1 **Determinants of functional connectivity of holm oak woodlands:**
2 **fragment size and mouse foraging behavior**

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18 **Highlights**

- 19 • Low acorn dispersal may override extensive pollen flow, limiting
20 genetic cohesiveness.
- 21 • Large forest fragments are key to maintain connectivity as they are
22 pollen sources.
- 23 • Seed crops in small forest fragments may better capture regional
24 genetic diversity.
- 25 • Scaling up fragment-level guidelines to landscape scale may not be
26 straightforward.
- 27 • Management practices aimed at raising connectivity should not
28 sacrifice local recruitment

29

30 **Abstract**

31 Demographic and genetic connectivity of fragmented plant populations
32 will depend on effective propagule flow across the landscape. We
33 analyze functional connectivity in a holm oak (*Quercus ilex*) fragmented
34 landscape by considering three important stages driving recruitment:
35 effective pollination, acorn production and acorn dispersal. We used a
36 network approach to (1) determine if pollen-mediated gene exchange
37 across the landscape was spatially structured; (2) estimate the effects of
38 limited acorn dispersal on functional connectivity; (3) identify which
39 landscape traits could drive source-sink dynamics of gene flow.

40 Although long distance dispersal was relatively frequent, most effective
41 pollen flow occurred over short distances (< 100 m). This resulted in a
42 significantly modular structure of the mating network, yielding higher
43 gene flow among nearby fragments. Limited mouse acorn hoarding
44 activity had a strong impact on landscape connectivity, decreasing male
45 gametic immigration rates into forest patches by one order of magnitude
46 Besides, our results show that big forest fragments (>10 ha) are the main
47 pollen sources, while small ones (<1 ha) are important pollen sinks.
48 Thus, big fragments are critical to maintain functional connectivity, while
49 small forest fragments may provide acorn crops better representing

50 regional genetic diversity. In addition to area effects, less isolated and
51 more central fragments showed higher migration rates and exchanged
52 effective pollen with more fragments. Hence, we expected that
53 landscapes with uniform or clumped distribution of big forest fragments
54 would show optimal connectivity traits. However, despite that simulated
55 gene flow was more evenly distributed across the landscape, connectance
56 and migration rates decreased. Our results call for caution before
57 translating patch-level management guidelines to the landscape scale.
58 They also show that the level of functional connectivity may change
59 throughout the recruitment process, suggesting that large-scale
60 conservation strategies may fail if local effective seed establishment is
61 disregarded.

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65 **Key words** *Quercus ilex*, mating network, seed dispersal, pollen
66 dispersal, forest fragmentation.

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81 **1. Introduction**

82 Land use changes have led to intense fragmentation of many temperate
83 woodland ecosystems, replacing large continuous forests by a mosaic of
84 isolated fragments, embedded in agricultural or urban matrices (Riitters
85 et al. 2000). The demographic and genetic connectivity of fragmented
86 plant populations depend on the effective dispersal of pollen and seeds
87 across the landscape (Sork et al. 1999; Sork and Smouse 2006). The
88 intensity and scale of both seed and pollen dispersal across forest
89 fragments are thus central to the decade-long debate about the extent to
90 which tree populations are resilient to fragmentation (Kramer et al.
91 2008). High tree genetic diversity and outcrossing rates, and extensive
92 long distance pollen dispersal may buffer the negative effects of forest
93 fragmentation (Hamrick 2004), while localized seed dispersal tends to
94 increase spatial genetic structure and relatedness. Seed dispersal
95 determines plant recruitment patterns, the successful establishment of
96 both male and female migrant gametes and the final distribution of
97 genotypes (Sork and Smouse 2006, Sork et al. 2015). Pollen movement
98 sets the template of male gametic gene flow, which depends on and is
99 subsequently shaped by effective seed dispersal (Fig. 1). Integrating the
100 joint effects of pollen and seed dispersal is thus necessary to gain realism

101 in functional connectivity studies (Sork and Smouse 2006; Jordano,
102 2010; Bacles and Jump 2011).

103 Analyzing fragmentation effects for trees using a metapopulation
104 perspective is a daunting task, due to their typically long life span,
105 delayed maturity, high recruit mortality, and long generation times
106 (Bacles and Jump 2011). Functional connectivity analyses provide a
107 middle way between data-intensive (and costly to validate)
108 metapopulation models and topological measures not underpinned by
109 biological processes. Functional connectivity usually refers to
110 demographic and genetic exchange among fragmented populations
111 (Taylor et al. 1993; Rico et al. 2012). The application of graph theory
112 methods to functional connectivity studies (Dyer and Nason 2004,
113 reviewed in Laita et al. 2011) has paved the way for evaluating which
114 factors govern mating patterns and effective pollen- and seed-mediated
115 gene flow at a landscape scale, and to detect genetic bottlenecks on
116 fragmented populations (Dyer et al. 2010; Fortuna et al. 2008; Herrera-
117 Arroyo et al. 2013). However, few landscape connectivity studies have
118 integrated the effects of fragmentation on the functionally-related
119 processes of pollen movement, effective mating, seed dispersal, and post-
120 dispersal seed mortality, even if connectivity patterns may vary
121 substantially throughout recruitment stages (Rico et al. 2012; Fig.1).

122 #Figure 1 approximately here#

123 Holm oak (*Quercus ilex*) forests are a suitable study system for
124 addressing the effects of limited seed dispersal in functional connectivity.
125 Like other wind-pollinated species, holm oaks typically exhibit
126 leptokurtic distributions of pollen dispersal distances, combining a rapid
127 decay at short distances with fat tails (Hampe et al. 2013; Ortego et al.
128 2014). As for acorns, forest management typically hampers their
129 effective dispersal over long distances (Santos and Telleria 1997; Pulido
130 and Diaz 2005; Morán-López et al. 2015). Eurasian jays (*Garrulus*
131 *glandarius*), the main long-distance acorn disperser in Europe, are absent
132 in small forest fragments (Andren 1992; Brotons et al. 2004), where
133 dispersal relies on wood mice (*Apodemus sylvaticus*), a moderately
134 efficient local acorn disperser. Most acorns handled by mice remain
135 within a close range of mother trees (< 5 m), and many of them are
136 finally predated (Gomez et al. 2008).

