

1 **Unraveling conflicting density- and distance-dependent effects on plant**
2 **reproduction using a spatially-explicit approach**

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13 **Running title:** Conflicting density- and distance-dependent effects

14

15 **Summary**

16 1. Density- and distance-dependent (DDD) mechanisms are important determinants of plant
17 reproductive success (PRS). Different components of sequential PRS can operate either in the
18 same or in different directions and thus reinforce or neutralize each other, and they may also
19 operate at different spatial scales. Thus, spatially-explicit approaches are needed to detect
20 such complex DDD effects across multiple PRS components and spatial scales.

21 2. To reveal DDD effects of different components of early PRS of the Iberian pear (*Pyrus*
22 *bourgaeana*) sampled over three consecutive years, we used marked point pattern analysis.
23 Our special interest is to identify conflicting processes that regulate populations at different
24 spatial scales, e.g. whether DDD on fruit initiation and on fruit development acted in opposite
25 directions. To evaluate the significance of observed mark correlation functions based on
26 empirical data (e.g. fruiting success) we compared them to expectations given by spatially-
27 explicit null models.

28 3. Diverse DDD processes affected several aspects of PRS in a variable extent over the three
29 seasons. First, early fruit set was higher for individuals with more neighbors at small
30 distances (i.e. up to 40m). However, late *P. bourgaeana* fruit set decreased with increasing
31 number of nearby neighbors, but these effects canceled for overall fruit set that did not show
32 DDD effects. Second, the absolute number of fruits produced (crop sizes) by trees showed
33 positive density dependence in 2011 and 2012 but not in 2013. Finally, the total number of
34 seeds produced did not show DDD effects, indicating that conflicting demographic processes
35 can disrupt the initial spatial pattern of tree investment in reproduction.

36 4. Synthesis: Understanding complex spatial effects of density- and distance-dependent
37 (DDD) processes requires dissection of component processes to attain the complete picture
38 since contrasting DDD processes may be hidden behind a single cumulative measure of
39 reproductive success. The combination of novel and classic mark correlation functions used
40 here constitute a powerful spatially-explicit tool that can be broadly applied to unravel
41 conflicting mechanisms of DDD regulating the persistence of sessile organisms at a range of

42 spatial scales. Our findings help to explain why some authors failed to find expected DDD of
43 PRS and highlight the importance of detailed multi-year field studies on plant reproductive
44 success.

45

46 **Key words:** aggregation, conflicting effects, density dependence, Doñana National Park,
47 mark correlation functions, plant-animal interactions, population regulation, pollination, plant
48 population and community dynamics, small populations

49

50 INTRODUCTION

51

52 Long-term persistence of natural populations is critical for the maintenance of community
53 structure, ecosystems functioning, and essential ecosystem services. Both plant and animal
54 populations are frequently regulated by density and distance dependence of their demographic
55 parameters that impose bounds on population size (Strong 1986, Hixon et al. 2002).

56 Contrasting density- and distance-dependent processes can operate during the often intricate
57 life cycles of organisms sequentially or even simultaneously (Roughgarden et al. 1988).

58 Diverse proximate mechanisms of density and distance dependence can thus act during
59 different ontogenic stages, spatial scales, and contrasting directions (e.g. positive vs. negative
60 density-dependence; see Courchamp et al. 2008 for a review).

61

62 In plant populations, the spatial distribution of individuals determines how a species uses
63 resources, how it is used as a resource, and how it reproduces (Condit et al. 2000, Wiegand et
64 al. 2007, Fedriani et al. 2010). For instance, isolated individuals are less often visited by
65 effective pollinators and thus produce fewer fruits than more aggregated individuals (i.e.
66 positive density-dependence; Nielsen & Ims 2000, Aizen & Vázquez 2006, Fox 2007). Such
67 negative effects of isolation on fruit initiation can be amplified or attenuated by density
68 dependence in other demographic processes acting on subsequent plant life stages (e.g., fruit
69 development). In particular, high conspecific density may either facilitate encounter and
70 exploitation by seed predators and pathogens (Janzen 1970) or promote predator satiation and
71 thus attenuate the *per capita* chances of predation (Augspurger 1981).

72

73 Competition for resources or pollinators can also lower fitness in high-density neighborhoods
74 (Harper 1977, Spigler & Chang 2008, Gunton & Kunin 2009). Recent investigations in self-
75 incompatible species have shown that negative density- and/or distance-dependence is most

76 likely when mating tends to occur among highly related neighbors, which results in low
77 quality of available pollen and lessened plant reproductive success (hereafter, PRS) (Ishihama
78 et al. 2006, Aizen & Harder 2007). Whether plant aggregation has an overall net positive or
79 negative effect on individual fitness or whether partial effects cancel each other is an
80 important question necessary to fully understand how plant populations are regulated. The
81 answer requires the identification of potentially conflicting density- and distance-dependent
82 (hereafter, DDD) effects that act upon different life stages, and may also act over different
83 spatial scales within a population. Like other ecological and evolutionary processes (Levin
84 1992, Peterson et al. 1998, Thompson 2013), density and distance dependence of PRS vary
85 with spatial scale and the distance between neighboring conspecifics. Surprisingly, however,
86 few studies have investigated such processes in a spatially-explicit way across spatial scales
87 and on multiple components of plant reproduction (Knight et al. 2005, Gunton & Kunin 2009,
88 Gómez et al. 2009). Spatially-explicit approaches are needed to reveal the complexity of
89 density and distance dependent effects that operate simultaneously over multiple spatial scales
90 and reproductive success components.

91

92 The analysis of marked spatial point patterns (Illian et al. 2008, Wiegand & Moloney 2014)
93 constitutes a powerful, albeit rarely used approach in ecology that allows identification of
94 distance- and density-dependence of PRS over a range of spatial scales. This technique
95 involves statistical analysis of mapped point patterns (e.g., reproductive plants) and additional
96 properties of the plants, called "marks" that represent, for example, PRS components (e.g.,
97 fruit initiation and development successes, number of seeds per fruit, etc). Analysis of such
98 quantitatively marked patterns allows detection of correlations in PRS across a range of
99 spatial scales (e.g., Illian et al. 2008, Getzin et al. 2011, Raventós et al. 2011, Wiegand et al.
100 2013, Fedriani & Wiegand 2014). This allows us to find out if, for example, whether
101 pollination success is larger for trees that have more neighbors compared to trees with fewer

102 neighbors. For detecting such density-dependent effects we specifically tailored a function
103 that directly measures the correlation between plant density and PRS. This new “density
104 correlation function” $D_{mk}(r)$ estimates the correlation coefficient between the reproductive
105 success of all trees and the density of neighbors located within distance r of a specific tree.
106

107 In this study, we investigate the occurrence of possibly conflicting DDD processes in different
108 components of pollination and fruiting success of the self-incompatible Iberian pear *Pyrus*
109 *bourgaeana* in a Mediterranean area of southern Spain. Our data comprise three consecutive
110 reproductive seasons. The low-density *P. bourgaeana* population studied here experiences
111 severe seed dispersal limitation that leads to small-scale aggregated establishment beneath
112 reproductive trees and eventually to adult tree clustering (Fedriani et al. 2010). These tree
113 clusters are readily located and exploited by diverse pollinators (Żywiec et al. 2012).

