density follow a bell-shaped curve for both year pairs (Shapiro test, Table 3), with both gains and losses (Fig. 2b).

Table 3. Basic statistics for *Quercus* density values (individuals per 100 m2) found in the study area in plots where at least one individual was present. P= P-values: (Shapiro test): * P<0.05, ** p<0.01, *** p< 0.001

	n	%	Mean	SD	Max	P
Qs Year 2003	30		15.4	16.1	58.2	
Others Year 2003	31		5.5	11.0	54.4	
Qs Year 2004	48		16.1	18.7	67.8	
Others Year 2004	48		6.1	10.7	58.9	
Qs Year 2005	55		14.7	18.4	76.2	
Others Year 2005	53		5.9	10.2	58.9	
Qs Difference 2004-2003	29		+1.6	4.7	13.4	*
Others Difference 2004-2003	30		+1.3	2.7	9.0	***
Qs Difference 2005-2004	48		-0.4	3.6	9.0	**
Others Difference 2005-2004	48		+0.2	1.9	5.8	***
Total (n=54)		100,0	15.0	17.7	67.8	
Seedlings		11.3	1.7	2.4	9.6	
Saplings		24.4	3.7	5.8	22.4	
Sprouting saplings		50.1	7.5	12.3	57.6	
Young trees		14.2	2.1	3.8	15.4	

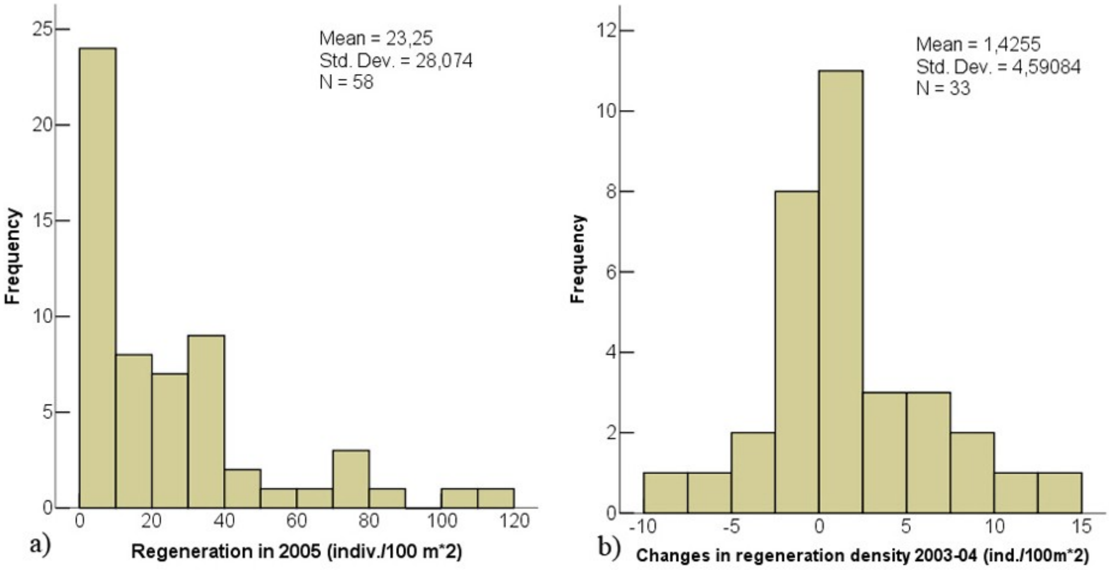


Figure 2. (a) Frequency distribution of regeneration (individuals/100 m^2) in 2005 and (b) changes in regeneration density (individuals/100 m^2) between 2003 and 2004 (positive values are increases and negative values decreases; right).

Overall, regeneration of other *Quercus* species represents 28% of the total *Quercus* regeneration, and ranged from 0 to 58.9 individuals/100 m^2 (mean for 2005 = 5.9 ± 10.2 SD), with a very strong skewed distribution: 30% of the plots had no regeneration of other *Quercus* species and 85% had less that 9 individuals/100 m^2. Changes in the regeneration density of these species are small and also follow a bell-shaped curve (Table 3). The species composition of this regeneration includes 54% of *Q.ilex*, 27 % of *Q.coccifera* and 19 % of *Q.faginea*.

Total *Q.suber* recruitment density for the 3 years of the study was significantly related to Vegetation Type (Vtype) and Site, and most explained variance was due to VType (R^2 in Table 4). Similar trends were observed for each regeneration class (Table 4) with the exception of small trees, for which the Site effect was more important than the VType effect. The highest recruitment was found in forest ecosystems, either pine (pineC) or cork oak forest (means for 2004 = 23 and 30.4 indiv./100m^2, respectively), while the lowest was in shrublands (mean = 0.27 indiv./100m^2). Old fields and shrubby pine forests (pineS) showed intermediate regeneration values (mean = 6.6 - 9.6 indiv. / 100m^2) (Table 5). Looking at the different recruitment classes (Figure 3) a pattern emerges: a) In old fields, there is a trend toward decreasing seedling and sapling density and increasing young trees with abandonment age, with very few levels of sprouting saplings in all old fields; b) in the forests, the distribution of recruitment classes is similar, with increasing density from shrubby forest to cork forest; and c) in shrublands, recruitment is almost negligible.

Table 4. ANOVA results for *Q.suber* density and height. P-values for the model with VType (V), Site (S), Quadrat nested within Site (Q (S)), and the interaction (V x S); and R^2 of the full model and the model with only Vegetation type, with only Site and with both Vegetation type and Site (V+S). Density was square-root-transformed previous to the analyses. ns indicates p > 0.1

	p-values					R^2		
	Model	V	S	Q(S)	VxS	V+S	V	S
Total density 2003	0.001	0.005	0.003	ns	ns	0.851	0.440	0.338
Total density 2004	0.000	0.000	0.002	ns	ns	0.783	0.484	0.237
Total density 2005	0.000	0.000	0.000	ns	ns	0.806	0.530	0.185
Difference 2003-04	0.082	ns	0.061	0.063	ns	0.683	0.424	0.278
Difference 2004-05	ns	ns	ns	ns	ns	0.250	0.072	0.068
Seedling density	0.002	0.023	0.001	ns	0.053	0.654	0.247	0.221
Sapling density	0.017	0.005	0.059	ns	ns	0.580	0.331	0.150
Sprout sap. density	0.000	0.000	0.006	ns	ns	0.789	0.582	0.121
Young tree density	0.000	0.008	0.000	ns	0.010	0.742	0.240	0.269

Table 5. Summary of the significance between VTypes for each regeneration class (Figure 3). Regeneration densities in different VTypes with different letters are significantly different. Differences for seedlings, sapling and recruits are not significant. The mean density values decrease from a to c, within each regeneration class

	VTypes						
Regeneration classes	Yaf	Maf	Oaf	Shrubs	PineS	PineC	Cork
Sprouting seedlings	bc	b	bc	bc	b	b	ab
Young trees	b	ab	a	b	ab	b	b

There is also some variation between sites, with Espadà presenting the highest plant density (22.35 ± 18 indiv./100m^2), Calderona the lowest (6.7 ± 9.7 indiv./100m^2), and

Pinet an intermediate value close to that of Espadà (19.2 ± 20.4 6 indiv./100m^2). These differences are due mostly to the number of sprouting saplings (Figure 4).

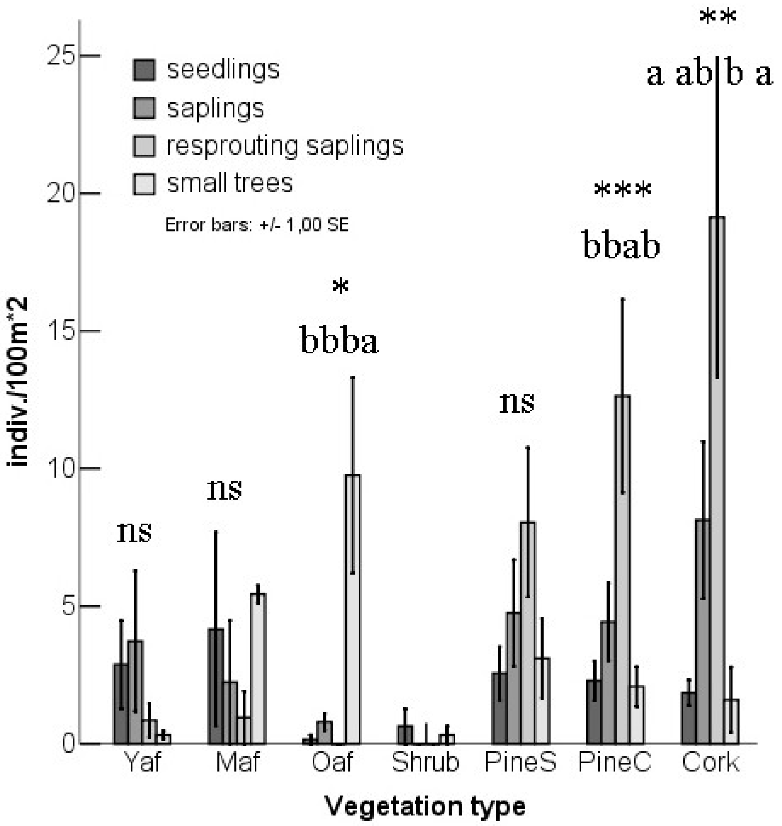


Figure 3. Mean *Q.suber* regeneration density by VType and regeneration class. Non-different regeneration class density means (indiv./100 m^2) are identified by the same letters in each VType. Table 5 shows the significance of density differences between VTypes for each regeneration classes.

The changes observed in *Q.suber* recruitment density among the 3 years studied were not related exclusively to VType; some of the changes (for 2003-04) were related to Quadrat or Site (Table 4).

In general, the regeneration distribution pattern of the other *Quercus* species considered (*Q.ilex*, *Q.faginea* and *Q.coccifera*) was similar to that of *Q.suber*, when respective adults were nearby (not shown). Nevertheless, the relative abundance of other *Quercus* species (from 0.5% at Quadrat 2 to 54.9 % in Quadrat 3) differs in each site and each Quadrat.

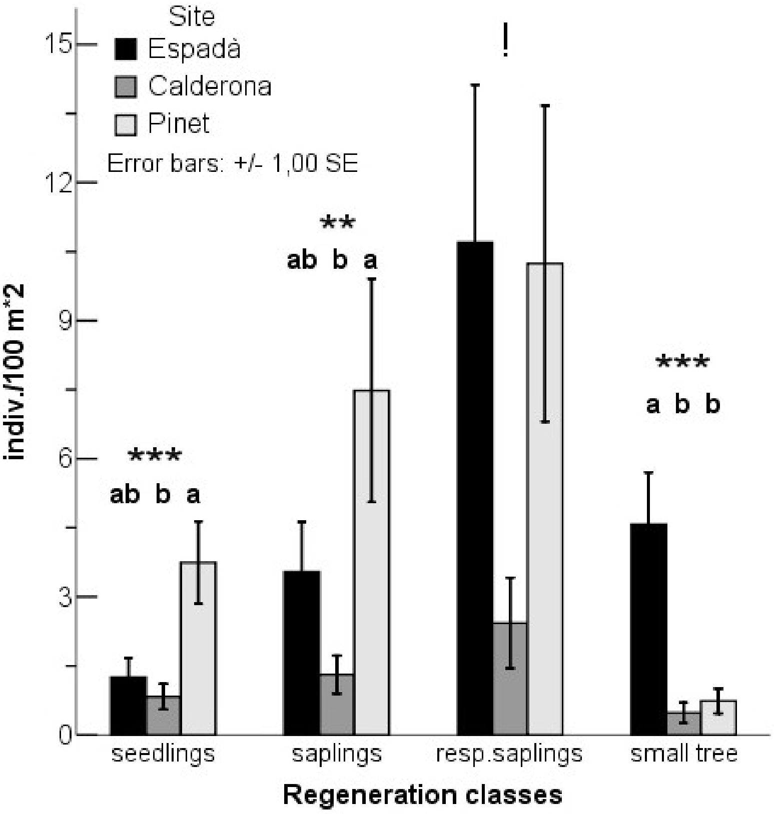


Figure 4. Mean regeneration density on the three studied sites for each regeneration class of Q recruits. Significant differences are coded by different letters. Symbols used for significant probability are: ! p<0.1, * p< 0.05, ** p< 0.01, *** p<0.001.

Discussion

Cork oak recruitment pattern

To our knowledge this is the first paper studying *Q.suber* recruitment at landscape level, and thus, most of the comparisons we make hereafter will be with other *Quercus* species, especially *Q.ilex*. Overall *Q.suber* recruitment densities in marginal cork oak populations of the eastern Iberian Peninsula are highly variable depending on the vegetation type considered, and they fall within the broad range of density values available for *Q.ilex* in nearby areas (see Table 6). In this region the habitat most similar to the western Iberian dehesa would probably be the old fields because both dehesas and old fields have non-continuous tree cover (absence of shaded microsites) with a large proportion of shrub-free soil. In our old fields, total densities are between 5 and 9 times larger than in the dehesas. This may be due both to the current low grazing levels in our area and the dispersal limitation found in dehesas (Pulido and Díaz 2005); a dispersal limitation has also been observed in North American forest-savannah ecotones (Weltzin and McPherson 1999). Nevertheless, the maximum densities of *Q.ilex* seedlings under cospecifics reported in a study on mature Holm oak in Catalonia

(NE Iberian Peninsula) were much greater than the maximum densities recorded in our study (Table 6).

Table 6. Mean, SD and maximum recruitment values observed for different European *Quercus* species in relation to their habitat. Species are *Quercus ilex* (Qi), *Q.suber* (Qs), *Q.petraea* (Qp). For the Iberian regions, cardinal locations within the Iberian Peninsula are given in brackets.

Habitat	sp	Mean ± SD	Max density recruits/ha	Study site	Reference
Dehesas[1]	Qi	136.4	>342	Extremadura (SW)	Plieninger et al. 2004
Old fields	Qs	708 ± 805	2176	València (E)	This study
Pine forest	Qs	2309 ±1698	5248	València (E)	This study
Pine forest	Qi	-	5461	València (E)	Own data (unpublished)
Pine forest[2]	Qi	1600	3800	Catalunya (NE)	Lookingbill and Zavala 2000
Cork forest	Qs	806		Extremadura (SW)	Currás et al 1995
Cork forest	Qs	3040 ± 2103	6784	València (E)	This study
Holm oak forest	Qi		29000	Catalunya (NE)	Espelta et al. 1995
Holm oak forest	Qi		40000	Catalunya (NE)	Gracia et al 2001
Holm oak forest[4]	Qi	1763-18024	-	Catalunya (NE)	Retana et al. 1999
Pine forest[5]	Qp		4255	Saxony (Germany)	Mosandl and Kleinert 1998

[1]Saplings; [2]Seedlings: individuals under 25 cm in height without a well-developed lignotuber; saplings: >25 cm in height but <2.5 cm DBH; [3]Variability between 6 years; [4]variability between 2 sites and 3 aspects. [5]Pinus sylvestris

The primary source of regeneration variation was found to be the vegetation type (habitat); moreover, the distribution of the regeneration between vegetation types was consistent (i.e., showing similar patterns) between sites, which suggests that similar processes were occurring on each site. These main processes are:

(a) There is very limited recruitment in shrublands (Figure 3). Although we cannot yet pinpoint the causes, possible hypotheses are: limited seed arrival, high seed predation, germination failure or competitive exclusion. As all of these are sequentially connected, the first seems to be the limiting one since the jay's habit of directing dispersal to open soil and actively avoiding closed shrublands has been widely reported (Bossema 1979, Darley-Hill and Johnson 1981, Kollmann 1996, Johnson et al. 1997, Frost and Rydin 2000, Gómez 2003). Furthermore, high acorn predator densities (mouse) are often found under shrublands (Wilson 1990, Alcantara et al. 2000, Hulme 1994, Hulme 1997). However, although limited, some recruitment occurred in shrublands composed mainly by *Erica* species under pines, and thus, a possible 'filtering' of recruits depending on shrub composition and structure (George and Bazzaz 1999) deserves future attention in Mediterranean systems.

(b) There is a clear dynamic process in old fields (Figure 3 left): recruitment is observed at the beginning of abandonment; then, as the vegetation cover increases acorn inputs decrease and seedlings develop into saplings. Finally, shrubs and herbs cover ca. 100% of soil and no new seedlings appear (as in the shrublands), suggesting that the recruitment window closes when saplings develop into young trees. This emphasises the importance of the temporal regeneration window in old field succession (Kollmann 1995). Although we do not have information on growth, the very low densities of sprouting saplings (i.e., low top killing) suggest very low stressful conditions in old fields, with the exception of eventual anthropogenic disturbances or grazing at the beginning of abandonment.

(c) In pine and oak forests, there is a high recruitment of new individuals; however, seedling desiccation and top killing is a very important process here, and many sprouting seedlings accumulate in a sprouting seedling bank without developing into trees (Figure 3 right). Thus, under these conditions, *Q.suber* form a typical seedling bank (Kohyama 1983, Marks and Gardesu 1998, Antos et al. 2005), that is, a pool of suppressed slow-growing individuals waiting for improved growing conditions. *Quercus* seedling banks under conifers seem to be widely spread for different species and environments (Mosandl and Kleinert 1998, Montero et al. 1994).