137 In fragmented holm oak woodlands, functional connectivity will thus
138 depend on effective pollen flow among fragments, and subsequent
139 mouse-mediated effective local acorn dispersal. The latter may in turn be
140 strongly negatively affected by fragmentation (Santos and Tellería 1997,
141 Morán-López et al. 2015). The resulting recruitment failure within

142 fragments may compromise the establishment of long-distance male
143 gametic migrants, which may explain the low genetic diversity of holm
144 oak saplings in small forest fragments (Ortego et al. 2010) in spite of
145 extensive pollen flow (Ortego et al. 2014). If this were the case, any
146 conservation strategy aimed at enhancing genetic cohesiveness at the
147 landscape scale should explicitly include measures aimed at restoring
148 local acorn dispersal.

149 The main goal of this study was to quantify functional connectivity of a
150 holm oak fragmented landscape and to detect critical demographic
151 factors potentially compromising gene exchange among fragments. For
152 this purpose we built spatial networks of gene flow among forest patches
153 considering effective pollination, acorn production and acorn dispersal.
154 This allowed us to (1) gauge if pollen-mediated gene exchange within the
155 landscape is spatially structured; (2) estimate the effect of mouse activity
156 on functional connectivity; (3) determine which patch traits define
157 source-sink dynamics within the network; and (4) evaluate if conclusions
158 drawn from patch-level approaches can be directly scaled up to
159 management guidelines at a landscape scale. We expected (a) a modular
160 structure of the gene exchange network due to predominantly local pollen
161 flow (Ortego et al. 2014), (b) a significant decrease of landscape
162 connectivity with diminishing effective acorn dispersal (Rico et al. 2012),

163 (c) an important effect of the spatial extent, centrality and isolation of
164 fragments on pollen source-sink dynamics, and (d) a problematic
165 extrapolation of these findings to the landscape scale, due to emergent
166 properties in the connectivity network (Baguette et al. 2013).

167 **2. Material and methods**

168 2.1 Study area

169 Field work was carried out in a Holm oak (*Quercus ilex*) archipelago
170 (14.4 x 10³ ha; see Appendix B Fig. B1) located in the southern plateau
171 of central Spain, near Quintanar de la Orden (39°35'N, 3°02'W, 870 m
172 a.s.l.). Cereal cultivation has reduced forest cover to ~8% in the study
173 area, with 401 patches ranging from 0.02 to 793 ha. The dominant tree is
174 holm oak and the understory is composed of shrubby kermes oak
175 (*Quercus coccifera*) and xeric Mesomediterranean shrubs (e.g. *Rhamnus*
176 *lycioides*, *R. alaternus*, *Cistus ladanifer*, and *Asparagus acutifolius*).
177 Annual precipitation and mean temperature are 421 mm and 14°C,
178 respectively. We chose this study site because it is representative of holm
179 oak woodlands in central Spain (Santos and Tellería 1998).

180 2.2 Sampling design

181 In autumn 2012, we simultaneously measured acorn production, acorn
182 dispersal patterns by wood mice (*Apodemus sylvaticus*) (Morán-López et
183 al. 2015) and pollen flow. Eurasian jays are supposed to be absent in
184 these patches (Tellería et al. 1999, Palomino et al. 2012), but we
185 surveyed corvid presence during autumn-winter anyways. Two observers
186 walked along 2 to 5 km transects, uniformly distributed throughout the
187 study area (over 150 km in total), stopping every 100 m. Monitoring was
188 performed at dawn and dusk (periods of peak bird activity). The
189 openness of the study area, both among and within forest fragments,
190 ensured easy acoustic or visual detection 200 m around observers, as
191 ascertained by frequent contacts with magpies *Pica pica*, carrion crows
192 *Corvus corone* and similar-sized birds. We did not detect any Eurasian
193 jay, either during transects or while performing field work with mice and
194 oak crops during 2012-2014 (Morán-López et al. 2015, 2016). Jay
195 absence was further corroborated by interviews to local farmers and
196 hunters.

197 We selected three large (> 100 ha) and 10 small (0.05 ha on average)
198 forest fragments. Within large fragments, we defined interior and edge
199 areas considering a 60 m threshold distance to the cultivated border
200 (García et al. 1998). We thus considered three fragmentation categories:
201 large fragment interior, large fragment edge, and small fragment, which

202 allowed us to assess global patterns of acorn production and seed and
203 pollen dispersal taking into account edge effects.

204 To assess local acorn production, we monitored acorn crops of 90 focal
205 trees (30 per fragmentation category) and their four nearest mature trees
206 in random directions, whenever possible. We visually estimated acorn
207 crop size with a semi-quantitative measure ranging from 0 (no crop) to 4
208 (more than 90% of canopy producing acorns), referred to as acorn score
209 hereafter (Koenig et al. 2013). Acorn dispersal patterns by mice were
210 evaluated for 45 focal trees (15 trees per fragmentation category). In each
211 focal tree we offered 27 acorns to rodents (1250 acorns in total). A metal
212 wire (0.6 mm $\varnothing$) with a numbered plastic tag was attached to each acorn
213 (Xiao et al. 2006). Marked acorns were placed beneath the canopies of
214 focal trees and protected with 35 cm x 35 cm x 15 cm wire cages with a
215 mesh size of 6 cm that only allowed the entrance of rodents. Offered
216 acorns were tracked and categorized as predated or cached (buried and
217 intact) (see Morán-López 2005, for further details). Finally, to estimate
218 pollen dispersal distances we selected and georeferenced 28 mother trees,
219 collecting young leaves and 15-20 fully mature acorns from each of them
220 (460 seeds in total; see next section).

221 2.3 Pollen dispersal kernel estimation

222 We used mother-embryo diploid genotypic data and the POLDISP
223 software (Robledo-Arnuncio et al. 2007) to estimate the probability
224 density function of pollen dispersal locations from a source tree (pollen
225 dispersal kernel), which was then used to parameterize landscape
226 connectivity models. POLDISP relies on the expected decay with
227 distance of a normalized measure of paternal identity among maternal
228 sibship pairs. To gauge such decay empirically, mother trees should
229 sample as many pairwise-distance classes as possible, from neighboring
230 to long-distance pairs. Guided by this requirement and by viable acorn
231 availability, the 28 sampled mother trees were distributed as follows: 10
232 in the interior of large fragments, 6 in large fragment edges, and 12 in
233 small fragments. Pairwise inter-mother distances ranged from 4 to 5477
234 m. We initially intended to estimate a separate kernel for each
235 fragmentation category, since changes in canopy structure are expected
236 to alter air flow (Dyer and Sork, 2001; Bacles et al. 2005). However,
237 sample sizes were insufficient to achieve good fits (results not shown), so
238 all 28 mothers were pooled to obtain an average dispersal kernel.