114 Therefore, we hypothesized that aggregated trees would experience higher pollination success
115 (i.e. fruit initiation) than isolated trees which are more difficult to locate by pollinators. Also,
116 because most recruitment occurs near parent trees and high-density neighborhoods tend to be
117 composed by highly related individuals (Rodríguez 2009), we predicted more fruit abortion
118 and lower fruit development (i.e. fruits that complete development) for trees with close
119 neighbors than for isolated trees (Herlihy & Eckert 2004, Aizen & Harder 2007). More
120 specifically, we seek to answer the following three questions: 1) Do measures of relative
121 reproductive success (percentage of flowers that set and develop fruit) show DDD effects and,
122 if so, at what spatial scale? 2) What is the net effect of density and distance among neighbors
123 on absolute measures of reproductive success of *P. bourgaeana* (i.e., crop size, total number
124 of seeds per tree)? and 3) Are the DDD effects of different reproductive components
125 consistent in sign and spatial scale, and among reproductive seasons? To answer these
126 questions, and to progress our ability to unravel density from distance dependent mechanisms
127 acting on PRS, we use standard mark correlation statistics in combination with a new density

128 correlation function that quantifies the correlation between a mark of the plants (e.g. a
129 measurement of PRS) and the number of conspecific neighbors within a given distance r .

130

131 MATERIALS AND METHODS

132 *Study system*

133 *Pyrus bourgaeana* (Rosaceae) is a small tree distributed across the southern Iberian Peninsula
134 and northern Morocco (Aldasoro et al.1996). Our focal population is located in Doñana
135 National Park (510 km²; 37°89'N, 6°26'W), on the west bank of the Guadalquivir River
136 estuary in southwestern Spain. The climate is Mediterranean sub-humid, characterized by
137 dry, hot summers (June-September) and mild, wet winters (November-February). In the
138 Doñana area, this tree population occurs at low densities (< 1 ind/ha) across the landscape but
139 tree local distribution varies from highly isolated to strongly aggregated (6-8 reproductive
140 individuals within ~25 m; Fedriani et al. 2010). The establishment and persistence of such
141 tree clusters arises from dispersal limitation and spatial contagion of dispersed seeds (Fedriani
142 & Wiegand 2014). These processes create considerable relatedness among individuals within
143 clusters (Rodriguez 2011). The fieldwork (see below) was undertaken in an irregular
144 quadrilateral plot of 49-ha in which the locations of all *P. bourgaeana* reproductive trees were
145 known.

146

147 *Pyrus bourgaeana* is a self-incompatible species that flowers during February-March and is
148 pollinated by a diverse insect assemblage (Żywiec et al. 2012). Flowers are hermaphrodite,
149 showing radial symmetry and usually five oval petals. Fruit crop size strongly varies among
150 individuals and seasons, though each individual usually produces 100-500 fruits that ripen
151 during fall. Mature fruits are globose pomes, comprising 1-5 viable seeds. Pre-dispersal seed
152 predation by invertebrates is generally low (<5%; Fedriani & Delibes 2009). However,

153 during the long period of fruit ripening (March-September) a considerable fraction of the
154 initial fruit set fails before completing development (Authors *unpublished data*).

155

156 *Fruit set, crop size, and total seed number*

157 Since *P. bourgaeana* trees produce many inflorescences and reproductive success often varies
158 within trees (Herrera 2009), among each pollination season (i.e. 2011, 2012, and 2013) and
159 for each reproductive individual, we monitored several inflorescences to ensure that we attain
160 a good representation of its reproductive success. Specifically, we selected 2-6 branches of
161 each flowering *P. bourgaeana* tree ($n = 71, 67, \text{ and } 67$, respectively) within the study plot
162 (most of the 73 trees flowered during all three seasons). On each branch, we tagged from 1-4
163 inflorescences, recorded the number of flowers per inflorescence, and monitored them **once**
164 per month until complete fruit fall (i.e. early December). During 2011, our monitoring started
165 in early May (i.e. after anthesis) and thus we marked 142 infrutescences with 440 recently set
166 fruits. Thus, for this season, we estimated fruit development (i.e. number of fruits that
167 completed their development until early September / number of set fruits). During 2012 and
168 2013 monitoring started early in March before anthesis; we monitored the fate of 5012 and
169 5048 flower buds placed in 529 and 531 inflorescences, respectively. For both seasons, we
170 estimated both fruit initiation (i.e. number of flowers that set fruit / initial number of flowers)
171 as well as fruit development (as defined above). Overall fruit set (fully developed fruits per
172 flower) for each of these seasons was then estimated as the product of fruit initiation and fruit
173 development successes. Though overall fruit set best describes female performance of
174 individual trees, distinguishing between fruit initiation and development at a range of spatial
175 scales can help to identify density dependent mechanisms acting on individual fitness
176 components.

177

178 During the three seasons, just before the initiation of fruit fall in early September, we
179 estimated the crop sizes of all reproductive trees within the study plot by counting their fruits
180 with the aid of binoculars, when needed. In *P. bourgaeana*, fruits are arranged in discrete
181 clusters which facilitated estimation of reliable crop size by visually counting fruits from the
182 ground (e.g., Janzen et al. 2008). Finally, during 2011, we estimated the total number of
183 seeds produced by each focal tree by quantifying average seed number per fruit (three fruits
184 per tree) and multiplying it by the corresponding crop size (e.g. Spligler & Chang 2008).