Variations at regional scale (between sites) occur primarily in the size of the seedling bank (Figure 4) and are difficult to attribute to one unique cause. Our initial hypothesis that the recruitment density would decrease as the *Q.suber* population size decreased must be rejected because the northern and southern populations (Espadà and Pinet) showed similar recruitment levels while the central population (Calderona) showed lower recruitment levels. Alternative hypotheses may be related to (a) competition for dispersal, and (b) landscape structure. All *Quercus* species have the same dispersal agents and acorns of different species may compete to be dispersed. Thus, considering all *Quercus* species, the northern population (Espadà) has the densest *Quercus* recruitment. This would suggest that the future of *Q.suber* may interact with the dynamics of other *Quercus* species, including different degrees of asynchrony in the masting (Kelly 2002). The landscape hypothesis suggests that the configuration and amount of suitable patches in relation to source patches may determine recruitment. For instance, it was expected that the Pinet population would have lower recruitment than the Calderona population both because Pinet is a small, marginal *Q.suber* population and because the amount of forest (jay habitat) in the area is very low (Table 2), but the opposite was true. Quadrat 4 in Calderona and Quadrat 5 in Pinet have a similar landscape composition (dominated by shrublands, Table 2), but the spatial configuration of the landscape is different (Figure 5) in such a way that in Quadrat 5 the habitats with higher recruitment (pine forests and old fields) are surrounded by the source of acorns (cork oak forest), while in Quadrat 4 they are more spatially segregated. Thus, in Quadrat 5 shorter dispersal distances (jay flights) are required, which may explain the higher recruitment in Quadrat 5 than in Quadrat 4.

Furthermore, the small amount of forest in the Pinet area, which we hypothesised to be negative because of the low jay habitat, may in fact be positive for regeneration because of the higher forest-to-jay pair ratio. Contrary to the results by Santos and Telleria (1997), overpressure by rodent populations on acorns in smaller forests does not seem to occur in our area as *A.sylvaticus* usually showed a lower preference for the forest habitat than for the surrounding matrix (shrubland), probably because of the higher predation risk in the forest (Díaz et al 2005). A further difference between both Sites is that red squirrels (*S.vulgaris*) were observed at Calderona (Q4) but not at Pinet (Q5); nevertheless, the role that this animal might have on recruitment is still unknown. All these hypotheses are at a smaller scale (Quadrat) than the Site, and they need further research.

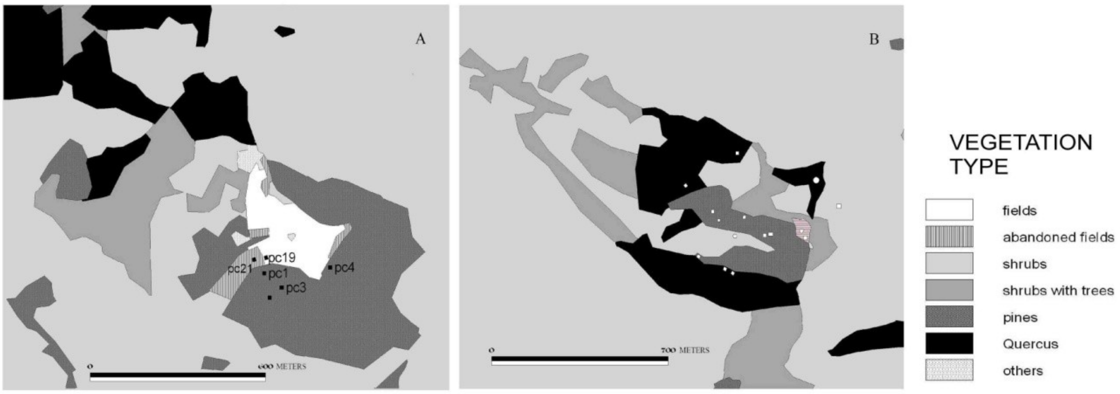


Figure 5. Differences in spatial vegetation pattern at (A) Portacoeli (Quadrat 4) and (B) Pinet (Quadrate 5) in relation to the position of studied plot (black dots in A and white dots in B). In A the susceptible regeneration area (pine forests and fields) is aggregated to SW, at longer distances from acorn sources (black patches) than in B. In B, *Q.suber* regeneration densities are greater, probably because the susceptible regeneration area is surrounded by acorn sources. Both areas are included in a shrubland matrix (pale grey).

Competitiveness from other *Quercus* at regeneration level seems to occur but our data are too limited to state general rules despite showing that some trends arise: in mesic forested areas with the absence of fires, *Q.ilex, Q.faginea* (and on more humid sites, *Q.pyrenaica*) seem to reduces *Q.suber* regeneration (Villamalur area, Quadrat 1). The same seems true for *Q.ilex* and *Q.coccifera* in xeric areas (Calderona). However, the current and future fire regime seems to favour *Q.suber* due to its fire resistance mechanisms (Pausas 1997).

Implications for cork oak regeneration

Our results indicate that good regeneration currently occurs on abandoned land. However, most of these fields were abandoned 25-40 years ago. As time passes, more fields will become incapacitated for new acorn arrival because of herb and shrub inhibition (Kollmann 1995). The lack of wild herbivores and the abandonment of extensive livestock-breeding in Mediterranean dry areas have contributed to the homogenisation and loss of open areas in the region. Nevertheless, this loss of heterogeneity and continuity of fire fuels may increase the annual fire frequency and area burned (Pausas 2004). And *Q.suber* will probably take advantage of this situation through 3 mechanisms: its strong fire resistance (Pausas 1997) may give it a competitive advantage; fire may act as a grazer (Bond and Keeley 2005) and re-open the regeneration window for *Q.suber* in old fields and shrublands; and despite the large amounts of recruitment in pine and oak forests (Fig. 3), regeneration does not occur, probably because the forest canopy reduces seedling growth. It has been proposed that close association with pines indicates a safe site for recruitment (Lookingbill and Zavala 2000); however, in such conditions, tree development is difficult without a disturbance and, in fact, seedling banks under pine cover may be released after fire.

In general, *Q.suber* regeneration in the Valencia region seems to be in good condition, and some growth at the expense of old fields and pine forests (after the more-than-probable fires) will most likely occur. On the other hand, because of the reduced size and poor substrate conditions of the Pinet population, there is a need for some kind of sylvicultural intervention to increase the population here. On this site we observe a lack of regeneration outside the forest and especially in old fields >1.5 km away. We believe that the matrix of shrublands (88.9% of the area) has limited the populations and the dispersal activities of the jay. Since the acorns are not arriving naturally, the most economical alternative would be to substitute the dispersal vector by artificial means prior to regeneration-window closure.

Acknowledgements

We thank Cristina Betseller, Eloi Ribeiro, Nestor Pons, Marcos Mata, Ana B. Ribes, and Alicia Roman for collaborating in the field sampling. This work was funded by the CREOAK European project (QLRT-2001-01594) and the VARQUS Spanish project (CGL2004-04325/BOS). CEAM is supported by *Generalitat Valenciana* and *Bancaixa*.

References

Alcantara,J.M. 2000. Factors shaping the seedfall pattern of a bird-dispersed plant. Ecology 81(7), 1937-1950.

Antos, J.A., Guest,H.J., Parish,R. 2005. The tree seedling bank in an ancient montane forest: stress tolerators in a productive habitat. J. Ecol. 93, 536-543.

Bond,W.J., Keeley,J.E. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol. Evol. 20, 387-394

Bossema,I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. Behaviour 70, 1-117.

Carmel,Y., Flather,C.H. 2004. Comparing landscape scale vegetation dynamics following recent disturbance in climatically similar sites in California and the Mediterranean basin. Landscape Ecology 19, 573-590.

Currás,R., Guara,M., Montero,G. 1995. Distribucion de los efectivos del sotobosque de un alcornocal extremeño sometido a diferentes tratamientos selvicolas. Ecologia 9, 177-190.

Dalling,J.W., Muller-Landau,H.C., Wright,S.J., Hubbell,S.P. 2002. Role of dispersal in the recruitment limitation of neotropical pioneer species. Journal of Ecology 90, 714-727

Darley-Hill,S., Johnson,W.C. 1981. Acorn dispersal by the Blue Jay (*Cyanocitta cristata*). Oecologia 50, 231-232.

Díaz,M., Torre,I., Peris,A., Tena,LL. 2005. Foraging behaviour of wood mice as related to presence and activity of genets. Journal of Mammalogy 86(6), 0000-0000.

Espelta,J.M., Riba,M., Retana,J., 1995. Pattern of seedling recruitment in West-Mediterranean *Quercus ilex* forests influenced by canopy development. Journal of Vegeation Science 6, 465-472

Frost,I., Rydin,H. 2000. Spatial pattern and size distribution of the animal-dispersed tree *Quercus robur* in two spruce-dominated forests. Ecoscience 7, 38-44.

George,L.O., Bazzaz,F.A. 1999. The fern understory as an ecological filter: Growth and survival of canopy-tree seedlings. Ecology 80, 846-856.

Gómez,J.M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26, 573-584.

Gómez,J.M. 2004. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. Plant Ecol. 172, 287-297.

Gómez,J.M., Valladares,F., Puerta-Piñero,C. 2004. Differences between structural and functional environmental heterogeneity caused by seed dispersal. Funct. Ecol. 18, 787-792.

Gracia,M., Retana,J., Pico,F.X. 2001. Seedling bank dynamics in managed holm oak (*Quercus ilex*) forests. Ann.For.Sci. 58, 843-852.

Grime,J.P., Hillier,S.H. 2000. The contribution of seedling regeneration to the structure and dynamics of plant communities, ecosystems and larger units of the landscape. In: Fenner, M. (ed.). The Ecology of Regeneration in Plant Communities. pp. 361-374. CAB International.

Hampe,A., Petit,R.J. 2005. Conserving biodiversity under climate change: the rear edge matters. Ecol. Lett. 8, 461-467.

Hulme,P.E. 1994. Post dispersal seed predation in grassland: its magnitude and sources of variation. Journal of Ecology 82, 645-652

Hulme,P.E. 1997. Post-dispersal seed predation and the establishment of vertebrate dispersed plants in Mediterranean scrublands. Oecologia 111, 91-98

Jiménez,P., Agundez,D., Alia,R., Gil,L. 1999. Genetic variation in central and marginal populations of *Quercus suber* L. *Silvae Genetica* 48, 278-284.

Johnson,W.C., Adkisson,C.S., Crow,T.R., Dixon,M.D. 1997. Nut caching by blue jays (*Cyanocitta cristata* L.): Implications for tree demography. American Midland Naturalist 138, 357-370.

Kelly,D., Sork,V.L. 2002. Mast Seeding in Perennial Plants: Why, How, Where? Annu. Rev. Ecol. Syst. 33, 427-447.

Kohyama,T. 1983. Seedling stages of two subalpine *Abies* species in distinction from sapling stage: a matter-economic analysis. *Botanical Magazine, Tokyo* 96, 49-65.

Lawton,J.H. 1993. Range, population abundance and conservation. Trends Ecol. Evol. 8, 409-413.

Kollmann,J. 1995. Regeneration window for fleshy-fruited plants during scrub development on abandoned grasslands. Ècosience 2, 213-222.

Lesica,P., Allendorf,F.W. 1995. When peripheral populations are valuable for conservation. Conserv. Biol. 9, 753-760.

Loftis,D.L., McGee,C.E. 1993. Oak regeneration: serious problems, practical solutions. Gen. Tech. Report SE-84 USDA Forest Service, Ashville, NC, 319 pp.

Lookingbill,T.R., Zavala,M.A. 2000. Spatial pattern of *Quercus ilex* and *Quercus pubescens* recruitment in *Pinus halepensis* dominated woodlands. *J. Veg. Sci.* 11, 607-612.

Lorimer,C.G., Chapman,W., Lambert,W.D. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. J. Ecol. 82, 227-237.

Marks,P.L., Gardesu,S. 1998. A case study of sugar maple (*Acer saccharum*) as a forest seedling bank species. J. Torrey Bot. Soc. 125, 287-296.

McGarigal,K., Marks,B.J. 1994. FRAGSTAT: Spatial pattern analysis program for quantifying landscape structure - Version 2.0. Forest Science Department, Oregon State University.

Mellanby,K. 1968. The effect of some mammals and birds on the regeneration of oaks. J. Appl. Ecol. 5, 359-365.

Montero,G., Torres,E., Cañellas,I. 1994. Regeneración de alcornocales. Síntesis biblográfica. Ecología 8, 271-283.

Mosandl,R., Kleinert,A. 1998. Development of oaks (*Quercus petraea* (Matt.) Liebl.) emerged from bird-dispersed seeds under old-growth pine (*Pinus silvestris* L.) stands. For. Ecol. Manage. 106, 35-44.

Pausas,J.G. 1997. Resprouting of *Quercus suber* in NE Spain after fire. J. Veg. Sci. 8, 703-706.

Pausas JG., 2004. Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). Climatic Change 63, 337-350.

Pausas,J.G., Pons,J., Vallejo,R. 2004. Cork Oak Restoration: developing techniques to enhance establishment of a threatened ecosystem (Spain). Ecological Restoration 22 (4), 289-290.

Plieninget,T., Pulido,F.J., Schaich,H. 2004. Effects of land-use and landscape structure on holm oak recruitment and regeneration at farm level in *Quercus ilex* L. dehesas. J. Arid Envir. 57, 345-364.

Pulido,F.J., Díaz,M. 2005. Regeneration of a Mediterranean oak: a whole-cycle approach. Ècoscience 12, 92-102.

Santos,T., Telleria,J.L. 1997. Vertebrate predation on holm oak, *Quercus ilex*, acorns in a fragmented habitat - effects on seedling recruitment. Forest Ecology and Management 98,181-187.

Shaw,M.V. 1968. Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in north Wales. J. Ecol 56, 565-583.

Schupp,E.W. 1990. Annual variation in seedfall, postdispersal predation, and recruitment of a Neotropical tree. Ecology 71, 504-515.

Schupp,E.W. 1995. Seed-seedling conflicts, habitat choice, and pattern of plant recruitment. American Journal of Botany 82, 399-409.

Retana,J., Espelta,J.M., Gracia,M., Riba,M. 1999. Seedling recruitment, in: Rodà,F., Retana,J., Gracia,C.A., Bellot,J. (Eds.), Ecology of Mediterranean evergreen oak forest, Springer-Verlag, Berlin, pp 89-103.

Tutin,T.G., Heywood,V.H., Burges,N.A., Valentine,D.H., Walters,S.M., Webb,D.A. (eds.) 1964. Flora Europaea. vol. 1. Cambridge University Press, Cambridge, UK.

Vucetich,J.A., Waite,T.A. 2003. Spatial patterns of demography and genetic processes across the species' range: null hypotheses for landscape conservation genetics. Conserv. Gen. 4, 639-645.

Weltzin,J.F., McPherson,G.R. 1999. Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones. Ecological Monographs 69, 513-534.

Wilson,M.F., Whelan,C.J. 1990. Variation in postdispersal survival of vertebrate dispersed seed: effects of density, habitat, location, season and species. Oikos 57, 191-198

Cork oak regeneration model[7]

ABSTRACT

Oak acorns are predated and dispersed by jays and rodents, but the balance between these two processes for each agent has seldom been quantified, especially at landscape level. To elucidate the relative contribution of these two species to oak regeneration we built a simple recruitment model, taking into consideration the coexistence of different oak species and the dispersers' acorn preferences. The model was based on field observations from five sites located in the eastern Iberian Peninsula. Specifically, we predicted cork oak (*Quercus suber*) regeneration under different scenarios. First we generated four scenarios combining two alternative acorn distributions by jays along with the occurrence of rodent dispersal. Then, we tested whether the acorn selection by jays modified the final densities of cork oak seedlings by computing four additional scenarios using a different acorn selectivity index. Predictions were validated against the field data to infer the most plausible scenario. The results indicate that both acorn dispersal and acorn dispersal efficiency are higher for jays than for rodents. Results also show that the jay tends to concentrate acorns in caches and that the jay preference for a particular oak species contributes to explain the uncoupling between acorn production and the observed recruitment pattern.

INTRODUCTION

Plant regeneration is the result of a complex balance between successive stages from seeds to adults (Harper 1977, Clark et al. 1999, Pausas et al. 2009). Biotic or abiotic factors may enhance one stage but not others, resulting in an uncoupled balance (Schupp 1995). For instance, enhanced seed production due to high resource availability would not necessarily lead to an increase in seedling density (Crawley and Long 1995). As these factors are variable over space and time, it is not easy to integrate results from different locations and different periods (Crawley and Long 1995, Pulido and Díaz 2005, Hampe et al. 2008).

The common jay (*Garrulus glandarius*) is the main acorn disperser for most European oaks, moving several thousand acorns/year (Haffer 1993, Cramp & Perris 1994), but showing different preferences for each species (Pons and Pausas 2007a). Moreover, different oaks have different acorn production patterns (Greenberg and Parresol 2003, Koening and Knops 2003, Chapter 2). Thus, in mixed oak forest landscapes, the link between acorn production and dispersal (and presumably recruitment) is further

---

[7] Pons, J. and Pausas J.G. Oaks, jays and mice: a simple model for *Quercus suber* regeneration, *in preparation*.

complicated by jay preferences for different acorns, a factor that has rarely been considered in oak regeneration models.