239 Acorns were soaked for 24 hours and then placed in a germination
240 chamber. Because some acorns did not contain viable embryos, the final
241 number of offspring per mother was 12 ± 0.32 (mean $\pm$ S.E). We used
242 Invisorb DNA Plant HTS 96 Kit/C to extract and purify genomic DNA

243 from adults and progeny. A total of ten nuclear microsatellites transferred
244 from *Quercus petraea*, *Q. robur* and *Q. macrocarpa* were used to
245 genotype all mothers and embryos (see Appendix Table A1). Primers
246 were dyed labeled (FAM, PET, VIC, NED) and DNA was amplified
247 following Ortego et al. (2014). Amplification products were sent to an
248 ABI Genetic Analyzer (ABI, St. Louis, MO) and genotypes were scored
249 using Genemarker (Holland and Parson 2011).

250 The rank correlation coefficient between the probability of paternal
251 identity among maternal sibship pairs and inter-mother distance was
252 negative and significant ($r_s = -0.13$; $p < 0.01$). We fitted a two-parameter,
253 two-dimensional exponential-power pollen dispersal kernel (Clark 1998;
254 Austerlitz et al. 2004):

$$255 \quad P(d|a, b) = \frac{b}{2\pi a^2 \Gamma(2/b)} \exp(-(d/a)^b) \quad \text{eq.1}$$

256 where d is the pollen movement distance, Γ is the gamma function, b is
257 the shape parameter, and a is the scale parameter. The effective number
258 of pollen donors was estimated as the inverse of the probability of
259 paternal identity within maternal sibships ($N_{ep} = 1/r_p$) (Ritland 1990),
260 calculated separately for small and large fragments.

261 2.4 Design of landscape connectivity network

262 We constructed the functional connectivity network of our landscape
263 through three consecutive steps: (1) computation of expected pollen
264 migration rates among fragments, based on the empirically estimated
265 pollen dispersal kernel; (2) simulation of the number of acorns produced
266 and the realized number of effective pollination (mating) events within
267 fragments and among fragment pairs, given the expected pollen
268 migration rates; and (3) simulation of acorn caching by rodents.

269 *2.4.1 Expected pollen migration rates*

270 A digital ortophotography of the study area (20 x 7.2 km) was used to
271 create a gvSIG shape file (Steiniger and Hay 2009) of all fragments. For
272 each forest fragment, we calculated its centroid, area and perimeter. The
273 shape file was then imported to Netlogo and rasterized (Wilensky 1999).
274 Final pixel size was 20 m x 20 m (1000 pixels x 360 pixels within the
275 landscape) and each pixel contained information of its habitat (cropland
276 vs forest) and the type of forest fragment.

277 For each pair of fragments i and j , we defined the expected pollen
278 migration rate from j to i (M_{ij}) as the probability that an acorn produced
279 by a mother in the i -th fragment has been fertilized by pollen dispersed
280 from the j -th fragment, which was calculated as

$$M_{ij} = \frac{1}{n_{\chi_i}} \sum_{\chi_i=1}^{n_{\chi_i}} m_{\chi_i,j} = \frac{1}{n_{\chi_i}} \sum_{\chi_i=1}^{n_{\chi_i}} \left(\frac{\sum_{\chi_j=1}^{n_{\chi_j}} P_{\chi_i \chi_j}}{\sum_{k=1}^K \sum_{\chi_k=1}^{n_{\chi_k}} P_{\chi_i \chi_k}} \right) \quad \text{eq. 2}$$

281

282

283 where $P_{\chi_i \chi_j}$ is the probability of pollen transport between the centres of
 284 recipient pixel χ_i and source pixel χ_j (from the i -th and j -th fragments,
 285 respectively), given by the assumed pollen dispersal kernel (eq. 1); and
 286 where n_{χ_i} is the total number of pixels in the i -th fragment and K the
 287 total number of fragments. The term $m_{\chi_i,j}$ is the probability that an acorn
 288 produced by a mother in the χ_i -th pixel of the i -th fragment has a paternal
 289 parent from (any of the pixels of) the j -th fragment, so M_{ij} is calculated as
 290 an average probability of pollen immigration from fragment j across all
 291 pixels of the recipient fragment i . Note that M_{ii} yields the probability of
 292 local mating within the i -th fragment. If M_{ii} is close to zero, then the i -th
 293 fragment can be considered a pollen sink. On the other hand, the j -th
 294 fragment can be considered an important pollen source if the average M_{ij}
 295 over all i recipient fragments is comparatively large. All the M_{ij} values
 296 are stored in the $K \times K$ matrix **M**.

297 *2.4.2 Simulating acorn production and mating events*

298 We estimated acorn production across the landscape in 2012. Each pixel
 299 was assigned to one of the three forest fragmentation categories. The
 300 number of acorns produced in the i -th fragment ($Prod_i$) was estimated as:

$$301 \quad Prod_i = \sum_{\chi_i=1}^{n_{\chi_i}} Prod_{type,\chi_i} \times 28.75 \times (\pi 2.5^2) \times 5 \quad \text{eq. 3}$$

302 where $Prod_{type,\chi_i}$ is the acorn score (see above) for the fragmentation
 303 category of the χ_i -th pixel of fragment i (1.28 ± 0.03 , 2.28 ± 0.07
 304 average $\pm$ SD acorn score for forest interiors and edges, respectively;
 305 $N=171$ and $N=153$ trees respectively); 2.5 is the average canopy radius in
 306 our study area (± 0.01 m; $N=96$; 32 per fragmentation category), 5 is the
 307 estimated number of stems per pixel (corresponding to an average stem
 308 density of 125 stems/ha). The constant 28.75 converts the semi-
 309 quantitative acorn score data into acorns per square meter of canopy
 310 projection, following the regression model developed by Díaz et al.
 311 (2011) from data taken in the National Park of Cabañeros during 2008-
 312 2010 ($\text{acorns/m}^2 = 28.75 * \text{acorn score}$; $P < 0.01$, $R^2 = 0.87$).