185

186 *Mark-correlation functions*

187 To detect DDD effects on different components of *P. bourgaeana* PRS, we used techniques of
188 marked point pattern analysis (Illian et al. 2008; Wiegand & Moloney 2014). One data set
189 comprises for each reproductive *P. bourgaeana* tree i the coordinates \mathbf{x}_i and given measure m_i
190 of reproductive success that can be in our case percentage of flowers that set and develop
191 fruit, crop size, or the number of seeds per tree. This data structure is a univariate
192 quantitatively marked point pattern (Illian et al. 2008, Wiegand & Moloney 2014) where the
193 coordinates \mathbf{x}_i represent the univariate point pattern and the measure of reproductive success
194 m_i represents a quantitative mark.

195

196 Mark correlation functions are based on all (ordered) pairs of trees which have inter-point
197 distances within the small interval $(r - h, r + h)$. The parameter h is called bandwidth and must
198 be wide enough to yield a sufficient number of pairs in each distance class r but small enough
199 to reveal relevant biological detail (Illian et al. 2008). The basic idea of mark correlation
200 functions is then to estimate the mean value $c_t(r)$ of a test function $t(m_i, m_j)$ of the two marks
201 m_i and m_j , taken over all (ordered) pairs i - j of trees which have inter-point distances of $r \pm h$.
202 This procedure is then repeated for a range of distances r taken at distance steps Δr to obtain a
203 non-normalized mark correlation function $c_t(r)$ (Illian et al. 2008). To obtain the final mark

204 correlation function, the $c_t(r)$ is normalized with the expectation c_t of the test function taken
 205 over all pairs of trees, irrespective on their spatial separation:

206

$$207 \quad k_t(r) = c_t(r)/c_t. \quad (1)$$

208

209 Many different test functions $t(m_i, m_j)$ are possible (Illian et al., 2008). We use here the r-mark
 210 correlation function $k_{m.}(r)$ which is based on the test function

211

$$212 \quad t(m_i, m_j) = m_i. \quad (2)$$

213

214 An estimator of the corresponding non-normalized mark correlation function is given by

215

$$216 \quad \hat{c}_i(r) = \hat{\mu}(r) = \frac{\sum_{i=1}^n \sum_{j=1, \neq}^n m_i \times k^h(\|\mathbf{x}_i - \mathbf{x}_j\| - r)}{\sum_{i=1}^n \sum_{j=1, \neq}^n k(\|\mathbf{x}_i - \mathbf{x}_j\| - r)} \quad (3)$$

217

218 where the “box kernel” function $k^h(d)$ yields a value of $1/2h$ if the two trees with coordinates
 219 \mathbf{x}_i and \mathbf{x}_j have inter-point distances of $r \pm h$ and zero otherwise (Illian et al. 2008; Wiegand &
 220 Moloney 2014). Thus, the denominator of equation (3) yields the number of ordered pairs of
 221 trees i and j which are distances of $r \pm h$ apart and therefore, equation 3 yields the mean value
 222 of the mark m_i of the first tree i of these pairs. The normalization constant c_t of the r-mark
 223 correlation function which is taken over all pairs of points, regardless of their spatial
 224 separation, is obtained by replacing in equation 3 $k^h(d)$ by $1/2h$:

225

226
$$\hat{c}_i = \frac{\sum_{i=1}^n \sum_{j=1, \neq}^n m_i / 2h}{\sum_{i=1}^n \sum_{j=1, \neq}^n (1 / 2h)} = \frac{1}{n} \sum_i m_i = \mu \quad (4)$$

227

228 and yields μ , the mean value of m_i taken over all trees i (Illian et al. 2008).

229

230 Thus, $k_{m.}(r) > 1$ indicates that the PRS of trees that have neighbors at distance r is on average
 231 larger than the average PRS, indicating a positive effect of nearby *P. bourgaeana* trees on
 232 PRS. Conversely, $k_{m.}(r) < 1$ indicates that the PRS component of trees that have neighbors at
 233 distance r is smaller than the average PRS, indicating a negative effect of nearby trees on PRS
 234 (for further methodological details see Illian et al. 2008 and Wiegand & Moloney 2014).

235

236 We also used a mark correlation function that characterizes the spatial covariance in PRS of
 237 two *P. bourgaeana* trees separated by distance r . The appropriate test function for this
 238 purpose was proposed by Schlather *et al.* (2004):

239

240
$$t(r, m_i, m_j) = [m_i - \mu(r)][m_j - \mu(r)] \quad (5)$$

241

242 which results in a Moran's I like summary statistic $I_{mm}(r)$, a spatial variant of the classical
 243 Pearson correlation coefficient (Shimatani 2002). $I_{mm}(r)$ is normalized by the mark variance
 244 σ^2 . Thus, the $I_{mm}(r)$ is the straight forward Pearson correlation coefficient between the two
 245 variables m_i and m_j defined by the ordered i - j pairs of trees separated by distance $r \pm h$. Note
 246 that a test function that adjusts for the mean $\mu(r)$ that considers only pairs of trees separated by
 247 at a given distance r , not the population mean μ , is required to yield a summary statistic with
 248 the interpretation of a correlation coefficient (Schlather et al. 2004).

249

250 Finally, we developed a new function that directly relates the PRS component of a *P.*
 251 *bourgaeana* tree to the density of its conspecific neighbors. This “density correlation
 252 function” $C_{m,K}(r)$ estimates the classical Pearson correlation coefficient between the
 253 reproductive success m_i of a tree and the number of neighbors within distance r [$=\lambda K_i(r)$].
 254 Thus, the density correlation function is based on the following test function:

255

$$256 \quad t(r, m_i, K_i) = [m_i - \mu][(\lambda K_i(r) - \lambda K(r))], \quad (6)$$

257

258 where m_i is the PRS of the focal tree i , μ is the mean PRS of the population, λ the overall
 259 density of trees in the study area, $\lambda K_i(r)$ the number of neighbors around the focal tree i within
 260 distance r , and $\lambda K(r)$ the mean number of neighbors within distance r for all trees. Because
 261 correlation functions are invariant under multiplication with a constant it does not matter if we
 262 use absolute number of neighbors (e.g., $\lambda K(r)$) or density of neighbors ($\lambda K(r)/\pi r^2$).

263

264 The $K_i(r)$ is basically a “local” K -function and the average over all $K_i(r)$ ’s yields the well
 265 known K -function $K(r)$. Estimation of $K_i(r)$ requires an edge correction factor w_i if the
 266 neighborhood around tree i is not fully within the observation window, which yields $\pi r^2/A_i$
 267 where A_i is the area of the disk around point i within the observation window. The density
 268 correlation function $C_{m,K}(r)$ is normalized by the product of the standard deviations $\sigma_m \sigma_K$ of
 269 the marks m_i and the individual K -functions $K_i(r)$, respectively. “ C ” stands for correlation,
 270 “ m ” for the first mark m_i , and “ K ” for the second mark $K_i(r)$. In Appendix S1 we use artificial
 271 data sets to test the ability of the density correlation function to reveal different known DDD
 272 effects (see Fig. S1- S2).