While jays disperse acorns from a few meters up to several Km from the mother tree (Bossema 1979, Gomez 2003, Pons and Pausas 2007a,c), the role of rodents as acorn dispersers is still under debate (Kollmann and Schill 1996, Li and Zhang 2003, Sun et al 2004, Gomez et al. 2008). Rodents probably act as acorn dispersers or predators depending on acorn production (Janzen 1971) and their own population dynamics (Sone et al. 2002). It is known that some rodent populations are driven by oak masting cycles (Stenseth 2002, Clotfelter et al. 2007, Suchomel 2007); thus, rodent acorn dispersal could also be enhanced during mast years (Vander Wall 2002, Zhang et al. 2008).

Recently, there have been several attempts to provide a model of the recruitment process for Mediterranean oaks (Cortés 2003, Pulido and Díaz 2005, Perez Ramos 2006, Acacio et al. 2007, Puerta-Piñero 2008). Here we offer a modelling approach based on transition probabilities, which takes into account the basic stages of the whole recruitment process with a spatio-temporal variability of six years, four sites, and seven vegetation types. As a novelty we have introduced the acorn production for all coexisting oak species in the area and a jay-oak specific coefficient of dispersal to account for dispersal competitiveness between oak species. We then generate six scenarios with an explicit transition model and compare the amount and type of recruits (final numbers of seedlings and saplings) with field data (Pons and Pausas 2006). The parameters of the model are largely based on our previous research performed in cork oak ecosystems (Pons and Pausas 2007a,b,c, 2008), plus references from the literature.

Specifically, our objectives are: 1) to evaluate the relative role of jays and mice in oak dispersal; 2) to test if the uncoupling between acorn production and recruitment can be attributed to the jay's acorn species selection; and 3) to evaluate the effect of the dispersal vectors on oak demography by calculating the total contribution of each disperser to the total number of recruits at landscape level (i.e., disperser effectiveness, or the proportion of the seed crop dispersed by a particular vector species which has recruited successfully in the adult population; Janzen 1971, Schupp 1993). To answer these questions we have built a simple oak recruitment model for *Quercus suber,* an evergreen oak from the western Mediterranean Basin, and we have compared the simulated results from different scenarios with field data.

Methods

Study area

The model is mainly based in previous research performed in three coastal mountain areas (Espadà, Calderona and Pinet) in the Valencia region, at the east of the Iberian Peninsula (Spain). The climate is typically Mediterranean and the landscape is a product of a long history of fire and land use. The study sites correspond to four of the five 3x3 km quadrats defined in Pons and Pausas (2006, 2008; Q1 and Q2 in Espadà, Q3 in Calderona and Q5 in Pinet) in which seven vegetation types were defined (Pons and Pausas 2006): fields, recently abandoned fields, oldfields, shrublands, cork oak forest, holm oak forest, and pine woodlands. Four oak species co-occur at landscape scale: *Quercus suber, Q. ilex, Q. coccifera,* and *Q. faginea*. We used *Quercus suber* (cork oak) as the study species because its populations are fragmented and threatened within the study area despite its socio-economic relevance and its status as a protected species at European level (Pausas et al. 2009).

The model

A simple model has been constructed using available published information on the oak regeneration process and our own observations. We used the year (2003-2008) as temporal units and the 3x3 km quadrats as spatial units, considering the seven vegetation units within the quadrats. The four oak species occurring in the study area were considered separately as there is evidence of differences in both acorn production (see Table 2 in Appendix 1) and acorn preference by jays (Pons and Pausas 2007a).

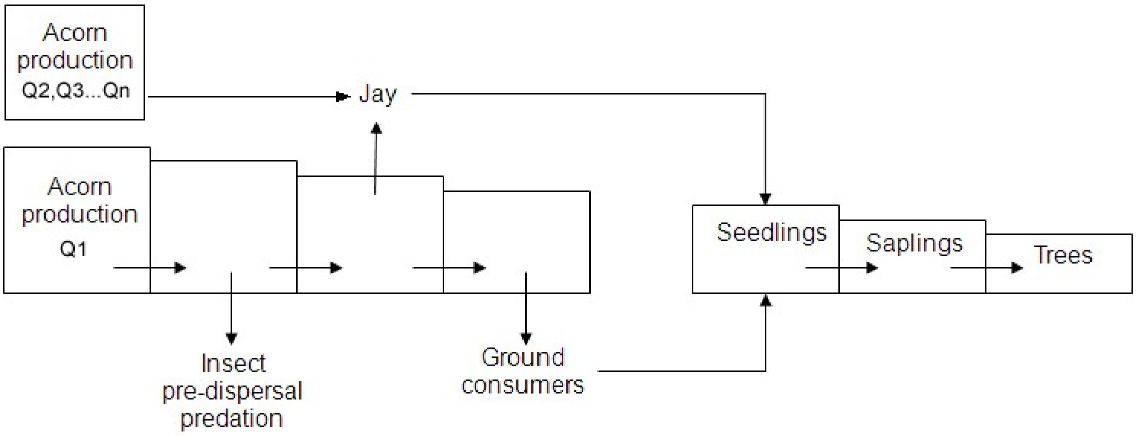


Fig.1. Simple general model for recruitment in *Quercus* species. As a novelty we have introduced a variable jay dispersal as a response to other *Quercus* species production

The model follows a direct timeline with five main stages (Fig. 1):

Acorn production: The mean Cork oak (*Q.suber*) crop (in number of acorns) per tree for each quadrat (2003-2007 from Chapter 2 plus 2008 data) was multiplied by the average tree density (200 trees/ha), estimated from available aerial photography of the study area. For the other oak species, the mean acorn production per tree was inferred from its proportionality to the cork oak crop and based on field surveys (2003-2008, see Appendix 1 for details).. Because the target species was *Q.suber*, more trees were counted for this species (981) than for the other oak species (*Q.ilex* n=542, *Q.coccifera* =369, *Q.faginea* =159).

Insect predation: Predispersal acorn infestation information was discounted from the acorn production numbers. Unfortunately, this type of data was available only for *Q.suber* and only for 2003-2005 (Chapter 2); infestation for 2006-2008 and for the other oak species was computed as the mean of 2003-2005 for each site. Thus our *1st assumption* was that predispersal insect predation was equal for the four oak species. Finally, to obtain sound acorn production per quadrat, the area occupied by each species was calculated from field data on species cover (Pons and Pausas 2008). Because *Q.coccifera* (a shrubby oak) is included in surveys in the shrubland category, an estimation of its proportion within the shrublands was obtained from field sampling (transects) in the study area (mean cover = 8.3%, n=9).

Jay dispersal: jays collected acorns from the tree crown (usually even before full maturation; pers.obs.), which implies an independent removal by other vertebrates that pick up acorns from the soil surface. It is known that the *field mouse* can carry out arboreal removals (Buesching et al. 2008), but the magnitude of this behaviour in our system is unknown and was not further considered. We selected an area of 300 ha with acorn crop availability for each pair of jays based on their estimated nest positions (Pons and Pausas 2008). The number of acorns removed by jays at each quadrat was computed as follows: a) the jay population was calculated as 2.5 times the number of nests to account for floating populations (Grahn 1990, Pons and Pausas 2008); b) a coefficient of acorn species selection by the jays was built on the basis of jays' acorn species preferences (Pons and Pausas 2007a), available acorn crop and mean production by tree as follows: (mean acorn production per tree of species *i*/sum of mean tree production of all oaks) x (total production of population of species *i*/total production of oaks) x (coefficient of acorn selection by jay); and c) the season crop per jay was set at 5000 acorns (Cramp & Perrins 1994) and the effectively dispersed proportion of acorns at 0.71 (Pons and Pausas 2007c). Afterwards, the proportion of acorn dispersal to each vegetation type was computed using data from Pons and Pausas (2007c).

Wildboar and rodent removal: after discounting the acorns removed by jays, we had to account for the acorns that fell to the ground and were available to forest-dwelling vertebrates, mainly rodents and wild pigs. The actual pattern of acorn removal by the two species is only speculative: we considered that wild pigs removed acorns in a density-dependent form, consuming a maximum of 50% of the acorns available on the soil surface and thus leaving the remaining acorns to rodents (*assumption 2*). Wild pig densities were set at 3.7 ind./Km^2 (mean value from Herrero (1995) for Aragón, the closest available data) and multiplied by a daily consumption of 2 kg (approx. 400 acorns; a conservative amount as compared with the 6-10 kg consumed by Iberian pigs in farmlands- cited in Rodriguez-Estevez et al. 2007). Although wild boar populations are known to oscillate depending on the acorn crop (Rosell et al. 1998), we did not introduce this variation as the heavy cynegetic pressure dilutes it (30-40 % annual population reduction, Rosell et al. 2001). The removal season was set at 90 days, which is approximately the period of acorn crop availability (Canellas et al. 2007). We estimated rodent densities (*Apodemus sylvaticus* mainly and *Mus spretus* when present; no data available on red squirrels) from available trapping experiments (Appendix 2). To obtain rodent acorn removals, densities were multiplied by a daily acorn removal of 20 acorns (*assumption 3*; estimated from video-tape recordings, Pons and Pausas 2007b) and by a season of 90 days. When there were still some acorns on the ground after the end of the season – i.e., saturation – we increased the rodent dispersal by a factor of 2 (*assumption 4*) to account for enhanced dispersal during masting years (Vander Wall 2002, Zhang et al. 2008). The proportion of acorns dispersed by rodents (3.2%, from Gomez et al. 2008) was multiplied by the proportion of acorns displaced out of the mother tree (55.1%, Gomez et al. 2008) as acorns under the mother tree cannot be considered effectively dispersed because their probability of becoming an adult plant is remote (Schupp 1993). Since rodents move acorns only a few meters from the origin, *Q.suber* dispersal was considered to be present only in cork oak forest. We are aware that secondary dispersal can increment the distances of acorn dispersal (Vander Wall 2002b), but this was not considered because of a lack of data in our study site. Also, for simplicity, acorn preferences by rodents were not considered.

Seedlings stages: to assess post-dispersal predation, germination and summer survival, we buried acorns at different vegetation types during a three-year period (2003-2005) and followed their fate. This methodology is used as an approach to simulate acorn dispersal (Herrera 1995, Gomez et al. 2003, Perez-Ramos and Marañon 2008). Monitoring finalized at the end of 2006, thus 3 summer effects were recorded for acorns seeded in 2003, 2 for the 2004 acorns and 1 for the 2005 acorns. Mean values were used for the 2006-2008 period. Detailed results are shown in Appendix 3.

The final output of the model was an estimated mean value of the number of seedlings for each year and site (and for each simulated scenario, see below). To provide an estimation of the variability of this mean value, we predicted the number of seedlings in 100 simulated plots assuming a Poisson distribution.

Scenarios

Relative role of jay vs rodents

We considered four scenarios, two in which only jays are considered acorn dispersers (J300, J30) and two in which both jays and rodents are considered dispersers (J300R, J30R, see Table 1). Two of the scenarios assume that jays patrol the acorn-crop territories (300 ha) and cache the acorns uniformly over the same area (J300, J300R). The other two scenarios (J30, J30R) consider that jays collect the acorns from the acorn-crop territories (300 ha, autumn-winter) but scatter-hoard in their nesting territories only (30 ha, spring-summer). The latter area is based on the idea that jays tend to concentrate acorns in their future nesting territory as a staple food supply for emergencies in nestling and young feeding (Grahn 1990, Ellenberg 2002). The seasonal difference in size of the jay territory was based on Rolando (1998). Our own observations suggested that this seasonal difference in the patrol and nest area could also be working in our study site. In the scenarios with rodent dispersal, we assumed that rodents only disperse acorns within the same vegetation type where they were collected (*Q.suber* in cork oak forest, *Q.ilex* in holm oak forest and *Q.coccifera* in shrublands). This is a plausible assumption as most acorns moved by rodents reach very short distances (average distance = 4.6±5 m; 90% of the acorns are moved less than 10 m; Pons and Pausas 2007b). Because of the lack of data on seedling recruitment for holm oak forest to perform the validation of the predictions, the role of rodents in recruitment was compared only in cork oak forests (see below).

Table 1. Summary of the simulated scenarios for testing the relative role of jays vs rodents (dispersal vector, jay caching area and jay acorn preferences considered). Mice dispersal was not considered in pine woodlands.

Scenarios	Dispersal in oak woodlands	Dispersal in pine woodlands	Jay caching area (ha)	Jay acorn preference Qi - Qf - Qs - Qc
J30	Jay	Jay	30	0.65 - 0.19 - 0.16 - 0.001
J300	Jay	Jay	300	0.65 - 0.19 - 0.16 - 0.001
J30R	Jay and mice	Jay	30	0.65 - 0.19 - 0.16 - 0.001
J300R	Jay and mice	Jay	300	0.65 - 0.19 - 0.16 - 0.001

Field data from Pons and Pausas (2006) (Table 2) was compared with the predicted recruitment to choose the most likely scenario. Specifically, we compared the number of seedlings (counts) in each field plot with the predicted number of seedlings in the 100 simulated plots, using box plots (percentiles). No statistical analysis was performed with the simulated data as our aim was not to test the differences, but rather to see which of the scenarios was closest to the observed data. In addition, our available field data (for each site and year) covered relatively few plots.. The scenarios with both jays and rodents (J30R, J300R) were validated for the cork oak forest only, while the scenarios with jays only (J30, J300) were validated both for cork oak forests and for pine woodlands. Observed data on seedling densities in pine woodlands were divided into two groups with respect to understory vegetation density (shrubby pinewoods and non-shrubby pinewoods, thereafter S-pines, and non-Spines, respectively), as there is evidence of differential jay dispersal in these two types of ecosystems (Pons and Pausas 2008). Because seedling age is difficult to assess, we used only 3 sets of field recruitment data (seedling density): the 2004 seedling cohort (corresponding to acorn production in autumn 2003), the 2005 seedling cohort (2004 crop), and saplings (plants equal to or older than 2 years of age but lower than 3 meters in height). To calculate accumulated saplings in the model we multiplied the mean of plants surviving 3 years by an estimated time of accumulation (40 years for pine woodlands and cork forest - *assumption 5*). This long period of sapling accumulation is plausible as sapling growth is reduced under forest cover (Pons and Pausas 2006).

Table 2. Field data on seedling (1 year old) and sapling (>1 year old and less than 3 m. height) densities (# individuals/156.25m^2; from Pons and Pausas 2006). SPines: pine woodlands with a dense understory of shrubs; non-Spines: pine woodlands without a dense understory of shrubs; Qs forest: cork oak forest. N refers to the number of plots.

Quadrat	Vegetation types	Seedlings Cohort 2003			Seedlings Cohort 2004			Saplings		
		Mean	SD	N	Mean	SD	N	Mean	SD	N
1	SPines	0.33	0.58	3	1.00	1.00	3	30.33	13.87	3
	non-Spines	2.75	1.89	4	3.75	3.30	4	66.00	32.30	4
2	Qs forest	2.33	2.52	3	1.00	1.00	3	87.00	35.04	3
3	SPines	0.00	.	1	0.00	.	1	1.00	.	1
	non-Spines	6.00	7.00	3	0.00	0.00	3	27.67	13.65	3
	Qs forest	2.00	1.63	4	0.00	0.00	4	26.25	21.70	4
5	SPines	1.00	1.73	3	1.33	2.31	3	37.67	15.37	3
	non-Spines	2.33	2.08	3	3.33	3.51	3	58.33	26.58	3
	Qs forest	1.00	1.00	3	1.00	1.00	3	83.00	58.41	3

Acorn production-recruitment uncouplement

Previous exploration work comparing data on *Q.suber* mean sound acorn production by tree for 2003 and 2004 (Chapter 2) with new seedling densities (Pons and Pausas 2006) showed a marginal correlation between acorn production and seedling densities in cork oak forest, but no correlation at all in pinewoods (Table 3). As acorn dispersal in pinewoods can only be attributed to jays (see above), this would seem to indicate an uncoupling due to jay acorn selection. To address this hypothesis we computed 6 scenarios (Table 4): two scenarios were the same as above (J30 and J30R) where jay acorn selection was based on observations (Pons and Pausas 2007a); two scenarios (J30NQc and J30RNQc) considered jay acorn selection equal for all species except *Q.coccifera,* where it was set at low values (0.01); and two scenarios (J30NQq and J30RNQq) in which jays showed no preference for any type of acorn. Three scenarios were set to rodent and jay acorn dispersal in cork forest (J30R, J30RNQc, J30RNQq), and three to jay dispersal only in pinewoods (J30, J30NQc, J30NQq) (Table 4).

Table 3. Correlations between acorn production and 1-year-old seedling densities in cork oak woodlands. Abbreviations as in Table 1. r: Person's coefficient of correlation. Vtype: vegetation type.

	vtype	n	r	sig
2004 seedlings vs 2003 tree production	Qs forest	10	0.333	0.347

	Spines	7	-0.235	0.612
	non-Spines	11	-0.077	0.821
2005 seedlings vs 2004 tree production	Qs forest	10	0.577	0.081!
	Spines	7	0.200	0.667
	non-Spines	11	0.093	0.786

Table 4. Summary of the simulated scenarios for testing acorn differential selection by jays (dispersal vector, jay caching area and jay acorn preferences considered). Mice dispersal was not considered in pine woodlands.