313 The mating network was then constructed by simulating acorn
 314 production. For each (recipient) forest fragment, we generated the
 315 number of acorns sired by pollen donors from each of the potential K
 316 (source) fragments by randomly drawing from a multinomial distribution
 317 with K classes with probabilities given by vector $\mathbf{M}[i,]$ (see eqn. 2), and

318 $Prod_i$ trials, using the multinomRob package (Walter et al. 2013). This
 319 way, network nodes represented forest fragments and link weights
 320 realized pollen migrant proportions among the corresponding $Prod_i$
 321 acorns. By replicating realized numbers of mating events using the
 322 multinomial distribution (rather than using the multinomial frequencies
 323 directly as link weights), we could assess the sensitivity of network
 324 structure to stochastic mating and acorn caching (see next section),
 325 conditional on differences in acorn production and caching rates between
 326 fragmentation categories.

327 *2.4.3 Simulating acorn caching vs predation*

328 We obtained average acorn caching rates per fragmentation category
 329 from our field acorn predation/removal experiments. We calculated the
 330 number of acorns cached per fragment using the equation:

$$331 \quad Cached_i = \sum_{\chi_i=1}^{n_{\chi_i}} Prod_i \times Cached_{type, \chi_i} \quad \text{eq.4}$$

332 in which $Cached_i$ is the estimated number of acorns cached in a pixel of
 333 forest fragment i , $Cached_{type, \chi_i}$ is the caching rate corresponding to the
 334 fragmentation category of the χ_i -th pixel of the i -th fragment (decreasing
 335 from 0.12 ± 0.05 in large fragment interiors and 0.09 ± 0.03 in large

336 fragment edges, down to 0.02 ± 0.01 in small fragments). $Prod_i$ is acorn
337 production, as calculated using eq.3.

338 The post-acorn-dispersal (effective) mating network was built in the
339 same way as the pre-acorn-dispersal mating network, but using $Cached_i$
340 (instead of $Prod_i$) as the number of trials of the corresponding
341 multinomial for the i -th fragment. In this case, the weights of network
342 links corresponded to realized migrant proportions among the
343 corresponding $Cached_i$ acorns (Fig.1), i.e., the (i, j) link weight was the
344 proportion of the $Cached_i$ acorns within fragment i whose paternal parent
345 was located at fragment j .

346 2.5 Quantifying network structure

347 We explored the structure of the two mating networks (before and after
348 acorn dispersal) by constructing 100 replicates for each and performing
349 modularity analyses. For each network, we calculated the following
350 parameters of functional connectivity: (1) connectance, defined as the
351 ratio between the number of realized links and the number of possible
352 links; (2) number of isolated (unconnected) patches; (3) modularity of the
353 network (raw and relative; see below); (4) number of modules; (5) mean
354 number of nodes per module; (6-7) minimum and maximum module size;
355 and (8) mean immigration rates.

356 The modularity function (M) determines if the network is organized in
357 well-defined separate modules, and was calculated using Newman and
358 Girvans' (2004) algorithm, as implemented in the igraph R package
359 (Csardi 2006):

$$360 \quad M = \sum_{s=1}^{Nm} \left[\frac{ls}{L} + \left(\frac{ds}{2L} \right)^2 \right] \quad \text{eq. 5}$$

361

362 where Nm is the number of modules, L is the number of links in the
363 network, ls is number of links between nodes in module s , and ds is the
364 sum of degrees (total number of links) of module s . A higher modularity
365 implies a more uneven distribution of gene flow across the landscape.
366 Modules represent subareas of the landscape within which among-
367 fragment gene flow is more intense. To test the significance of
368 modularity we compared the observed M value with values of 100
369 randomization of the network, keeping the same connectance, (Guimera
370 and Amaral 2005) using the package tnet (Opsahl 2009). The modularity
371 of the networks depends on their connectance and hence, to control for
372 this difference when comparing modularity between networks, we
373 calculated relative modularity following (Fortuna et al. 2008).

$$M^* = (M_{real} - \bar{M}_{random}) / \bar{M}_{random} \quad \text{eq. 6}$$

Wilcoxon rank sum tests were used for comparing topological parameters (connectance, relative modularity, number of isolated nodes etc.) between pre- and post-acorn-dispersal mating networks. To compare immigration rates we used generalized binomial regression models (link logit). Besides, to evaluate the impact of seed dispersal by mice on functional connectivity (Fig. 1), we calculated the percentage of variation between pre- and post-acorn-dispersal mating networks for each parameter of functional connectivity, represented in equation 7 as P ($\Delta_{pre-post}$).

$$\Delta_{pre-post} = \left(\frac{P_{post} - P_{pre}}{P_{pre}} \right) \times 100 \quad \text{eq. 7}$$

2.6 Factors determining effective pollen source-sink dynamics

We evaluated which factors determined the role of forest fragments as sources or sinks of effective pollen across the landscape (i.e. source vs sink nodes within the network). Our response variables were migration rates and the degree of the fragments within the network. Immigration rates are given by the proportion of non-local mating (equal to $1 - M_{ii}$ for each fragment i). Emigration rates for every fragment j were calculated

392 as the average proportion of seeds sired by pollen donors from j over all
393 recipient fragments i (average M_{ij} over all i). The degree of a node is
394 defined as its number of outgoing and ingoing links, which in our case
395 translates into the number of source or recipient fragments exchanging
396 effective pollen with the target fragment. We divided out forest
397 fragments into five size categories: ≥ 100 , $[10, 100)$, $[1, 10)$, $[0.1, 1)$ and
398 ≤ 0.1 ha. Our fixed effects were fragment area, distance to the center of
399 the archipelago, mean distance to other forest fragments (isolation) and
400 their interaction. Distance to the center of the archipelago and isolation
401 were not correlated ($P = 0.22$, Pearson correlation = -0.06). We used
402 generalized quasibinomial and quasipoisson models for the analysis of
403 migration rates and fragment degrees, respectively.