273

274 To test whether the data show spatial correlations in the marks, we contrast the three mark
 275 correlation functions of the data to that of repeated simulations of a null model without spatial

276 correlation in the marks. This null model was implemented by randomly shuffling the marks
277 over all *P. bourgaeana* trees (Illian et al. 2008; Wiegand et al. 2013). We conducted 199
278 randomizations to estimate simulation envelopes for our summary statistics $k_{m.}(r)$, $I_{mm}(r)$, and
279 $C_{m,k}(r)$, being the 5th lowest and highest values of the summary statistics among the 199
280 simulations of the null model (e.g., Wiegand et al. 2013, Fedriani & Wiegand 2014). We
281 observe a departure from the null model at particular distances r if the summary statistic of
282 the observed data is outside the simulation envelopes.

283

284 To test the overall fit of the random marking null model over a range of distances we used the
285 “Diggle-Cressie-Loosmore-Ford” Goodness-of-Fit (GoF) (Baddeley et al. 2014) for the entire
286 distance interval up to 50m. The GoF test returns a P -value that indicates significant
287 departures of the observed mark correlation function from the random marking null model
288 over the distance interval of interest. If a significant departure occurs, we can inspect the plot
289 of the mark correlation function together with the simulation envelopes to identify the specific
290 distances r where departures occurred.

291

292 We estimated the two mark correlation functions and the pair correlation function every five
293 metres up to distances of 50m, where the distance bins centered on $r = 2.5\text{m}$, 7.5m , 12.5m , ...
294 included all pairs of trees within distance $(r - h, r + h)$, being $h = 2.5\text{m}$ the bandwidth. The
295 distance bins for the cumulative density correlation function yield $r = 5\text{m}$, 10m , 15m , ... All
296 point pattern analyses were conducted with the software *Programita* (Wiegand & Moloney
297 2014) available at <http://programita.org/>

298

299 RESULTS

300 *Aggregation of P. bourgaeana trees*

301 We first estimated the degree of clustering of our focal tree population. The non-cumulative
302 neighborhood density varied with distance from focal trees. Within 5-10 m away from a focal
303 tree, it was on average 29 times higher than expected by a completely random pattern, at 15-
304 20 m it was still 12 times higher, but beyond 40 m it approximated the overall density λ (see
305 Appendix S1). As expected, the cumulative relative neighborhood density $K(r)/(\pi r^2)$ declined
306 somewhat slower and approximated the overall density λ at radius r of about 100 m (Fig. S3).
307 Thus, we expect the strongest density-dependent effects to occur within 20-30 m which
308 should slowly fade away after 40-50 m (see Fedriani et al. 2010 for a more details on *P.*
309 *bourgaeana* clustering).

310

311 *Fruit initiation*

312 Fruit initiation during 2012 and 2013 was low (12% and 8.5% on average) and highly variable
313 (range 0-40%) among *P. bourgaeana* trees during both years (Table 1). As expected, the r-
314 mark-correlation function for the percentage of flowers that initially set fruits during 2012
315 was significantly higher for individuals with conspecific neighbors within 35 m (Fig 1A; $P =$
316 0.01). For example, a tree that had other trees at distance 25 m set about 1.4 times more fruit
317 than the mean of all trees in the study area, and such differences declined quickly for above
318 35 m (Fig. 1A). Schlather's I_{mm} correlation function showed that fruit initiation of trees
319 separated by less than 20 m were positively correlated (Fig 1B; $P = 0.015$). The density
320 correlation function $C_{m,K}$ indicated a highly significant and positive density dependence at tree
321 neighborhoods > 5 m ($P < 0.01$; Fig. 1C) with a peak at 30m [$C_{m,K}(r) = 0.5$]. The 2013 data
322 exhibited very similar patterning, i.e. positive DDD of fruit initiation that was somewhat
323 stronger than that of the previous season (Fig. 1D-F).

324

325

326

327 *Fruit development*

328 Fruit development rate from the total number of flowers that had set fruits (i.e. 440, 579, and
329 541 in 2011, 2012, and 2013, respectively) was over 3-fold higher than fruit initiation rate, but
330 also very variable among reproductive trees during the three seasons (Table 1). As predicted,
331 and in contrast with the observed trend for fruit initiation, fruit development showed negative
332 density dependence during two of the three years. During 2011, fruit development was
333 significantly lower for individuals with neighbors within 50 m (Fig 2A; $P < 0.01$). For
334 example, the mean r-mark-correlation value for fruit development of trees with neighbors at
335 30 m was only about 0.54 times that of the population mean fruit development (Fig. 2A). The
336 spatial correlation in fruit development of two trees r apart was higher than expected for
337 individuals with conspecifics up to 50 m away (Fig 2B; $P < 0.01$). This was caused by the
338 consistently lower fruit development of nearby trees as shown by the r-mark correlation
339 function. As a consequence we observed strong negative density dependence with maximal
340 correlations between 40 and 80 m ($P < 0.01$) where trees within clusters showed lower than
341 expected fruit development (Fig. 2C).

342

343 During 2012 the trend in fruit development was the same, being lower for *P. bourgaeana*
344 individuals with close conspecific neighbors, though the observed values were not significant
345 and fall within the simulation envelopes (Fig 2D-F). During 2013, the r-mark correlation
346 function indicated that fruit development was again significantly lower for individuals with
347 conspecific neighbors up to scale of 40 m ($P = 0.04$; Fig. 2G). Also, fruit development
348 exhibited a significant negative density dependence at neighborhoods with radius larger than
349 10m ($P = 0.015$; Fig. 2I).

350

351 *Overall fruit set*

352 Overall fruit set of *P. bourgaeana* trees during 2012 and 2013 (0.054 ± 0.006 and 0.028 ± 0.007
353 fully developed fruits per flower, respectively) was generally low and variable among
354 reproductive trees (Table 1). Interestingly, all three summary statistics during both seasons
355 were always non-significant and fall within the simulated envelopes (always, $P > 0.250$; Fig.
356 3A-C [2012], Fig. 3 D-F [2013]). This result indicates lack of distance and density
357 dependence of overall fruit set as well as lack of spatial correlation among tree in overall fruit
358 set, thus the positive density dependence of fruit initiation was just neutralized by the negative
359 density dependence of fruit development.