Scenarios	Dispersal in oak woodlands	Dispersal in pine woodlands	Jay caching area (ha)	Jay acorn preference Qi - Qf - Qs - Qc
J30		Jay	30	0.65 - 0.19 - 0.16 - 0.001
J30R	Jay and mice		30	0.65 - 0.19 - 0.16 - 0.001
J30NQc	-	Jay	30	0.33 - 0.33 - 0.33 - 0.001
J30NQq	-	Jay	30	0.25 - 0.25 - 0.25 - 0.25
J30RNQc	Jay and mice	-	30	0.33 - 0.33 - 0.33 - 0.001
J30RNQq	Jay and mice	-	30	0.25 - 0.25 - 0.25 - 0.25

Dispersal efficiency

Efficiency of the dispersal vector is defined here as the mean of the number of plants surviving 3 summers whose origin can be attributed to the disperser, divided by the total number of acorns used (eaten or transported) by the disperser. This (3-year) sapling age was chosen because it is the length of time we had been monitoring the saplings; nevertheless, it can be regarded as a good approximation for Mediterranean conditions (i.e., with strong summer drought) where most seedling mortality occurs after emergence (Pausas et al. 2004).

RESULTS

Cork oak forest

Recruitment (2004 and 2005 cohorts) in rodent scenarios (J300R and J30R) was higher than the observed annual seedling recruitment. The opposite occurred for predicted values for jay-only scenarios (J300 and J30), with the exception of the 2004 cohort in quadrat 3 where no seedlings were either observed or predicted (fig. 2). In all scenarios, accumulated sapling densities were lower than observed densities, but with different magnitudes: 3 times lower for J30R in quadrat 3, 1.5 times for quadrat 2 and slightly lower for Q3. J30RNQc and J30RNQq scenarios produced similar results to the jay and rodent scenarios with observed jay acorn selection (J30R and J300R).

Pine woodlands

Pine woodlands with a low density of shrubs have a higher density of seedlings than shrubby pine woodlands (Table 3 and observed values in Fig.3). As a consequence, the best scenario is different for each pine woodland type: for non-shrubby woodlands, J30 was closer to observed densities than J300; the opposite was true for shrubby woodlands in Q1 and Q3 for 2004 and in Q1 for the 2005 cohort. In 2004, it was again higher than J30 in Q1. Q5 shows a different pattern with close to zero seedlings predicted in the 2004 cohort for both pinewoods, and values closer to J300 for the 2005 cohort. Predicted sapling densities were lower than observed densities at all sites with the exception of shrubby pine woodlands in quadrat 3 (but only one plot was available for this woodland type). In non-shrubby pine woodlands, the J30Nqc scenario was closer to observed data than other scenarios in Q3 and Q5 in 2004 and Q1 in 2005. When we consider saplings, J30Nqc was closer to observed data than other scenarios in all pinewoods with the exception of shrubby pinewoods in Q3, Q5. J30Nqq was closer to observed data than other scenarios only in Q5 for 2005.

Regeneration cycle and dispersal efficiency

The predicted mean annual proportion of recruitment after 3 summers considering the 4 study sites together was 0.4% of the sound acorns. The acorn crop was mostly used by rodents (39.0%) and insects (36.3%), followed by wild boars (14.1%) and jays (5.1%). Estimated dispersal efficiency for J30 was 0.10-16.20% for jays and 0.03-1.00% for rodents (fig.4). The efficiency ratio between jays and rodents was greater than 1 for all sites and years, with the exception of Q3 at 2006. Mean for all sites and years was 31.2 and varied between 0.26 (q3, 2006) and 165.43 (q1, 2004) (tab 3).

Tab3. model (J30R) estimation of jay/rodent Qs recruitment efficiency ratio by quadrat and year.

g/r Qs	q1	q2	q3	q5
2003	16.21	29.25	26.68	71.07
2004	165.43	7.60	10.18	54.55
2005	32.15	9.64	1.53	55.36
2006	25.52	9.66	0.26	55.60
2007	25.77	28.21	22.18	48.90
2008	30.63	4.75	22.92	48.51
Mean	49.28	14.85	13.96	55.66

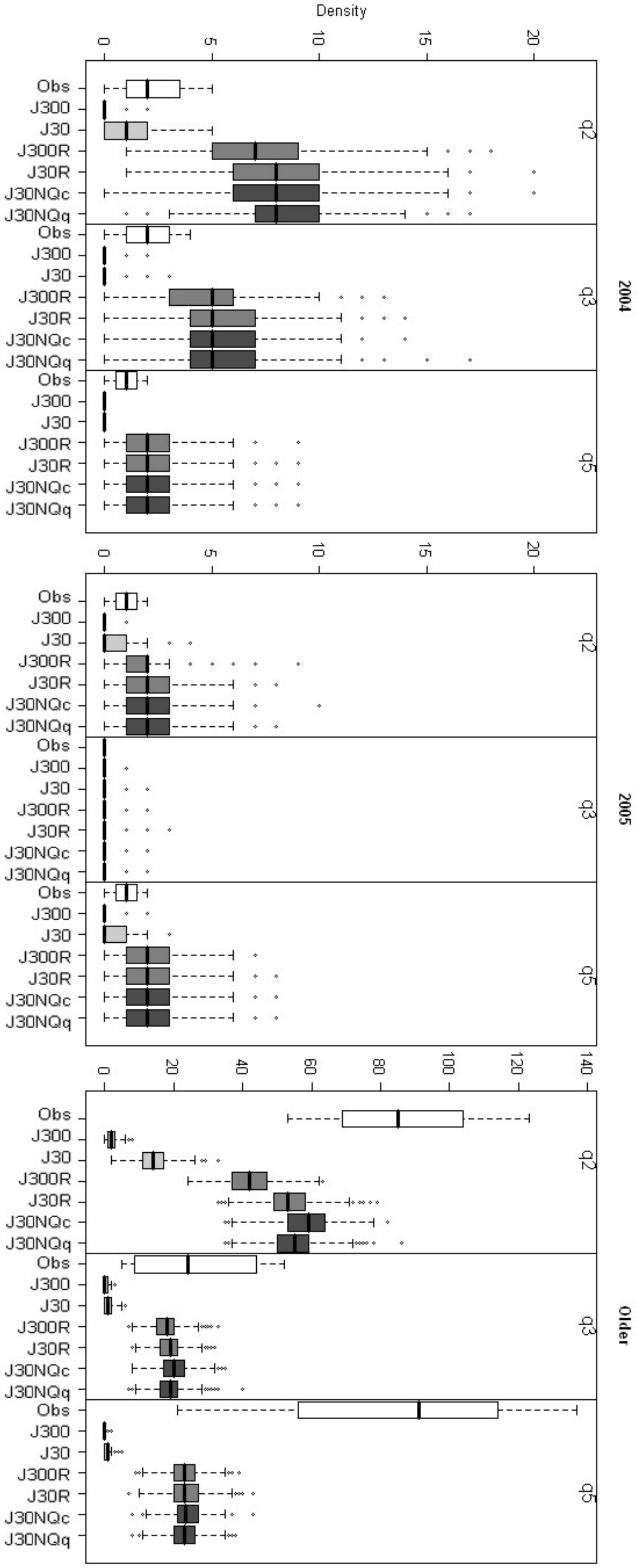


Fig. 2. Observed cork oak seedling density (plants / 156.25m², boxplot) in cork forest and the prediction from the 6 scenarios for each quadrat. a) 2004 cohort, b) 2005 cohort, c) older seedlings. See methods for scenario description.

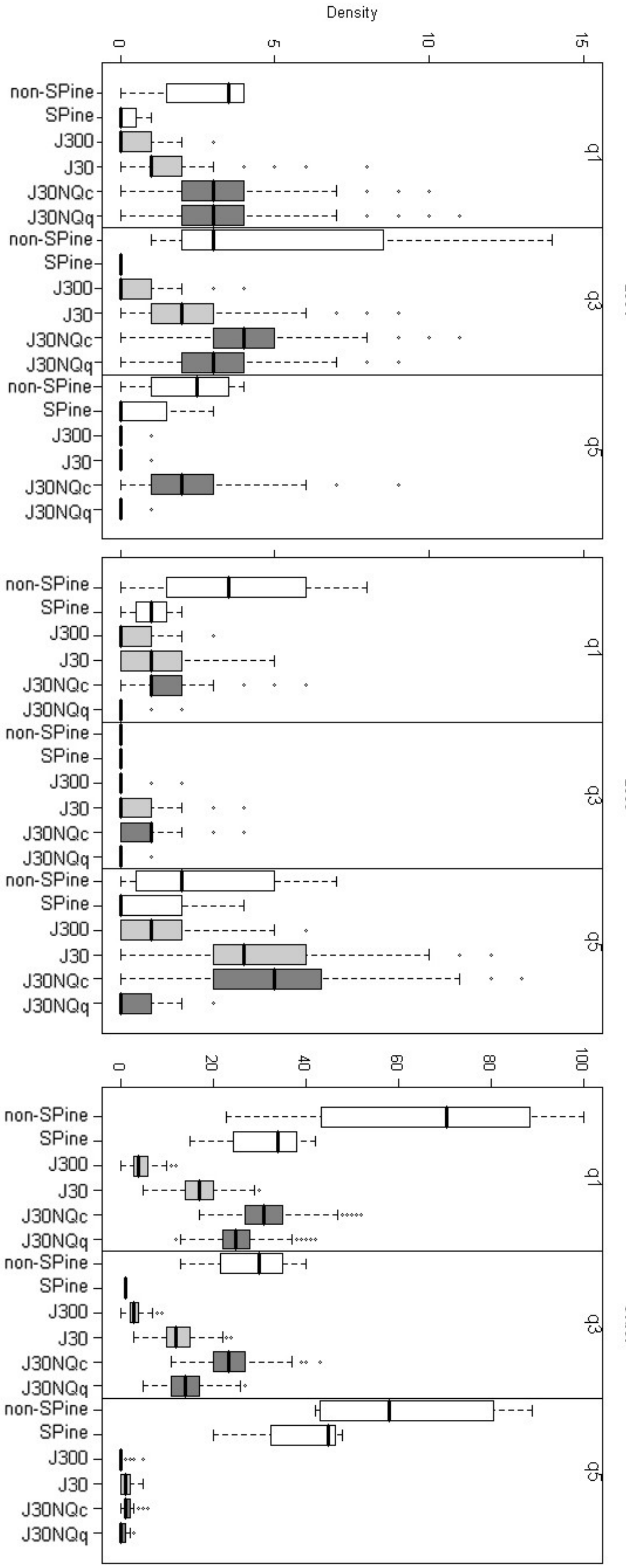


Fig. 3. Observed cork oak seedling densities (plants / 156.25m²) in pine woodlands with (A) and without (B) a dense shrubs understory, and the predicted values for the two jay scenarios (J300, J30) in each quadrat. 2003 cohort (1); 2004 cohort (2); and older seedlings (3). See methods for scenario descriptions.

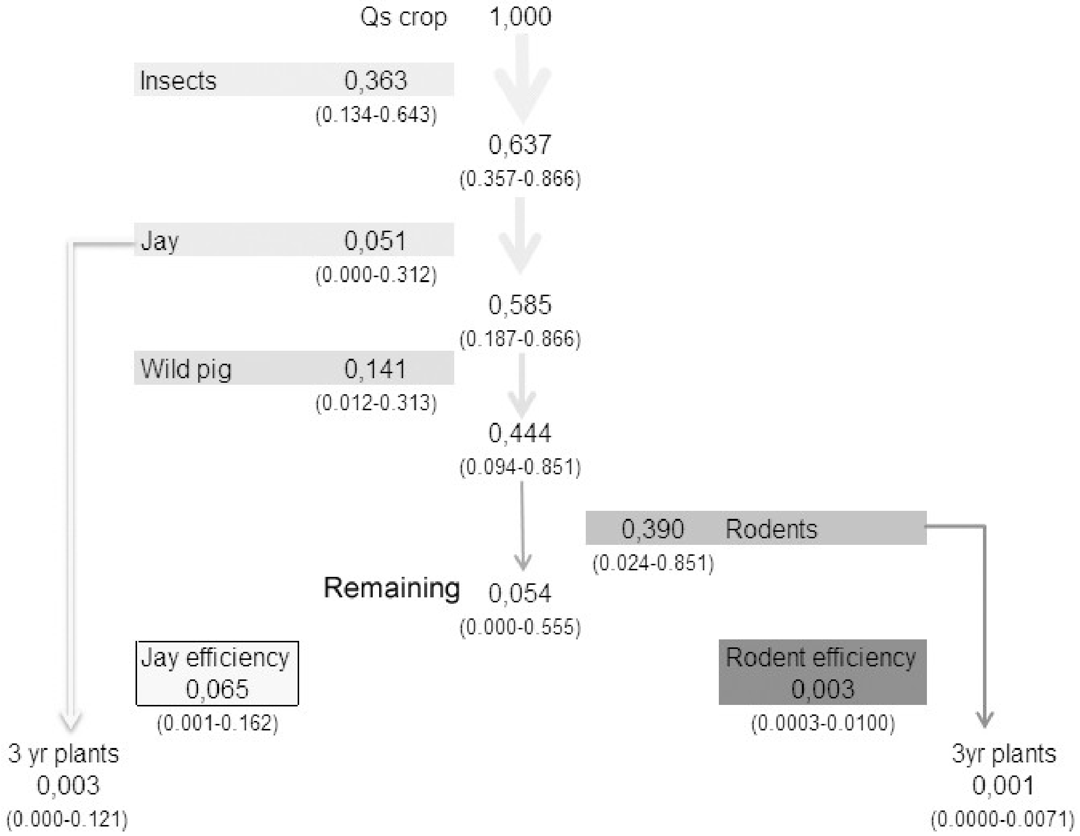


Fig.4. Relative proportion of acorns through the different steps of the regeneration process, as mean J30R scenario of the 6 years of data and 5 sites. Range values in brackets.

Discussion

Both jays and rodents currently disperse acorns. Predictions with the jay-only scenarios yield lower recruitment values than those actually observed in cork forest. Indeed, rodents are responsible for many new seedlings under cork oaks. Predictions with rodent scenarios overestimate seedling recruitment of 1-year cohorts, but underestimate older (cumulative) recruitment. Several possible explanations for this contrasting result arise. One is that because rodent populations are highly variable, there could be exceptional years with high recruitment, but we lack parameters for modelling these rare events. These high recruitment years could be attributable to enhanced acorn scattering in mast years (Vander Wall 2002, Li and Zhang 2007, Zhang et al 2008). Other possible explanations could be that a proportion of the observed accumulated recruitment was of vegetative origin (Espelta et al.1995), and/or there was enhanced recruitment in the past due to some soil-cover clearance (e.g., human or fire disturbance), that is, a re-opening of the regeneration window (Kollmann 1995).

Seedling densities at pine woodlands with low understory were predicted relatively well by J30 scenarios. In contrast, at pine woodlands with shrubby understory, observed densities were lower than scenario-forecasted densities, suggesting that for natural regeneration purposes, shrub cover can reduce new recruitment via jays, even under canopy cover. It also suggests greater rodent activity in these forests. The discordant observed sapling densities, with values close to 0 in quadrat 5 (the isolated cork oak patch in Pinet), can be attributed to high current mortality caused by the isolated forest effect (heavy use by wild boars and humans searching for mushrooms-see Pausas et al. (2006) for details on this forest). Obviously, the currently observed seedling survival does not match with seedling survival in the past. On the whole, we conclude that enhanced dispersal by jays varies by site and vegetation type : J30 scenarios fitted well in non-shrubby pine woodlands, but the J300 scenario fitted better in shrubby ones. Nevertheless, the ultimate reason why jays concentrate acorns remains unsolved. A possible explanation is that jays move acorns towards nesting territories as a future food supply for nestlings and youngsters (Ellenberg 2002)

The seedling densities predicted by J30NQc improved those of other scenarios in pinewoods. This improvement was even more pronounced when the sapling densities in this scenario were compared with the observed ones. In general, this suggests that jays avoid *Q.coccifera* acorns. At the moment we cannot provide any explanation for the disagreement between these results in which jays seemed to select acorns equally between the 3 *Quercus* tree species considered (*Q.suber*, *Q.ilex* and *Q.faginea)* and the cafeteria tests (Where Q.ilex were preferred over the two others species; see Pons and Pausas (2007a) for cafeteria test details). In the case of *Q.coccifera*, jays actively avoided its acorns, as corroborated by the low seedling densities forecasted by the J30Nqq scenario. Thus, with the data available to us, we cannot attribute the observed uncoupling between acorn production and seedling-sapling densities to jay selection of the acorn species, with the probable exception of *Q.coccifera*.

Jay efficiencies are one or two orders of magnitude higher than rodent efficiencies, suggesting that the jay is the main acorn disperser of *Q.suber*, probably exceeded by rodents only in mast years (Vander Wall 2002, Zhang et al. 2008). However, rodents and jays are complementary: the jay moves acorns out of the forest to habitats where rodents are scarce to avoid pilfering of its scattered-hoarded acorns (Pons and Pausas 2007c). Thus, acorn scatter-hoarding by jays is, in fact, indirectly driven by rodent populations.

The population model proposed provides a variable output that reflects the spatial and temporal heterogeneity of the cork oak forests in the Valencia region, as well as the interaction between the acorn productions of the several coexisting oaks. Final recruitment depends not only on the dispersal vectors but also on the competitive ability of each oak species to attract them, especially in the case of the highly mobile jay. In other words, good cork oak recruitment does not depend solely on good seed crop years that saturate pre-dispersal predators; it probably also requires a reduced production of other oaks (especially holm oak in our system). An explanation might be that productions of holm oak and cork oak used to occur in alternate years so that there was no competition between them for jay dispersal. However this point needs to be validated.