404 2.7 Scaling up to regional-scale management from patch-level measures

405 To explore whether our fragment-level analyses can be extrapolated to
406 landscape management guidelines, we generated six alternative
407 landscape scenarios: (1) Control landscape, in which the centroid and the
408 area of forest fragments are equal to those of the real landscape; (2) Area
409 reduction landscape, in which the area of large forest fragments (>10 ha)
410 is reduced by 10%; (3) Uniform landscape, in which centroids of large
411 forest fragments are uniformly distributed within the landscape, while

412 keeping the same area; (4) Clumped landscape, in which centroids of
413 large fragments are aggregated in the center of the archipelago following
414 an exponential decay function; (5) Combined uniform and area reduction
415 landscape; (6) Combined clumped and area reduction landscape. Each
416 fragment was built by spreading the forest habitat from its allocated
417 centroid to neighbor cells until the desired area was reached, producing a
418 tumor-like shape. The control landscape was used as a benchmark
419 (excluding shape effects) in our connectivity simulations. A 10% of area
420 reduction corresponds to reported values of habitat loss (per decade) in
421 evergreen woodlands of the Iberian Peninsula (Costa et al. 2014). For
422 each theoretical landscape scenario, we built a mating network following
423 the same protocol as for the real landscape, and compared the
424 corresponding functional connectivity parameters against those of the
425 control landscape ($\Delta control_{LANDS}$).

426 To assess the impact of enhanced caching rates on landscape
427 connectivity, we built two post-acorn-dispersal mating networks in the
428 control landscape: a control one, in which caching rates were the same as
429 those observed in the study area, and an alternative increased-caching
430 network in which caching rates were fixed to 0.17 for all pixels,
431 corresponding to observed values in the interior of well-preserved forests
432 (Morán-López et al. 2015). As before, we calculated landscape

connectivity parameters and compared them between both caching scenarios (control and increased-caching; $\Delta control_{INCREASES}$).

3. Results

3.1 Structure of pre- and post- acorn dispersal networks

The estimated pollen dispersal kernel had an average of 1149 m, was fat-tailed ($b = 0.16$) and rather leptokurtic, with a rapid decay of pollen dispersal probability within 100 m of source trees (see Appendix Fig. A1). Modeled effective pollen movement across the landscape was significantly modular, both for the pre- and post-acorn-dispersal networks (Table 1). In the modularity analysis of the pre-acorn-dispersal mating network, Newmans' algorithm (see Methods) detected an average (over independent replicates) of seven subareas of more intense gene flow (modules). Modules were of highly variable size (ranging from 5.87 to 129.66 nodes per module, Fig 2A). Almost no isolated fragments were detected in any of the replicates of the network, even if only 22% of potential links between fragments were realized on average (Table 1).

#Table 1 approximately here#

After simulating mouse foraging decisions (caching vs predation), the post-acorn-dispersal mating network was globally less connected (-36.62%), more spatially structured (61.62%), and with one order of

453 magnitude lower immigration rates, relative to the mating network before
454 seed dispersal (Table 1). Besides, the probability distribution of effective
455 pollen immigration rates became substantially positively skewed after
456 acorn dispersal, with one third of fragments showing very low ($\leq 2\%$)
457 immigration rates (Fig.2B, 2C). Overall, the considered post-seed-
458 dispersal demographic filter resulted in a more labile effective mating
459 network, due to the disappearance of low probability links and a lower
460 strength of the remaining ones.

461 #Figure 2 approximately here#

462 #Figure 3 approximately here#

463 3.2 Factors determining effective pollen source-sink dynamics

464 Considering first the pre- acorn-dispersal mating network, we found that
465 large fragments (>10 ha) acted predominantly as sources of effective
466 pollen, while small forest fragments (<0.1 ha) were mostly effective
467 pollen sinks (Fig. 3A and B, grey bars). Fragment area positively affected
468 the number of ingoing and outgoing links, though this effect was weak
469 (Fig. 3C and D, grey bars), resulting in a lower link number to fragment
470 area ratio in large forest fragments (mean $\pm$ s.e. links per pixel, 17.69 ± 1.14
471 and 0.01 ± 0.00 in fragments <0.1 ha and >10 ha, respectively). In
472 agreement with these results, the effective number of pollen donors was

473 much higher in trees located in small forest fragments than those from
474 large ones (32.29 ± 9.74 vs 12.66 ± 1.95 in small and large forest fragments
475 respectively). Pollen emigration rates and the degree of fragments also
476 depended on their spatial configuration. More isolated stands donated
477 less pollen and to a lower number of neighbor fragments. In addition to
478 isolation, distance negatively affected the number of ingoing and
479 outgoing links. In general, spatial configuration effects were stronger in
480 smaller fragments (Table 2, pre-acorn-dispersal network).

481 #Table 2 approximately here#

482 Considering now the post- acorn-dispersal mating network (Fig. 3, black
483 bars), results were similar in terms of emigration rates and fragment
484 degree (in and out). However, immigration rates showed a bell-shape
485 response (Fig. 3A, black bars, Table 2, post-acorn-dispersal network).
486 Medium-sized fragments showed the highest immigration rates. In fact,
487 as a consequence of strong post-dispersal seed mortality, small forest
488 fragments showed rather low effective pollen immigration rates (<2%),
489 relative to the high proportion of immigrant pollen at the seed-crop stage
490 (>60%).

491 3.3 Scaling up to regional-scale management from patch-level measures

492 A 10% area reduction of large fragments (>10 ha) in the control
493 landscape resulted in a lower number of links within the mating network
494 (−9.34%), smaller modules (−6.99%) and weaker links (−3.13%), but the
495 modular structure of the network did not change significantly, as
496 indicated by the relative modularity index (Table 3, see area reduction
497 landscape). Contrary to our expectations, both clumped and uniform
498 spatial distributions of large forest fragments negatively impacted
499 landscape connectance (−36.60 and −33.99% respectively) and average
500 immigration rates (−24.6 and −16.7%, respectively). Nevertheless, links
501 were more homogeneously distributed across the landscape (Fig. 4),
502 resulting in a reduction of network modularity (−49.59 and −52.88%
503 respectively). Besides, the size of the smallest modules was about three
504 times larger (2.87 and 3.20 respectively, for clumped and uniform
505 landscapes; Table3). Superimposing a fragment area reduction on the
506 clumped or uniform landscapes had low additional impact on observed
507 parameter changes (Table3, Uniform area and Clumped area landscapes).

508 #Table 3 near here#

509 The simulated enhancement of acorn caching rates increased all
510 connectivity parameters. It increased network connectance (15.51%),
511 decreased the number of isolated patches down to about 1 (vs 7 in the

control network), and increased immigration rates by a factor of two (2.35% vs 5.15%). Besides, increased seed caching relaxed the modular structure of the network (-8.99%), which showed bigger modules (12.33%) and a smallest module much larger (100.36%) (Table 3, Increased caching effect).