360

361 *Crop size and total seed number per tree*

362 Fruit crop size varied extensively among *P. bourgaeana* trees during the three seasons,
363 ranging over three orders of magnitude (Table 1). On average, trees produced twice as many
364 fruits during 2011 as during 2013 (Table 1). Crop sizes exhibited similar spatial patterning
365 during 2011 and 2012, but differed in 2013 (Fig. 4) when fruit crops were smallest. During
366 2011 and 2012 individuals with nearby conspecific neighbors produced more fruits than
367 average (i.e., up to 30-40 m; Fig. 4A [2011], Fig. 4D [2012]), with differences being
368 significant in 2011 ($P = 0.015$). During 2011, fruit production was subject to significant
369 positive density dependence at scales greater than 10m ($P < 0.01$; Fig. 4C). During 2012, the
370 pattern of density dependence was very similar to that in 2011, but somewhat weaker ($P =$
371 0.015 ; Fig. 4F) and restricted to scales from 20-60 m. In contrast, during 2013, all three
372 summary statistics indicated no spatial structures in crop sizes at any smaller spatial scale (P
373 > 0.44 ; Fig. 4G-I).

374

375 During 2011, the estimated total number of seeds per reproductive *P. bourgaeana* tree varied
376 widely (i.e. up to two orders of magnitude; Table 1). However, all three summary statistics
377 indicated a general lack of DDD effects on total number of seeds ($P > 0.145$; Fig. S4A-C).

378 These results indicate that the strong effect of conspecific neighbors at small scales for crop
379 size (Fig. 4) did not influence the number of seeds per fruit. This is probably caused by trees
380 with larger crops that produce fruits with fewer seeds, though such a trend was only
381 marginally significant ($r_s = -0.207$, $P = 0.096$).

382

383 DISCUSSION

384 We used detailed data from three consecutive seasons to examine DDD effects on sequential
385 PRS components over a range of spatial scales. Application of the framework of marked point
386 pattern analysis allowed us to answer our three guiding questions. First, fruit initiation, fruit
387 development and crop size showed DDD effects over spatial scales that correspond to that of
388 the highest neighborhood density of *P. bourgaeana* trees (some 30-40m, somewhat smaller
389 than the diameter of the typical cluster which yields 44m; Fedriani et al. 2010) as indicated by
390 the maximal correlation between reproductive success and neighborhood density. Second, we
391 found the surprising result that the net effect of DDD on the overall fruit set of *P. bourgaeana*
392 trees just canceled because DDD effects on its two components (i.e., fruit initiation by fruit
393 development) acted on opposite directions and with similar strengths. Finally, though the
394 DDD effects of different reproductive components of *P. bourgaeana* were conflicting in sign
395 (fruit initiation and crop size showed positive DDD effects whereas fruit development showed
396 negative DDD effects), they showed similar critical scales imprinted by the strong clustering
397 of the trees. However, DDD effects did not appear every year.

398

399 *Conflicting DDD processes*

400 Density and distance dependence in demographic parameters may be critical for the
401 regulation of many plant populations and thus for ecosystem functioning (Courchamp et al.
402 2008 review). Few studies, however, have considered DDD effects on several fitness
403 components simultaneously over a range of spatial scales which, as we illustrate, is needed

404 given that both sort of effects can emerge at contrasting plant life stages and spatial scales
405 (Aizen & Harder 2007). Our results provided clear evidence that different DDD processes
406 affect different aspects of fruit production (Aizen & Vazquez 2007, Gómez et al. 2009, Jones
407 & Comita 2010). First, as expected, *P. bourgaeana* individuals with nearby neighbors (up to
408 40 m) initiated more fruits during both seasons studied, which is consistent with results from
409 other temperate and tropical species, including some hermaphrodite species (e.g., Kunin 1993,
410 Aizen 1997; but see Spigler & Chang 2008). Such findings are generally attributed to the
411 attraction of pollinators to larger floral displays, and increased pollen transfer per visit at high
412 conspecific densities (Ishihama et al. 2006, Aizen & Harder 2007).

413

414 However, fruit development showed negative density and distance dependence during two out
415 of the three monitored seasons (Fig. 2). One hypothesis to explain this result is that most
416 mating occurred between highly related *P. bourgaeana* individuals (e.g., Ishihama et al. 2006,
417 Jones & Comita 2008). In entomophilous species pollen deposition from genetically related
418 donor conspecifics can strongly contribute to qualitative pollen limitation given that insect
419 pollinators typically disperse pollen locally (Harder & Barrett 1996, Aizen & Harder 2007).
420 Though the initiation of fruit set can occur despite low-quality pollen, such developing fruits
421 are likely to abort because embryos homozygous for deleterious alleles tend to die during
422 development (Herlihy & Eckert 2004, Aizen & Harder 2007). Several lines of evidence
423 support this hypothesis in our system. Genetic analyses indicates strong relatedness among
424 individuals within clusters (Rodríguez 2009), which is consistent with limited seed dispersal
425 and spatial contagion of dispersed *P. bourgaeana* seeds (Fedriani et al. 2010, Fedriani &
426 Wiegand 2014). Such local genetic structure also occurs in other tree species experiencing
427 limited seed dispersal (Dutech et al. 2002, Ng et al. 2004, Voigt et al. 2009). Moreover,
428 thorough hand-pollination experiments revealed that *P. bourgaeana* flowers supplemented
429 with pollen from individuals away from the focal cluster produced more fruits than

430 individuals supplemented with pollen from neighboring conspecifics (Fedriani et al. 2012).
431 Comparing levels of inbreeding in fully developed versus aborted seeds is a pending relevant
432 task (Jones & Comita 2008).

433

434 *Further influential factors*

435 Other factors, such as availability of soil resources, intraspecific competition, and tree size
436 could potentially affect fruit initiation and development, and hence overall fruit production
437 (Pacala & Silander 1985, Obeso 2002, García-Camacho et al. 2009). However, we did not
438 find any effect of tree size (i.e. dbh and crown area) on fruit production and the locally
439 dominant sandy substrate appears homogeneous across our study area (Fedriani & Delibes
440 2009). Furthermore, by sampling all reproductive individuals within our study plot and
441 performing detailed analyses at a range of spatial scales, we have minimized any potential
442 effect of spatial heterogeneity, thus providing robust results. On the other hand, though it
443 cannot be ruled out that high competition for resources and pollinators in high density
444 neighborhoods lessened tree reproductive success, high pollinator visitation and relatively
445 high initial fruit sets and crop sizes are often observed in these tree clusters. Nonetheless, at
446 least during 2011, although individuals in large clusters produced more fruit (Fig. 4) their
447 seed production (a more pertinent aspect of female reproductive success) did not show such
448 marked positive DDD pattern. This result indicates that although fruit production may
449 depend on flower production, subsequent conflicting DDD processes (including intraspecific
450 competition) can modify the spatial pattern of tree reproductive investment.