Some parts of the model were speculative due to a lack of data (noted as assumptions in the methods section). For instance, jay acorn selection was obtained from an experimental design using several acorn species on the same feeding pole (Pons and Pausas 2007a); however, real selection coefficients probably vary with the spatial structure of the vegetation and the jay's use of the territory (spatial configuration). We tried to minimize this bias by using an acorn selection coefficient (see coefficient of acorn species selection by the jays in the methods section) that takes into account acorn production both at individual tree level and at stand level, as well as acorn selectivity in the jay; nevertheless, this point requires further research under real conditions. Another question still open is the role of the red squirrel in oak recruitment: it is feasible that squirrels play a role in dispersing acorns, especially in pine woodlands, but this role has not yet been considered due to lack of information.

To build our model we have considered seedling survival rates in each vegetation type up to the third summer. However, jays disperse farther away from parents, often in places with better growing conditions, e.g., oldfields (Darley-Hill and Johnson 1981, Gomez 2003, Pons and Pausas 2006). Thus, greater differences in acorn dispersal efficiency between both dispersers could be expected if growth is also considered. As a consequence, our estimation of the higher importance of jays over rodents in seed dispersal in oak landscapes may even be underestimated.

The fact that jays provide ecosystem services has been recognised in previous studies (Hougner et al. 2006, Whelan et al 2008). Here we show that the jay is also the main disperser of acorns and we provide the first explicit quantitative estimation of its role in the recruitment of cork oak at landscape level. A direct consequence of this for forest management is to confirm that the benefits of protecting jays are very high. Moreover, the enhancement of jay activity should be considered as an alternative to expensive and sometimes aggressive human reforestations.

References

Acacio,V., Holmgren,M., Jansen,P.A., Schrotter,O. 2007. Multiple recruitment limitation causes arrested succession in mediterranean cork oak systems. Ecosystems 10: 1220-1230.

Bossema,I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. Behaviour 70: 1-117.

Buesching,C.D., Newman,C., Twell,R., Macdonald,D.W. 2008. Reasons for arboreality in wood mice *Apodemus sylvaticus* and Bank voles *Myodes glareolus*. Mammalian Biology 73: 318-324.

Canellas,I., Roig,S., Poblaciones,M.J., Gea-Izquierdo,G., Olea,L. 2007. An approach to acorn production in Iberian dehesas. Agroforestry Systems 70: 3-9.

Clark,J.S., Beckage,B., Camill,P., Cleveland,B., HilleRisLambers,J., Lichter,J., McLachlan,J., Mohan,J., Wyckoff,P. 1999. Interpreting recruitment limitation in forests. American Journal of Botany 86: 1-16.

Clotfelter,E.D., Pedersen,A.B., Cranford,J.A., Ram,N., Snajdr,E.A., Nolan,V., Ketterson,E.D. 2007. Acorn mast drives long-term dynamics of rodent and songbird populations. Oecologia 154: 493-503.

Cortés,P. 2003. Distribución y dinamica de un *Quercus* caducifolio (*Q.cerrioides* Willk.and Costa) y uno perennifolio (*Q.ilex* L.) en catalunya. Análisis de la ecología de la reproducción, la respuesta de las plantulas a factores ambientales y la respuesta a las perturbaciones. Thesis, Universitat Autonoma de Barcelona, Bellaterra.

Cramp,S., Perrins,C.M. 1994. The birds of the western Palearctic, vol VIII. Oxford University Press, Oxford.

Crawley,M.J., Long,C.R. 1995. Alternate Bearing, Predator Satiation and Seedling Recruitment in *Quercus robur* L. Journal of Ecology 83: 683-696.

Darley-hill,S., Johnson,W.C. 1981. Acorn dispersal by blue jays (*Cyanocitta cristata*). Oecol. 50: 231-232.

Elias,S.P., Witham,J.W., Hunter,M.L. 2004. *Peromyscus leucopus* abundance and acorn mast: Population fluctuation patterns over 20 years. Journal of Mammalogy 85: 743-747.

Ellenberg,H. 2002. Warum und mit welchen Folgen tragen Eichelhäher (*Garrulus glandarius*) Eicheln oft über große Strecken? In: Corax, Band 18, Heft 4/2002: 444-447.

Espelta,J.M., Riba,M., Retana,J. 1995. Pattern of seedling recruitment in West-Mediterranean *Quercus ilex* forests influenced by canopy development. Journal of Vegeation Science 6: 465-472.

Gomez,J.M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26: 573-584.

Gomez,J.M., Garcia,D., Zamora,R. 2003. Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. Forest Ecology and Management 2003 Jul 17;180: 125-134.

Gomez,J.M., Puerta-Pinero,C., Schupp,E.W. 2008. Effectiveness of rodents as local seed dispersers of Holm oaks. Oecologia 155: 529-537.

Grahn,M. 1990. Seasonal changes in ranging behaviour and territoriality in the european jay *Garrulus g. glandarius*. Ornis Scand. 21: 195-201.

Greenberg,C.H., Parresol,B.R. 2003. Dynamics of acorn production by five species of Southern Apalachian oaks. In: McShea,W.J. and Healy,W.M. (eds.), Oak Forest Ecosystems, pp. 149-172. John Hopkins Univ.Press, Baltimore, Mariland.

Haffer,J. 1993. *Garrulus glandarius* (Linnaeus 1758) – Eichelhäher. – In: GLUTZ und BAUER (Hrsg.), 1993, S. 1380-1435.

Hampe,A., Garcia-Castano,J.L., Schupp,E.W., Jordano,P. 2008. Spatio-temporal dynamics and local hotspots of initial recruitment in vertebrate-dispersed trees. Journal of Ecology 96: 668-678.

Harper,J.L 1977. Population biology of plants. Academic Press, London.

Herrera,J. 1995. Acorn predation seedling production in a low-density population of cork oak (*Quercus suber* L.). Forest Ecology and Management 76: 197-201.

Herrero,J., García-Serrano,A., García-Gonzalez, Y.R. 1995.. Wild boar (*Sus scrofa* L.) hunting in south-western Pyrenees (Spain): preliminary data. Journal of Mountain Ecology, 3: 228-229.

Hougner,C., Colding,J. Soderqvist,T. 2006. Economic valuation of a seed dispersal service in the Stockholm National Urban Park, Sweden. Ecological Economics 59: 364-374.

Janzen,D.H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2: 465-492.

Kollmann,J. 1995. Regeneration window for fleshy-fruited plants during scrub development on abandoned grassland. Ecoscience 2: 213-222.

Kollmann,J., Schill,H.P. 1996. Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. Vegetatio 125: 193-205.

Li,H.J., Zhang,Z.B. 2003. Effect of rodents on acorn dispersal and survival of the Liaodong oak (*Quercus liaotungensis* Koidz.). Forest Ecology and Management 176: 387-396.

Li,H.J., Zhang,Z.B. 2007. Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in *Prunus armeniaca* (Rosaceae). Forest Ecology and Management 242: 511-517.

Margaletic,J., Bozic,M., Grubesic,M., Glavas,M., Baumler,W. 2005. Distribution and abundance of small rodents in Croatian forests. Journal of Pest Science 78: 99-103.

Pausas,J.G., Marañón,T., Caldeira,M., Pons,J. 2009. Chapter 10. Natural regeneration. In: Aronson,J., Pereira,J.S., Pausas,J.G. (eds). Cork Oak Woodlands on the Edge: conservation, adaptive management, and restoration. pp. 115-124. Island Press.

Perez-Ramos,I.G. 2006. Factores que condicionan la regeneracion natural de especies leñosas en un bosque mediterraneo del sur de la Peninsula Iberica. PHD, University of Sevilla.

Perez-Ramos,I.M., Maranon,T. 2008. Factors affecting post-dispersal seed predation in two coexisting oak species: Microhabitat, burial and exclusion of large herbivores. Forest Ecology and Management 255: 3506-3514.

Pausas,J.G., Blade,C., Valdecantos,A., Seva,J.P., Fuentes,D., Alloza,J.A., Vilagrosa,A., Bautista,S., Cortina,J., Vallejo,R. 2004. Pines and oaks in the restoration of Mediterranean landscapes of Spain: New perspectives for an old practice - a review. Plant Ecology 171: 209-220.

Pausas,J.G., Ribeiro,E., Dias,S.G., Pons,J., Beseler,C. 2006. Regeneration of a marginal *Quercus suber* forest in the eastern Iberian Peninsula. Journal of Vegetation Science 17: 729-738.

Pons,J., Pausas,J.G. 2006. Oak regeneration in heterogeneous landscapes: The case of fragmented *Quercus suber* forests in the eastern Iberian Peninsula. Forest Ecology and Management 231: 196-204.

Pons,J., Pausas,J.G. 2007a. Not only size matters: acorn selection by the European jay (*Garrulus glandarius*). Acta Oecologica 31: 353-360.

Pons,J., Pausas,J.G. 2007b. Rodent acorn selection in a Mediterranean oak landscape. Ecological Research 22: 535-541.

Pons,J., Pausas,J.G. 2007c. Acorn dispersal estimated by radio-tracking. Oecologia 153: 903-911.

Pons,J., Pausas,J.G. 2008. Modelling jay (*Garrulus glandarius*) abundance and distribution for oak regeneration assessment in Mediterranean landscapes. Forest Ecology and Management 256: 578-584.

Pons,J., Pausas,J.G. (*submitted*). Acorn production in *Quercus suber* is explained by both adaptive and non-adaptive hypotheses.

Puerta-Piñero,C. 2008. Ecologia de la regeneración de *Quercus ilex* a escala de paisaje: importancia del los dispersores y/o depredadores de semillas para el reclutamiento. Tesis doctoral, Universidad de Granada.

Pulido,F.J., Diaz,M. 2005. Regeneration of a Mediterranean oak: A whole-cycle approach. Ecoscience 12: 92-102.

Rodriguez-Estevez,V., Avilez,J.P., Felix,E., Perea,J., García,A., Gomez,G. 2007. Eficiencia del cerdo iberico en el decorticado de la bellota. Arch. Zootec. 56: 535-539.

Rolando,A. 1998. Factors affecting movements and home ranges in the jay (*Garrulus glandarius*). J. Zool. Lond. 246: 249-257.

Rosell,C., Carretero,M.A., Bassols,E. 1998. Seguimiento de la evolución demografica del jabalí (*Sus scrofa*) y efectos del incremento de presión cinegética en el parque natural de la zona volcánica de la Garrotxa. Galemys 10: 59-74.

Rosell,C., Herrero,J., Fernandez-Llario,P. 2001. El jabalí (*Sus scrofa* L.). Galemys 13: 1-25.

Saitoh,T., Osawa,J., Takanishi,T., Hayakashi,S., Ohmori,M., Morita,T., Uemura,S., Vik,J.O., Stenseth,N.C., Maekawa,K. 2007. Effects of acorn masting on population dynamics of three forest-dwelling rodent species in Hokkaido, Japan. Population Ecology 49: 249-256.

Schupp,E.W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107/108: 15-29.

Schupp,E.W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany **82**: 399-409.

Selas,V., Framstad,E., Spidso,T.K. 2002. Effects of seed masting of bilberry, oak and spruce on sympatric populations of bank vole (*Clethrionomys glareolus*) and wood mouse (*Apodemus sylvaticus*) in southern Norway. Journal of Zoology 258: 459-468.

Sone,K., Hiroi,S., Nagahama,D., Ohkubo,C., Nakano,E., Murao,S., Hata,K. 2002. Hoarding acorns by granivorous mice and its role in the population processes of *Pasania edulis* (Makino) Makino. Ecological Research 17: 553-564.

Stenseth,N.C., Viljugrein,H., Jedrzejewski,W., Mysterud,A., Pucek,Z. 2002. Population dynamics of *Clethrionomys glareolus* and *Apodemus flavicollis*: seasonal components of density dependence and density independence. Acta Theriologica 47: 39-67.

Suchomel,J. 2007. Contribution to the knowledge of *Cletrhrionomys glareolus* populations in forests of managed landscape in Southern Moravia (Czech Republic). Journal of Forest Science 53: 340-344.

Sun,S., Gao,X.M., Chen,L.Z. 2004. High acorn predation prevents the regeneration of *Quercus liaotungensis* in the Dongling mountain region of north China. Restoration Ecology 12: 335-342.

Vander Wall,S.B. 2002. Masting in animal-dispersed pines facilitates seed dispersal. Ecology 83: 3508-3516.

Vander Wall,S.B. 2002b. Secondary Dispersal of Jeffrey Pine Seeds by Rodent Scatter-hoarders: the Roles of Pilfering, Recaching and a Variable Environment. *In* Seed Dispersal and Frugivory: Ecology, Evolution and Conservation (eds D.J. Levey, W.R. Silva and M. Galetti)'ch.13, D.J. Levey, W.R. Silva and M. Galetti eds.

Whelan,C.J., Wenny,D.G., Marquise,R.J. 2008. Ecosystem services provided by birds. Ann. N. Y. Acad. Sci. 1134: 25-60.

Zhang,H.M., Cheng,J.R., Xiao,Z.S., Zhang,Z.B. 2008. Effects of seed abundance on seed scatter-hoarding of Edward's rat (*Leopoldamys edwardsi* Muridae) at the individual level. Oecologia 158: 57-63.

Appendix 1.

Acorn production data for the four Quercus species considered.

Several point-count stations dispersed within the quadrats were established in 2003 and their exact location recorded with a GPS for subsequent recounts. In some quadrats, new point-count stations were added in subsequent years. The methodology corresponds to a modified version of the one described by Koenig et al. (1996): at each counting point, an observer counted as many acorns as possible for 30 seconds by tree, for 3 to 6 individuals of each species present at the point. Because the study was centred on Qs most of the 6 individual counts were from this species. The observer was the same for the whole period and for all sites. Table 1 shows the total number of trees sampled for each species and the mean number of acorns per tree and species. To compute the quadrat mean for each tree, we used the mean of the tree-counted acorns at each counting point.

Table. 1. a) Mean tree number of acorns by species, year and quadrat, calcualted from prior tree mean number at point counts. b) Number of individuals of each *Quercus* species counted (Qi=*Q.ilex*, Qs=*Qsuber*, Qc=*Q.coccifera*, Qf=*Q.faginea*) by year and quadrat (1-5) at point counts.

		a) mean acorns by tree						b) n					
		Quadrat						Quadrat					
Year	Species	1	2	3	4	5	Total	1	2	3	4	5	Total
2003	Qi	12	10	57	.	16	23	9	6	7	0	11	33
	Qs	9	12	33	.	1	12	53	34	25	0	28	140
	Qc	1	.	34	.	43	37	1	0	6	0	9	16
	Qf	4	.	.	.	0	4	13	0	0	0	2	15
	Total	9	12	38	.	12	15	76	40	38	0	50	204
2004	Qi	1	11	4	20	1	5	14	9	22	6	12	63
	Qs	2	9	2	5	12	6	47	34	25	5	30	141
	Qc	24	.	49	39	35	42	3	0	22	6	15	46
	Qf	0	.	0	.	.	0	17	0	3	0	0	20
	Total	3	10	17	22	16	12	81	43	72	17	57	270
2005	Qi	23	28	8	11	31	19	27	14	30	15	20	106
	Qs	4	4	1	1	6	3	36	54	25	30	30	175
	Qc	20	25	17	19	29	22	6	3	24	21	22	76
	Qf	13	.	1	.	0	11	24	0	6	0	1	31
	Total	13	10	8	9	20	12	93	71	85	66	73	388
2006	Qi	40	34	13	12	37	27	27	17	30	16	22	112
	Qs	11	10	0	3	9	7	36	54	25	30	30	175
	Qc	5	3	15	14	40	21	6	3	24	21	23	77
	Qf	13	.	0	.	.	11	24	0	6	0	1	31
	Total	20	15	9	9	26	16	93	74	85	67	76	395
2007	Qi	26	64	31	37	46	38	28	17	30	16	23	114
	Qs	6	14	4	4	1	7	36	54	25	30	30	175
	Qc	43	107	53	62	36	52	6	3	24	21	23	77
	Qf	5	.	0	.	.	4	24	0	6	0	1	31
	Total	14	29	27	30	25	25	94	74	85	67	77	397
2008	Qi	35	66	48	19	61	46	28	17	30	16	23	114
	Qs	44	68	5	20	15	37	36	54	25	30	30	175
	Qc	40	84	47	49	61	52	6	3	24	21	23	77
	Qf	16	.	0	.	.	13	24	0	6	0	1	31
	Total	34	68	32	29	42	41	94	74	85	67	77	397
Total	Qi	27	42	23	19	37	29	133	80	149	69	111	542
	Qs	12	21	7	7	7	12	244	284	150	125	178	981

Qc	26	55	36	36	41	37	28	12	124	90	115	369
Qf	10	.	0	.	0	8	126	0	27	0	6	159
Total	16	26	20	19	25	21	531	376	450	284	410	2051

References

Koenig,W.D., Knops,J.M.H., Carmen,W.J., Stanback,M.T., Mumme,R.L. 1996. Acorn production by oaks in central coastal California: Influence of weather at three levels. Canadian Journal of Forest Research-Journal Canadien de la Recherche Forestiere 26: 1677-1683.

Appendix 2

Estimation of rodent densities.