#Figure 4 near here#

4. Discussion

We analyzed functional connectivity in a holm oak fragmented landscape taking into account three key stages of the recruitment processes: effective pollen dispersal, acorn production and local acorn dispersal.

As expected, effective pollen flow within the landscape was spatially structured. As with other *Quercus* species (Streiff et al. 1999; Pakkad et al. 2008; Pluess et al. 2009), most mating events occurred over short distances, while showing at the same time a fat-tailed distribution. The modular structure of the mating network implies that there are landscape subareas within which effective pollen exchange is substantial and that show comparatively less frequent mating with other subareas. Notably, decreased effectiveness of local seed dispersal had a great impact on the landscape reproductive connectivity, diminishing the robustness of the mating network modules. Not only the number of connections in the

532 mating network decreased after accounting for post-dispersal seed
533 mortality, realized effective pollen immigration rates were an order of
534 magnitude lower on average. In line with previous work, our results show
535 that limited acorn dispersal can have pervasive effects on the
536 maintenance of reproductive and genetic connectivity of fragmented oak
537 populations (Fernandez-M and Sork 2007; Grivet et al. 2009; Luisa
538 Herrera-Arroyo et al. 2013, Sork et al. 2015).

539 The role of forest fragments in the mating network reflected both their
540 sizes and locations. Large fragments (>10 ha) were the main sources of
541 effective pollen, enabling mating and thus pollen gene flow among
542 fragments across the landscape. This result suggests that the system may
543 become more genetically disjoint and fragile if a minimum number of
544 large oak woodlands are not preserved. Conversely, small forest
545 fragments (<1 ha) acted as major pollen sinks, showing the highest
546 effective pollen immigration rates. Likewise other anemophilous species,
547 our model predicts that as population size decreases the paucity of local
548 mating neighbors results in higher immigration rates, as a consequence of
549 the mass-action law (reviewed in Sork and Smouse 2006). In addition to
550 the amount of immigrant pollen, the diversity of sources is important in
551 maintaining the genetic diversity of the acorn pool. Although larger
552 fragments received migrant pollen from a higher number of external

553 sources, the number of external pollen sources per area unit was larger
554 for smaller fragments. Thus, individual trees within large fragments
555 sampled less diverse pollen clouds (also reflected in N_{ep} estimates).

556 It has been advocated that small fragmented populations should be
557 avoided in seed-collection management practices, due to impoverished
558 genetic diversity of seed pools (Breed et al. 2013), but our results suggest
559 that potential trade-offs between fewer effective mothers and more
560 effective fathers need not invariably result in reduced seed pool genetic
561 diversity. Germplasm bank sampling strategies should consider including
562 acorns not only from mothers in large forest fragments, but also from
563 small ones, scattered across the landscape. The number of sampled
564 mothers per fragment could in principle be proportional to fragment area
565 (since the effective pollen pool diversity per unit area appears to be
566 inversely related to fragment size), but more precise recommendations
567 would require empirical genotypic and phenotypic information (e.g.
568 common garden experiments). Given that fine-scale spatial genetic
569 structure in adult trees is not uncommon in *Quercus* species (e.g. Aldrich
570 et al. 2005; Soto et al. 2007), and also that correlated paternity among
571 maternal families decreases with distance, usual recommendations about
572 separation distance between sampled mother trees should also be
573 considered.

574 In addition to area effects, the spatial distribution of forest fragments
575 across the landscape modulated gene flow source-sink dynamics. As
576 could be expected, forest patches located in central areas or less isolated
577 played a more important role within the network. This suggests that a
578 uniform or a clumped distribution of large forest fragments would
579 enhance landscape connectivity. In the former case, gene flow would be
580 more evenly distributed across the landscape. In the second one, a large
581 central core area with a high number of patches and redundant
582 connections would be created. However, functional connectivity may
583 emerge from a complex interplay between habitat availability and
584 landscape topology (Minor and Urban 2008; Laita et al. 2011; Baguette
585 et al. 2013), leaving aside potentially important selective effects
586 influencing gene flow patterns across the landscape.

587 By simulating gene flow in theoretical landscape scenarios we were able
588 to test whether fragment-level analyses can be scaled up to landscape
589 management guidelines. In relation to area effects, the mating network
590 was quite resilient to a ten percent area reduction of large forest
591 fragments, even if the latter act as landscape connectivity hubs. Although
592 reproductive connectivity may be minimally impacted by such a habitat
593 loss, it is important to bear in mind that acorn predation may be
594 exacerbated by increasing edge areas (Costa et al. 2014; Morán-López et

595 al. 2015). As expected, the spatial arrangement of large forest fragments
596 significantly impacted functional connectivity. However, not all the
597 effects followed the expected connectivity enhancement. For instance, a
598 uniform distribution of large forest fragments decreased the modularity
599 of the network and increased the size of the smallest module, but
600 diminished the number of connections among patches and average
601 immigration rates. Similar results were obtained in the clumped
602 landscape scenario. Overall, these results suggest that translating patch-
603 centered approaches into conservation planning strategies may not be
604 straightforward, due to the interaction between landscape configuration,
605 habitat availability and edge effects. On the contrary, caching rate
606 enhancement in edge areas improved all connectivity parameters.
607 Process-based models, like our network approach, can help to evaluate
608 the potential effectiveness of costly, large scale conservation measures
609 before their implementation (Bolliger et al. 2014; Humphrey et al. 2015).
610 Used carefully, they draw the attention to the potential of local
611 management practices in the maintenance of functional connectivity at
612 the landscape scale.

613 Our network approach allowed us to evaluate concomitantly pollen and
614 seed dispersal considering the structure of the entire landscape. However,
615 several simplifying assumptions should be acknowledged. Due to

616 sampling constraints, we estimated a single global pollen dispersal
617 kernel, without considering potential variation in pollen movement
618 probabilities associated with local heterogeneity in vegetation structure
619 or wind direction. Therefore, our model could be underrating pollen flow
620 in open areas or along certain directions (Robledo-Arnuncio et al. 2014).
621 However, estimated pollen dispersal distances and simulated immigration
622 rates were comparable to those found in previous studies developed in a
623 variety of landscape scenarios and *Quercus* species (Streiff et al. 1999;
624 Nakanishi et al. 2004; Lorenzo 2006; Soto et al. 2007; Pakkad et al.
625 2008; Pluess et al. 2009; Gerber et al. 2014; Ortego et al. 2014).