451

452 *Conclusions*

453 Our study revealed that complex scale-dependent processes operate at different components
454 of pollination and fruiting success of the self-incompatible Iberian pear *Pyrus bourgaeana* in
455 a Mediterranean area of southern Spain. Interestingly, DDD processes for sequential tree

456 reproductive success components operated in opposition and neutralized each other. This
457 result may help to explain why some authors failed to find expected DDD of plant
458 reproductive performance (see Ghazoul 2005 review). Understanding of the complex spatial
459 effects of DDD processes requires thus dissection of component processes to obtain the
460 complete picture since contrasting DDD processes may be hidden behind a single cumulative
461 measure of reproductive success.

462

463 Our approach can be widely applied to mapped plant populations for which detailed data on
464 reproductive success are available or attainable. Furthermore, point pattern analyses similar
465 to those presented here could be conducted using reproductive success components
466 concerning subsequent plant stages (e.g. dispersed seeds, seedlings, saplings; Fedriani &
467 Wiegand 2014, Jacquemyn et al. 2010, Wiegand & Moloney 2014) and thus foster
468 understanding of population regulation. Because DDD effects concern many active areas of
469 ecological and evolutionary research (e.g., humanization, invasive species, density-dependent
470 selection; Courchamp et al. 2008, Thompson 2013), the combination of novel and classic
471 mark correlation functions presented here could be broadly applied to unravel conflicting
472 mechanisms regulating the persistence of sessile organisms at a range of spatial scales.

473

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484 We do not perceive any potential source of conflict of interest influencing our objectivity in
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486

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605
606

607 **Supporting Information**

608

609 Additional supporting information may be found in the online version of this article:

610

611 **Appendix S1.** Test of the density correlation function with artificial data

612 **Figure S1.** Analysis of the spatial pattern of adult *P. bourgaeana* trees.

613 **Figure S2.** The mark correlation functions for total seed number produced by target *Pyrus*
614 *bourgaeana* trees during 2011

615

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620

621 **Table 1:** Sample sizes, mean, standard error, minimum, and maximum values of different *Pyrus*
 622 *bourgaeana* reproductive success components used in our marked point pattern spatial analyses for
 623 each of the three years (2011, 2012, and 2013) encompassed during the study. N₁, summation of
 624 flower buds, seeds, or fruits monitored to estimate fruit initiation and fruit development, as well as
 625 total seed numbers. Note that fruit set is given as a proportion. N₂, number of reproductive trees
 626 considered for the estimation of each reproductive success component.

	N ₁	N ₂	Mean	SE	Minimum	Maximum
2011						
Fruit initiation	-					
Fruit development	440	71	0.595	0.047	0	1
Overall fruit set	-					
Crop size	36215	71	510.07	57.69	16	1858
Total seed number†	78064	63	1239.1	188.2	59	7263
2012						
Fruit initiation	5012	67	0.120	0.011	0	0.345
Fruit development	579	61	0.455	0.046	0	1
Overall fruit set	5012	67	0.054	0.006	0	0.190
Crop size	17434	67	257.75	37.76	0	1448
2013						
Fruit initiation	5048	67	0.085	0.011	0	0.399
Fruit development	541	50	0.276	0.044	0	1
Overall fruit set	5048	67	0.028	0.007	0	0.351
Crop size	15725	72	218.40	30.58	0	1249

627

628 †Estimated only during the 2011 fruiting season.

629

630 FIGURE LEGENDS

631 **Figure 1:** Fruit initiation. The three mark correlation functions (r-mark correlation function,
632 Schlather's I function, and density correlation function) to detect a potential spatial structure
633 in *P. bourgaeana* fruit initiation during 2012 (A-C) and 2013 (D-F). The r-mark correlation
634 function is the mean reproductive success component (i.e., fruit initiation) m_i of a tree at
635 distance r of another tree, Schlather's I_{mm} correlation function is the correlation between the
636 fruit initiation m_i and m_j of two trees i and j separated by distance r , respectively, and the
637 neighborhood correlation function $C_{\text{mK}}(r)$ is the correlation between the mark m_j and the
638 number of neighbors within distance r . The observed mark correlation functions (closed
639 disks), the expected function under the null model of random mark i (grey solid line), and the
640 corresponding simulation envelopes (solid lines), being the 5th lowest and highest values of
641 the functions created by 199 simulations under the null model, are shown. To test the overall
642 fit of the random marking null model over a range of distances we used Goodness-of-Fit
643 (Baddeley et al. 2014) for the entire distance interval up to 50m. The GoF test returns a P -
644 value (shown in each panel) that indicates significant departures of the observed mark
645 correlation function from the random marking null model over the distance interval of
646 interest.

647

648 **Figure 2:** The mark correlation functions for fruit development in *Pyrus bourgaeana* during
649 2011 (A-C), 2012 (D-F), and 2013 (G-I). Other conventions are as described in Figure 1.

650

651 **Figure 3:** The mark correlation functions for the overall fruit set (i.e. the product of fruit
652 initiation by fruit development) in *Pyrus bourgaeana* during 2012 (A-C) and 2012 (D-F).
653 Other conventions are as described in Figure 1.

654

655 **Figure 4:** The mark correlation functions for crop size in *Pyrus bourgaeana* during 2011 (A-
656 C), 2012 (D-F), and 2013 (G-I). Other conventions are as described in Figure 1.