We estimated rodent densities (mainly *Apodemus sylvaticus*, but also *Mus spretus*, which is sometimes present) from the following three trapping and removal rate experiments:

(1) Several trapping sessions in quadrats 2 and 5 in 2003 and 2004 totalling 1091 trap-nights; The traps used were 20x20x10 cm galvanized wire cages; they were set in the field with a design of 5 x 5 traps per station, separated by 10 meters. Trap sessions lasted 3 nights, with at least one of the nights separated by a day from the other two. When the weather was cold and to avoid hypothermal losses, traps were visited in intervals of 6 hours or less. Data are shown at Table 1.

Table 1. Rodent trap session results.

Quadrat	Year	Vegetation type and replica number	Total rodents captured	N valid traps / night	Mean captured rodents
Q5	2003	medium oldfield	2	95	0.021
		shrubs 1	19	65	0.292
		shrubs 2	18	92	0.196
		shrubs 3	11	95	0.116
		pinewood 1	0	73	0.000
		pinewood 2	0	100	0.000
		cork oak forest 1	22	69	0.319
		cork oak forest 2	9	94	0.096
		corc oak forest 3	24	87	0.276
Q2	2003	shrubs 1	64	62	1.032
		shrubs 2	61	61	1.000
		shrubs 3	59	57	1.035
	2004	shrubs 1	29	47	0.617
		shrubs 2	7	49	0.143
		shrubs 3	12	45	0.267

(2) Data from the rodent removal experiment: using the same wire cages as above, 12 traps lines were set in a parallel disposition in 3 shrublands in la Pobla Tornesa (close to quadrats 1 and 2). Several trapping sessions were conducted and trapped rodents were liberated 2 km away (removal trapping). The maximum density of rodents was obtained from the sessions in which saturation was reached on the first day (all 25 traps with captures) of the removal experiment, and density was calculated as the sum of captures till stabilization by migration.

Table2. Results from the rodent removal experiment.

Days from the beginning of the experiment	1	4	5	18	19	20	25	26
Number of captured rodents	23	14	7	9	5	5	3	7

(3) Data on acorn removal rates in Pons and Pausas 2007.

Rodent abundances are highly variable (Elias et al 2004) and follow acorn crops (Selas et al 2002, Margaletic et al 2005, Saitoh et al 2007). Approaches considered for quadrats without rodent density data were as follows: for Q1, rodent density was considered equal to Q2 because of their proximity; for Q3, mean of available data was used. For subsequent years, rodent density was calculated as (last year density) x (0.5+ available current year amount of acorn/ maximum amount of acorns available in the study period).

References

Elias,S.P., Witham,J.W., Hunter,M.L. 2004. *Peromyscus leucopus* abundance and acorn mast: Population fluctuation patterns over 20 years. Journal of mammalogy 85: 743-747.

Pons,J., Pausas,J.G. 2007. Rodent acorn selection in a Mediterranean oak landscape. Ecological Research 22: 535-541.

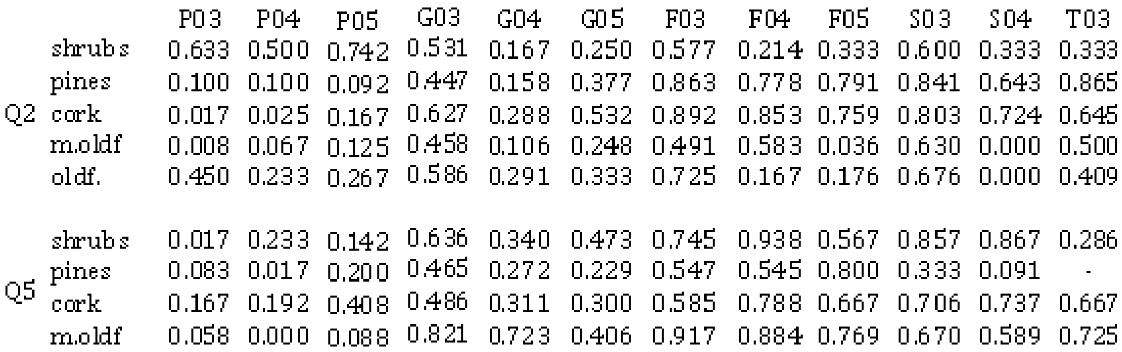
Saitoh,T., Osawa,J., Takanishi,T., Hayakashi,S., Ohmori,M., Morita,T., Uemura,S., Vik,J.O., Stenseth,N.C., Maekawa,K. 2007. Effects of acorn masting on population dynamics of three forest-dwelling rodent species in Hokkaido, Japan. Population Ecology 49: 249-256.

Selas,V., Framstad,E., Spidso,T.K. 2002. Effects of seed masting of bilberry, oak and spruce on sympatric populations of bank vole (*Clethrionomys glareolus*) and wood mouse (*Apodemus sylvaticus*) in southern Norway. Journal of Zoology 258: 459-468.

Appendix 3

Germination, predation and summer survivals: in November 2003, at quadrats 2 and 5, we established three lines per vegetation type (shrubland, cork forest, pine forest and abandoned fields for both quadrats, plus oldfields for quadrat 2), and buried 100 acorns collected from nearby trees in groups of two at a depth of 1-3 cm and at 1-meter intervals (50 points per line, 2 acorns per point). Half of the points (alternating design) were protected by a wire mesh to avoid predation. The experiment was repeated in 2004 and 2005. Approximately 3-4 weeks after seeding, the lines were checked and predation activity recorded. Afterwards, germination was recorded in May-June, and summer mortality was estimated by revisiting the lines during the following autumn-early winter. Results are shown in table 1.

Table 1: proportion of post-dispersal predation (P), germination (G), first (F), second (S) and third summer survival (T), for the lines established in 2003 (03), 2004 (04) and 2005 (05) at different vegetation types in quadrats 2 and 5; cork= cork oak forest; oldf= oldfieields; m.oldf. = medium oldfields.



		P03	P04	P05	G03	G04	G05	F03	F04	F05	S03	S04	T03
Q2	shrubs	0.633	0.500	0.742	0.531	0.167	0.250	0.577	0.214	0.333	0.600	0.333	0.333
	pines	0.100	0.100	0.092	0.447	0.158	0.377	0.863	0.778	0.791	0.841	0.643	0.865
	cork	0.017	0.025	0.167	0.627	0.288	0.532	0.892	0.853	0.759	0.803	0.724	0.645
	m.oldf	0.008	0.067	0.125	0.458	0.106	0.248	0.491	0.583	0.036	0.630	0.000	0.500
	oldf.	0.450	0.233	0.267	0.586	0.291	0.333	0.725	0.167	0.176	0.676	0.000	0.409
Q5	shrubs	0.017	0.233	0.142	0.636	0.340	0.473	0.745	0.938	0.567	0.857	0.867	0.286
	pines	0.083	0.017	0.200	0.465	0.272	0.229	0.547	0.545	0.800	0.333	0.091	-
	cork	0.167	0.192	0.408	0.486	0.311	0.300	0.585	0.788	0.667	0.706	0.737	0.667
	m.oldf	0.058	0.000	0.088	0.821	0.723	0.406	0.917	0.884	0.769	0.670	0.589	0.725

Consideracions finals

La regeneració en les espècies del gènere *Quercus* és el balanç final d'un procés, no només perquè les diferents fases poden estar desacoblades sinó també perquè hi ha una gran variabilitat espaciotemporal. A més a més, aquest procés es caracteritza per tenir fortes interaccions no només entre individuus de la mateixa espècie, sinó també amb d'altres espècies. Hem vist al llarg d'aquest estudi que en el cas de les sureres, la periodicitat en la producció de glans ès encara desconeguda per causa de l'acció simultània de la producció de dos tipus de glans (anuals/biennals), als factors metereològics, a la sacietat dels predadors predispersius i, probablement també, a la competència pels dispersors. Tot i això, els nostres resultats indiquen que si hi ha una veritable periodicitat en la surera, l'interval de producció seria superior al d'altres *Quercus* coexistents (probablement de 5 o més anys). La contribució i connexió exacta entre els factors que controlen la vecería de la surera queda per a ser descrita i quantificada en una major precisió a mesura que obtinguem sèries de producció més llargues. Cal tenir també present que aquesta periodicitat pot estar relacionada amb la d'altres espècies amb les quals competeix, com són la carrasca, el roure valencià i el coscoll. Tots ells comparteixen el gaig com a principal dispersor del glans, i el ratolí de bosc com el principal predador i dispersor secundari de glans.

Al camp hem pogut observar que, almenys a la Península Ibèrica oriental, el reclutament de plançons dels *Quercus* està funcionant, especialment als camps de conreu abandonats on totes les fases de la regeneració són concordants i els arbres adults apareixen després d'un període de temps relativament curt (diguem 20 anys). Tot i això, la finestra de regeneració es veu reduïda als anys immediats després de l'abandonament; tal com va recobrint-se el sòl de vegetació herbàcia i arbustiva, el gaig va deixant de dispersar glans fins a parar completament amb recobriments del sòl pròxims al 100%. Açò és a causa probablement d'un augment del robatori dels glans per part dels rosegadors, puix que aquestos augmenten la seva activitat amb l'increment de la cobertura vegetal. És necessari recalcar que açò només passa en els conreus abandonats propers a àrees boscoses amb presència de gaigs; aquesta sembla la raó principal de la falta de regeneració en boscos oberts com les deveses. Per altra part, els boscos de *Quercus* tenen suficient regeneració a partir de les dispersions de curta distància fetes pels rosegadors, que reomplin els clars i mantenen unes densitats de plançons suficients per a la regeneració després de possibles perturbacions, almenys en les actuals condicions de poca pressió de pasturatge d'ungulats salvatges i ramats domèstics.

Podem imaginar-nos una seqüència probable de successos que explicarien l'actual regeneració dels *Quercus* als boscos de l'orient ibèric: l'ús de la terra va ser tan intens fins a mitjans del segle passat que la superfície forestal estava reduïda a la mínima expressió de la qual tenim constància i, com a conseqüència, les poblacions de gaigs hi devien ser molt reduïdes també. Després de l'abandonament generalitzat del anys seixanta, els pins, afavorits per una dispersió anemòfila, i per les reforestacions, van ocupar gran part de les terres agrícoles abandonades i part de les forestals. Mestrestant, la regeneració dels bosquets remanents de *Quercus* es reduïa al seu 'manteniment' dirigida pels rosegadors. Pels vuitanta-noranta moltes de les pinedes de l'etapa anterior ja estaven en fases madures de desenvolupament. Aquest ambient forestal devia permetre un augment significatiu de les poblacions de gaigs, que a la vegada van activar una dispersió de mitja-llarga distància dels *Quercus* cap a conreus abandonats i (novetat) les cada vegada més freqüents zones incendiades. Esta seqüència de successos, encara que especulativa, està plenament en corcondància amb el que sabem actualment del procés de regeneració dels *Quercus*. Una qüestió pendent és si la dispersió pel gaig serà suficient per a mantenir les actuals taxes de reclutament al futur pròxim després de les més que probables grans pertorbacions (focs de gran extensió) i els efectes del canvi climàtic.

En conjunt, els resultats tenen implicacions d'importància des del punt de vista de la gestió dels forests de *Quercus*. En primer lloc, pel que fa als gestors, caldria parar atenció a les fases clau de la regeneració (especialment a la dispersió) per tal de potenciar-la. A l'hora de desevolupar estratègies de gestió i de l'execució dels treballs caldria tenir en compte certs punts: (a) Els *Quercus* no es regeneren adequadament a sota coberta, però el banc de plançons és crucial per a la regeneració després de fortes pertorbacions com per exemple els focs o les netejes forestals. En conseqüència, en les feines d'extracció de fusta cal para atenció per tal de minimitzar l'impacte sobre aquestos bancs de plançons; (b) a l'hora de planificar una tala, és preferible fer molts rodals menuts (clarianes) que no àrees extenses, puix que els gaigs soterren les glans no gaire allunyats d'una coberta forestal protectora per prevenir els atacs per part dels rapinyaires; dit d'un altra manera, els gaigs són habitants de bosc i no d'espais oberts; C) per tal de mantenir bones densitats de gaigs, molts tipus diferents de rodals són preferibles a pocs rodals homogenis de gran mida; els paisatges en mosaic es regeneren millor que, per exemple, grans reforestacions; (d) les distàncies de regeneració natural se situaran a no més de pocs quilòmetres de la vora del bosc. Però, caldrà tenir en compte que si hi ha bons llocs perquè els gaigs puguen soterrar les glans a prop del lloc on les obtenen, aquestes distàncies rarament superaran el mig quilòmetre; (e) els matollars (coberts o no per arbres) no són zones que puguen regenerar-se amb *Quercus* per si mateixes (exceptuant segurament el coscoll), i caldrà netejar-les si volem potenciar-hi la regeneració forestal. (f) En la planificació de reforestacions, la gla emprada per a la producció de plançons o per a la sembra directa no hauria de ser de mida (molt) superior al màxim que solen dispersar els gaigs; pel contrari estaríem reduint les possibilitats que el bosc resultant veja limitada la seva dispersió.

Segon, pel que fa als investigadors en tècniques de reforestació amb *Quercus*, la sembra directa de glans en grans reforestacions a sòl descobert sembla possible, però si volem minimitzar les pèrdues de glans prèviament necessitem desenvolupart de forma simultània (a) protocols per a mesurar fàcilment les densitats de rosegadors, i (b) indicadors per a quantificar fonts d'aliment alternatives per als rosegadors presents. En aquesta línia, cal desenvolupar previsions més precises i fiables de la producció de glans, puix que la variació de les poblacions de rosegadors segueixen les variacions en la disponibilitat de glans. Respecte a la potenciació de la regeneració natural, s'haurien de validar menjadors artificials amb glans per a gaigs i ratolins sota diverses condicions. També cal dedicar esforços a la dinàmica de població dels esquirols i a quantificar la seva implicació en la dispersió de glans a nivell de territori. El desenvolupament de noves tècniques de potenciació i mimetisme de la regeneració natural en els *Quercus* sembla un tòpic interessant per a la investigació futura, a la qual esperem que aquest estudi haja contribuït d'alguna manera.

Principals conclusions:

- La producció de glans en la surera és més variable que no en els altres *Quercus* que s'han estudiat fins ara, no només a nivell individual sinó també a nivell de població. Aquesta alta variabilitat està produïda probablement per factors metereològics (acoblament als recursos), a la dinàmica endògena i a l'habilitat de produir dos tipus de glans de forma simultània (glans de maduració anual i biennal). La sacietat de predadors predispersius és més elevada en suraredes monoespecífiques que no en mixtos amb carrasques o roures. La mida de la gla és major a baixes taxes d'infestació, més disponibilitat hídrica durant la maduració i major nombre de dies de gelades a la primavera.

- El gaig viu a zones heterogènies forestals (combinacions de boscos diversos, conreus en ús, conreus abandonats, etc), i presenta als forests mediterranis densitats 6-7 vegades més baixes que no a les poblacions atlàntiques. En la setmana posterior a l'abandonament del niu, les seves poblacions reproductores es poden censar fàcilment amb el registre de les posicions del polls volanders. Amb l'ús de mapes de vegetació generats a partir de fotografies aèries i posterior validació sobre el terreny, hem pogut estimar la densitat i la distribució espacial de les poblacions de gaigs. Tot i això, per a fer una anàlisi més acurada serà necessari un desenvolupament futur del model proposat, el qual probablement haurà d'incloure les comunitats d'ocells presents.

- El gaig prefereix les glans de les carrasques i rebutja, si té altres opcions, les de coscoll; la selecció de les glans de roure valencià i surera és intermèdia entre les anteriors dues espècies. Respecte a la mida, el gaig selecciona preferentment glans grans, però tenint en compte que hi ha un òptim de mida seleccionat, immediatament per sota dels límits imposats per les dimensions de la gola, que cal tenir en compte a l'hora de planificar reforestacions amb glans grans.

- S'hi han trobat glans dispersats pel gaig des de 3 fins a 550 metres de distància dels menjadors experimentals, amb una distribució de distàncies Log-Normal. El patró espacial de dispersió va ser d'agregacions de glans distribuïts en funció de la composició i configuració de la vegetació. A majors distàncies que la de les agregacions es troben glans aïllats. Les zones preferides per a soterrar les glans són rodals amb percentages baixos de cobertura del sòl per la vegetació (p.e. conreus recentment abandonats, pistes i camins forestals, pinars amb poc recobriment arbustiu, etc). Per contrapartida, el gaig evita rodals amb elevat recobriment del sòl (conreus abandonats vells, matollars i pinars amb matolls). El robatori de glans dispersats pel gaig per part de ratolins va ser baix (sobre un 8%). No vam trobar diferències en les distàncies de soterrament de glans de carrasca i surera. El seguiment de glans amb radiotransmissors és una tècnica òptima per al seguiment de la dispersió de glans a distàncies mitjes i llargues, i pot ser utilitzat per al seguiment de la destinació de les glans (predació, dispersió secundària, escapament, etc).

- Els ratolins van seleccionar glans de carrasca abans que els de surera o coscoll, és a dir, són capaços de diferenciar les distintes espècies de glans. Pel contrari, no hem trobat una clara selecció de les glans per la seva mida, si exceptuem les glans de coscoll, o el que és el mateix, la selecció de la mida de la gla va ser depenent de l'espècie. Després de selecionar la gla a l'assaig tipus cafeteria, no s'hi van trobar diferències en la destinació de la gla (predada, soterrada, distància de transport...), a excepció de les glans de coscoll que van ser més soterrades del que esperàvem. Les taxes de desaparició i les distàncies de transport de les glans van variar amb el tipus de vegetació considerat: s'hi van trobar baixes taxes de desaparició i llargues distàncies de transports en les zones amb poca cobertura del sòl (p.e. pinedes sense matolls). Els resultats poden tenir coseqüències rellevants per a boscos mixtos de *Quercus* i per les planificacions de reforestacions amb sembra directa de glans.