626 For the sake of simplicity, our model did not assume differences in male
627 fecundity among individuals, which is substantial in many empirical
628 studies (e.g. Kang et al. 2003). However, this assumption should not have
629 biased our pollen dispersal kernel estimation, since the employed method
630 has been shown to be accurate under non-uniform fecundity scenarios
631 (Robledo-Arnuncio et al. 2006). The sensitivity of the mating network
632 topology to potential variation in male fecundity among fragmentation
633 categories across space, is more difficult to predict, and would be worth
634 exploring theoretically and empirically. We additionally assumed that
635 fragmentation did not induce pollen limitation. It is not clear whether
636 pollen availability is a limiting factor of acorn production as density

637 decreases in holm oak stands (Garcia-Mozo et al. 2007; Ortego et al.
638 2014), but the positive edge effect on acorn production observed in our
639 study area may suggest that this is not the case in our landscape. Our
640 model did not include fragmentation effects on seedling establishment,
641 even if cropland ploughing will reduce recruitment success in edge areas
642 and may act as a subsequent filter in functional connectivity (Fig 1).
643 However, we were interested in evaluating the endogenous potential of
644 patchy woodlands to maintain genetic connectivity. The massive
645 disappearance of emerging seedlings due to ploughing would make
646 unfeasible to tease apart differences in recruitment driven by changes in
647 disperser behavior from purely anthropogenic impacts. Acorn tracking
648 experiments in abandoned croplands would help to incorporate edge
649 effects on potential seedling recruitment in the model. Finally, in long
650 lived species like holm oaks, the contribution of individuals to population
651 demography and genetics occurs over decades. Albeit our network
652 approach is based on extensive field data, it is temporally fine-scaled and
653 hence it is difficult to evaluate the overall impact of fragmentation on the
654 long term population structure and dynamics. For instance, although
655 seedlings of managed holm oak woodlands show lower genetic diversity
656 (Ortego et al. 2010), recent studies suggest that long distance dispersal
657 may prevent genetic erosion in extremely isolated populations (Hampe et

658 al. 2013). Models including multiple generations, based on mechanistic
659 demographic and genetic approaches, could help to scale up our findings
660 (Robledo-Arnuncio et al. 2014).

661 **5. Conclusions**

662 Our results showed that limited seed dispersal can constrain genetic
663 cohesiveness of fragmented populations despite extensive pollen flow.
664 Besides, they suggest that the preservation of large forest fragment
665 (>10ha) is essential to maintain functional connectivity, as they act as
666 predominant pollen sources. By contrast, acorn crops at small forest
667 fragments may potentially harbor higher genetic diversity. Despite the
668 clear source-sink dynamics found here, our results highlighted the need
669 for caution when scaling up patch-centered approaches into landscape
670 conservation guidelines. Overall, our study shows that costly large scale
671 management practices envisioned to enhance landscape connectivity may
672 not be effective if local recruitment processes are disregarded

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Table 1. Summary of modularity analysis on pre-acorn and post-acorn dispersal networks. *Connect*, connectance; *Isol*, number of isolated patches; *Mod*, Newmans' modularity; *S*, significance of the network modularity; *M**, relative modularity; *Nmod*, number of modules of the network; $\bar{N}$, average number of nodes per module; *Min* and *Max*, minimum and maximum number of nodes per module, respectively; *Mig*, immigration rates (% with respect to acorns produced). $\Delta pre-post$, percentage of variation between pre- and post-acorn dispersal network parameters. Significant values of $\Delta pre-post$ are in bold (** denotes $P < 0.01$)

Network	Filter	<i>Connect</i>	<i>Isol</i>	<i>Mod</i>	<i>S</i>	<i>M*</i>	<i>Nmod</i>	$\bar{N}$	<i>Min</i>	<i>Max</i>	<i>Mig</i>
Pre-acorn dispersal	Landscape	0.22±0.00	0±0.0 0	0.47±0.0 0	**	0.91±0.00	6.88±0.2 2	62.63±1.49	5.87±0.1 8	129.66±0 .81	46.64
Post-acorn dispersal	Acorn predation	0.14±0.00	0±0.0 0	0.51±0.0 0	**	1.47±0.01	6.97±0- 23	63.15±1.81	5.82±0.1 6	109.61±3 .30	3.11
$\Delta pre-post$		-36.36**	--	--	--	61.54**	1.30	0.83	-0.85	-15.46**	-93.32**

Table 2. Effects of fragment area, distance to the center of the archipelago, and isolation on immigration and emigration rates, and number of ingoing and outgoing links. Only significant effects are shown. *LRT*, likelihood ratio test; *df*, degrees of freedom; *Sign*, sign of the effect.

Network	Response	Effect	<i>LRT</i>	<i>df</i>	<i>Sign</i>	<i>pseudoR2</i>
Pre-acorn dispersal	Immigration rates	Area	4152.20	4	-	0.91
	Emigration rates	Area	1018.06	4	+	0.77
		Isolation	16.05	1	-	
		Area*Isolation	10.88	4	-	
	Degree(in)	Area	20.45	4	+	0.30
		Distance to center	87.00	1	-	
		Isolation	41.24	1	-	
		Area*Distance	9.12	4	-	
		Area*Isolation	15.00	4	-	
		Distance*Isolation	12.05	1	+	
	Degree(out)	Area	29.51	4	+	0.18
		Distance to center	42.92	1	-	
		Isolation	96.8	1	-	
		Area*Distance	11.36	4	-	
		Area*Isolation	15.75	4	-	
		Distance*Isolation	12.11	1	+	
Post-acorn dispersal	Immigration rates	Area	5093	4	-/+	0.92
	Emigration rates	Area	1164.31	4	+	0.79
		Distance to center	3.69	1	-	
		Isolation	18.63	1	-	
		Area*Isolation	15.24	4	-	
	Degree (in)	Area	1141.54	4	+	0.29
		Distance to center	25.36	1	-	
		Isolation	12.00	1	-	
		Distance*Isolation	5.81	1	+	
	Degree(out)	Area	165.89	4	+	0.35
		Distance to center	34.95	1	-	
		Isolation	23.28	1	-	
		Area*Distance	33.25	4	-	
		Area*Isolation	14.17	4	-	

Table 3. Landscape configuration effects on connectance (*Con.*), number of isolated patches (*Isol*), raw modularity (*Mod*), relative modularity (*M**), number of modules (*Nmod*), mean number of nodes per module ($\bar{N}$), number of nodes of the smallest module (*Min*), number of nodes of the biggest module (*Max*) and migration rates (*Mig*). $\Delta control_{LANDS}$, percentage of variation of pre-acorn dispersal network with respect to the control landscape; $\Delta control_{INCREASE}$, percentage of variation between post-acorn dispersal and increased-caching networks in the control landscape. Significant differences are in bold (* $p < 0.05$, ** $p < 0.01$). *S* indicates the significance of modular structure of the landscape in relation to null networks (see text). *Pre-disp* and *Post-disp*, pre- and post-acorn dispersal networks, respectively.