657

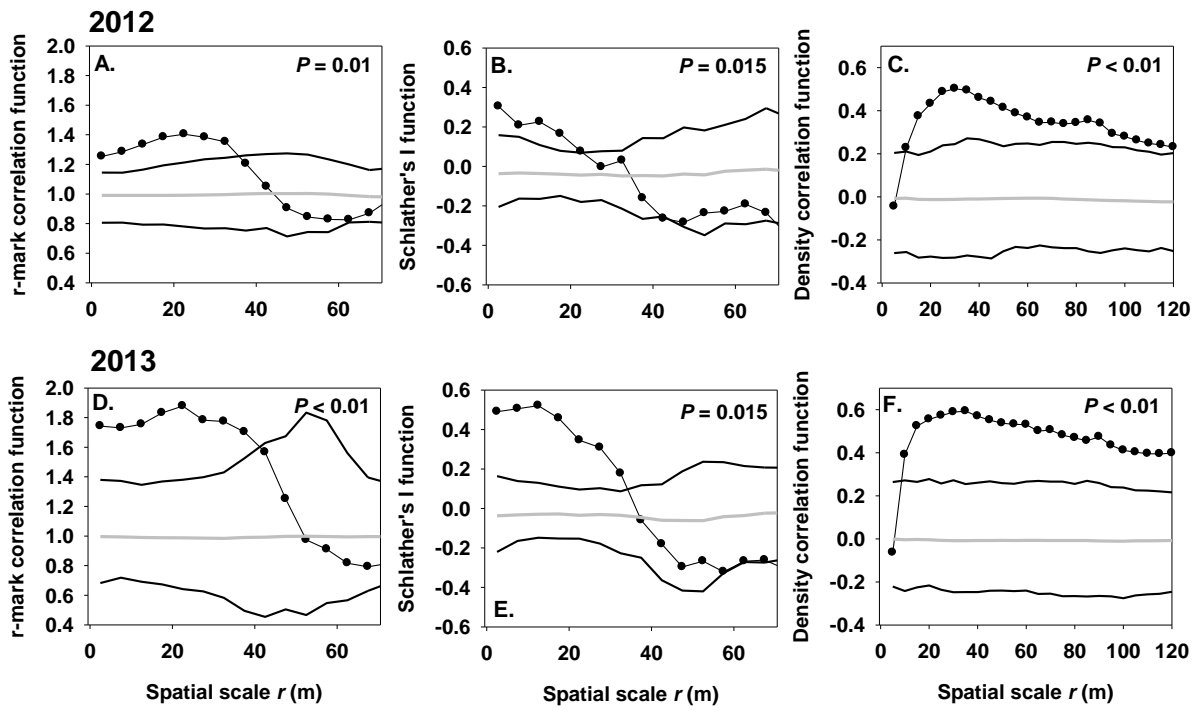


Figure 1.

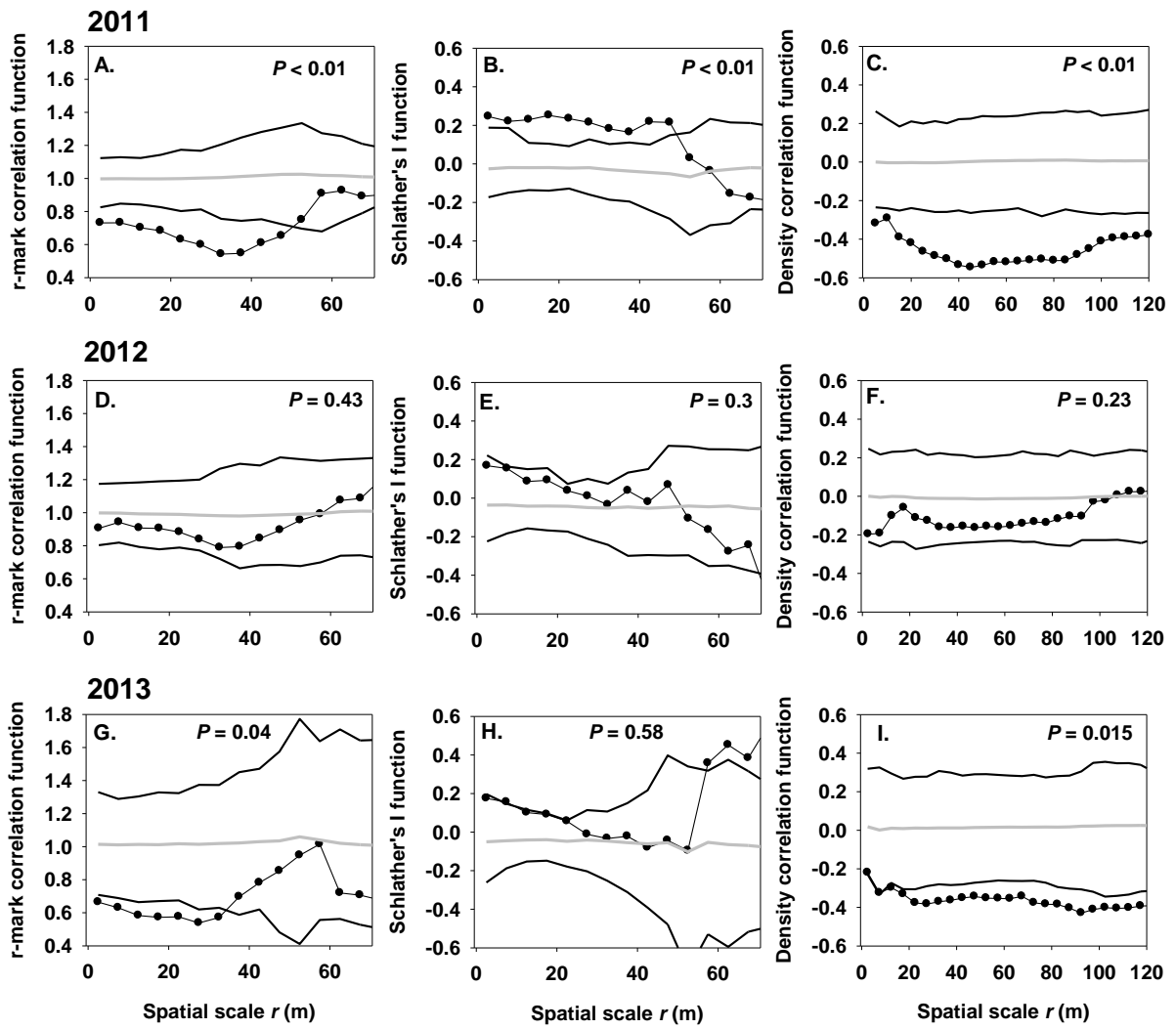


Figure 2.