- Les densitats de plançons van ser molt variables en funció de les unitats (tipus) de vegetació però en conjunt superiors a les trobades a les deveses. Resumint, hem trobat: (a) regeneració limitada en els matollars, el més probable a conseqüencia d' una falta de dispersió de glans; (b) regeneració completa en els conreus abandonats propers a boscos, però amb una finestra de regeneració que es tanca ràpidament amb el recobriment del sòl per la vegetació; (c) grans densitats de plançons sota les suredes i els pinars, amb taxes d'aparició i mortalitat de nous plançons elevades (banc de plançons dinàmic). Aquestos plançons asseguren el reompliment de la coberta de la sureda i el remplaçament del pins després d'una pertorbació (p.e. incendis).

- Tant el gaig com els ratolins dispersen glans, però el 75% dels plançons amb 3 anys d'edat es correspondrien a dispersions efectuades pel gaig en aquelles zones on són presents. L'eficàcia del gaig en la dispersió de glans seria d'un ordre de magnitud superior a la dels ratolins. Les acumulacions d'arbrets als escenaris de la sureda van ser inferiors a les observades sobre el terreny, probablement perquè la dispersió per part dels ratolins podria ser superior en certs anys (p.e. anys de collita abundant) respecte als dos anys dels quals disposem dades i/o a causa d'una proporció desconeguda de regeneració vegetativa. El millor escenari que explica les densitats observades de plançons i arbrets es correspon a aquell en què (a) la dispersió és compartida pel gaig i el ratolí i (b) els gaigs obtindrien glans des d'una zona de campeig hivernal àmplia i els dirigirien cap al territori de nidificació que seria més reduït (dispersió dirigida). En condicions naturals sembla que els gaigs refusen les glans de coscoll, però no hi hem trobat efectes d'una possible selecció d'espècie sobre el banc de plançons.

Agraïments

A totes les persones que han col·laborat d'una o d'altra manera. La major part d'aquesta tesi s'ha fet a la Fundació CEAM i ha estat finançada pel projecte VARQUS (Ministeri de Ciència i Tecnologia, CGL2004-04325/BOS) i el projecte CREOAK (Comissió Europea, QLK5-CT-2002-01594).

Resum

Introducció general

La mediterrània és una terra poblada més o menys intensivament des d'abans de l'Imperi Romà. Com a resultat d'aquesta llarga història d'ús del territòri, el paisatge està típicament fragmentat en zones amb distints usos. El podríem definir com a un paisatge en mosaic que comprén conreus, pastures, matollars, pinars, alzinars, suredes, ... etc. L'ocupació rural i l'explotació de les terres d'aquest mosaic va tenir possiblement el seu màxim històric durant el primer terç del segle XX .

Tradicionalment, els arbres del gènere *Quercus* (carrasques, suredes, roures i coscoll) han estat molt apreciats per l'alta energia calòrica continguda en la seva fusta, especialment en les carrasques (*Q.ilex*). Açò va donar peu a una explotació d'aquestes espècies sense mesura per a llenyes i per a carbó vegetal. Fins i tot moltes vegades se n'extreien les arrels, especialment quan s'havia de a canviar l'ús del sòl (per exemple per a fer conreus). Cap als anys seixanta del segle passat, la migració a les ciutats i el canvi energètic cap a combustibles fòssils (gas i benzines principalment) va ser decisiu perquè es deixés d'emprar les llenyes i els carbons de manera generalitzada. Mentrestant, es va empendre la reforestació de terres abandonades amb pins. Pels anys vuitanta, alguns autors van assenyalar que els *Quercus* no regeneraven bé. La major part de les terres abandonades en anys anteriors van ser ocupades per matollars i pinedes, la qual cosa va contribuir de manera decisiva a l'augment de la freqüència i dimensions dels incendis forestals. La causa de la falta de regeneració dels *Quercus* es va atribuir sovint a la necessitat d'intervals de temps llargs perquè la vegetació evolucionés des dels matollars i pinars (comunitats prèvies) cap als carrascars, suredes i rouredes (comunitats clímax). Aquesta visió era hereva directa de les teoria de la succesió de les comunitats vegetals exposada per Clemence a principis de segle.

Als darrers anys, aquesta visió de l'evolució del bosc mediterrani ha estat parcialment desestimada i s'ha passat (en no poques vegades) a abandonar els pins en favor de l'ús directe dels *Quercus* en les reforestacions. Però, prompte hom es va adonar que la supervivència a la sequera dels plançons de *Quercus* era molt variable, i en conseqüència van aparèixer dubtes sobre la viabilitat del l'ús d'aquestes varietats en les repoblacions forestals. Per a millorar la implantació i desenvolupament dels plançons al camp s'han obert distintes línies d'investigació com són la millora dels plançons en el viver, les tècniques de plantació o l'ús d'hidratants i esmenes. La sembra directa de glans no ha estat una tècnica de reforestació massa acceptada per la incertesa que es deriva de la depredació que en fa la fauna i les variabilitats en les taxes de supervivència en funció del lloc i l'any.

El present estudi esta concebut sota la hipòtesi que la regeneració natural dels *Quercus* es pot millorar emprant o simulant els dispersors naturals. Aquestes tècniques podrien ser més econòmiques i menys agressives pel medi ambient que les tècniques de restauració tradicionals. Aleshores, el nostre objectiu principal és el desenvolupament de la base científica per augmentar o reproduir la regeneració natural dels *Quercus*. Al llarg de l'estudi utilitzem principalment la surera (*Quercus suber*) com a espècie bàsica perquè: 1) té processos de regeneració semblants a d'altres *Quercus* (generalitat), 2) té una gran importància socioeconòmica (transferibilitat a la societat), i 3) és una espècie protegida amb una distribució fragmentada a la Península Ibèrica oriental on la seva viabilitat ha estat qüestionada (respon a un problema específic).

El reclutament vegetal és un procés que comença amb la producció de llavors i finalitza amb la incorporació de nous adults a la població. Aquest procés es compon de diverses fases que poden o no entrar en conflicte entre elles: floració, producció de glans, predació de glans abans de la dispersió, dispersió del glans, predació de glans posterior a la dispersió, germinació, establiment dels plançons i creixement dels arbrets. L'interés per aprofundir en el coneixement de cadascuna de les fases del reclutament dels *Quercus* ha augmentat significativament els últims anys. Per tal de comprendre els factors que limiten la regeneració dels *Quercus* cal parar atenció a totes i cadascuna de les seves fases. Dit d'un altra manera, la regeneració dels *Quercus* pot estar limitada per una o diverses de les seves fases a la vegada, cosa que es coneix amb el terme de 'colls d'ampolla'.

En qualsevol cas, el que cal saber per a identificar un 'coll d'ampolla' és la proporció de la collita de glans que es perd en cadascuna de les fases del reclutament i el balanç final. Tot i això, estudis del cicle complet de regeneració són més bé escassos. Aproximacions alternatives al problema com pogués ser la integració d'estudis parcials de la regeneració, no són de molta utilitat perquè és complicada la interpretació de dades de diversos llocs i períodes, cosa que fa que es reduïsca la possibilitat d'obtenir conclusions fiables que reflectisquen situacions reals.

Pel que fa referència a la producció de glans, el gènere *Quercus* són espècies anyívoles, o dit d'altra manera, amb alternança d'anys amb grans quantitats de glans i anys sense producció o molt escassa. La periodicitat de les grans collites és específica de cada espècie, amb períodes de recurrència de 2, 3 i més anys. En algunes espècies, com en la surera, desconeixem encara la recurrència de les grans collites o és dubtosa perquè en disposem de poques dades. Nó és sorprenent puix que hi manquen sèries llargues (probablement >15 anys) de dades de producció de glans per a les sureres necessàries per tal d'extraure patrons de producció fiables.

Les causes de la vecería són confuses i estan encara en debat. Actualment les hipòtesis més acceptades són a) adequació als recursos disponibles b) sacietat dels predadors de glans, i c) la dispersió per animals . En general, els períodes curts s'associen a espècies en què la maduració de les glans es produeix el mateix any que van ser polinitzades (espècies anuals), mentre què el fet contrari resulta cert per a espècies que tarden 2 anys a madurar des de la polinització (espècies biennals). Entre els *Quercus* mediterranis, la carrasca (anuals) sembla produir glans en anys alterns. En el cas de la surera el patró de producció de glans es complica pel fet que pot produir glans d'1 i de 2 anys d'edat al mateix arbre. Com a conseqüència la vecería en la surera sembla variable segons la proprorció de cada tipus de gla en la població. Sobre el roure valencià, (anual, *Q.faginea*) i el coscoll (biennal, *Q.coccifera*) disposem també de poques dades. Al *Capítol 2* el nostre objectiu és descriure el patró de producció de glans en la sureda i validar: 1) la importància relativa dels factors metereològics (precipitació i temperatura) en els patrons espacials i temporals de la producció de glans, tant en el nombre com en la mida de les glans; 2) la importància de la duració del període vegetatiu en el patró de producció anual-biannual de glans i les seves conseqüències a nivell de població.; i 3) si les densitats de predadors predispersió són depenents de la producció de glans.

La dispersió de glans va ser atribuïda tradicionalment a la barocòria (dispersió per gravetat) i a un moviment difús per animals que s'alimenten de glans. Per exemple, era freqüent sentir coses com que a conseqüència que les glans no són llavors recalcitrants, la germinació massiva només es dóna els anys especialment humits que eviten la dessecació de les glans. Aquesta ambigüetat és deu bàsicament a la dificultat de seguir físicament la dispersió de les glans, especialment a distàncies de dispersió mitjanes i llargues. La barocòria, encara que que juga un cert paper als boscos de *Quercus*, ha estat rarament validada. Probablement es necessita clarificar dos conceptes per tal d'avançar en l'ecologia de la dispersió: què entenem per dispersió? i quina és la implicació del terme 'quantitatiu' intrínseca en el concepte mateix de dispersió? Tot al llarg del present estudi entenem per dispersió el desplaçament de la llavor des del seu origen a la planta mare fins a un lloc amb algunes probabilitats que el plançó s'hi establisca, i amb el temps, esdevinga un nou adult. A més a més, el concepte de dispersió té un component quantitatiu puix que el que és dispersat és una collita o una quantitat (producció) determinada de llavors. Aquesta part quantitativa del concepte implica que quan p.e. hom diu que la barocòria és un mecanisme de dispersió en els *Quercus*, és necessari afegir quina proporció de la dispersió total és a causa de la barocòria. L'evidència indica que la barocòria no és la norma al clima mediterrani: la majoria de glans que cauen de l'arbre mare per gravetat es queden a la superfície del sòl i a) se sequen o b) són consumides per diferents animals atrets per grans acumulacions de glans (p.e. rosegadors, ungulats i porcs senglars; predació densodepenent). Encara més, si les glans aconsegueixen sobreviure i germinar, la coberta forestal les suprimeix per competència directa, cosa que es veu reflectit en creixements molt baixos o fins i tot negatius. En aquestes circumstàncies molts plançons perden la part aèria i tornen a rebrotar després de l'estiu de forma recurrent. En conclusió, quan hom diu que la barocòria és un mode de dispersió en els *Quercus*, cal afegir quina proporció de la collita de glans està incrementant la població d'adults per aquesta via (p.e. 0.001% de la collita anual; deixem per al debat si un mecanisme amb molt baixes proporcions de dispersió de la collita val la pena mantenir-lo com un mètode de dispersió).

La majoria dels animals que s'alimenten de glans són considerats només consumidors i no dispersadors puix que les glans no sobreviuen a la ingesta. Atès que la major part de les glans que queden a la superfície del sòl es sequen o són predades, els veritables dispersadors són aquells que escampen glans soterrant-les, és a dir, els gaigs (*Garrulus glandarius*), els esquirols (*Sciurus vulgaris*) i els ratolins (bàsicament el ratolí de bosc *Apodemus sylvaticus* i el ratolí mediterrani *Mus spretus*). El gaig sembla haver desenvolupat una relació simbiòtica especial amb els *Quercus*, i se li ha dedicat una atenció especial. Com que una reducció en una de les fases del procés de regeneració pot portar a l'absència total de regeneració, per tal de compendre el reclutament en els *Quercus* hom necessita conéixer l'existència i les densitats dels dispersadors de glans. Al *Capítol 3* ens preguntem fins a quin punt la presència, densitat i distribució espacial del gaig està relacionada i es pot predir a partir de les característiques del territori. L'anàlisi està feta a dues escales espacials: 1) a l'escala de territori per validar la relació entre els atributs del territori (composició i configuració) i l'abundància de gaigs; i 2) a l'escala del territori de nidificació del gaig per validar quines parts del paisatge són seleccionades per les parelles de gaigs. L'objectiu final (pràctic) és l'obtenció d'un model predictiu de la distribució dels gaigs aplicable posteriorment a grans extensions de terreny (com podria ser la totalitat d'un parc natural).

Freqüentment hi trobem distintes espècies de *Quercus* juntes en el mateix bosc (boscos mixts de *Quercus*) o en boscos adjacents (paisatges mixts de *Quercus*) a causa que la major part dels territoris de la Mediterrània tenen una llarga història d'ús pels humans, amb el resultat d'un paisatge característic en mosaic. Tots els *Quercus* comparteixen els dispersors, cosa que dóna peu a la possibilitat d'una competència inter i intraespecífica per tal de dispersar les llavors pròpies. Aleshores, la qüestió de si els dispersadors són o no igualment atrets per glans de distintes espècies, formes o mides no és trivial per tal d'entendre la dinàmica demogràfica dels *Quercus*. Al *Capítol 4*, ens preguntem fins a quin punt el gaig mostra una preferència per les glans d'uns *Quercus* determinats, per les glans d'una mida determinada o, si ambdues preferències hi existeixen, quina de les dues (espècie o tamany) és dominant.

L'eficàcia del dispersant depén també dels llocs on soterra les glans. Per exemple, el picot americà transporta grans quantitats de glans a troncs prèviament foradats on són acumulades com si fos un graner. Clarament per als glans un tronc no és un lloc òptim per a germinar. En el cas del gaig, els llocs on les glans són soterrades solen ser òptims per a la germinació: sòls aclarits bons per a l'establiment, i a distàncies d'entre pocs metres a alguns quilòmetres de l'arbre mare. Aquesta dispersió a microllocs 'bons' per a la germinació suggereix que el gaig es pot considerar com un dispersant òptim de glans. Però, com de 'bons' per a la germinació i el creixement són els llocs que seleciona el gaig per a soterrar les glans és encara una incògnita a causa de les dificultats de seguir els vols del gaig al lloc exacte on amaga les glans. Aquesta questió és encara més rellevant als hàbitats en mosaic, ja que una gran varietat de rodals amb diferent vegetació són a l'abast del gaig. Al *Capítol 5* hem emprat radiotransmissors col·locats a dins del gla per a localitzar-ne amb precisió el lloc de soterrament, i per a: (a) conéixer la distribució de distàncies de dispersió dels glans; (b) determinar la forma del l'ombra de dispersió (p.e., ens demanem fins a quin punt les glans amagades pel gaig són agregades o distribuïdes a l'atzar); (c) determinar quins tipus de vegetació prefereix el gaig per amagar els glans; i finalment, (d) corroborar la idioneïtat d'aquesta metodologia per a l'estudi de les ombre de llavors i les característiques de dispersió del gaig.

Els rosegadors, especialment el ratolí de bosc a la zona mediterrània, consumeix grans quantitats de glans, però se sap també que dispersa glans a distàncies d'entre pocs a algunes dotzenes de metres. La seva eficiència sembla ser més baixa que la dels gaigs, atés que la major part de les glans són consumides i els llocs de soterrament són de més baixa qualitat per al reclutament dels plançons. Tot i això, cal dir que rarament aquesta eficiència ha estat validada. En qualsevol cas, les altes densitats de població dels ratolins probablement fan de contrapés a aquesta baixa eficàcia i sembla ser un dispersor adient i suficient per tal de regenerar els clars als boscos de *Quercus*. Les preferències del ratolí per una espècie de gla sobre d'altres, o les diferències de les taxes d'activitat en diferents tipus de vegetació són encara desconegudes en hàbitats mediterranis. Al *Capítol 6* els nostres objectius són: (a) determinar si els ratolins tenen preferències per distintes glans (en concret per a distintes espècies o mides), i (b) quantificar variacions en les taxes de remoció i distàncies de transport de glans en funció del tipus de vegetació. La nostra hipòtesi de treball és que els rosegadors són els màxims depredadors de glans i seleccionen les glans més nutritives. Aquestes glans seleccionades es deuen transportar més lluny pels avantatges energètics. Tot i això, aquest patró podria variar en les distintes unitats de vegetació degut a diferents densitats de rosegadors, diferències en el risc de predació per als rosegadors, fonts d'aliment alternatives presents i/o diferent disponibilitat dels llocs segurs per a soterrar les glans.