Effect	Landscape	Analysis	<i>Con.</i>	<i>Isol</i>	<i>Mod</i>	<i>S</i>	<i>M*</i>	<i>Nmod</i>	$\bar{N}$	<i>Min</i>	<i>Max</i>	<i>Mig</i>
No effect	Control	<i>Pre-disp</i>	0.14	0.00	0.62	**	1.45	9.39	45.47	8.73	89.31	30.27
		<i>Post-disp</i>	0.10	7.23	0.63	**	1.79	11.19	36.63	2.78	84.45	2.35
Area	Area reduction	<i>Pre-disp</i>	0.12	0.03	0.63	**	1.45	9.88	42.29	10.10	91.41	29.33
		$\Delta control_{LANDS}$	-9.34**	--	--	--	-0.04	5.16	-6.99*	15.74	2.35	-3.13**
Configurati on	Clumped	<i>Pre-disp</i>	0.09	0.00	0.63	**	0.73	8.59	48.86	25.95	72.49	22.83
		$\Delta control_{LANDS}$	-36.30**	--	--	--	-49.59**	-8.56**	7.43*	197.34**	-18.84**	-24.6**
	Uniform	<i>Pre-disp</i>	0.09	0.00	0.66	**	0.68	7.87	54.64	27.87	79.96	25.22
		$\Delta control_{LANDS}$	-33.99**	--	--	--	-52.88**	-16.22**	20.16**	219.34**	-10.47**	-16.7**
Configurati on & area	Clumped Area	<i>Pre-disp</i>	0.09	0.00	0.61	**	0.65	8.64	49.18	24.38	72.30	21.12
		$\Delta control_{LANDS}$	-34.54**	--	--	--	-55.36**	-8.03*	8.14*	179.35**	-19.05**	-30.23**
	Uniform Area	<i>Pre-disp</i>	0.09	0.00	0.66	**	0.69	7.15	59.01	21.76	90.10	24.45
		$\Delta control_{LANDS}$	-31.23**	--	--	--	-52.11**	-23.88**	29.77**	149.37**	0.88	-19.43**
Increased caching	Control	<i>Post-disp</i>	0.12	0.84	0.63	**	1.63	10.13	41.15	5.57	82.43	5.15
		$\Delta control_{INCREAS}$	15.51**	-88.38*	--	--	-8.99**	-9.47**	12.33**	100.36**	-2.39	118.88**

678 **Figure legends**

679 Fig.1. Conceptual model of functional connectivity including changes
680 along different recruitment stages (modified from Rico et al. 2012).

681 Fig.2. (A) Modular organization of the mating network of *Quercus ilex*
682 population (pre-acorn dispersal). Nodes represent forest fragments. Each
683 color depicts a module detected by the algorithm (areas of higher estimated
684 gene flow). (B-C) Histogram of immigration rates of the pre and post-
685 acorn-dispersal networks.

686 Fig. 3 Area effects on (A) immigration and (B) emigration rates, (C) links
687 arriving to the fragment (degree in), and (D) links emerging from the
688 fragment (degree out). Grey and black bars represent the pre- and post-
689 acorn-dispersal networks, respectively. Letters represent homogeneous
690 groups according to Tukey tests (capitals for pre-acorn-dispersal, lower
691 case for post-acorn-dispersal). Note that the axes of immigration and
692 emigration rates have different scale for each network.

693 Fig.4. Modular organization of connectivity in theoretical landscapes.
694 Nodes represent forest fragments (N = 401; solid-color circles and light-
695 color squares represent large (> 10 ha) and small (<10 ha) fragments,
696 respectively). Each color represents a module (group of patches highly
697 connected, as detected by Newmans' algorithm). Lines indicate pollen-

698 flow links between fragments (increasing grey darkness of links indicates
699 larger pollen migration rates). (a) Control landscape, preserving the
700 centroid and area of the fragments; (b) Clumped landscape, where
701 centroids of large fragments are aggregated in the center of the
702 archipelago, following an exponential decay function; (c) Uniform
703 landscape, where centroids of large forest fragments are uniformly
704 distributed within the landscape.

705

707 **Figure 1**

710 **Figure 2**

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713 **Figure 3**

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716 **Figure 4**

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901 **Appendix A**

Table A1. Microsatellite loci used to genotype *Quercus ilex*. Ne = number of effective alleles, Ho: observed heterozygosity, He: unbiased expected heterozygosity, Ta = annealing temperature. Data corresponds to the analysis of the 28 mother trees.

Primer	Ne	Ho	He	T _a	Primer origin
MSQ13	5.92	1	0.85	50	Dow et al. (1995)
ZAG7	2.48	0.96	0.62	57	Kampfer et al. (1998)
ZAG9	4.98	0.64	0.76	55	Steinkellner et al. (1997)
ZAG11	1.55	0.43	0.36	50	Kampfer et al. (1998)
ZAG15	9.56	0.96	0.91	50	Steinkellner et al. (1997)
ZAG20	4.09	0.86	0.77	55	Kampfer et al. (1998)
ZAG112	2.88	0.64	0.66	55	Kampfer et al. (1998)
ZAG46	3.74	0.71	0.75	53	Steinkellner et al. (1997)
PIE020	2.27	0.57	0.57	50	Durand et al. (2010)
PIE258	6.37	0.68	0.86	55	Durand et al. (2010)

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908 FigA1. Pollen dispersal kernel for *Quercus ilex* estimated with
 909 the exponential power function using the indirect method
 910 KINDIST. In the upper right corner is a log-plot version of the
 911 same curve providing a better representation of the tail.

909

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922 Fig B1. Map of the study area. Fragments are depicted in
923 grey. Not all the study area is represented in order to
924 visualize small forest fragments.
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