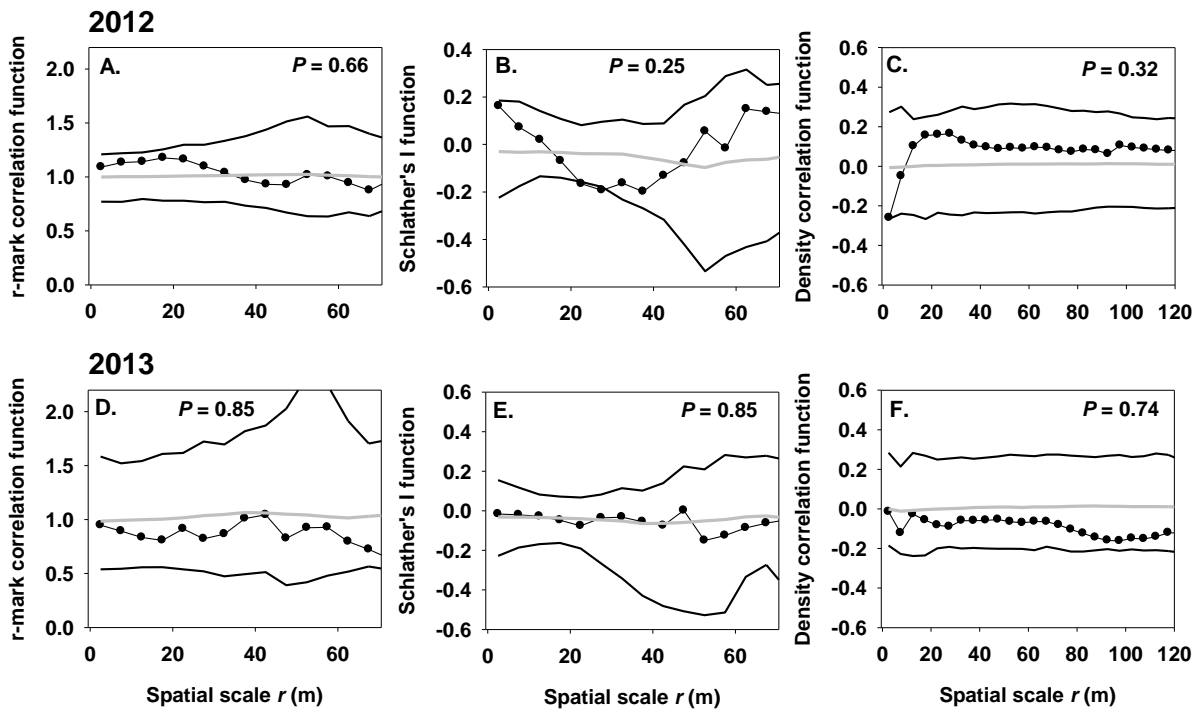


Figure 3

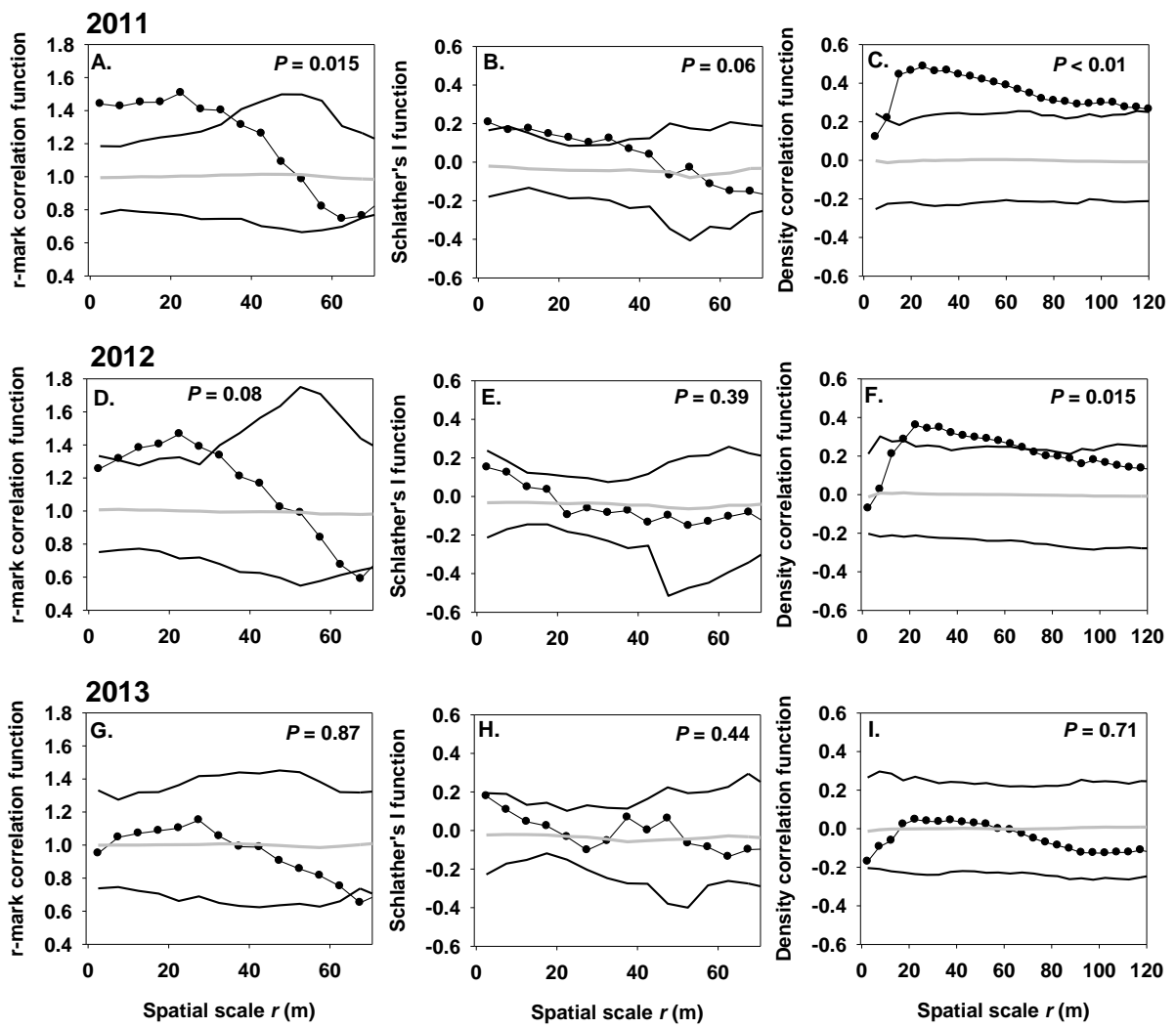


Figure 4