En la pràctica, com a resultat de la variabilitat en les fases de regeneració (producció, predació, dispersió, germinació, i supervivència) el que veiem al camp són diferents densitats de plançons i arbrets amb diferents dinàmiques de creixement. Quines zones són colonitzades pels *Quercus*? Sobreviuen i creixen els plançons igual de bé a totes les unitats del territori? En el cas de la surera, com que les poblacions orientals de la Península Ibèrica són relativament menudes (de desenes a milers d'hectàries) una altra qüestió rellevant és si els boscos menuts estan patint una falta de regeneració. Al *Capítol 7* (a) es mostrem els resultats de les prospeccions de camp fetes per quantificar les densitats de plançons i arbrets, i (b) es validen 3 hipòtesis de treball: en primer lloc ens demanem si la regeneració de sureres en les poblacions orientals és superior a la de les deveses (formacions sabanoides de l'oest de la Península Ibèrica, anomenades 'montados' en portugués). En les deveses la regeneració de carrasques i sureres sembla molt més baixa que als ecosistemes forestals, probablement a causa d'un impacte acusat de les activitats cinegètiques i ramaderes que han derivat en una mancança de dispersió de glans i una pressió a causa del pasturatge excessiva a sobre els plançons. A l'orient ibèric, la pressió per pasturatge i les activitats humanes s'ha reduït els últims anys a causa de l'èxode rural i dels processos d'abandonament de la terra en concordància amb la resta de zones costeres mediterrànies europees (veure més amunt, Pausas 2004).

La nostra segona hipòtesi al *Capítol 7* és que la regeneració decreixerà amb la reducció de la mida del bosc de sureres i açò podria ser conseqüència de diferents factors: és ben conegut que les poblacions menudes poden presentar efectes negatius a causa de l'endogàmia i l'erosió genètica, que podrien repercutir en una reducció en la producció i qualitat de les llavors, reduint la viabilitat de la població i augmentant el risc d'extinció, i reflectint-se tot plegat en el procés de regeneració. En aquest context, s'ha demostrat que les poblacions marginals de sureres tenen una diversitat genètica menor comparades amb les poblacions centrals. Aleshores, podríem esperar un patró de regeneració decreixent paral·lel a la mida de la població, i en especial pel que fa a la població més menuda estudiada (Pinet), a la qual es pot considerar menuda per a una població d'arbres (aprox. 70 ha de baixa densitat d'arbres). Més encara, el fet que els boscos són l'hàbitat principal del gaig fa que una reducció de la seua mida repercutisca en una reducció de la densitat de gaigs, i que a la vegada repercutisca en una reducció de la regeneració de les sureres. Finalment, cal assenyalar també que les poblacions menudes presenten un major 'efecte vora' que pot suposar una major predació dels glans i sensibilitat a les alteracions. Tots aquest processos plegats suggereixen que la regeneració de sureres podria reduir-se amb la mida del bosc en les poblacions ibèriques orientals.

La nostra tercera hipòtesi al *Capítol 7* és que, a l'escala de territori, la regeneració no es distribueix a l'atzar per què les condicions ambientals i els factors biòtics diferents (dispersió, predació i competència) afecten de manera distinta a les distintes unitats del paisatge. Aleshores, a causa de l'actual heterogeneïtat del territori per a les diferents unitats espacials esperem diferents processos de regeneració i densitats de reclutament.

Al *Capítol 8*, s'integren totes les dades, pròpies i la informació disponible a la bibliografia, en un model demogràfic de regeneració, i intentem mantenir tant com siga possible la variabilitat existent. L'objectiu del model és analitzar dades reals per tal d'entendre la dinàmica actual de la regeneració dels *Quercus* a escala de territori. El model està basat en la surera perquè ès l'espècie de la qual disposem de més dades, però probablement és transferible a d'altres *Quercus*. Com a novetats pel que fa a uns altres models basats en transicions recentment apareguts, hi ha la integració de tots els *Quercus* simpàtrics i tots els dispersors (per desgràcia amb l'excepció de l'esquirol, ja que no en tenim dades), i l'ús d'un índex de selecció/diponibilitat de glans per part del gaig. A partir del model es van simular diversos escenaris per validar les implicacions relatives del gaig i dels ratolins en la dispersió de la surera. Altres escenaris intenten esbrinar si la seleció de glans pels gaigs contribueix a la falta de correlació entre la producció de glans i les densitats de planços. Per tal d'avaluar l'efecte relatiu de cada dispersor sobre la demografia de la surera, es va calcular també la contribució total de cada dispersor al nombre total de reclutaments i l'efectivitat de cadascun a nivell de territori, entenent per efectivitat la proporció entre arbrets atribuïbles a cada dispersor i la proporció de la collita emprada per cada dispersor.

Principals resultats

- La producció de glans en la surera és més variable que no en els altres *Quercus* que s'han estudiat fins ara, no només a nivell individual sinó també a nivell de població. Aquesta alta variabilitat està produïda probablement per factors metereològics (acoblament als recursos), a la dinàmica endògena i a l'habilitat de produir dos tipus de glans de forma simultània (glans de maduració anual i biennal). La sacietat de predadors predispersius és més elevada en suraredes monoespecífiques que no en mixtos amb carrasques o roures. La mida de la gla és major a baixes taxes d'infestació, més disponibilitat hídrica durant la maduració i major nombre de dies de gelades a la primavera.

- El gaig viu a zones heterogènies forestals (combinacions de boscos diversos, conreus en ús, conreus abandonats, etc), i presenta als forests mediterranis densitats 6-7 vegades més baixes que no a les poblacions atlàntiques. En la setmana posterior a l'abandonament del niu, les seves poblacions reproductores es poden censar fàcilment amb el registre de les posicions del polls volanders. Amb l'ús de mapes de vegetació generats a partir de fotografies aèries i posterior validació sobre el terreny, hem pogut estimar la densitat i la distribució espacial de les poblacions de gaigs. Tot i això, per a fer una anàlisi més acurada serà necessari un desenvolupament futur del model proposat, el qual probablement haurà d'incloure les comunitats d'ocells presents.

- El gaig prefereix les glans de les carrasques i rebutja, si té altres opcions, les de coscoll; la selecció de les glans de roure valencià i surera és intermèdia entre les anteriors dues espècies. Respecte a la mida, el gaig selecciona preferentment glans grans, però tenint en compte que hi ha un òptim de mida seleccionat, immediatament per sota dels límits imposats per les dimensions de la gola, que cal tenir en compte a l'hora de planificar reforestacions amb glans grans.

- S'hi han trobat glans dispersats pel gaig des de 3 fins a 550 metres de distància dels menjadors experimentals, amb una distribució de distàncies Log-Normal. El patró espacial de dispersió va ser d'agregacions de glans distribuïts en funció de la composició i configuració de la vegetació. A majors distàncies que la de les agregacions es troben glans aïllats. Les zones preferides per a soterrar les glans són rodals amb percentages baixos de cobertura del sòl per la vegetació (p.e. conreus recentment abandonats, pistes i camins forestals, pinars amb poc recobriment arbustiu, etc). Per contrapartida, el gaig evita rodals amb elevat recobriment del sòl (conreus abandonats vells, matollars i pinars amb matolls). El robatori de glans dispersats pel gaig per part de ratolins va ser baix (sobre un 8%). No vam trobar diferències en les distàncies de soterrament de glans de carrasca i surera. El seguiment de glans amb radiotransmissors és una tècnica òptima per al seguiment de la dispersió de glans a distàncies mitjes i llargues, i pot ser utilitzat per al seguiment de la destinació de les glans (predació, dispersió secundària, escapament, etc).

- Els ratolins van seleccionar glans de carrasca abans que els de surera o coscoll, és a dir, són capaços de diferenciar les distintes espècies de glans. Pel contrari, no hem trobat una clara selecció de les glans per la seva mida, si exceptuem les glans de coscoll, o el que és el mateix, la selecció de la mida de la gla va ser depenent de l’espècie. Després de selecionar la gla a l'assaig tipus cafeteria, no s’hi van trobar diferències en la destinació de la gla (predada, soterrada, distància de transport...), a excepció de les glans de coscoll que van ser més soterrades del que esperàvem. Les taxes de desaparició i les distàncies de transport de les glans van variar amb el tipus de vegetació considerat: s’hi van trobar baixes taxes de desaparició i llargues distàncies de transports en les zones amb poca cobertura del sòl (p.e. pinedes sense matolls). Els resultats poden tenir coseqüències rellevants per a boscos mixtos de *Quercus* i per les planificacions de reforestacions amb sembra directa de glans.

- Les densitats de plançons van ser molt variables en funció de les unitats (tipus) de vegetació però en conjunt superiors a les trobades a les deveses. Resumint, hem trobat: (a) regeneració limitada en els matollars, el més probable a conseqüencia d’ una falta de dispersió de glans; (b) regeneració completa en els conreus abandonats propers a boscos, però amb una finestra de regeneració que es tanca ràpidament amb el recobriment del sòl per la vegetació; (c) grans densitats de plançons sota les suredes i els pinars, amb taxes d’aparició i mortalitat de nous plançons elevades (banc de plançons dinàmic). Aquestos plançons asseguren el reompliment de la coberta de la sureda i el remplaçament del pins després d’una pertorbació (p.e. incendis).

- Tant el gaig com els ratolins dispersen glans, però el 75% dels plançons amb 3 anys d’edat es correspondrien a dispersions efectuades pel gaig en aquelles zones on són presents. L’eficàcia del gaig en la dispersió de glans seria d’un ordre de magnitud superior a la dels ratolins. Les acumulacions d’arbrets als escenaris de la sureda van ser inferiors a les observades sobre el terreny, probablement perquè la dispersió per part dels ratolins podria ser superior en certs anys (p.e. anys de collita abundant) respecte als dos anys dels quals disposem dades i/o a causa d’una proporció desconeguda de regeneració vegetativa. El millor escenari que explica les densitats observades de plançons i arbrets es correspon a aquell en què (a) la dispersió és compartida pel gaig i el ratolí i (b) els gaigs obtindrien glans des d'una zona de campeig hivernal àmplia i els dirigirien cap al territori de nidificació que seria més reduït (dispersió dirigida). En condicions naturals sembla que els gaigs refusen les glans de coscoll, però no hi hem trobat efectes d'una possible selecció d'espècie sobre el banc de planços.

Conclusions i discussió general

La regeneració en les espècies del gènere *Quercus* és el balanç final d'un procés, no només perquè les diferents fases poden estar desacoblades sinó també perquè hi ha una gran variabilitat espaciotemporal. A més a més, aquest procés es caracteritza per tenir fortes interaccions no només entre individuus de la mateixa espècie, sinó també amb d'altres espècies. Hem vist al llarg d'aquest estudi que en el cas de les sureres, la periodicitat en la producció de glans ès encara desconeguda per causa de l'acció simultània de la producció de dos tipus de glans (anuals/biennals), als factors metereològics, a la sacietat dels predadors predispersius i, probablement també, a la competència pels dispersors. Tot i això, els nostres resultats indiquen que si hi ha una veritable periodicitat en la surera, l'interval de producció seria superior al d'altres *Quercus* coexistents (probablement de 5 o més anys). La contribució i connexió exacta entre els factors que controlen la vecería de la surera queda per a ser descrita i quantificada en una major precisió a mesura que obtinguem sèries de producció més llargues. Cal tenir també present que aquesta periodicitat pot estar relacionada amb la d'altres espècies amb les quals competeix, com són la carrasca, el roure valencià i el coscoll. Tots ells comparteixen el gaig com a principal dispersor del glans, i el ratolí de bosc com el principal predador i dispersor secundari de glans.

Al camp hem pogut observar que, almenys a la Península Ibèrica oriental, el reclutament de plançons dels *Quercus* està funcionant, especialment als camps de conreu abandonats on totes les fases de la regeneració són concordants i els arbres adults apareixen després d'un període de temps relativament curt (diguem 20 anys). Tot i això, la finestra de regeneració es veu reduïda als anys immediats després de l'abandonament; tal com va recobrint-se el sòl de vegetació herbàcia i arbustiva, el gaig va deixant de dispersar glans fins a parar completament amb recobriments del sòl pròxims al 100%. Açò és a causa probablement d'un augment del robatori dels glans per part dels rosegadors, puix que aquestos augmenten la seva activitat amb l'increment de la cobertura vegetal. És necessari recalcar que açò només passa en els conreus abandonats propers a àrees boscoses amb presència de gaigs; aquesta sembla la raó principal de la falta de regeneració en boscos oberts com les deveses. Per altra part, els boscos de *Quercus* tenen suficient regeneració a partir de les dispersions de curta distància fetes pels rosegadors, que reomplin els clars i mantenen unes densitats de plançons suficients per a la regeneració després de possibles perturbacions, almenys en les actuals condicions de poca pressió de pasturatge d'ungulats salvatges i ramats domèstics.

Podem imaginar-nos una seqüència probable de successos que explicarien l'actual regeneració dels *Quercus* als boscos de l'orient ibèric: l'ús de la terra va ser tan intens fins a mitjans del segle passat que la superfície forestal estava reduïda a la mínima expressió de la qual tenim constància i, com a conseqüència, les poblacions de gaigs hi devien ser molt reduïdes també. Després de l'abandonament generalitzat del anys seixanta, els pins, afavorits per una dispersió anemòfila, i per les reforestacions, van ocupar gran part de les terres agrícoles abandonades i part de les forestals. Mestrestant, la regeneració dels bosquets remanents de *Quercus* es reduïa al seu 'manteniment' dirigida pels rosegadors. Pels vuitanta-noranta moltes de les pinedes de l'etapa anterior ja estaven en fases madures de desenvolupament. Aquest ambient forestal devia permetre un augment significatiu de les poblacions de gaigs, que a la vegada van activar una dispersió de mitja-llarga distància dels *Quercus* cap a conreus abandonats i (novetat) les cada vegada més freqüents zones incendiades. Esta seqüència de successos, encara que especulativa, està plenament en corcondància amb el que sabem actualment del procés de regeneració dels *Quercus*. Una qüestió pendent és si la dispersió pel gaig serà suficient per a mantenir les actuals taxes de reclutament al futur pròxim després de les més que probables grans pertorbacions (focs de gran extensió) i els efectes del canvi climàtic.

En conjunt, els resultats tenen implicacions d'importància des del punt de vista de la gestió dels forests de *Quercus*. En primer lloc, pel que fa als gestors, caldria parar atenció a les fases clau de la regeneració (especialment a la dispersió) per tal de potenciar-la. A l'hora de desevolupar estratègies de gestió i de l'execució dels treballs caldria tenir en compte certs punts: (a) Els *Quercus* no es regeneren adequadament a sota coberta, però el banc de plançons és crucial per a la regeneració després de fortes pertorbacions com per exemple els focs o les netejes forestals. En conseqüència, en les feines d'extracció de fusta cal para atenció per tal de minimitzar l'impacte sobre aquestos bancs de plançons; (b) a l'hora de planificar una tala, és preferible fer molts rodals menuts (clarianes) que no àrees extenses, puix que els gaigs soterren les glans no gaire allunyats d'una coberta forestal protectora per prevenir els atacs per part dels rapinyaires; dit d'un altra manera, els gaigs són habitants de bosc i no d'espais oberts; C) per tal de mantenir bones densitats de gaigs, molts tipus diferents de rodals són preferibles a pocs rodals homogenis de gran mida; els paisatges en mosaic es regeneren millor que, per exemple, grans reforestacions; (d) les distàncies de regeneració natural se situaran a no més de pocs quilòmetres de la vora del bosc. Però, caldrà tenir en compte que si hi ha bons llocs perquè els gaigs puguen soterrar les glans a prop del lloc on les obtenen, aquestes distàncies rarament superaran el mig quilòmetre; (e) els matollars (coberts o no per arbres) no són zones que puguen regenerar-se amb *Quercus* per si mateixes (exceptuant segurament el coscoll), i caldrà netejar-les si volem potenciar-hi la regeneració forestal. (f) En la planificació de reforestacions, la gla emprada per a la producció de plançons o per a la sembra directa no hauria de ser de mida (molt) superior al màxim que solen dispersar els gaigs; pel contrari estaríem reduint les possibilitats que el bosc resultant veja limitada la seva dispersió.

Segon, pel que fa als investigadors en tècniques de reforestació amb *Quercus*, la sembra directa de glans en grans reforestacions a sòl descobert sembla possible, però si volem minimitzar les pèrdues de glans prèviament necessitem desenvolupart de forma simultània (a) protocols per a mesurar fàcilment les densitats de rosegadors, i (b) indicadors per a quantificar fonts d’aliment alternatives per als rosegadors presents. En aquesta línia, cal desenvolupar previsions més precises i fiables de la producció de glans, puix que la variació de les poblacions de rosegadors segueixen les variacions en la disponibilitat de glans. Respecte a la potenciació de la regeneració natural, s’haurien de validar menjadors artificials amb glans per a gaigs i ratolins sota diverses condicions. També cal dedicar esforços a la dinàmica de població dels esquirols i a quantificar la seva implicació en la dispersió de glans a nivell de territori. El desenvolupament de noves tècniques de potenciació i mimetisme de la regeneració natural en els *Quercus* sembla un tòpic interessant per a la investigació futura, a la qual esperem que aquest estudi haja contribuït d’alguna manera.

Reunido el Tribunal que suscribe en el día de la fecha acordó otorgar, por a la Tesis Doctoral de Don/Dña. la calificación de .

Alicante de de

El Secretario,

El Presidente,

UNIVERSIDAD DE ALICANTE

Comisión de Doctorado

La presente Tesis de D. ____ ha sido registrada con el nº ____________ del registro de entrada correspondiente.

Alicante ___ de __________ de _____

El Encargado del Registro,